Methods for the study of large mammals in forest ecosystems

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Research Institute for Nature Management

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Methods for the study of large mammals in forest ecosystems

Proceedings of a workshop organized by the
Research Institute for Nature Management,
Arnhem, The Netherlands, 15-17 December 1988

G.W.T.A. Groot Bruinderink and S.E. van Wieren (eds.)

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PREFACE

The Research Institute for Nature Management has accumulated twenty years of experience with the study of effects of the introduction of large herbivorous species into different habitats. The species involved were generally domesticated animals such as heifers, sheep, and goats; in most cases the new habitats consisted of land formerly used for agriculture, for example heathland, salt meadows, and riverine pastures. The main issue in all of these experiments was the conservation of plant communities that had gradually become very rare and therefore valuable. They were the product of several forms of traditional land use such as mowing, cutting of peat, or grazing by domestic stock.

Although the research performed was of a highly empirical nature, it yielded useful management tools and was completely in line with the prevailing conservation strategy. However, it was inadequate from the ecological point of view because no attention was paid to the zoological aspects of the ecosystem. The animals in question were simply considered as tools to realize pre-set management goals. Qualities of vegetation were never described in terms of food supply, and little attention was given to the problem of whether such animals could survive and produce offspring simply by exploiting the naturally available food supply. In general, the "application" of domestic stock for year-round grazing was thought to be impossible without supplementary feeding at least in the winter and early spring. This view was even held with respect to red deer and wild boar management where densities were kept high for hunting purposes.

In this field the concept of nature management has changed positively in recent years, the animals interests being taken into account in the sense that they were more and more considered to be a valuable part of the ecosystem. The "tools" were considered worthy of study, and the lack of knowledge about them in this context was repeatedly underlined in official publications. In 1987, the Institute decided to start a long-term project dealing with this relatively untouched field. At this time, 1200 ha of fenced heath and woodland inhabited by small populations of red deer, roe deer, and wild boar were generously offered as a study area by the forester of the Royal Forestry of Het Loo, in the Veluwe region. Since it came into use as such, the animals have not been fed supplementarily and have been kept at constant spring densities.

At the start of this research program it was the late Dr. D.C.P. Thalen, former head of the Botany Department of the Institute, who suggested the organization of a workshop on the main issues related to the combination of large herbivores and forest management, the objective being to benefit from international experience and bring the participants up to date quickly. Although we originally had a smaller scope in mind for the workshop, I now consider that we are indebted to all of the participants for having dealt with most aspects of the problem in a more general way allowing a wider audience to benefit from the proceedings presented here, and I thank all of them for that. Unfortunately, Dr. Thalen, the workshop's initiator, died at the end of 1988, and I wish to dedicate these *Proceedings* to the memory of this fine colleague.

Dr. W.J. Wolff

Director of Research

THE WORKSHOP

Geert Groot Bruinderink and Sip van Wieren

In February/March 1988, specialists from all over Europe working in various fields pertaining to herbivorous species in forest ecosystems, were invited to participate in a workshop organized by the Research Institute for Nature Management, to be held in December of that year. The main goal set by the organizers of this workshop was to collect all recent information on the interaction between red deer, roe deer, and wild boar and their forested environment, with special attention to methods for the study of these secretive animals and the analysis of the data obtained.

In view of the limited time available, all participants were asked to submit in advance a list of the main issues they would like to raise during the workshop and a resumé of the most recent results of their own work. Copies of this material were distributed to all participants, which saved time for the workshop and facilitated preparation of the proceedings. Needless to say, the papers making up the proceedings were never intended to provide a complete review of the subject.

The workshop started on Thursday, the 15th of December, with an evening session on the catching and handling of deer species, a paper presented by Dr. R. Harrington (Ireland). On the following day there was an excursion to a specific habitat of the three herbivore species. In the afternoon Dr. M. Petrak (Federal Republic of Germany) and Dr. R. Putman (Great Britain) presented their paper on habitat use by red deer. The evening program comprised papers on food supply and consumption by Dr. K. Perzanowski (Poland) and Dr. R. Putman. The final session on Saturday, the 17th of December, dealt with condition and biotelemetry, the respective papers being presented by Dr. F. Tataruch and Dr. F. Schober (both from Austria).

Most of the papers were followed by ample time for discussion, the only exception being Dr. Schober's. All discussions were taken down by two Dutch colleagues, to whom we are of course greatly indebted.

The sessions were chaired by Groot Bruinderink, van Wieren, Ratcliffe, and Putman.

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PART ONE: VEGETATION-BASED TECHNIQUES

I. HABITAT USE AS ASSESSED BY VEGETATION SURVEY

M. Petrak

Introduction

Since direct assessment of habitat use by secretive herbivores is frequently impossible, we must resort to various indirect techniques, for example by studying feeding traces left by large herbivores in the vegetation. Important components of vegetation surveys include the phenological calendar and classification of the degree of damage.

Seasonal variation in habitat use and food preferences: the need for a phenological calendar

Habitat use and browsing intensity vary with the phenological phases of the food plants. Recording of only the dates of field surveys is not sufficient for analysis of the seasonally fluctuating intensity of browsing of the plants or for comparison of the results obtained in different regions. Timing of field studies must be planned and be defined in terms of the phenological phases of the food plants. Within any given phenological phase, food and cover are comparably available. The annual development of plant indicators indicates the phenological phases: 1: the period before spring, 2: early spring, 3: spring, 4: early summer, 5: summer, 6: late summer, 7: early autumn, 8: autumn, 9: late autumn, and 10: winter.

The phenological phases to be recorded are shown in the next page:

1. The first flowers are fully open, exposing the pollen-bearing stamens (b).
2. The first leaves have unfolded and show their typical shape but not necessarily their final size (BO).
3. Half of the flowers are fully open (ab).
4. The first fruits are ripe, enough of them for the first picking to be worthwhile (f).
5. More than 50% of all leaves (including those already fallen) show autumnal tints (LV).
6. Onset of leaf fall (BF).

Phenological	b	BO	ab	f	year remarks
1. time before spring					
Corylus avellana	--				
Galanthus nivalis	--				
Alnus glutinosa	--				
Tussilago farfara	--				
Salix caprea	--				
Narcissus pseudonarcissus	--				
2. early spring					
Anemone nemorosa	--				
Betula pendula	--	--			
Quercus robur		--			
Prunus spinosa	--	--			
Fagus sylvatica		--			
Taraxacum officinale	--				
3. spring					
Syringa vulgaris	--				
Malus domestica	--				
Cytisus scoparius	--				
Chrysanthemum leucanthemum	--				
Picae abies	--				
Vaccinium myrtillus	--				
Rubus idaeus	--				
4. early summer					
Symphoricarpos rivularis	--				
Robinia pseudacacia	--				
Fragaria vesca or dom.				--	
Prunus avium (early)				--	
Alopecurus pratensis			--		
5. summer					
Centaurea cyanus	--				
Prunus avium (late)				--	
Vaccinium myrtillus				--	
Ribes uva-crispa				--	
6. late summer					
Calluna vulgaris	--				
Sorbus aucuparia				--	
Symphoricarpos rivularis				--	
Prunus domestica (early)				--	
Malus domestica (early)				--	
	b	f	LV	BF	
7. early autumn					
Colchicum autumnale	--				
Aesculus hippocastanum		--			
Pyrus communis (late)		--			
Malus domestica (late)		--			
Sambucus nigra		--			
8. autumn					
deciduous trees			--		
Fagus sylvatica		--			
Quercus robur		--			
9. late autumn					
deciduous trees				--	
10. winter					
Helleborus niger	--				

Application of the following simple guidelines should improve the value of data recorded in the field:

1. Note only one date (day, month, year) for all phenological observations.
2. Be sure that habitat conditions (climate, soil, height above sea-level, inclination, exposure) are comparable for all observations.
3. Restrict observations to typical plants.
4. Add remarks, i.e., record supplementary observations (e.g. beginning and end of agricultural procedures).
5. Permanent recording of observations is imperative.
6. Additional observations on important food plants are helpful.

The vegetation developing in any given situation tells a great deal about habitat conditions. The plants can be used to evaluate habitat conditions as indicators of climate, soil conditions, moisture conditions, past disturbance, and agricultural conditions. Indicator plants and plant communities have received considerable attention; Ellenberg's (1979) publication in particular gives a comprehensive synopsis of the indicator values of about 2000 species of vascular plants in the western part of Central Europe that is very useful for wildlife vegetation surveys.

Direct observation of deer feeding

Studies on the extent to which animals use various habitat types can be carried out by means of direct observation throughout the year. Direct observations on deer feeding in the study area are helpful for assessment of the reliability of the vegetational surveys. The classification of biotopes must be based on the identification and phytosociological classification of well-defined plant associations.

The number of feeding deer counted in a certain habitat type (A) divided by the percentage of habitats of that type in the study area as a whole (B) multiplied by 100 gives the value of the index of intensity of feeding by animals (RSF):

$$RSF = A/B \times 100$$

Plots

Vegetational surveys are considered to be a method for the analysis of habitats as well as of habitat use, including feeding behaviour. Plant-sociological surveys as a technique to investigate wildlife have been described according to the method developed Braun-Blanquet (1964) and modified by Petrak (1987). The number, scale, timing, and place chosen for such surveys have a strong influence on the results.

The size of the sample plot is determined mainly by the homogeneity of the plant community and the type of vegetation and the animal species under study. The size of the sample plot is of considerable practical as well as statistical importance. Determination of the minimal sample-plot size that will supply adequate data is advantageous. One of the methods used for this purpose is based on a species area curve. Such curves are obtained by plotting the cumulative number of species counted in the samples on the y axis and the sizes of plots on the x axis. The curve rises sharply and then levels off, the peak indicating the approximate point beyond which further sampling will give diminishing returns. Each plant community must be considered individually, or at least plot sizes must be chosen in relation to the vegetation type, e.g. heathland and forest.

For determination of the minimum plot size, habitat use by the animals must be taken into consideration, especially when feeding behaviour is not homogeneous, for example because human activities make increasing demands on shared natural habitats. Normally, the minimum plot size for the study of wildlife must be larger than the minimum plant-sociological size.

Plant-sociological surveys should be carried out during all phenological seasons.

Bite marks

Vegetational surveys offer an indirect method to analyse habitat use. Although it is impossible to distinguish species-specific bite marks - only in a few cases will the height of a bite mark above the ground give this information - it is possible to identify the species by such signs as the shape of tracks and droppings found near bite marks. The field worker must be able to read the deer trail accurately, just as he must be familiar with the behaviour of the animals in their biotopes. Field observations on deer feeding in any habitat should be done by the same person(s). Since the nutritional requirements of red deer, roe deer, and wild boar differ substantially, experience can be gained in multispecies areas by locating sample plots for quantitative vegetational surveys such that a single species is dominant among those feeding on within the plot.

Large herbivores will never be the only animals using a habitat. Insects, rabbits, rodents, and other organisms will all compete for the available food. This point should always be kept in mind when planning a browse survey for ungulates, because it helps to avoid confusion about bite marks of different species.

It is rather difficult to investigate the productivity and utilization of dwarf shrubs and other woody species during the vegetative period. The species-specific growth of the stem system only provides a reference within one year. Careful and repeated checking of individual plants provides indications showing whether a bite mark is older than four weeks. After that interval changes occur so slowly that it is not possible to conclude whether a bite mark is say five or ten weeks old. Under these conditions the research worker must be familiar with the sample plots.

Only for nanophanerophytes (shrubs or small trees, height 0.5-5 m) and phanerophytes (trees normally reaching heights over 5 m) occurring in a plot is it necessary to record whether the stem apex is damaged. Here, the growth stage must be taken into consideration.

An approved system for the classication of browse damage to woody species (1988) has been given by Pollanschütz (see Appendix 1). Bark-stripping should be given as frequency, i.e., expressed as the percentage of trees in a plot that have been damaged by bark-stripping, and a distinction must be made between bark-stripping on standing trees and stripping due to breaking of branches by the wind.

Vegetational survey as a method combining forage inventory and assessment of forage utilization should not be restricted to woody species but rather should cover all plant species present.

Index of utilization

Vegetational surveys usually begin with the estimation or measurement of the height and cover of the tree, shrub, and herb layers and in certain cases also the bryophyte layer. Cover is defined as the vertical projection of above-ground parts on to the ground.

The empirical material is presented as plant sociological tables. The plant species in all layers are listed. For each species at least the degree of coverage and of grazing or browsing are given according to the following two scales:

Degree of coverage (AM)

r - very rare
+ - 2-5 individual plants, coverage 5%
1 - 6-50 individual plants, coverage 5%
2 - more than 50 individual plants, coverage 5%, or any number of individuals, coverage 5-25%
3 - coverage 26-50%, any number of individuals
4 - coverage 51-75%, any number of individuals
5 - coverage 76-100%, any number of individuals

Degree of plant damage due to grazing/browsing (AS):

0 - all plants of a given species showing no signs of consumption
1 - up to 5% of the individuals of the given species damaged or up to 5% of the shoots (stalks, leaves, sometimes roots, etc.) of several individuals are grazed/browsed
2 - 5-25%, as for 1
3 - 25-50%, as for 1
4 - 51-75%, as for 1
5 - 76-100%, as for 1

Only current year/season damage should be recorded.

The sum of all products of the degree of coverage (AM) and the extent of plant damage (AS) is divided by the sum of all degrees of coverage (AM) and the quotient is multiplied by the relative coverage of the herbaceous layer, which gives the value of the index of utilization intensity (AS+) for the plot in question:

$$AS+ = \frac{n_1 \times 1 + n_2 \times 2 \ldots n_5 \times 5}{(n_0 + n_1 \ldots\ldots\ldots\ldots\, n_5)} \times Kr\text{-}D$$

where Kr-D is the relative coverage of the herb layer, 0...5 is the degree of plant damage due to the feeding behaviour, and n_0+n_5 is the sum of the degrees of coverage of all species suffering the same degree of damage.

If a herb layer is absent, the relative coverage of the shrub layer should be substituted for Kr-D.

Note: Only one value is used for each plant species occurring in the plot. If a woody species occurs in both the herbaceous and the shrub layers, the value for the herb layer is used. If the species is only found in the shrub layer, that value is taken.

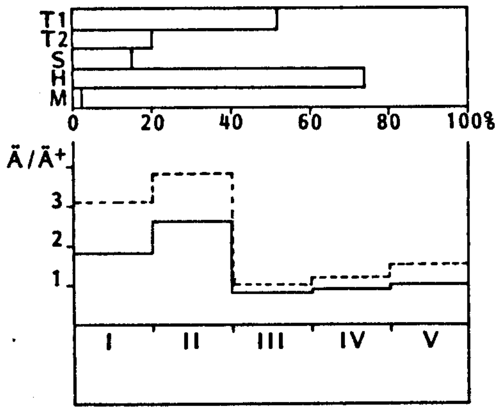


Figure 1. Mean index of utilization intensity. $\bar{A}^+$ for I (winter), II (time before spring and early spring), III (spring and early summer), IV (summer and late summer), and V (early autumn). Tl, T2: tree layer, S: shrub layer, H: herbaceous layer, M: moss layer (for fallow deer, Lower Saxony) Pine forest, 80-100 years old.

An example of the mean index of the utilization intensity AS+ for all plots (mean value) of a certain vegetation unit is given in Figure 1. For all plant species in the study area the ratio of all values for plant damage (from all sample plots) to all values for the degree of coverage gives the value of the index of feeding preference for the plant species under study (BM): BM - AS/AM

The mean of all values for plant damage (AS) gives the average intensity of grazing/browsing on the species. For woody species both BM and AS should be given for all layers in which the species occurs.

The reliability of the vegetational surveys can be assessed on the basis of the relationship between the data from direct observations of deer feeding (RSF) and the index of utilization intensity (A+). For a population of red deer in the Eifel this correlation was found to be highly significant (Fig. 2).

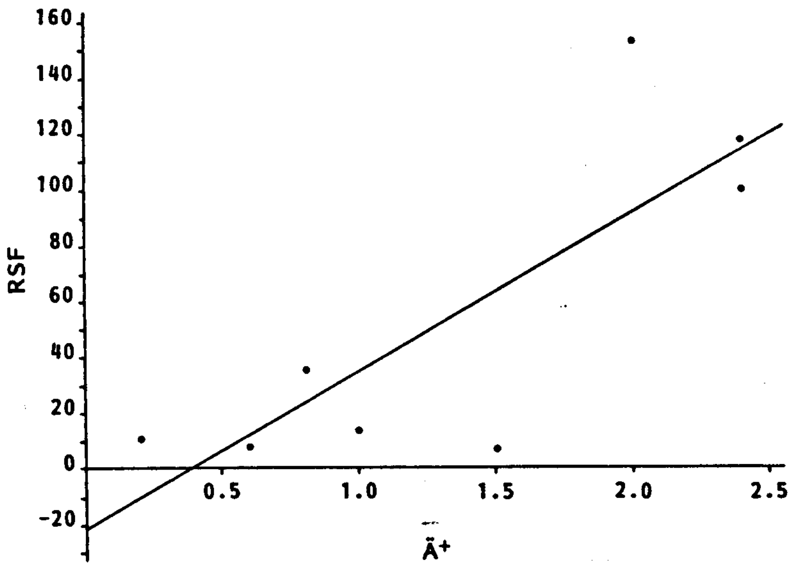


Figure 2. Graph showing correlation between the average index of utilization intensity ($\bar{A}^+$) and the index of feeding intensity by animals (RSF); $\bar{A}^+$ based on indirect observation, RSF based on direct observation (red deer, summer, Eifel), ($y = -21.33 + 56.21\,x$; $r = 0.8066$, $p < 5\%$).

Typical phenological response of a spruce tree to repeated browsing.

Vegetational surveys can show patterns of habitat use that cannot be detected by direct observation of deer feeding, e.g. where feeding occurs proceed in thickets where observation is virtually impossible.

Vegetational surveys offer a method for the analysis of habitat use, and are almost the only way to study interdependences between the vegetation of the habitat and the ecological requirements of deer. Browse intensity can only be interpreted in terms of habitat use if vegetational surveys are not limited to woody species alone.

References

Ahlen, I. 1975. Winter habits of moose and deer in relation to land use in Scandinavia. Viltrevy 9:45-192.

Aldous, S. 1944. A deer browse survey method. Journal of Mammalogy 25: 130-136.

Borowski, S. & S. Kossak 1975. The food habits of deer in the Bialowieza primeval forest. Acta Theriologica 20: 463-506.

Braun-Blanquet, J. 1964. Pflanzensoziologie: Grundzuge der Vegetationskunde. 3. Aufl. Springer, New York.

Dzieciolowski, R. 1969. The quantity, quality, and seasonal variation of food resources available to red deer in various environmental conditions of forest management. Warsaw.

Klötzli, F. 1965. Qualität und Quantität der Rehäsung in Wald- und Grünland-Gesellschaften des nördlichen schweizer Mittellandes. Veröffentl. Geobot. Inst. ETH Zürich 38. Huber, Bern.

Ellenberg, H., G. Spatz, L. Pletzt & A. Mangstl 1979. Zeigerwerte der Gefässpflanzen Mitteleuropas. Scripta Geobotanica 9. 2. Aufl. Goltze, Göttingen.

Koss, G. 1969. Einflüsse auf Pflanzengesellschaften und Äsungs-Präferenzen von indigenen Ungulaten in Kenia und Deutschland. Diss. Giessen.

Lavsund, S. 1976. The ecology of red deer, Cervus elaphus L., in areas in southern and central Sweden with recently established populations. Diss. Stockholm, Research Notes 25, Royal College of Forestry.

Petrak, M. 1982. Etho-ökologische Untersuchungen an einer Rothirsch-population (Cervus elaphus Linne, 1758) der Eifel unter besonderer Berucksichtigung des stoffwechselbedingten Verhaltens. Schrft. AKWJ JLU Giessen 10. Enke, Stuttgart.

Petrak, M. 1984. Strategien einer Rothirschpopulation (Cervus elaphus Linné, 1758) in der Eifel zur Realisierung ihrer Lebensansprüche. Schrft. AKWJ JLU Giessen 13. Enke, Stuttgart.

Petrak, M. 1987. Zur Ökologie einer Damhirschpopulation (Cervus dama Linné, 1758) in der nordwestdeutschen Altmoränenlandschaft des niedersächsischen Tieflandes. Schrft. AKWJ JLU Giessen 17. Enke, Stuttgart.

Pollanschütz, J. 1988. Entwicklung der Verbiss-Situation von Forst-pflanzen im Versuchsgatter Stammham (Kurzfassung plus Übersichten und Tabellen). Rehwild-Symposium der Justus-Liebig-Universität Giessen, (in press).

Veen, H.E. van de 1979. Food selection and habitat use in the red deer (Cervus elaphus L.). Diss. Groningen.

Appendix 1. Example of grading of intensity of browsing on woody species (Pollanschütz 1988).

Degree of damage	*Picea abies*	*Fagus sylvatica*
0	no damage	no damage
1	up to 60% of the lateral twigs of the 3 top whorls damaged	up to 60% of the twigs damaged
2	60-90% of the lateral twigs of the 3 top whorls damaged	60-90% of the lateral twigs damaged
3	more than 90% of the lateral twigs of the 3 top whorls damaged	more than 90% of the lateral twigs damaged
4	stem apex and up to 30% of the lateral twigs of the 3 top whorls damaged	stem apex and up to 30% of the lateral twigs damaged
5	stem apex and 30-60% of the lateral twigs of the 3 top whorls damaged	stem apex and 30-60% of the lateral twigs damaged
6	stem apex and 60-90% of the lateral twigs of the 3 top whorls damaged	stem apex and 60-90% of the lateral twigs damaged
7	stem apex and more than 90% of the lateral twigs of the 3 top whorls damaged	stem apex and more than 90% of the lateral twigs damaged

Approved sample plots measure 5x5 or 6x6 m^2, and each of the plants must be checked individually. The average damage to plots can be given. Damage below the tree top whorls has no consequences for individuals of *Picea abies*.

To a certain extent habitat use by large herbivores can be assessed by qualifying grazing intensity.

II. PATTERNS OF HABITAT USE: AN EXAMINATION OF THE AVAILABLE METHODS

R.J. Putman

Introduction

This paper will concentrate for the most part on an evaluation of the various indirect methods available for trying to assess the patterns of habitat occupance by secretive wild herbivores. To establish context however, I wish briefly to review the major alternatives in terms of direct methods (visual observation and radiotelemetry) in order to consider their relative strengths and weaknesses.

Direct methods

Direct observation

The most commonly-quoted objections to assessment of habitat use from direct observation are the difficulty, with secretive animals in concealing habitats, of obtaining sufficient records in a given time period to provide an adequate data set for analysis, and the problem of interpreting observations from complex habitat mosaics of different relative visibility. Less often considered - yet potentially equally serious in introduction of potential bias - are the problems which can arise in interpretation of data collected opportunistically problems of animal aggregation. Opportunistic observations tend to be very heavily biased in favour of those habitats or parts of the range where animals are more easily seen. Problems due to animal aggregation may be illustrated by the imaginary example of an observer who scores no animals at all in three blocks of deciduous woodland he has surveyed and thus concludes the animal make no use of this habitat-type; while in practise all the animals were gathered in a cluster in the fourth, unsurveyed patch of the same habitat.

Many of these problems can be overcome by careful sampling. Records should not be taken opportunistically but should be based on regular and repeated suvey of a fixed transect route running through the study area and designed to sample all vegetation types in the same proportion to each other as they occur in the study area as a whole. Surveys should be taken along this route regularly throughout all times of the day (24 h or daylight hours, depending on the base of study), to eliminate biases due to changes in habitat use during the day, and should be repeated in exactly the same format monthly or on a seasonal basis.

Records can be corrected for differential visibility by assessing how far the observer can see into each different vegetation type and thus assessing for each the true area surveyed. This figure will however vary at different times of day and at different times of year. Further, when applied to really dense vegetation types where the observer can really only see into the edge, there remains the problem that the animals' use of such communities may itself not be homogeneous : that is it may use very differently the dense core - into which the observer cannot penetrate, and the edge which is surveyed. Problems of animal aggregation merely required more comprehensive sampling of all blocks of any given community-type within the area. None of these devices however can serve to overcome possible paucity of observations overall.

Radiotelemetry

While radiotelemetry may seem an elegant answer to many of the problems outlined above for direct observation, in that it does not rely on visual location of either total lack of visibility of differential visibility, nor from spatially-biased sampling, the technique has its own problems. While results offer very detailed information on movement patterns of those animals which are tagged, analysis is restricted to a very small sample of individuals which may or may not be representative of the population as a whole.

Furthermore it is clear that there are problems with topography and range and that there is limited (and variable) precision of triangulation, which make it difficult to place a given animal precisely within a particular habitat class if habitat patch size is small or if habitat edges are important.

Indirect methods

Such considerations as these have led many workers - particularly those concerned with secretive animals at low population densities to look for indirect methods of assessing habitat occupance - looking for signs left behind by animals using a given part of a range as evidence of that usage. Such methods have the additional argued advantage that they accumulate over time and are thus in a sense an 'integrated' picture of the animals' pattern of habitat use over an extended period and as such are more likely to be truly representative than records based on the necessarily more limited hours an observer can put in in the field in direct observation. 'Signs' available for interpretation in this way are bite marks on vegetation, tracks and faecal depositions.

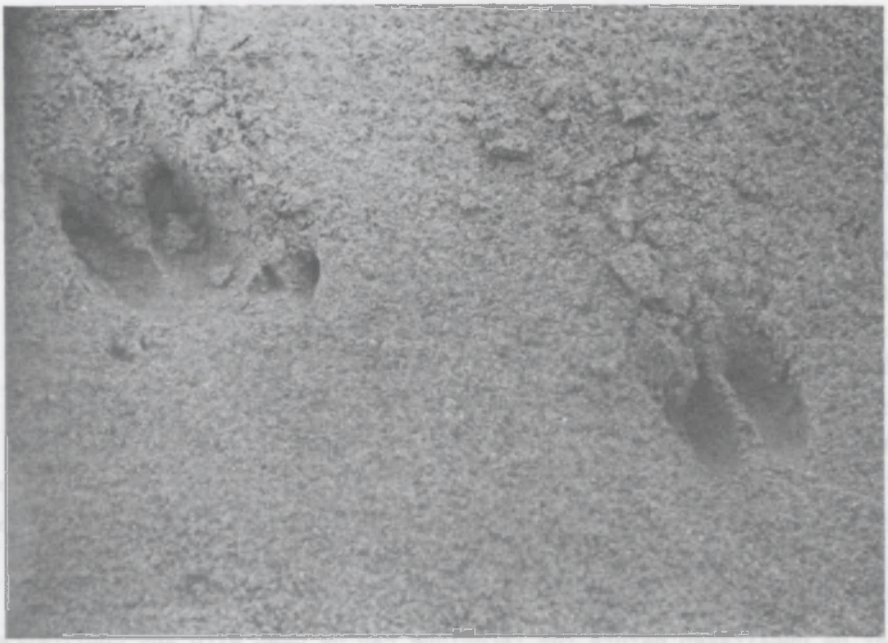
Bite marks

Although Dr. Petrak has made very satisfactory use of this technique in assessing patterns of habitat use, I have serious reservations about the method and its interpretation.

It restricts analysis to use overall; it is difficult to apply in vegetational communities where the predominant foods are grasses and related food plants rather than browse and it is not applicable in multi-species systems since it is impossible in such systems to determine which herbivore left the bite. As a technique it is also only applicable if the observer records feeding pressure on all levels and all species of forage. If measurement is restricted to only one or a few forage species, comparisons of intensity of use of different habitats become extremely difficult since I) most herbivore species are mixed feeders - and do not take all foods in equal proportion: thus few bite marks on plant species x may not reflect low animal activity, merely low preference for x; even where the same foodstuff occurs in a variety of habitats, II) its chemical composition varies widely, so preference may change, III) it will occur in different proportion in relation to other foodstuffs in different habitats and thus again, relative preference may change. In each case changing preference will affect the 'absolute' assessment of relative animal usage.

Track counts

Once again, while occurrence of fresh tracks in an area may be useful evidence of presence/absence of animals in that area, I have no confidence in the technique as a more quantitative method. The probability of leaving tracks varies between habitats, dependent on soil type, soil moisture and how heavily vegetated may be the ground layer. Further, large numbers of tracks may represent large numbers of animals, but may equally represent frequent use of a pathway by one or two individuals. Finally tracking does not distinguish between actual use of an area and mere movement through it; i.e. it cannot give information on



Track counting is a relatively inaccurate method for assessment of the size or structure of a population, in this case of wild boar.

the relative length of time any animal has spent in the area.

Most workers have in the end come to rely, among the indirect methods available, on some form of analysis of faecal depositions.

Faecal counts

Standing crop or plot clearance

Interpretation of patterns of habitat use from patterns of faecal deposition may be based on either of two basic forms of analysis - the assessment of the standing crop of faeces (pellets or pellet groups) in a series of quadrats or along given transects, or measurement of the accumulation of dung in fixed quadrats which are cleared of dung on a regular basis. Actual methods, and the relative advantages and disadvantages of both are discussed by, for example, Neff (1968), Putman (1984) and Leopold et al. (1984). Here I will review briefly some of the major potential problems of both techniques, and consider possible solutions.

Much controversy surrounds the initial dichotomy of basic methodology; whether to use standing crop or plot clearance methods to assess dung accumulation. To a large extent the resolution of this dichotomy depends on the particular circumstances obtaining in any given study. The clear disadvantage of standing crop methods is that the recorder has no intrinsic knowledge of the time period over which dung collected has been accumulating: dung present in a quadrat at any one time is in effect the net result of a dynamic equilibrium between rates of accumulation and rates of decomposition. Since not only accumulation rates (the statistic in which we are ultimately interested as a reflection of animal usage) but also decay rates, may differ between habitats, some correction must be made for rates of dung decomposition in all the different habitats considered. Dung, even from one species of animal, decays at widely differing rates at different times of year, in different habitats, and under different climatic conditions. Thus in practise, extremely detailed study of the decay patterns of the dung must be undertaken before the technique can be used with any confidence (e.g. Mitchell et al. 1983).

Plot clearance methods overcome this problem by removing all dung present in a plot at the outset, recording only that which has accumulated by the time the plot is next cleared; as long as the time interval between clearances is less than the minimum time taken for total disappearance of a faecal deposit, the method can give a direct assessment of dung accumulation rates, without the need for cumbersome studies of relative decay rates in different habitats and resultant (potentially inaccurate) corrections. However, plot clearance methods have their own problems, particularly where animal densities are low, in that in the short time periods plots are left to accumulate dung, many plots will not receive any depositions: the data set thus suffers from low overall numbers of faecal groups recorded and high aggregation of depositions even within habitats, making statistical interpretation difficult.

Statistical analysis to be presented below may help to overcome these problems to some extent, but the fact remains that the high variance resulting from data sets containing many 'zero' plots may render results as inaccurate in practise as those derived from standing crop methods. In this context it should be recorded that, working with red deer in coniferous forests in Scotland (which offered to the deer a complex mosaic of blocks of a mixture of different ages and structures), Ratcliffe found that standing crop methods gave extremely consistent results (Ratcliffe 1987, Staines and Ratcliffe 1987). He found that actual deer densities within a forest/habitat showed a linear relationship with the mean number of pellet groups recorded in random 7 x 7 m plots; variation about the line was further reduced when corrections were incorporated for measured decay rates. Ratcliffe concludes (1987), that if standing crop methods can be used to give consistent results, they may have advantages over plot clearance methods in that less time is required in sampling and no follow-up visits are necessary to a site. An even more important advantage is that, because pellet group density is higher than on cleared plots, sampling efficiency is higher, and a significantly reduced samplingintensity is required (Neff 1968, Rogers, Julander and Robinette 1958).

Practical problems common to both techniques are differential search ability by the recorder in different habitats, differential search efficiency between observers, and necessary inaccuracies, again in multispecies systems, of identification of pellets to species (of dunger). These problems are however purely practical and can be overcome by careful sampling. Recorders can check their relative search abilities in relation to each other and in relation to the habitat searched, in a series of preliminary trials - where an independent 'examiner' has previously set up plots with known numbers of artificial faecal groups; similar tests (using faecal piles collected from known individual animals of the different herbivore species likely to be encountered) can be undertaken to assess accuracy of dung identification. I might note that all these tests are not only possible: they must be carried out. To me the classic study in conceiving and carrying out all possible cross-checks and validation of the methodology is that of Koster and Hart (1988) in their analysis of ungulate populations in tropical forest.

Sampling statistics

Other problems to be addressed in use of any faecal technique are questions of sampling and analysis/interpretation. Various authors have considered the merits and demerits of plots of different size or shape. Some have proposed that circular plots should give better results since they present the smallest perimeter for a given are and thus minimise the risk of 'edge' groups; in practice this does not represent a great problem in normal experience - and square or rectangular plots are easier to establish. Belt transects can be used to survey larger areas if standing crop methods are to be employed, but in general, for both techniques, square plots are most commonly employed. Quadrat size depends again on faecal density. Plots of 50 m2 are generally employed. In tests of plot sizes varying from 3 x 3 m to 25 x 25 m Bailey and Putman (1981), working with fallow deer, showed that variability in the number of pellet groups recorded per quadrat was rather high in plotsizes of 10 x 10 m or below and was considerably reduced by using plots of 15 x 15 m. (Above this size no further significant improvement was achieved). However, searching efficiency declines in the larger plots and as a compromise, plots of 50 m2 (7.1 x 7.1 m) are widely employed.

Considerations of the number of plots required to minimise variance suggest a minumum for any habitat of 8 plots (the number required to give a sufficient number of degrees of freedom in any subsequent analysis). In practice sample size should be increased above this minimum until it is felt that adition of further replicates no longer substantially deceases variance. Opinion is divided as to whether all habitats should be sampled equally, irrespecitve of their relative area within the study site as a whole, or whether the number of samples in each should be weighted in relation to that relative area (in an attempt to overcome heterogeneity in use by the animals of large patches of habitat, and heterogeneity in dung deposition resulting form this). On balance, I myself would advocate proportional sampling in an attempt to overcome this latter non-uniformity, but with a minimum number of 8 plots retained in the samller community-types.

Whatever the basic approach (standing crop or plot clearance) and whatever methodological steps are undertaken in an attempt to overcome some of these potential sources of bias, one final major problem remains in interpretation; for whatever biological reason, dung groups tend to be highly aggregated in distribution. This problem is more acute in plot clearance methods which by their nature are concerned with only fresh depositions, but is nonetheless apparent even in data sets derived for standing crop counts. Analysis of mean values is thus unhelpful. The data more closely fit a negative binomial distribution (White and Eberhardt 1980) which can be described by two parameters, the mean (m) and the positive skew or positive exponent (k). Ideally the application of the negative binomial distribution to pellet group data requires a common value for k in order to test for differences in the means from two samples. White and Eberhardt however, present a protocol for testing differences between samples even where these do not have a common exponent (k), proposing four models encompassing a range of distributions where either m or k remain constant. These analytical techniques certainly do help to improve the resolution of and interpretation of pellet group data. Alternative methods of analysis based on calculated nearest neighbour distances between adjacent dung groups in different habitats have been suggested by, for example, Batcheler (1975) but White and Eberhardt's analysis is now most commonly employed.

All these considerations suggest that faecal techniques may be used in analysis of habitat use patterns of large herbivores: perhaps, dung clearance methods to be preferred where animals are present at high densities so that faecal accumulation rates are relatively rapid, standing crop methods - (with their associated extra requirement of additional experiments to determine decay rates) - to be favoured where animal densities are low and thus use of clearance plots would result in too many quadrats with no dung recorded within them. Interpretation of results in relation to expressed patterns of habitat use must however be made only with caution. All that the data really offer is an analysis of habitat use for defaecation. To interpret the results in terms of patterns of habitat use overall is to make a number of as yet unsubstantiated assumptions: that I) animals defaecate at regular and constant intervals throughout the 24 h of a day, so that the amount of faecal matter accumulated in an area is a reflection of the amount of time spent in that area, II) that defaecation rate is not affected by behaviour, III) that defaecation behaviour is independent of habitat and is not itself, either directly, or indirectly (through positive association with some other habitat-specific behaviour) influenced by habitat occupied. Not only are these assumptions unsubstantiated; such evidence as we do have is that animals do not defaecate at entirely regular intervals.

Defaecation rhythms are suppressed while animals are lying resting; the dung accumulated is passed in numerous defaecations in quick succession on rising. Dunging is thus very positively associated with behaviour and habitat, if animals choose particular sites for resting; in addition, at least some ungulates, (e.g. horses: Edwards and Hollis

1983, Pratt et al. 1986) show specific latrine behaviour - seeking particular community-types/cover-types for defaecation. How far such observations invalidate the technique remains to be discussed!

References

Bailey, R.E. & R.J. Putman, 1981. Estimation of fallow deer (Dama dama) populations from faecal accumulation. J.appl.Ecol. 18: 697-702.

Batcheler, C.L., 1975. Development of a distance-method for deer census from pellet groups. J.Wildl.Mgmt. 39: 641-652.

Dzieciolowski, R., 1976. Estimating ungulate numbers in a forest by track counts. Acta theriologica 21.

Eberhardt, L.E. & R.C. van Etten, 1956. Evaluation of the pellet-group count as a deer census method. J.Wildl.Mgmt. 20: 70-74.

Edwards, P.J. & S. Hollis, 1982. The distribution of excreta on New Forest grasslands used by cattle, ponies and deer. J.appl.Ecol. 19: 953-964.

Koster, S.H. & J.A. Hart, 1988. Methods of estimating ungulate populations in tropical forests. Afr.J.Ecol. 26: 117-126.

Leopold, B.D., P.R. Krausman & J.J. Hervert, 1984. The pellet-group census technique as an indicator of relative habitat use. Wildl.Soc.Bull. 12: 325-326.

Mitchell, B., D. McCowan & D. Campbell, 1983. Faecal depositions as indicators of site use by red deer. Ann.Rep. Institute of Terrestria Ecology, 1982: 85-87.

Neff, D.J., 1968. The pellet-group count technique for big game trend, census and distribution. J.Wildl.Mgmt. 32: 597-614.

Pucek, Z., B. Bobek, L. Labudzki, K. Morow & A. Tomek, 1975. Estimates of density and number of ungulates. Polish Ecol. Studies 1: 121-136.

Putman, R.J., 1984. Facts from faeces. Mammal Review 14: 79-97.

Ratcliffe, P.R., 1987. The Management of Red deer in the Commercial forests of Scotland, related to Population Dynamics and Habitat ÉrÉ changes. PhD thesis. University of London.

Rogers, G., O. Jolander & W.L. Robinette, 1958. Pellet-group counts for deer census and range-use index. J.Wildl.Mgmt. 22: 193-199.

Staines, B.W. & P.R. Ratcliffe, 1987. Estimating the abundance of red deer (Cervus elaphus L) and roe deer (Capreolus capreolus L) and their current status in Britain. Symp. Zool. Soc. Lond. 58: 131-152.

Welch, D.C., 1982. Dung properties and defaecation characteristics in some Scottish herbivores with an evaluation of the dung-volume method of assessing occupance. Acta theriologica 27: 191-212.

White, G.C. & L.E. Eberhardt, 1980. Statistical analysis of deer and elk pellet group data. J.Wildl.Mgmt. 44: 121-131.

III. WHAT CAN WE LEARN ABOUT HABITAT CHOICE BY INDIRECT METHODS?

A.W. Illius

Indirect methods for estimating feeding-niche breadth are prone to considerable experimental error. The usefulness of these methods depends on the investigator being aware of the sources of potential errors and estimating the magnitude of errors relative to the degree of variation known to occur within each botanical category. The main limitation on the definition of feeding niches by indirect methods is that observations on where animals feed, and even what plants they choose, may not be closely correlated with the actual intake from each type of vegetation. Corroboration may be sought from data pertaining to the impact of grazing or browsing on vegetation, but such attempts encounter the equally intractable problem posed by attempts to measure something after it has been removed. Furthermore, assessment of the number of bites taken from vegetation may be biased by differences in the visibility of bites on different vegetation types. These problems can be partially overcome by using tame animals to assess the average size and visibility of bites taken from vegetation carefully chosen as representing the range usually encountered. Once that is done, observation of feeding time, biting rates, grazing impact, and botanical distribution, can be combined to obtain estimates of niche selection.

Definitions of measurements

B_i - bite numbers on plant species i counted during survey

V_i - proportion of bites visible to a trained observer

BR_i - mean rate of biting

BM_i - mean bite mass, estimated on the basis of studies in tame animals, plant weighing performed before and after

A_i - area occupied by plant species i

M_i = biomass concentration (dry mass per unit area)

Variables and indices of habitat use

Area distribution of plant species, AD_i = (proportion occupied by i_{th} species)

$$AD_i = \frac{A_i}{\sum_{i=1}^{n} A_i}$$

Mass distribution of plant species, MD_i = (proportion of total biomass)

$$MD_i = \frac{A_i \; M_i}{\sum_{i=1}^{n} A_i \; M_i}$$

Numbers of bites on the i_{th} species, BN_i =

$$BN_i = \frac{B_i}{V_i}$$

Diet composition PBM_i = (proportion of i_{th} species in diet)

$$PBM_i = \frac{BN_i \; BM_i}{\sum_{i=1}^{n} BN_i \; BM_i}$$

Time spent by the animal on i_{th} species T_i = (proportion)

$$T_i = \frac{BN_i BR_i}{\sum_{i=1}^{n} BN_i BR_i}$$

Selection index of i_{th} species for consumption = $\dfrac{PBM_i}{MD_i}$

Time allocation index = $\dfrac{T_i}{AD_i}$

Appropriate methods

The first question to be answered concerns the objectives of the study. The purpose of research can range from understanding foraging strategies and assessing niche overlap to evaluating the effect of management decisions on herbivore performance and the impact on vegetation. Studies on feeding ecology done with indirect techniques have very limited value

The assessment of browse supply, which should be based on a phenological calender, requires very laborious and time-consuming research.

for the establishment of causal relationships between vegetation characteristics and animal behaviour. The lack of universality also limits extrapolation of results to other sites. What is required is controlled experimentation allowing manipulation of vegetation variables. The alternative comparative study of a series of different sites by indirect methods depends on weak analytical techniques such as detection of correlation, which cannot establish causality and is very expensive in terms of the resources used. In general, therefore, indirect methods yielding vegetation-based estimates of food intake and selection are not suitable for animal-orientated questions pertaining to such subjects as foraging strategy or adequacy of nutrition.

Where the objectives of the study are plant-orientated, vegetation-based methods become more appropriate. This holds particularly for situations where the impact on sensitive vegetation categories can be intensively monitored, because diffuse assessment over a wider range of vegetation entails reduced sampling frequency and hence poorer estimation. It is evident that the level of sampling required for such estimations should be determined in advance, since the distribution of sampling effort across vegetation categories should reflect both the importance and the variability of each category.

Reliability

The reliability criteria, i.e., accuracy, precision, and repeatability, are seldom given sufficient attention. Small-scale trials using simulated grazing or browsing can serve to obtain an idea of how accurately and with what precision the indirect methods can estimate off-take. Lack of repeatability is mainly a problem of variability between observers. Human operator differences can be reduced by a careful training program, but since this factor is likely to remain a significant source of variation, allowance should be made for it in the statistical design. Thus, operator effects can be estimated and controlled for. Subjective estimation techniques are of course dependent on the skill and experience of personnel, who should be backed up by a carefully recorded description of techniques and frequent reference to 'standards' or reference samples, which will help to control longer-term drift with respect to the criteria used for assessment.

The value of experimentation

The relevance and validity of indirect methods and the interpretation of the findings can be greatly improved where preliminary or concurrent experimentation is possible. Tame animals fed weighed food samples presented in a natural way, can be used to estimate the range of bite weights obtained from plants and show how plant variables affect this range. Although a comprehensive understanding of the latter is generally lacking, this interaction is one of the most important influences on foraging behaviour. Consequently, it is essential to know which plant parts are selected by tame animals in each stage of their growth if field techniques are to be based on vegetation survey.

IV. HABITAT USE OF WILD UNGULATES: DISCUSSION

H.H.T. Prins and J. Bokdam

Introduction

Many methods for the measurement of habitat use were discussed, but two received the most attention, i.e., faecal pellet counting and direct observation. The discussion touched several times on problems concerned with the measurement of food intake, diet selection, and impact on the vegetation. The importance of defining in advance what one wants to know and why one wants to know it was underlined, because these two questions determine to a large extent the choice of methods for the research. Methodology concerns the selection of the study site, the study population, the parameters, and the sampling methods. Extrapolation from one study area to other areas is impossible without experimentation, because otherwise the causality of the processes cannot be understood: a description of habitat use by a study population alone will not yield enough information to provide a model of even the study site itself, let alone to serve for predictions concerning other sites. The discussion dealt with methods that can be used:

I. to assess the occupancy of the habitat by the animal species under study;

II. to assess food intake or to arrive at a description of the diet of the animals in question;

IIIa. to assess the amount of food on offer and the impact of these consumers on the vegetation and, b. on the use of the phenological calendar.

The discussion dealt primarily with wild ungulates, but parts were also valuable for free-ranging domestic animals. The methods discussed can be divided into two groups, viz., direct methods in which direct visual or other contact with the animal to be observed is used to establish its presence or activity and indirect methods, in which traces of various kinds are interpreted as indicating presence or activity.

Direct methods

Visual observation

It was generally felt that direct visual observation of the species under study is the best way to collect reliable information about habitat use, food selection, etc. Even when telemetry is feasible, it should be used in conjunction with direct visual observation for control. Several direct visual methods were discussed, roughly divided according to sit-and-wait and search-and-follow. With the sit-and-wait method a hide is erected and the observer remains in it as long as necessary. Only when the density of animals is quite high, the chance that one will observe the animals quite good; at low density 'you will sit and see nothing'. It was pointed out that one major drawback of this method is that the selection of sites for the hides will introduce a stong bias against the presence of all habitat types. Nevertheless, it can provide excellent information in some open types of habitat. The method can also be used at night with night vision equipment (and if necessary with infra-red floodlighting).

The search-and-follow method is strongly dependent on the habitat type (e.g., inapplicable if too steep or too densely vegetated) and on the wariness of the animals. The search-and-follow method is easily biased - and to an unknown degree - by the disturbance caused by the observer. Observation from a vehicle is preferable but the observer should never use the same type of vehicle as the hunters employ. Cessation of hunting is recommended for a study area where direct observation is to be carried out; sometimes animals (e.g. deer) react quickly, becoming tamer (Ireland after the Chernobyl fall out), but in many areas they take a long time to do so. It was suggested that admittance of the general public (without dogs) could promote tameness of the study population. A last resort could be observation on horseback.

Observers should arrange to be as comfortable as possible (a nice temperature for working and a comfortable place to sit), because there is a strong correlation between the quality of the observations and the comfort of the observer(s). Nocturnal observations do not pose a problem if one is seated in a vehicle or in a hide. Many animals quickly become accustomed to spotlight, and night vision equipment gives good results, but moving around is more difficult at night. Telemetry can help to locate the animals. It is not clear why some populations have nocturnal feeding habits and other diurnal. There is no reason to expect a quick change from nocturnal to diurnal if hunting is stopped in a study area. The easiest way to solve this problem is to find another population which is not nocturnal; if that is impossible, the difficulty must be coped with in some other way.

Visual marking of individuals

Individual recognition is not only imperative for studies involving the social organization of the population, but also for dealing with problems of biased sampling (e.g., good data on food selection might concern some tame deer happening to use a specific habitat type that is hardly used by the majority of the population). An attempt should therefore be made by preference to mark all individuals of a population (or use natural markings) but this marking system means having to capture the animals. Paint spraying or paint shooting was not discussed, but these methods may give good results too. Patterns of movement can only be studied if a number of individuals have been marked, and 'radio-marking' of individuals can also serve this purpose.

Radio-marking of individuals

After individuals have been caught they can be tagged and fitted with transponders. In connection with the present discussion on habitat use, it was agreed that telemetric methods can determine where the individuals are at a given moment with some precision, but will tell nothing about *why* the animals are there; furthermore, it remains doubtful whether they will supply enough information about *what* the animals are doing there. Some felt that with sufficient effort enough information can be obtained with telemetry if heart rate, head up/down movements, number of bites, etc., are recorded with different sensors. It was emphasized that one should strive to collect data that can be analysed in a straightforward fashion and with statistical methods.

Other participants were more catholic in their approach, and pointed out that one ends up with many notebooks full of 'data' that are impossible to analyse ('two roomfulls of collected and unanalysed data for each publication'). Although the majority agreed that this was a valid point, they preferred to use notebooks because they needed them later on

Automized radiotracking demands major investments of time and money.

for their analysis of the numerical data. Moreover, they did not believe that any telemetry system will function all of the time, so they felt a need for the back-up system supplied by their notebooks.

It also was remarked that the social structure of a group of animals is often habitat dependent (e.g., small groups in closed habitat, larger ones in open habitats). Thus, if one relied exclusively on telemetry and only a few individuals had been fitted out or could be tracked, erroneous information would be obtained about habitat use by the population as a whole. As capturing of all individuals or getting all transponders to work is unlikely, 'old-fashioned' methods must be relied on as well.

Indirect methods

Hoofprints

One of the so-called old-fashioned methods is to look for tracks left by the animals. If there is an extensive network of unmetalled roads in the study area one could consider tying brushwood (e.g., *Crataegus*, *Prunus spinosa*) on the rear of a vehicle to obliterate old tracks so one could check for new tracks every day. If these roads lie along the perimeter of different habitats, the tracks left by the animals could yield some information about the differential use of the habitats. However, the number of tracks is not dependably correlated with such items as percentage of habitat occupancy or of time spent in different habitats, and therefore the data will give only a general idea about habitat use by the population. The 'track method' can nevertheless supply additional information in some study areas.

Dung depositions

In this respect, too, the group had grave reservations about the usefulness of methods based on the distribution of faecal pellet groups and interpretation concerning the habitat occupancy. Droppings tell where animals have defaecated, but the interpretation of dung densities in different habitats is not simple. Experienced participants agreed that the methods work better in areas with little variation compared with areas showing a complex pattern (many types of habitat). Used together with stratified sampling in different habitats, the method could provide good estimates of the total population size, but it is uncertain whether it could lead to a reliable estimate of densities in different habitats. Even the best searchers show a differential success in pellet finding in different habitats, but a correction can be established by scattering a known number of pellets in a plot and scoring the number of retrieved pellets.

The identification of pellets is also more difficult than might be expected (in a known mixture of pellets of red and roe deer, 25% of the pellets were wrongly identified; so, test yourself). For statistical reasons the number of plots in each habitat must be at least eight, irrespective of the relative area of that habitat type, but one should try to have at least 20 plots. Systematic sampling, which gives better covering of the area than a random sampling of plots, is not statistically inferior to the latter, but some of the participants still felt that a dung method to study habitat use only gives information about differential defaecation in the habitat types. This drawback could be overcome by calibrating the pellet counts against information on habitat use obtained by direct visual observation or telemetry, even though the telemetric results are biased too. This problem was not discussed further but is of paramount importance. It is felt that two sources of imperfect information can yield better results than one source (as suggested by e.g. Baeysian methods of interference).

For comparison of the use of different habitats on the basis of the dung method, it is very important to establish the smallest possible confidence limits for each estimate of dung density in the habitats in question. Although the decay rate of the dung is not important when the clearance method is used (i.e., all pellets removed from a plot after each count), this method is less reliable than the faecal standing-crop method (i.e., counting all pellets in a given area), because the latter method yields fewer zero values (theoretically this cannot be true). Zeros are extremely difficult to interpret, and for the analyses it must be assumed that the values from the different plots have a negative binomial distribution.

Information from bite marks

Since participants showed a general mistrust of indirect methods, it is hardly surprising that they voiced reservations about the use of bite marks for the study of habitat use, the quantification of foraging time, and the assessment of off-take. They were less doubtful with respect to woody species than about bite marks on grass or herbs. The main problem associated with bite marks is the difficulty of estimating the number of bites on herbs. One misses too many bites (but no one knows how many) to reach any quantitative conclusion about habitat use on the basis of scoring of bite marks. Even if one could score all bite marks on a sward and knew the total herbage mass, a 10% error in assessing the bite depth would lead to an error of +40% in bite weight and thus in forage offtake. This is rather depressing if you have worked 14 hours in the field to collect data of these types. Furthermore, certain food items completely escape notice with the bite mark technique, e.g. acorns.

Assessment of food intake and diet composition

Direct visual observation and telemetry

During the present discussion this subject was only touched upon briefly. Estimation of bite size cannot be based on gravimetric quantification. The same applies to telemetry: the number of bites can be recorded via sensors attached to the jaw but an estimation of bite size is very difficult (Chapter VII).

Faecal analysis: reliable information on the defaecation rate and the amount of faeces produced is difficult to obtain for wild animals

(Chapter VII). Faecal analysis has been used extensively for the assessment of the botanical diet composition, but bias with respect to the qualitative and quantitative composition should be checked by means of controlled experiments.

Rumen analysis: rumen analysis is unreliable not only because of the differential passage rates of the particles of different sizes but also the different rates of digestion of plant species/plant parts.

Bite marks: the tallying of bite marks was considered completely unreliable for grassy vegetation and herbs; it appeared to be more reliable for animals feeding on woody species.

Exclosures and standing-crop assessment: during the discussion several participants repeatedly emphasized the point that both the food on offer and the offtake can be measured quite reliably by the use of temporary exclosures. This method was considered especially necessary for grassy vegetation or herbs. It must be kept in mind, however, that certain types of exclosure, particularly those using a cage, can induce an increase of primary production. This method is more suitable for estimation of the offtake from a certain habitat type or location than for assessment of the animals intake, because most areas are heterogeneous.

Assessment of food supply and grazing impact

Exclosures and standing-crop assessment

Although this method was only touched on briefly, it appears to be the most reliable. Knowledge of phytomass on offer and food offtake in a given type of habitat or location and the animals' intake (per unit of time, per day) is essential if one wants to know why the animals are at a given place in the area at certain times. Information of this kind can only be obtained by the expenditure of much care and effort.

Vegetation description and impact assessment based on bite marks

This subject was not adequately discussed. The Braun-Blanquet method, as advocated by Petrak, makes use of a non-linear scale to weigh the importance of different plant species, and attaches too much weight to rare species. The method is apparently appropriate to describe plant species associations but is not adequate for estimation of the relative importance of the amount of food offered by the individual plant species. In this respect the point-quadrat method seems to be superior. The impact on vegetation was not adequately defined, but if it is taken as damage to e.g. trees as interpreted by foresters, Petrak's method could be of value. The problems would then be what foresters view as damage and the ecological meaning of their interpretation of bite marks. Petrak agreed that if interest is concentrated on biomass removal and its effect on the plants, use must be made of exclosures and harvesting techniques.

Habitat description

One of the major problems encountered in the study of habitat selection is how to understand a situation from the animal's angle. Many aspects must be taken into account here, not only the vegetation but also the degree of shelter, steepness of slope, height of shrubs, amount of timber, etc. Even cluster analysis of these data will not show how to weigh the various factors. When aspects and parameters are selected, the potential limiting factors for the animal should be considered and availability in the research area assessed. Factors such as available *ad libitum* level will have no influence. An attempt should be made to rank factors according to their relative importance and relative availability. Habitat classification - which must of course precede mapping for habitat-use studies - has proven to be very difficult. Perhaps the only satisfactory approach is to describe the habitat units in a very old-fashioned way, i.e., to use terminology to distinguish one 'unit' from another (e.g., heathland, shrub, thicket, forest, meadow), and then use these units in the classification, mapping, and description of the habitat. But it is evident that this would give only a poor approximation of the animals' 'view' of the area.

Incidental and unpredictable habitat characteristics can have a strong impact on habitat use, e.g., the presence of leaves or branches on the forest floor after a storm.

Usefulness of the phenological calendar

The participants agreed that the phenological calendar can be useful for the comparison of study sites within a large geographical area (e.g. Europe). The relevant data are often collected in botanical gardens belonging to the network of phenological stations in Europe. (The U.S.A. has a network of this kind too.)

V. ASSESSMENT OF BROWSE SUPPLY

K. Perzanowski

Introduction

Any method used to estimate browse supply should fulfill two crucial requirements: accuracy and efficiency. For an appropriate method, the cost, effort, and reliability of the data obtained must be optimal. Unfortunately, the clumped distribution of browse means that the variability of the data will be high; furthermore, the available techniques are rather laborious.

Many factors besides variable coverage of the forest floor by trees and shrubs are responsible for the extreme spatial variability of the browse supply. The amount of available browse is also dependent on such factors as forest type, age of the stand, density of the canopy, degree and direction of slope, and soil and water conditions.

Plots

In the selection of a method the first question to be answered is where plots for sampling browse should be located. Sites can be chosen systematically, i.e., along set transects with well-defined distances, or randomly, i.e., according to a randomly selected azimuth and distance between plots or according to a random drawing of plot numbers from a previously established grid. The selection should include typical stands of the forest under study, possibly in the same proportion as they occur in the habitat (Fig. 3).

The second question concerns decisions about the necessary number of plots. For this purpose, use is often made of the formula:

$$n = s^2t^2/d^2$$

where n is the required number of plots, s the standard variation, t the normal deviation at confidence limit and given degrees of freedom (from t table), and d is the margin of error. Determination of the size of plots should be based on the value of the coefficient of variability. The larger the plots, the lower the variance. Older stands usually require larger plots.

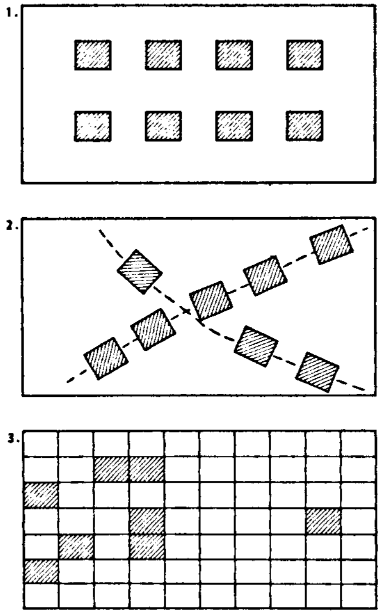


Figure 3. Placement of plots for the sampling of browse according to three approaches: 1. systematic assignment; 2. on the basis of random selection of azimuth and distance between individual plots; and 3. on the basis of random drawing of plot numbers from a grid.

Comparison of the results for plots measuring 18, 21, 24, 27, and 30 m^2 in a hornbeam forest showed no differences greater than 10% in thickets and young plantations. For pole-sized and timber stands, the minimal plot size was over 21 m^2 (Bobek & Dzieciolowski 1972). Because of the high variability of the distribution of browse, it is impossible to give a general formula for the minimal size and number of plots. To assure comparability of results, an accuracy of 20% and a 0.05 confidence limit are generally accepted. In any case, preliminary sampling leading to an estimate of the potential variablility of the data is indispensable.

The shape of plots influences the quality of the data too. Rectangles (long strips) are preferable to round or square plots, because the results show less variability (de Vos & Mosby 1969) (Fig. 4). Methods to estimate browse resources that yield relative data without the use of plots are usually time-saving and less costly, but such data, although valuable for monitoring long-term changes in a habitat, are difficult to interpret in terms of carrying capacity and are therefore not very useful for wildlife management.

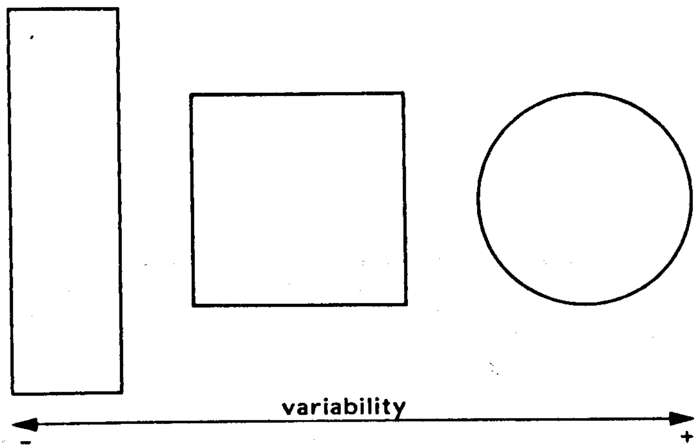


Figure 4. Plot shape and variability of results.

Clipping height

The next factor to be decided is the distance from the ground at which browse supply should be estimated. This depends on the game species concerned. For roe deer the accepted height is 1.5 m above the ground, for red deer 2.0 m, and for moose or bison 2.5 m. The height at which measurements are made in the winter season depends on the depth and toughness of snow as well. According to data presented by Telfer (1974), snowshoe hares in Alberta took about 20% of their winter food above 1.8 m and only 1.7% lower than 0.6 m above the ground. Similarly, moose in the province of New Brunswick took over 11% of their winter food above 2.9 m (Fig. 5). These data also showed that browsing deer were supported by snow at between 52-76 cm above the ground. After a heavy snowfall the weight of accumulated snow can bend branches and bring them within the reach of browsing mammals, which means that sampling must be done up to the highest visible marks of browsing. Some modifications can be applied, depending on whether the measurements are to be made in deciduous or coniferous stands. For estimation in the summer in a deciduous forest it is important to determine the ratio of leaves to twigs, but this is usually not taken into account for estimates of coniferous species. In certain habitats where some coniferous species are not browsed (e.g. spruce, in high mountain forests) (Perzanowski et al. 1986), such trees can be omitted to save time and effort.

For fenced plots it should be kept in mind that although the smaller the fenced area the less fencing is required, small fenced areas are subject to border effects, because the fence can locally modify such parameters as wind speed, sunlight, and snow accumulation, and this can affect the growth rate of twigs.

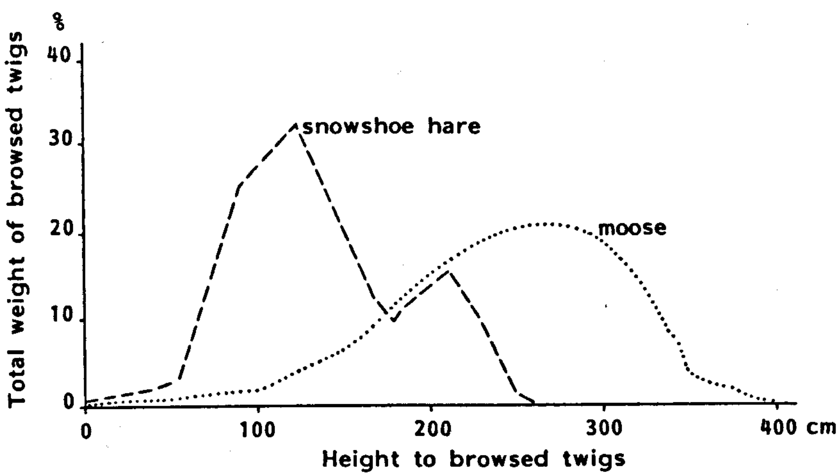


Figure 5. Weight of browsed twigs in the menu of the snowshoe hare and moose in relation to the height of these twigs from the ground (after: Telfer 1974).

Plot techniques

Harvest plot technique

The harvest plot technique is considered standard because it gives the most reliable results, but it has some drawbacks; it is undoubtedly the most laborious method and thus the most expensive and time consuming, not to mention the additional costs of fencing.

Usually, clipping of twigs (current growth) is applied in fenced plots (7x3 or 10x2 m), which allows estimation of the potential browse supply in the absence of animal feeding. Furthermore, the consumption and the total destructive effect of herbivores on vegetation can be estimated by simultaneous clipping of browse on adjoining unfenced plots. The harvest method can be recommended for use where manpower is amply available.

Twig count

A less expensive method but one considered very reliable is twig counting (Shafer 1963, Perzanowski et al. 1986). This technique requires advance estimation of the average biomass of a twig for all browse species in the habitat under study. Because the amount of current growth usually differs considerably among the age classes occurring in a tree stand, the standard mass of a twig should be established for each species and each age class separately. Application of the technique does not necessarily require fencing, since the number of browsing points can be added to the number of recorded twigs. When the browse supply is very low, greater accuracy can be obtained by concomitant measuring of the twig diameter at the base of each counted twig. This permits calculation of the biomass of browse according to an established ratio between the diameter of the twig and its biomass for each species of browse (Bobek et al. 1979).

Height/diameter index

A method tested by Bobek and Bergstrom (1978) employs the height/diameter index and is especially suitable where even the twig-count technique is too laborious in an area with a very dense current growth of twigs, as in thickets and young plantations. The method can be applied to trees not exceeding 3.5 m in height and requires plots each measuring 15x5 metres and divided into 5 subplots (3x5 m). In each subplot, the diameter of tree trunks is measured 5-10 cm above the ground as well as the height of each tree not taller than 3.5 m. Browse is then clipped in the subplot. The relationship between the height/diameter index (which is the logarithm of the diameter divided by the height and browse supply) can then be calculated. With this index, browse supply is estimated for the 5x15 m plots. Comparison of the results obtained by clipping and this method showed differences of less than 10%, and the method using the height/diameter index was found to be much faster.

Basal tree area

The following method is particularly recommended for browse estimates in timber stands with a variable canopy density due to selective logging. The method is based on the known relationship between the browse supply (BS) in an understory and the basal tree area (BTA), which is the sum of cross-sections of tree trunks and is calculated from the diameter of tree trunks at a level 1.3 m above the ground (called breast height). In mountain beech forest (Fagetum Carpaticum type) the following correlations have been found (Perzanowski et al. 1986):

Winter BS [g dry wt./sq. m] = 63.9 - BTA [sq. m/ha] 1.63 (r = -0.79),

Summer BS [g dry wt./sq. m] = 106.7 - BTA [sq. m/ha] 2.78 (r = -0.94).

This method too starts with clipping or twig counting on standard plots (20 m^2) where the BTA is estimated at the same time. This is also the only method permitting predictions about the browse supply according to prescribed logging.

Photographic technique

This last of the discussed techniques, described by Krebs, Sinclair, Boonstra and Smith (1986), is suitable for non-destructive determination of the growth rate of twigs and can be used for long-term studies. A certain number of twigs are tagged with soft wire and aluminium tags, and selected twigs are photographed against a white background. The areas of enlarged twig images can then be read from the screen (using an image analyser), and the biomass calculated according to the biomass/area ratio determined from previously clipped random samples of twigs. The repeatability of such measurements was reported by the authors to be very high, i.e., between 1 and 2 per cent, depending on the degree of contrast in the photographs.

Places were red deer and wild boar feed make good observation sites.

Concluding remarks

It is sufficient to assess browse supply twice a year, i.e., at the end of the vegetative season (to determine summer standing crop) and either late in the autumn (end of November) or at the onset of spring (early March). In the latter period the winter use of browse resources can be estimated at the same time.

Although deciduous browse is undoubtedly an important element of the deer's diet in the spring and summer, the estimation of food resources for deer should indisputably include the ground-flora (i.e., dwarf shrubs, dicotyledonous forbs, and moonocotyledons), which provide much more nutritious forage for deer, especially during the winter season. Due to the seasonal dynamics of ground flora supply, estimation requires sampling at short intervals. Spring sampling should by preference be repeated every two weeks (or at least once a month). After that, samples should be taken in the summer (August), fall (September/October), and winter just before the first snowfall (December). For these estimates, the clipping method applied to rectangular plots (0.5 x 2 m) is recommended (Bobek et al. 1979, Perzanowski et al. 1982).

References

Bobek, B. & P. Bergstrom 1978. A rapid method of browse biomass estimation in a forest habitat. J. Range Mgmt. 31: 456-458.

Bobek, B. & R. Dzieciolowski 1972. Method of browse estimation in different types of forests. Acta Theriol. 17, 14: 171-186.

Bobek, B. and K. Perzanowski, J. Siwanowicz & J. Zielinski 1979. Deer pressure on forage in a deciduous forest. Oikos 32: 373-380.

Krebs, C.J., A.R.E. Sinclair, R. Boonstra & J.N.M. Smith 1986. A photographic technique for estimating browse growth and use. Wildl. Soc. Bull. 14: 286-288.

Perzanowski, K., A. Pradel, M.D. Sikorski & J. Mydlarz 1982. Food resources for deer in Niepolomicka Forest. Acta Theriol. 27, 36: 509-519.

Perzanowski, K., T. Putec & W. Podyma 1986. Browse supply and its ulitization by deer in Carpathian Beechwood, Fagetum carpaticum. Acta Theriol. 31, 8: 107-118.

Shafer, E.L. 1963. The twig count method for measuring hardwood deer browse. J. Wildl. Mgmt. 27: 428-437.

Telfer, E.S. 1974. Vertical distribution of cervid and snowshoe hare browsing. J. Wildl. Mgmt. 38, 4: 944-946.

Vos, A. de & H.S. Mosby 1969. Habitat analysis and evaluation. In: R.H. Gills (ed.), Wildlife management techniques. The Wildlife Society: 135-172. Washington D.C.

VI. FEEDING BY LARGE HERBIVORES IN FORESTS: METHODS FOR ESTIMATING SUPPLY AND CONSUMPTION OF FORAGE

R.J. Putman

Introduction

This paper is presented as a companion piece to Dr Perzanowski's detailed analysis of methods of assessing supply and will deal for the most part with methods of assessing consumption of forage by large herbivores.

Since, however, many of the techniques available for assessing forage consumption must simultaneously measure productivity of the vegetation in order to calculate offtake, some consideration will necessarily, be paid in this paper also to the available methods for assessing forage supply. Further, since animals in forest systems will not restrict their feeding activities to browsing, but may feed on vegetation on the woodland floor or in communities beyond the woodland boundary, I will extend consideration here to estimation of consumption of all forage types: grasses and forbs, ericaceous dwarf shrubs, woody trees and shrubs. For all these forage types there are available two basic approaches towards assessing animal offtake - in looking purely at the vegetation itself and in looking at the animals.

Vegetational assessment

Basic methods to be discussed here are outlined in Putman et al. (1981) or Putman (1986) and were developed, tested and refined in our studies of the interactions between large herbivores and their vegetational environment within the New Forest in southern England. Conceptually the easier forage classes to work with are the grasses and forbs - low, fast-growing, sward-forming species, where simple measures of standing crop in relation to productivity as measured within temporary grazing exclosures can be used to assess offtake. Measurements of vegetation standing crop both inside and outside an exclosure are recorded at the beginning and end of the exclosure period. Standing crop recorded inside the enclosure at the end of the exclosure period, minus the standing crop recorded inside, before exclosure, offers an estimate of production over the period. The difference between standing crop inside the

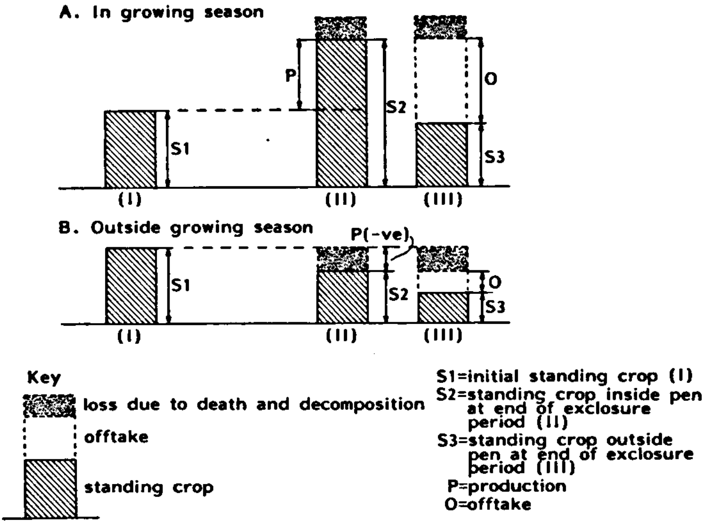


Figure 6. Diagram illustrating the significance of production and offtake data obtained by the exclosure method.

exclosure and outside recorded at the end of the exclosure period, represents offtake. The basic idea is shown diagrammatically in Figure 6.

Despite the appealing simplicity of such an approach however, there are in practice many problems: I) the growth pattern and productivity of vegetation in exclosures protected from grazing may be markedly different from that under normal grazing pressure; II) growth patterns may also be influenced by the shade/shelter effects of the exclosure itself (the so-called 'fence effect'); III) length of time exclosures are left before clipping has a pronounced effect on apparent production; IV) loss of standing crop may reflect senescence as much as offtake; V) mechanical constraints are usually such that exclosures are relatively small and thus the area enclosed may not be truly representative of the community as a whole. Finally, VI), when the proportion of forage species within the sward is low or changes in standing crop sought are small, such changes may be lost/masked by a high and unchanging standing crop of non-forage species within the same sample.

To examine further this catalogue of potential error: within an exclosure, released from grazing pressure, the sward plants may show a totally different patterns of growth. Rather then being kept perpetually in vegetative phase by continued grazing and regeneration, the plants may mature, and thus slow growth, they may flower and thus change both pattern and rate of growth. Growth pattern may also be influenced by the 'fence effect' of small enclosures. To some degree these problems may be overcome by careful sampling. Exclosures should be as large as possible and sampling should be restricted to those areas in the centre of the pen well away from the edge. Exclosures should be maintained for as short a time period as possible; to minimize the effects of release from grazing they should be left only as long as is required to get a measurable amount of vegetational growth within the pen and no longer. Even this is fraught with problems however, because the duration of exclosure (and frequency of clipping) themselves have a very sensitive effect on measured production. Total accumulated yield from plots established on New Forest grasslands which were left in place for two months but clipped weekly, fortnightly, monthly or only once in the two month period varied from 78 g per m2 to 96 g per m2.

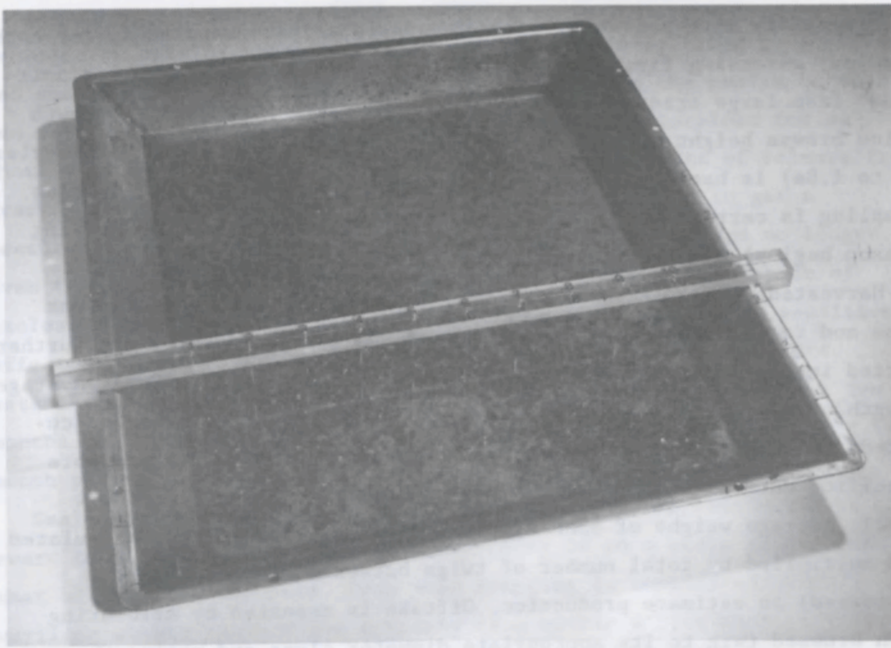
Small enclosures may not contain an area truly representative of the sward to be sampled, if sward heterogeneity is on a scale larger than that of the area enclosed. Even when sampling is replicated, high variance within results for standing crop within a treatment, may result in anomalous results such as negative production or even negative offtake. Finally, as noted, when the proportion of forage species within a sward is low, changes in standing crop of these forage species may be masked by high and unchanging standing crop of non-forage species. In this case studies of production and offtake must be undertaken at the level of individual species, not entire swards - and changes then are often so low as to be immeasurable. All these various problems are further compounded at low grazing pressures when offtake is in any case a small proportion of standing crop. We found results un-interpretable in one study of roe deer at a low density (Johnson 1984). Our approach to estimate of offtake from ericaceous shrubs has for the most part been this last one of considering standing crop inside and outside exclosures, but measuring the standing crop very specifically for a single species at a time. In this case sampling was at longer intervals because of the slower growht rates - and in our studies, very low offtake.

Sampling in a heterogeneous environment

Problems of sampling in a heterogeneous environment become more apparent when assessing production and offtake of trees and taller shrubs, which are more patchily distributed in space. Perhaps because the problems are so much more obvious they are less likely to cause unforeseen problems, because sampling must clearly be such as totake the heterogeneity into account. We have assessed offtake separately for each species, assessing first 'average density of individual trees per unit area' from large transects. Following this, all current year's growth below browse height of the animals in question (roe: 1.4m; other species up to 1.8m) is harvested from a sample of c. 20 trees of each species. Sampling is carried out at the end of winter (just before the growing season begins) and in autumn, at the end of the period of growth.

Harvested twigs are sorted to calculate total number of twigs per tree and to calculate % browsed. Browsed and unbrowsed twigs are further sorted into groups of common basal diameter (after Telfer 1969). Average length and weight of each diameter class of unbrowsed twig are calculated - and samples resorted, or diameter classes made more and more specific, until variance within each category is at an acceptable level. Average weight of each diameter class of twig is then calculated and multiplied by total number of twigs harvested (browsed and unbrowsed) to estimate production. Offtake is assessed by allocating each browsed twig to its appropriate diameter class and noting the difference in weight and length from the average measure for unbrowsed twigs in the same diameterclass. Measurements in autumn give an estimate of available forage production (and any summer offtake); those in late winter offer an estimate of overwinter offtake.

It is only fair to note that this technique is extremely laborious and labour-intensive. As with analysis of 'sward samples' differences between browsed and unbrowsed twigs may be lost because of high variance in the unbrowsed sample. Browsing during the growing season is underestimated and has an unknown effect on subsequent growth of that browsed twig (see, for example: Bobek et al. 1979, Miquelle 1983, Daneel et al. 1985). Finally - a problem common to all methods focussing on the vegetation itself: it is hard to attribute offtake with any confidence to any given species of herbivore in studies dealing with a multispecies system.



Shy animals like these are often in sight for only a few seconds. → p58

Animal-based techniques

Rumen contents

The most commonly used techniques for assessing vegetational consumption by animals is analysis of ruminal or stomach contents. Techniques are widely reviewed (e.g. Martin 1960, Chamrad and Box 1964, Staines 1976 among many others). Such approach has certain possible limitations. The animal needs to be dead before the samples are taken, so it is restricted to 'once-off' sampling for any individual. In many cases it is not legal to kill throughout the year, so sampling is restricted to certain seasons, or at very least sampling is not uniform throughout the year; sample sizes may be small. Finally, the rumen contents properly represent only the most recent meal (potentially important if the animal in question is a mixed feeder). In addition, the method is not immune from problems of differential digestibility.

Particles of foodstuffs of low digestibility will be retained in the rumen considerably longer than items of high digestibility and thus may be consistently overrepresented in analysis. While this effect may be minimised if rumen contents are seived before analysis and consideration is restricted only to particles above a certain minimum size, it cannot be completely resolved. However, results of ruminal or stomach content analysis may be expressed relatively easily as percentage by volume of ingesta (by calibration, for each foodstuff taken of the number of fragments required to make up a volume of say 10 ml: Staines 1976), and may be extended to analysis of actual nutritional quality of ingesta (e.g. Staines and Crisp 1978, Staines et al. 1982).

Faecal analysis

The other widely-used technique of dietary analysis, that of identification of plant remains in faecal material may be considered in many ways to complement ruminal analysis. Techniques are standard (see, for example, Storr 1961, Steward 1967, Steward and Steward 1970), and are based essentially on the identification under the microscope of plant fragments regularly or randomly located within a suspension spread over some form of grid, by relation to reference materials prepared from known plant species. Faecal analysis can overcome some of the problems experienced with analysis of rumen contents, while undoubtedly suffering other problems of its own. Faecal analysis offers the advantage that samples may easily be obtained throughout the year and samplesize is not restricted. Sampling may be repeated on known, marked individuals. Some estimate of the nutritional quality of the diet may be assessed from chemical composition of the dung itself (see for example Erasmus et al. 1978, Putman and Hemmings 1986, Leslie and Starkey 1985, Hobbs 1987). However, identification of dung to the species of herbivore that deposited it may be difficult in multi-species systems, unless sampling is restricted only to those occasions when individual animals are actually seen to deposit the faecal pile collected. Age of dung (time since deposited) may equally be hard tot assess. Recognition of plant fragments to species level is often extremely difficult (although in general the problem is no more difficult than in analysis of rumen contents). Further, reconstruction from proportions of material in the dung to actual proportions in ingesta is problematic, due to possible underrepresentation of highly digestible species, and problems of differential digestion and differential fragmentation (see Johnson et al. 1983, Putman 1984). Finally we face a tremendous problem in trying to

Assessment of diet composition by the point-frame method → p.56

calculate absolute quantities ingested (in terms of actual dry matter). Many people dismiss faecal methods from further consideration because of these perceived difficulties of both analysis and interpretation. In practice, many of the problems can be overcome with appropriate methodology, as, for example the milling of dried faecal pellets before analysis to render all fragments of similar size, or better preparation of samples to remove mucus and other contaminants, so that they yield a higher proportion of potentially-identifiable fragments. But all such corrections have the potential to introduce further bias and Johnson et al. (1983) found that problems due to differential fragmentation were in fact only of minor significance. Correction of proportional representation of forage species in faeces to proportional representation of those same species in the ingesta is also possible (i.e. correction for differences in digestibility of different foodstuffs as they pass through the alimentary tract). Thus, if all plant fragments in the faecal sample are of equal size and if all are assumed of equal thickness (most fragments encountered are epidermal fragments of single cellthickness), then fragment number for any plant species can be considered equivalent to relative fragment weight. If these values are then multiplied by 100/[100-CWD] (where CWD is % cell wall digestibility by weight, determined in vitro) corrected figures will approximate to the relative proportion by weight of each forage type in the ingesta (see Putman 1984 for full rationale). But is such correction worth it in practice? It is arguable that it incorporates too many assumptions and potential sources of error.

In practice, too, where forages are of at least a similar range of digestibility, the laborious correction offers makes little difference to the actual dietary profile obtained. (Table 1 shows uncorrected and corrected profiles for the diet of sika deer in the New Forest over a period of months: data from Mann, 1983).

Table 1. Composition of Sika-deer diet determined monthly in the New Forest in per cent, according to particle counts (1980). A. On the basis of faecal analysis. B. Based on faecal analysis after correction for cell-wall digestibility. Abbreviations: Call. - *Calluna vulgaris*; A.t. - *Agrostis tenuis*; A.s. - *Agrostis setacea*; Mol.- *Molinia caerulea*; T.G. - Total Grasses; T.L. - Total Leaves

A. Uncorrected values

	Apr	May	Jun	Jul	Aug	Sep
Call.	20.7	33.1	38.8	36.7	33.0	33.6
Pine	15.0	4.4	0	1.0	1.1	0
Ilex	1.1	1.6	0.7	0.5	1.9	2.9
Ulex	8.1	5.1	6.7	3.0	2.5	5.1
A.t.	6.6	9.2	8.8	9.4	12.1	17.8
A.s.	21.1	13.9	14.2	13.8	17.1	5.7
Mol.	4.7	5.9	3.7	3.7	6.0	0.8
T.G.	40.9	39.6	34.9	42.7	50.1	36.8
T.L.	11.4	13.9	16.5	14.3	10.8	21.6

B. Corrected values

	Apr	May	Jun	Jul	Aug	Sep
Call.	20.1	29.9	38.6	39.4	34.4	34.2
Pine	15.4	3.8	0	0.9	1.0	0.1
Ilex	1.6	2.1	1.0	0.7	2.4	3.4
Ulex	10.1	5.5	7.6	3.2	3.5	6.2
A.t.	7.6	13.0	10.6	12.3	13.7	21.2
A.s.	25.5	18.4	18.4	18.2	22.8	6.9
Mol.	5.3	10.4	4.8	4.5	7.4	1.0
T.G.	41.7	48.5	36.0	42.5	49.7	37.4
T.L.	9.5	10.1	16.9	12.8	8.7	18.6

Comparing ruminal and faecal analysis

Either ruminal or faecal analysis may thus be used to offer an estimate of the dietary composition, in terms of species content and nutritional quality, of a given herbivore. Absolute accuracy of neither method is fully established, though some validation of the ruminal technique has been attempted (e.g. Staines 1976) and precision of faecal analysis has been assessed, for example, with hand-fed Sika deer by Takatsuki (1978). Comparisons of results obtained from the two techniques together are offered by for example Anthony and Smith (1974), Kessler et al. (1981) and Hanley et al. (1985). From a comparison of dietary profile revealed by ruminal and faecal samples for 13 black-tailed deer, Hanley et al. conclude that forbs and ferns appear to be consistently more abundant in those profiles based on ruminal analyses, while grasses, mosses lichens and woody browse were more abundant in faecal profiles.

Whichever method of analysis is used to provide information on food habits and dietary composition however, estimation of forage offtake by a population, or within a given study site, requires translation of this dietary profile into figures for actual bulk of each forage consumed. Such calculation can be done assuming values from the literature on energetic requirements, but these are necessarily 'global' figures and are based in the main on captive or restrained individuals. The generality of their applicability to field studies offree-ranging ungulates is perhaps debatable. Other methods involve the use of radiotracers - and again require regular handling and manipulation of study animals. It may be possible to estimate actual bulk intake from ruminal analysis, where percentage volume of different foodstuffs has been assessed and total volume of rumen content also recorded. We have essayed another approach - based on an extension of faecal analysis techniques. During 24h follows of individual (habituated) animals- in this instance, New Forest ponies - we have collected the total faecal output for that day; sampling was repeated in every month.

Subsamples were analysed for species composition as above - but were not corrected for differential digestibility: results thus represent proportional composition of the faecal matter not ingesta. Making the same assumption as above, that fragment of equivalent size might be taken as of equivalent weight, analyses can be taken to contribution to the dung by weight. If multiplied by total weight of dung eliminated in 24h, results approximate to total faecal output by weight of each forage species recognised. Results for each forage class are now concerted by species specific dry matter digestibility values [DDM], derived in vitro, to offer an estimate of the actual ingested weight of that forage type by one animal in 24 h.

Specimen calculations are presented by way of example in table 2 for New Forest ponies in one particular month: July. While the technique is clearly highly dubious, and compounds an impressive array of assumptions and potential sources of error, it is striking that when estimated intake of different foodstuffs is summed across all forages to offer an estimate of total dry matter intake overall, this figure is remarkably plausible for a 250 kg horse! Despite this, however, I would emphasise that such analysis is highly speculative and requires further validation before it is more widely applied.

Table 2. From total faecal output to estimated intake of forage type: example giving results of calculation for New Forest ponies (July).

Forage type	Total faecal output in 24 h (kg)	% of faecal frag-ments	Faecal output for each forage type (g)	Digesti-bility of each forage type (%)	Estimated intake of each forage type (g)
Molinia		24.3	950.4	20.5	1386
Other grasses		67.7	2647.7	23.9	4144
Juncus spp.		2.6	101.7	16.2	42
Heather		0.7	27.4	10.7	33
Bracken		2.2	86.0	31.2	157
Mosses		0.7	27.4	6.0	31
Forbs		0.2	7.8	28.0	12
Tree leaves		0.2	7.8	30.2	14
Gorse		0	0	36.6	0
unidentified material		1.2	46.9	-	?
TOTAL	3.91	100	3911.0	-	5819

In overall summary, I believe that animal-based techniques, while useful in exploring the dietary selection of the animal, in regard to both species composition and nutritional quality, and in monitoring changes in that diet over time, are not appropriate in an analysis of actual vegetational offtake overall; such analysis should for the present rely on direct sampling of the vegetation itself.

References

Anthony, R.G. & N.S. Smit 1974. Comparison of rumen and faecal analysis to describe deer diets. J. Wildl. Mgmt. 38: 535-540.

Bobek, B., K. Perzanowski, J.Siwanowicz & J.Zielinski 1979. Deer pressure on forage in a deciduous forest. Oikos 32: 373-379.

Chamrad, A.D. & T.W. Box 1964. A point frame for sampling rumen contents. J. Wildl. Mgmt. 28: 473-477.

Danell, K., K. Huss-Danell & R. Bergstrom 1985. Interactions between browsing moose and two species of birch in Sweden. Ecology 66: 1867-1878.

Erasmus, T., B.L. Penzhorn & N. Fairall 1978. Chemical composition of faeces as an index of veld quality. S. Afr. J. Wildl. Res. 8: 19-24.

Hanley, T.A., D.E. Spalinger, K.A. Hanley & J.W. Schoen 1985. Relationships between fecal and rumen analysis for deer diet assessments in southeastern Alaska. Northwest Science 59: 10-16.

Hobbs, N.T. 1987. Fecal indices to dietary quality: a critique. J. Wild. Mgmt. 51: 317-320.

Holisova, V., I. Kozena & R. Obrtel 1986. Rumen content vs. faecal analysis to estimate roe deer diets. Folia Zool. 35: 21-32.

Johnson, M.K., H. Wofford & H.A. Pearson 1983. Digestion and fragmentation: influence on herbivore diet analysis. J. Wildl. Mgmt. 47: 877-879.

Johnson, T.H. 1984. Habitat and social organisation of roe deer (Capreolus capreolus). Ph.D. thesis, University of Southampton.

Kessler, W.B., W.F. Kasworm & W.L. Bodie 1981. Three methods compared for analysis of pronghorn diets. J. Wildl. Mgmt. 45: 612-619.

Leslie, D.M. & E.E. Starkey 1985. Fecal indices to dietary quality of cervids in old-growth forests. J. Wildl. Mgmt. 49: 142-145.

Leslie, D.M. & E.E. Starkey 1987. Fecal indices to dietary quality: a reply. J. Wildl. Mgmt. 51: 321-325.

Martin, A.C. 1960. Food-habits procedures. In: H. Mosby (ed.), Manual of game investigation techniques. Ann Arbor.

Miquelle, D.G. 1983. Browse regrowth and consumption following summer defoliation by moose. J. Wildl. Mgmt. 47: 17-24.

Putman, R.J. 1984. Facts from faeces. Mammal Review 14: 79-97.

Putman, R.J. 1986. Grazing in temperate ecosystems: large herbivores and the ecology of the New Forest. Croom Helm, London. 210 p.

Putman, R.J., P.J. Edwards, J.R. Ekins & R.M. Pratt 1981. Food and feeding behaviour of cattle and ponies in the New Forest: a study of the interrelationship between the large herbivores of the Forest and their vegetational environment. Report HF3/03/127 to Nature Conservancy Council, Peterborough.

Putman, R.J. & G.J. Hemmings 1986. Can dietary quality of free-ranging ungulates be simply determined from faecal chemistry? Acta Theriologica 31: 257-270.

Staines, B.W. 1976. Experiments with rumen-canulated red deer to evaluate rumen analysis. J. Wildl. Mgmt. 40: 371-373.

Staines, B.W. & J.M. Crisp 1978. Observations on food quality in Scottish red deer (Cervus elaphus) as determined by the chemical analysis of the rumen contents. J. Zool. Lond. 185: 353-359.

Staines, B.W., J.M. Crisp & T. Parish 1982. Differences in the quality of food eaten by red deer (Cervus elaphus) stags and hinds in winter. J. Appl. Ecol. 19: 65-77.

Steward, D.R.M. 1967. Analysis of plant epidermis in faeces: a technique for studying the food preferences of grazing herbivores. J. Appl. Ecol. 4: 83-111.

Steward, D.R.M. & J. Steward 1970. Food preference data by faecal analysis for African plains ungulates. Zool. Africana 5, 2: 5-29.

Storr, G.M. 1961. Microscopic analysis of faeces; a technique for ascertaining the diet of herbivore animals. Austr. J. Biol. Sci. 14: 157-164.

Takatsuki, S. 1978. Precision of fecal analysis: a feeding experiment with penned Sika deer. J. Mamm. Soc. Japan 7: 167-180.

Telfer, E.S. 1969. Twig weight-diameter relationship for browse species. J. Wildl. Mgmt. 33: 917-921.

VII. ASSESSMENT OF BROWSE SUPPLY AND BROWSE CONSUMPTION: DISCUSSION

S. de Bie and H.E. van de Veen

Introduction

Because the majority of the herbivores in terrestrial ecosystems forage (at least) partially on the leaves, twigs, flowers, and fruits of shrubs and trees, assessment of the supply of these food items and their consumption has received considerable attention but less than has been given to the production and offtake of herbaceous vegetation.

Browse and browse supply

The assessment of browse supply and consumption encounters a variety of problems right from the start. Browse is defined rather unanimously as the current year's growth of woody plant species (leaves and twigs) and bark of trunks and branches. Supply is more difficult to define. It could simply mean the quantitative presence of leaves and twigs of woody plant species. However, supply is often understood as indicating the amount of usable or consumable browse, the classification of what is usable (or consumable) depending on the type of user, i.e., herbivore species, but also on the management objectives. For example, red deer are able to reach at higher levels and take longer twigs with a larger diameter than roe deer are, which means that the same browse supply for red deer could be larger than that for roe deer. However, both species might consume more than is desirable or acceptable from the objectives of management. The plant species involved, the potential users, and the management objectives determine the amount of browse available as a source of food. Thus, browse supply should be specified according to the species of herbivores and the woody plants concerned. Consumption is the quantitative removal of all or part of the browse.

Sampling techniques for browse supply

Shrubs and trees occur in patches as the result of differences in soil and water conditions, the degree of slope and its direction, etc. Estimation of the supply and consumption of browse per unit area requires a sampling program.

Heterogeneous landscapes necessitate stratification of the area into (more) homogeneous subunits. The mode of stratification is partly determined by the reason for it. Although such stratification should by preference be based on criteria relevant for the consuming herbivore (e.g. occurrence and density of woody plant species), other criteria such as geomorphology, drainage patterns, and socio-ecological relationships between plant species are generally used instead. The latter criteria have more relevance for the researcher concerned with stratification.

The planning and execution of sampling of shrubs and trees for the estimation of browse supply (and consumption) raise a variety of problems. Any methodology evokes discussions. A thorough treatment of the subject is given by Perzanowski, who deals with two ways of sampling browse supply, i.e., in unfenced plots, transects, etc. and in fenced plots.

The use of unfenced plots or transects has several advantages in that it is relatively cheap and the sampling more rapid. Fenced plots have some advantages too. The latter method offers the best way to measure browse production, because consumption by herbivores is excluded. Moreover, regrowth cannot be measured accurately unless controlled clipping procedures are used.

From the point of view of forage supply for herbivores, the main disadvantage is the exclusion of browsing as a determinant factor with respect to plant growth and regrowth (pattern, rate, quantity), and plant shape. The growth pattern of shrubs and trees inside fenced plots differs from that outside such plots, e.g. as to leaf fall, time of flowering, etc.

In the first place, the rate of production differs as well. This means that the duration of exclosure will influence the amount of browse to be measured. Second, due to the high cost of fencing, fenced plots are small and variations between plots are likely to be larger than differences between estimation of browse inside and outside the enclosure. Third, the fencing itself leads to vegetational changes inside the plot, because it causes changes in microclimatic conditions and might even induce changes in the vegetation, because browse species might start to dominate less preferred species.

We conclude that fenced plots should only be used for short periods to avoid underestimation of actual production and supply.

Sampling in plots (fenced or unfenced), along transects, or by some other method means that many choices (see Chapter V) must be made. These choices concern the location of the plots or transects (random or systematic), the number of plots or transects, the plot size/transect length, the shape of the plots (rectangular plots give less variation than e.g. circular plots, because vegetational diversity is greater), the number of sampling points per transect, and the sampling height. Statistical methods can provide a basis for such choices.

Several techniques are available to measure browse quantitatively within individual plots or at each transect point. These include (see also Chapter V):

a. Total harvesting, which gives reliable results but is time-consuming and extremely laborious.

b. Twig counting combined with weighing of a sample of twigs to estimate average phytomass per twig; this requires differentiation of twigs according to age, length, and diameter. Results are reliable and the method is less time-consuming than total harvesting.

c. Measurement of characteristic features of plants (e.g. height, crown diameter, etc.) related to browse production.

d. Photographic techniques.

e. Measurement of tree and shrub density or canopy cover (e.g. PCQ and SPM methods), both of which are related to browse production.

All but the first of these techniques rely on sampling within a plot/transect point to estimate browse production, and three of them (b, c, and e) require harvesting to relate the parameter(s) to the quantity browse.

The frequency of sampling to determine browse supply (and consumption) deserves special attention. In general, assessment of browse production and supply is carried out twice, e.g. in the autumn to estimate total production (and summer consumption) and in the spring for winter consumption. However, this approach neglects two important aspects:

1. Browse production and browse supply are not identical. During the spring all growth could in principle be consumed by a herbivore, but during the growing season annual growth of twigs and leaves would become lignified, the level of polyphenolic and other chemical digestion-inhibiting compounds could rise sharply, and therefore the consumable part of the production would show a relative decrease. Hence, supply is not a constant fraction of production, which includes the potential consumption as well.

2. Browsing influences plant growth. Because traces of browsing may disappear rapidly, a sampling frequency of twice a year or less will lead to serious underestimation of the production, supply, and consumption of browse, especially in areas with a moderate to low browsing pressure. The relative importance of these aspects differ, between plant species and management objectives.

From the foregoing it is clear that accurate estimation of browse production and supply for one or more species of herbivores demands considerable work, and that for exact measurements it is essential to follow the plant's phenological stages as closely as possible.

Assessment of browse consumption

As explained by Putman, the consumption of browse by herbivores can be assessed by vegetational and animal-based techniques, but there are no sharply defined criteria available to facilitate the choice between these two categories. For a sward-like vegetation it holds that when the offtake is above approximately 20%, vegetational techniques are to be preferred because they demand relatively less time and are more accurate than animal-based techniques.

All vegetational techniques for the assessment of browse consumption start at the level of plant species, because these species differ both physically and chemically. Twig counting is a widely applied technique (see Chapter VI) but is quite laborious. In the growing season traces of browsing may disappear rapidly, and will be missed if the sampling frequency is not sufficiently high. Because of the difficulty of distinguishing between 'old' and 'new' scars, this technique can give a bias as to species composition and thus lead to underestimation of consumption. Moreover, determination of traces at the animal-species level is often difficult too, which means that if more than one herbivore species is involved, total offtake can be assessed but not the proportion for which each animal species is responsible.

Calculation of offtake on the basis of unbrowsed twigs can evoke another source of error. These twigs are either consumable but not browsed and are for some reason actively selected or avoided by the herbivore(s). This source of error can be avoided by marking subpopulations of twigs at the start of the growing season and then following these twigs at intervals. Although this is time-consuming, it is worth doing if the effect of herbivore selection on plant quality is studied.

Signs of rooting by wild boar

Furthermore, actual offtake is the difference between browsed and unbrowsed twigs (per age, length, and diameter class) and depends on what is available 'nearby' and what has already been eaten, and thus on animal density.

Other vegetational techniques such as total plot harvesting or analysis of photographs encounter comparable difficulties.

For the assessment of browse consumption also several animal-based techniques are available. Direct observation of animals can provide valuable information about diet composition and patterns of food selection. Often wild herbivores apply 'compensatory feeding' by active selection of particular food items to optimize the digestive process. Indirectly - via bite counts per unit of time - direct observations can be used to estimate feeding rate and intake. Unfortunately observational techniques rely on prolonged visibility of the animals to be observed and visibility in daylight offers great advantages over night observations. Low density and shyness of the animals and poor visibility of their habitat are among the factors that often force the researcher to use more indirect techniques.

Commonly used techniques include analysis of the stomach/ruminal contents and of faeces. A wealth of information has been published on these techniques (for more details about some of the advantages and disadvantages of both, see Chapter VI). A few aspects frequently discussed during the meetings should be mentioned here.

With respect to the applicability of these techniques, a useful distiction is made between qualitative aspects (plant-species composition of the diet) and quantitative aspects (intake).

It is generally agreed that analysis of both the stomach contents and (especially) the faeces provides sufficient reliable information on the diet composition of herbivores.

Stomach-content analysis has the following main disadvantages: a) data are often only available for a limited period of the year (due to hunting regulations), b) samples are small, and c) often only a small part of the diet spectrum is sampled due to differential fermentation rates of plant parts and species, and selective, non representative habitat use. Results obtained with this technique may have limited value in view of the usually small samples from identical conditions with respect to season and place.

Apart from the advantages offered by faecal-content analysis (samples available throughout the year, no restrictions on sample size), this technique encounters other problems, e.g. the identification of the producer of the faeces and the identification of plant fragments. All samples contain unidentifiable plant fragments, the proportions depending on the animal species involved (in ruminants there are more fragments unidentifiable than in non-ruminants) and on the minimum fragment size to be considered for identification (the larger this size, the more easily the fragments can be fractured, and digestible plant species will be underestimated or missed).

Assessment of intake

Calculation of total and proportional intake based on the diet composition indicated by both techniques requires knowledge of plant-species characteristics, especially the differential digestibility of plant species and plant parts, and also of the kinetics of the material during passage through the digestive tract and intestines.

The digestibility of plant species determined by in-vitro digestibility trials is often taken as the basis for reconstruction of dietary intake according to the proportional presence of these plant species in the faeces. Ruminal fluid from the animal species concerned should by preference be used in these in-vitro trials. With mixed diets use must be made of inocula derived from well-adapted rumen biota to avoid in-vitro fermentation that will lead to unreliable estimates of digestion rates or no results at all. But since use of inocula is often impossible, domestic animals (sheep) are used as the suppliers. Inocula from 'grazers' like sheep and cattle are an important source of error if digestibility of browse or browse-based diets is at stake. Feeding trials might provide accurate data on plant species-specific digestibility, but even if tame animals are not difficult to obtain, the reliability of such data remains questionable. Plant-species digestibility will vary much with the quantitative composition of the diet. This digestibility is determined not only by the quantitative proportion of the plant species concerned but also by the presence of other plant species in the diet. A second and often neglected source of error is due to the more fibrous parts of the browse ingested, especially twigs and bark. In the faeces this material often has no characteristics permiting plant-species determination. In Western Europe wood structure will help identification, because the number of woody species is limited, but this material is often removed from the faeces by the treatments applied.

Another source of error in the reconstruction of dietary intake from faecal fragments can lie in the conversion of surface area of plant fragments into quantity ingested without taking into account leaf thickness, which differs between plant species and groups. Because the ratio between weight and surface of plant leaf is comparable for the majority of plant species, this source of error is probably negligible.

Fistulation and feeding trials are alternative techniques used to avoid the limitations associated with the above-described animal-based methods. Apart from their specific problems (e.g. availability of tame or tamed animals), feeding trials (cafetaria system) can indeed provide information on food choice, but it must be kept in mind that the results obtained in this way concern the choice of plant species under controlled, i.e., non-natural conditions. In nature an animal's decision to feed on plants of a certain species depends upon several factors besides the presence of those plants; for example, browse with a certain amount of secondary plant metabolites (e.g. tannins) might be taken if other species with nutritional compensation for these compounds can be selected for. The optimization of foraging in nature is difficult if not impossible to simulate in feeding trials.

Fistulated animals need constant medical attention and care. Under free-ranging conditions, optimal care is difficult to guarantee. This explains the reluctance to use this type of research unless conditions can be tightly controlled. Moreover, the limited number of fistulated animals used might lead to bias concerning the choice and intake of plant species according to individual preferences. However, in habitats with few plant species this bias is probably small.

Rooting of wild boar imitated by the forester to stimulate forest rejuvenation

Concluding remarks

In view of the many problems involved, it is concluded that animal-based techniques for assessment of the quantitative intake of browse by herbivores should be used to supplement vegetational methods. At least for the estimation of total browse consumption, animal-based techniques should not be used.

Finally, with respect to the assessment of browse supply and consumption, two criteria are considered important: accuracy and sampling efficiency. The accuracy of the information obtained is strongly influenced by the amount of time and funds available. Optimization of both accuracy and efficiency often means the acceptance of a certain arbitrary level of inaccuracy; a certain accepted deviation from the (unknown) true value. This estimation can, however, be very precise. Much attention is often paid to a high degree of precision, but the methodology applied leads to a rather inaccurate estimation. A certain balance between accuracy and precision is just as important as an optimal balance between efficiency and accuracy.

PART TWO: ANIMAL-BASED TECHNIQUES

VIII. GUIDELINES FOR THE CAPTURE AND HANDLING OF DEER

R. Harrington

Introduction

The capture of deer is often an essential prerequisite for a wide variety of studies and management needs. Frequently, the undertaking of range studies depends upon whether deer can be captured, in what numbers, and how frequently.

During the past 25 years many techniques have been developed for the capture of large mammals. These developments have greatly benefited from the experience made in capturing deer and, more recently, the latter techniques have greatly improved the scope and effectiveness of the capture of other wild mammals.

There are basically two types of capture method, one physical and the other chemical, both of which can be either active (e.g. netting or darting) or passive (e.g. trapping or oral administration of drugs, which I shall call the *per os* method); a combination of methods is frequently the most effective approach. The decision as to the type of method to be employed will depend upon such factors as types and numbers of deer, tractability of the deer, number of recaptures required, kind of investigation/measurements to be made in the captives, prevailing season/weather conditions, ground conditions (grassland, heath, forest, etc.), accessibility for air or ground transport, time scale, presence of public, interaction or interference by other species (particularly ungulates), and the extent of range and boundaries.

The ease with which any capture method can be employed is greatly enhanced by an understanding of the behaviour of the deer. Generally, they are intelligent and show acute awareness of their environment and changes within it. Unpleasant experiences are long remembered and such situations avoided. Pleasant experiences, especially those associated with feeding or cover, are also remembered and recurrence is sought.

Circumstances under which deer are captured and handled vary to such a degree that it is impossible to define a procedure for all situations. The following discussion deals with the basics of the more common and some of the less widely used methods of capture.

Physical methods for capture and restraint

Enclosure traps

It is generally accepted that the use of enclosure traps is one of the most effective methods for capturing deer. When well designed and managed, these traps also cause the least stress. Their use is most appropriate when deer movement is known and groups of deer are required. Such traps are also generally the most effective for recaptures, and perhaps offer the sole method for capture and restraint when measurements in deer must be performed with minimal interference from the effects of stress and restraining chemicals. Enclosure traps may be permanent or of a temporary design.

Permanent enclosure traps

Permanent enclosure traps are used where there is continuous or regular seasonal presence of deer. These traps are erected in situations where the following conditions apply: there is adequate cover of trees or tall vegetation occupying not less than one-third of the enclosed area; natural feeding is available and/or supplemental feeding can be provided; the edge of the enclosure is accessible for wheeled transport; public interference is minimal or absent; dogs are absent; and there is shelter preventing exposure to wind and human presence. The specifications are given in Appendix I.

Temporary and portable enclosure traps

Temporary and portable enclosure traps are widely used. Recent innovations in New Zealand have made such traps the most effective for capturing a wide variety of deer and other mammalian species. The use and function of temporary/portable enclosure traps is basically the same as that for permanent structures, but they are often smaller and their temporary nature means that posts and netting must be made of stronger and more flexible materials. A wide range of materials and techniques can be used for the construction of this type of enclosure. The following items must, however, be considered indispensable:

a. Steel (or fibreglass) posts with provisions for effective bracing.

b. Wire/rope in continuous lengths and connected to corner posts by secure and easily adjusted fixtures, with no protusions into the enclosure.

c. Design allowing easy transport and handling.

As to the gates, both of the two types used for permanent enclosures are suitable (Appendix I). Now that considerable developmental work in New Zealand has been completed, a third kind, permitting erection of the whole perimeter in one operation, is now available. The basics of the third type are discussed below.

Other traps

A wide variety of other trapping techniques have long been available, such as leg, box, net, and pit traps, but all of these are less relevant within the scope of this workshop. In addition, new inventions and re-inventions appear constantly, and some of them have been usefully applied in specific circumstances, e.g. the 'Alpine spring net' trap which is the most successful net trap introduced in recent times. For this trap, corner posts are weighted and connected to a perimeter net, which is folded and placed in a trench. When triggered, the net is hauled into position by the weights. The deer thus enclosed are unable to escape and generally adapt quickly to captivity.

Capture and tagging of a large proportion of a population of animals facilitates assessment of population size and structure.

Netting

Long nets are universally applied, especially to capture smaller deer species and fallow deer. This technique is labour intensive and can be very stressful for deer - in particular to red deer and Sika deer, which often do not survive the effects.

General points concerning physical capture:

1. A thorough knowledge of the area where trapping is planned is essential.

2. Traps should usually be rapidly erected and left in an open position for at least two weeks before use.

3. The combination of pre-baiting of traps with supplementary feeding and the use of high levels of fertilizer containing nitrogen, phosphorus, and potassium on surrounding vegetation and the grass areas inside the trap enclosure, assures the best enticement.

4. Rehearsal of trapping by all involved is imperative.

5. Final checking of the trap-closing mechanism is essential.

6. It is desirable and generally more effective to capture all of the deer belonging to a group.

7. It should be possible to close the trap without disturbing the deer.

8. Under no circumstances should an approach be made to the trap until the trapped deer have settled down, which sometimes takes more than one day.

9. Movement of the captured deer into the race and thence to the handling/loading area should be done quietly.

10. Wild (feral) and even domesticated deer will require varying degrees of physical restraint during handling. It is essential that this be done in a quiet and firm manner in the handling area. Under no circumstances should this area be entered by anyone who shows hesitation or is in any way intimidated. Quiet, smooth, confident, and firm action is required. The less tractable the deer, the more relaxed and patient the handler must be. It is best to handle a number of a deer at one time, in confined space. A hinged side to the handling unit can serve as an adequate crush for dealing with stags in hard antler.

Chemical restraint

There are two basic ways to administer restraining chemicals to deer, by injection and via the oral route (ingestion).

Injection

The injection of chemicals is by far the most commonly used method for deer capture. Various techniques, often involving quite elaborate and sophisticated devices, have been developed for this purpose. They are divided into two types: the hand-held syringe (usually a long-handled syringe) and the automatic syringe on dart.

Hand-held syringes

Hand-held syringes are excellent devices for injecting deer in races or small enclosures and deer tame enough to allow the operator to come within 2-3 m of the animal. Such devices consist of a syringe provided with a short needle and mounted on a light-weight pole. This offers by far the safest way of injecting non-restrained animals.

Automatic syringes

Automatic syringes represent a wide range of design, construction, operation, and reliability. They are often crude and unreliable. Each type of automatic syringe has a specific set of advantages and drawbacks. The over-all problem is that of placing the dart accurately with minimal velocity. Few systems are consistently accurate at 35 m and almost none of those delivering 2-5 ml over greater distances. Light syringes appear to travel best when designed sufficiently long; short thick syringes need weight. Automatic syringes can be divided into two broad categories on the basis of how they are propelled, i.e., the blowpipe type and the firearm type.

Blow pipes

Velocity, accuracy and the degree of manoeuverability are determined by the length of the blow pipe. A length of 2 m seems to be the most suitable for most situations where 1-3 ml is to be delivered over distances of up to 12 m. Their low impact velocity, as well as the ease of operation and lower cost are all attractive features.

Accuracy and effectiveness in the use of blowpipes are dependent upon practice and regular usage. Such pipes have wider application than is realized and deserve far more use than they get. For those whose blowing capacity is limited, gas and hand-pumped propellants are available.

Firearm delivery systems

By far the most sought after system for deer capture is the firearm type (rifles, pistols, etc.). However, it must be kept in mind that 'Too many people are still under the impression that catching animals with a projectile dart is simply a matter of marksmanship. This aspect is important but skills in weapon handling can be taught quickly. The more difficult part of the procedure of catching animals by this method is the degree of personal judgement required to arrive at soundly based decisions on the drugs needed, their dosage rates, the type of dart, the length of needle, the method of approach and the likely range at which the animals will have to be hit' (David Jones, Director, London Zoo).

Firearm delivery systems add one more danger factor to deer capture. It is imperative that those who operate them are competent in all aspects of the use of this type of equipment and that they continuously receive opportunities for practice under realistic conditions.

The general guidelines for the use of firearms will apply. The veterinary practitioner supervising the use of chemicals for restraint must also issue clear directions about safety.

The use of most chemicals for restraining deer is generally regulated by prescription and is usually under the direct supervision of a practicing veterinarian. Various chemical cocktails for use in the three deer species living ferally in Ireland are available. Alternative compounds are continually being developed, but those listed in Table 3 have proved generally to be the most suitable under most conditions.

With the advent of the firearm delivery systems the use of the crossbow type of delivery is no longer considered appropriate for deer.

Table 3. Chemical compounds used for immobilizing deer species.

Species	Adult wt. range (kg)	1st choice & dose range	2nd choice & dose range
Red deer *Cervus elaphus*	105-180	2.0-4.5 mg etorphine & 9.0-20.0 mg acepromazine	30-40 mg xylazine
Sika deer & hybrids *Cervus nippon*	45- 85	2.0-3.5 mg etorphine & 9.0-20.0 mg acepromazine	20-40 mg xylazine
Fallow deer *Dama dama*	35- 70	1.2-2.0 mg etorphine & 35-70 mg xylazine	200-500 mg ketamine & 35-70 mg xylazine

Oral administration

Many claims have been made about the efficiency of administering drugs to deer orally. However, experience has shown that the oral administration of restraining chemicals is only effective under very specific conditions. In principle this route should only be used: in enclosures where the deer cannot be approached for darting, netting, etc. without subjecting the animals to considerable stress, and in association with capture enclosures. This route has special merits particularly for fallow deer.

Oral administration is accomplished best in a molasses-beet-pulp-brewers' grain mix to which 80 g of Diazepam has been added together with about 30 liters of feed. The animals are unlikely to receive an overdose by taking too much (though this can happen). Warm surroundings are essential to ensure recovery (1-2 days). Diazepam works best when ambient temperatures are below 2 °C.

Difficulties in administering chemicals *per os* are due not only to the lag time required for ingested substances to reach the bloodstream but also the uneven intake under field conditions, which means that some deer are more affected than others. There is also a substantial environmental influence on the intake and on the effects of ingested drugs in different deer species.

It must be kept in mind that the taste and smell of chemicals is remembered by deer for a long time; once deer have been affected by a chemical compound, they may refuse to ingest it a second time, certainly over periods of several months.

Drugs for oral administrations

Diazepam is by far the most effective restraining drug for oral administration to deer, but because the range of effectiveness is dependent on many factors, it must only be used in deer under the specific conditions mentioned above, and affected deer must be kept in enclosed and sheltered conditions until they recover.

Chloral hydrate and alphachloralose can be used together with Diazepam or alone. However, this demands even closer monitoring of the affected deer and the bitter taste of these substances makes them difficult to administer.

General points on chemical restraint

1. A thorough knowledge of the area where deer are to be captured is essential.

2. Because deer are rarely restrained within four minutes, there is considerable time for movement away from the place where a compound has been administered. It is essential that the deer are exposed to minimal stimuli during this induction phase.

3. Downed or restrained deer must be attended to immediately.

4. Essential safety procedures connected with the treatment of the deer must be applied under veterinary guidance.

5. The cardiac function and respiration are likely to falter in animals that have been under stress prior to administration of drugs or during the induction period. It is essential that stressed animals only be treated under conditions of last resort.

6. Recovery of deer must be allowed to proceed in seclusion and quiet.

7. Deer should not be transported before a reasonable degree of recovery has been achieved.

APPENDIX I

Specifications for a permanent enclosure

Area (Fig. 7A): A minimum of 0.1 ha for relatively small species, e.g. Sika deer, and 0.3 ha for larger deer, e.g. red deer.

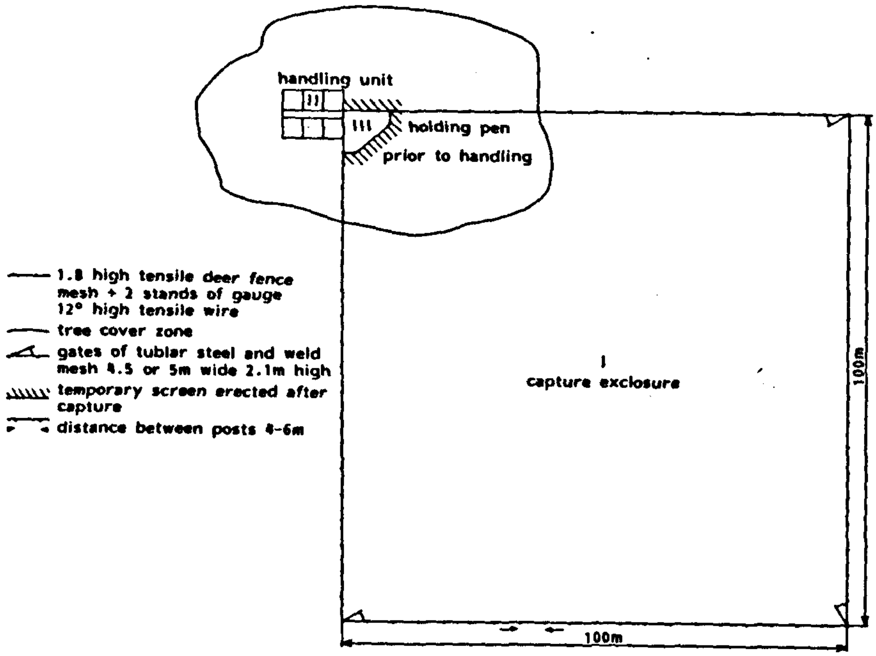
Vegetation: By preference mixed forest and grassland, ideally with shrubs. The grassland should be manured and mowed to ensure production of highly palatable forage or, alternatively, be baited with palatable food.

Fencing (Fig. 7B,C): High tensile (H.T.) wire (minimum gauge 4 mm) and strong posts (15 cm in diameter). Mild steel-wire or plastic mesh can be hung on supporting H.T.-line wires for the capture of small deer e.g. Sika and fallow. H.T. mesh with a minimum mesh size of 15 cm is needed for red deer. Posts can be placed 5 m apart. The height of the fence must be at least 1.8 m; higher fences may be required if excessive pressure is put on the fence, particularly by red deer and fallow deer.

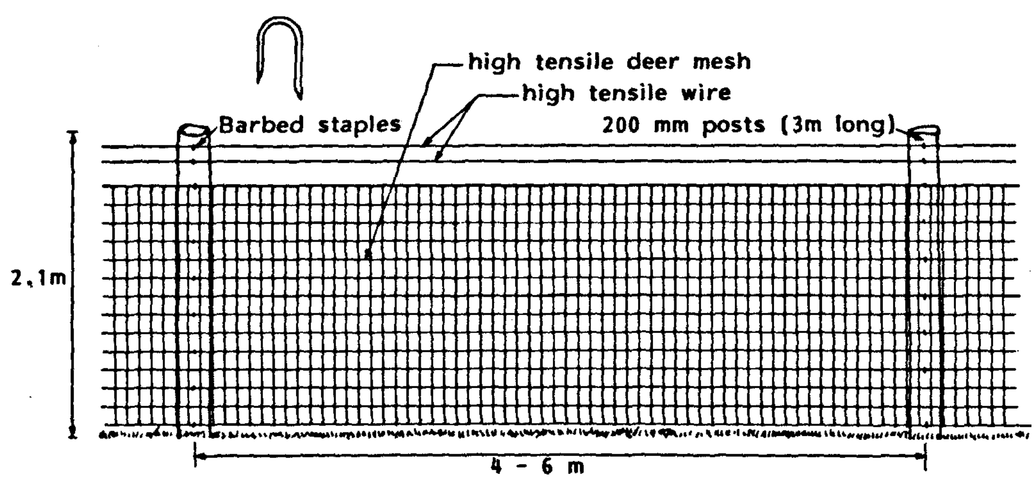
Gates (Fig. 7D): Two kinds of gate can be used: drop gates made of 5 cm plastic rope mesh or hinged gates made of light-weight metal tubing and wire mesh. It is essential that the gates function smoothly at all times, without hesitation or obstruction. All gates should be kept fully open to entice the deer to enter the enclosure. After acceptance of the pen, all but one gate can be closed. It is essential to allow the deer to settle after capture.

Sub-compartments (Fig. 7E,F): It is essential that the enclosure have divisions that can function as a raceway to a handling section. The area adjacent to the handling area should be screened off by cloth boarding or plastic sheeting to obstruct the vision of the enclosed deer.

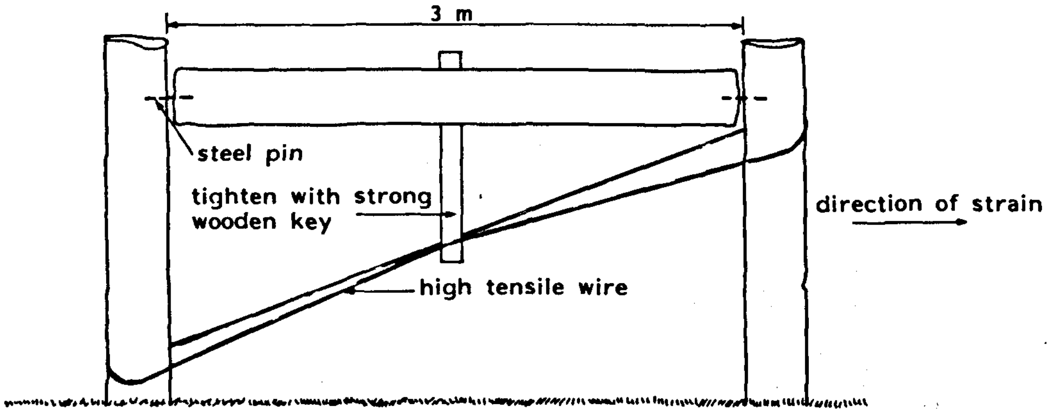
Handling area (G-J): A double compartment is a minimal requirement. A crush consisting of a covered area measuring about 1.5 m^2 is ideal. A hinged wall within this box will suffice for handling most deer, but might be placed externally if it is probable that large stags in hard antler will have to be handled. Fallow deer require completely darkened crush and handling areas. Sika deer and red deer can be adequately handled in subdued light in the absence of external visual stimuli.


handling unit
holding pen
prior to handling
1.8 high tensile deer fence mesh + 2 stands of gauge 12° high tensile wire
tree cover zone
gates of tublar steel and weld mesh 4.5 or 5m wide 2.1m high
temporary screen erected after capture
distance between posts 4-6m
I
capture exclosure
100m
100m

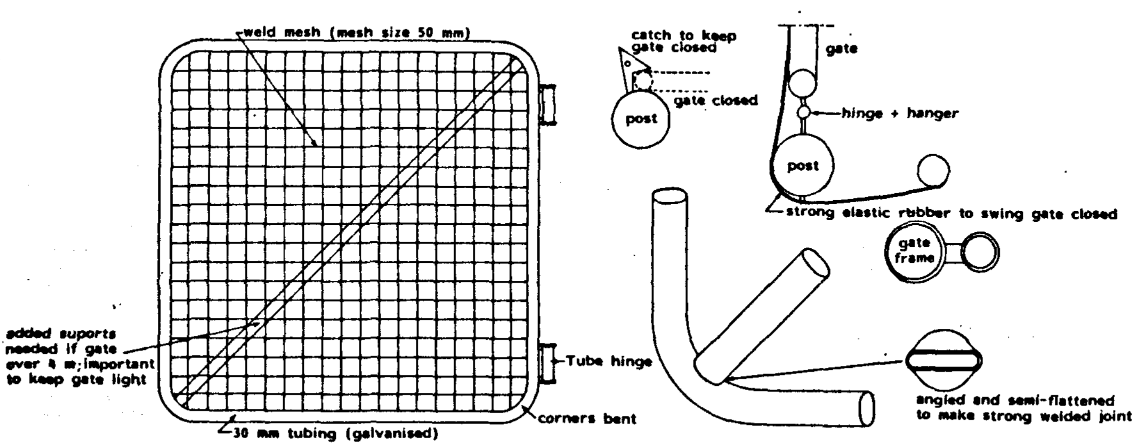
a


high tensile deer mesh
high tensile wire
Barbed staples
200 mm posts (3m long)
2,1m
4 - 6 m

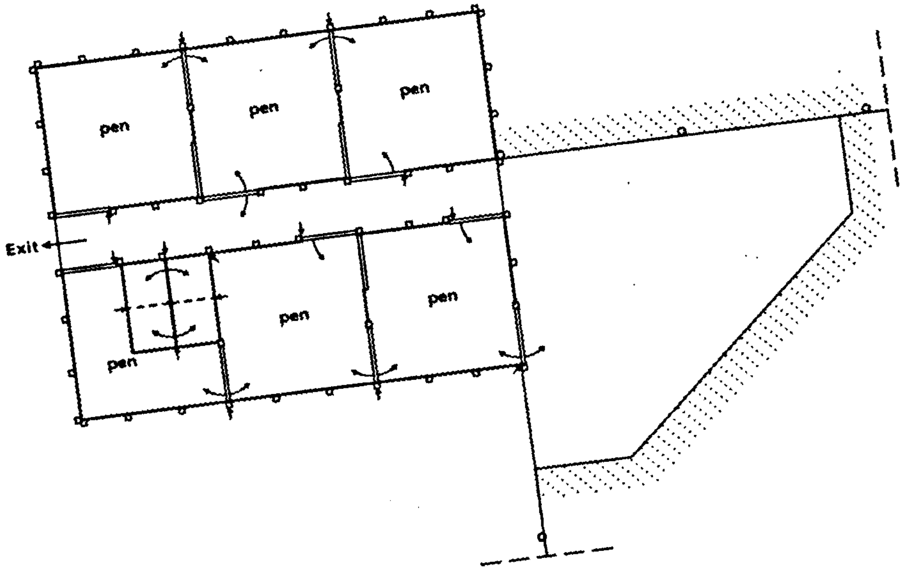
b

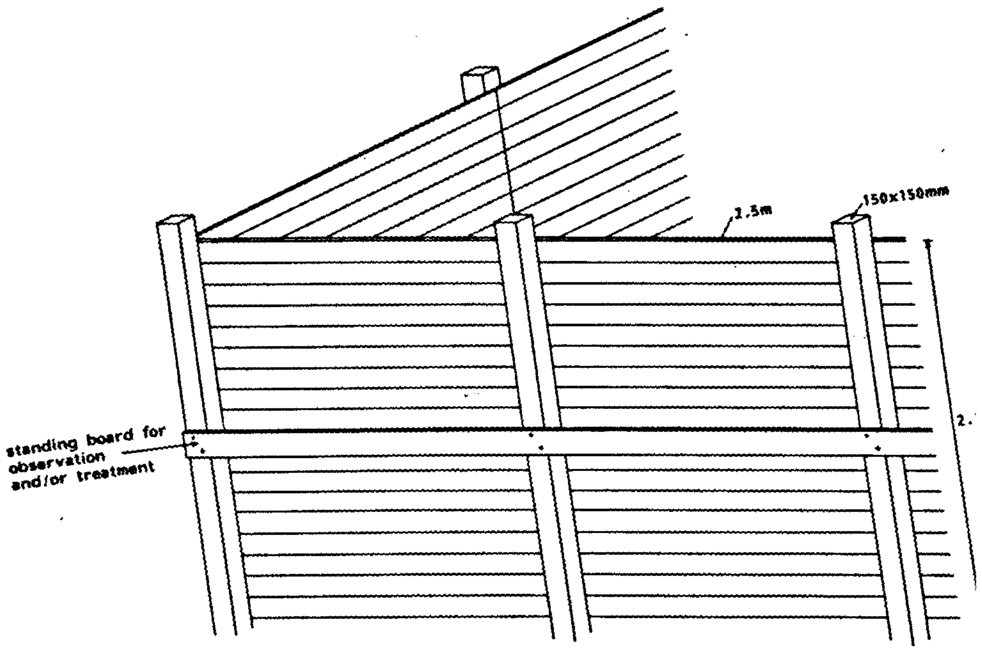

3 m
steel pin
tighten with strong
wooden key
high tensile wire
direction of strain

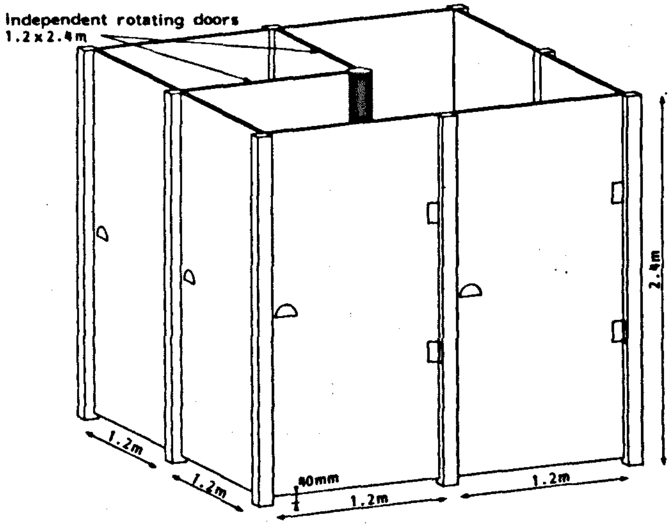
c


weld mesh (mesh size 50 mm)
added suports
needed if gate
over 4 m; important
to keep gate light
Tube hinge
corners bent
30 mm tubing (galvanised)
catch to keep
gate closed
gate closed
post
gate
hinge + hanger
post
strong elastic rubber to swing gate closed
gate
frame
angled and semi-flattened
to make strong welded joint

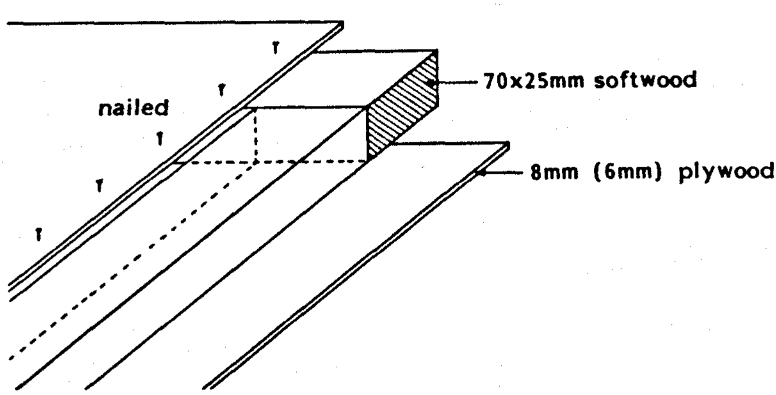
d


pen
pen
pen
Exit
pen
pen
pen

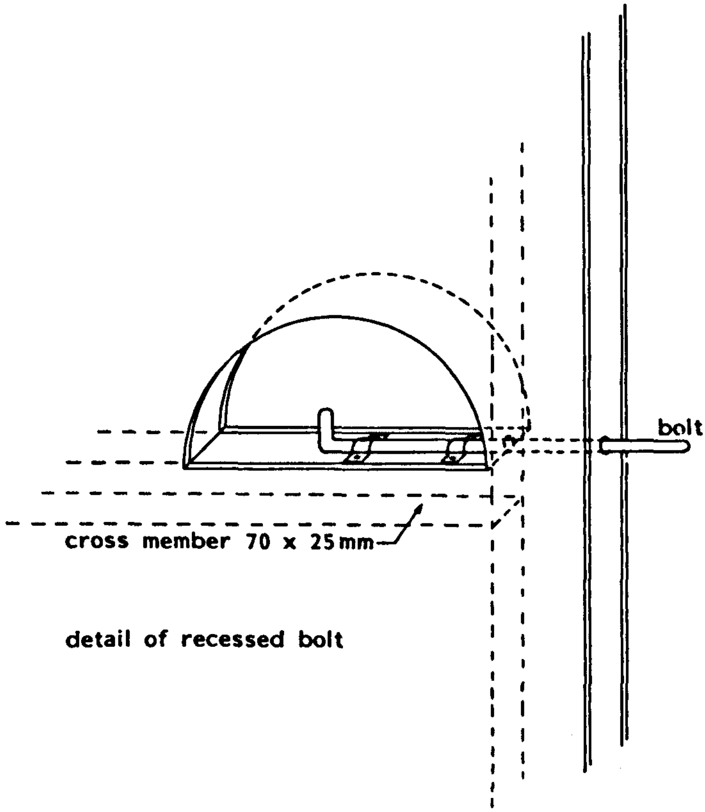

150x150mm
standing board for
observation
and/or treatment


Independent rotating doors
1.2 x 2.4m
2.4m
1.2m
1.2m
40mm
1.2m
1.2m

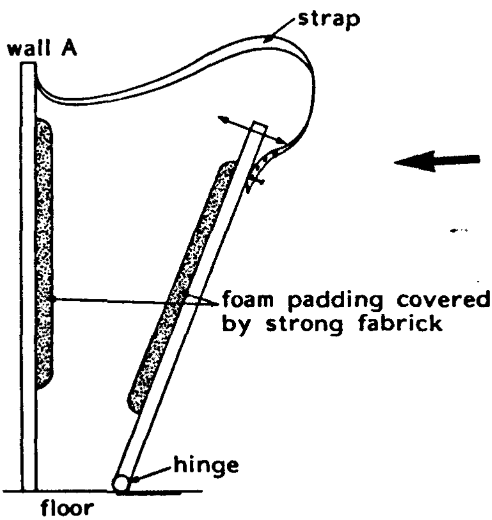
g

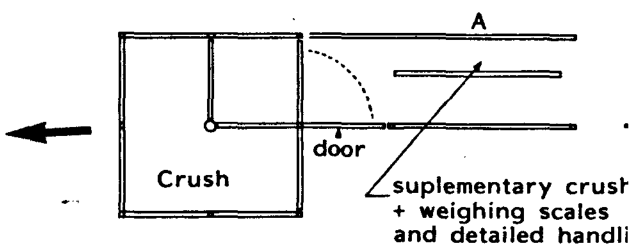

nailed
70x25mm softwood
8mm (6mm) plywood

h



detail of recessed bolt





IX. THE CAPTURE AND HANDLING OF DEER; DISCUSSION

M.H. den Boer and E. Hazebroek

The discussion focused on three areas: catching techniques, the use of chemicals and their influence, and handling techniques.

Catching techniques

Ratcliffe warned about situations where red deer refuse to enter enclosures. Together with Putman he suggested creating attractive areas just outside the fencing, e.g. by the application of artificial fertilizer in the catching area.

Van de Veen knew that in this area the red deer are accustomed to fences and do not even hesitate to enter enclosed areas when gates are left open.

Perzanovski described a catching area in which only the handling section is closed, i.e., by a wall 2.3 m high.

Putman suggested having permanent poles for use with temporary netting. For roe deer, Schober advised the use of drop-nets.

Drugs and their influence

Immobilon is by far the most effective chemical for this purpose. Illius uses Immobilon as a starter, to immobilize the animals, followed by an intramuscular injection of Diazepam. Harrington observed a loss of appetite in animals given Immobilon.

Other drugs, although less effective, might be used, e.g. Azaparon or Rhompun. Hellabrunner Mischung is not appropriate; it has too little effect on stressed animals and even the effect of an overdose is very uncertain (Hellabrunner Mischung is a mixture of Rhompun and Ketalar).

Most chemicals, if not all, affect blood parameters. In Tataruch's experience, xylazine decreases the haemoglobin concentration in the blood. However, stress itself can affect blood parameters, which makes their use disputable (see also Chapter XI).

Handling

Maintenance of quiet is of paramount importance to prevent or diminish stress. Trembling animals with glazed eyes must be released immediately, which means that an emergency escape route should be provided. Blindfolding is advised for fallow deer and roe deer but seems to be less effective in red deer. Extreme caution must be exercised, because red deer, especially if they are in hard antlers, can be extremely dangerous. A riot-shield may be useful, but better still would be to build a few permanent wooden shields like the ones used in Spanish arenas, behind which one can retreat.

About twenty minutes after Diazepam has been consumed, someone enters the enclosure quietly, walking slowly, to get the animals to the sub-division. It may be advantageous to let the animals enter and leave the handling area to familiarize them with it. The handling itself, inside the handling area, will be easier if several animals are present together. A very fine spray of water may calm them down. Illumination must be reduced by roofing the handling area. By preference, one animal is handled while the operator is leaning over another one.

An alternative handling contraption consists of a Y-shaped crush with a collapsing floor so the animal drops down slightly, looses its footing, and then becomes wedged in the Y-shaped narrow race. Information on the Y-shaped deer crush can be obtained from: Mr. D.N. Wallace, Livestock Officer (MAF) Animal Health Division, Tauranga, New Zealand.

The rather complicated type of harness needed for a wild boar to carry a transponder

X. HOW TO DETERMINE THE CONDITION OF WILDLIFE

F. Tataruch

Introduction

Blood parameters and their interpretation have become virtually indispensable for diagnosis in human medicine. In veterinary medicine, too, normal values established for various domestic animals offer a useful basis for the diagnosis of several diseases and forms of metabolic malfunction. Several years ago we started to establish normal values for blood parameters in wildlife as well. To this end, a number of problems had to be solved. One important question was whether normal values for domestic animals could be extrapolated to wildlife relatives, e.g. values for goats to chamois, those from domestic rabbits to the brown hare, or pigs' normal values to those of the wild boar. This proved to be impossible for several parameters, especially haematological factors. But other blood constituents also vary from species to species (Fig. 8), which made it imperative to determine normal values for each species.

Problems associated with blood sampling

In the procedure we use, blood is drawn from the jugular vein or directly from the heart. We prefer to use heparinized syringes, which yields more plasma than serum and reduces the danger of haemolysis. The blood is then centrifuged in the field, 2-3 hours after sampling. Plasma isolated by centrifugation is deep-frozen to be analysed in the laboratory. Serum samples are only used for the analysis of serum proteins; all other parameters are determined in plasma. For glucose samples, special syringes treated with fluoride are used; under these conditions the concentration of glucose does not change and can be determined later.

The representative samples we obtain in this way are of good quality, the only disadvantage being that the determinations cannot be repeated in samples of the same material. So far we have collected values for blood parameters from several hundreds of free-ranging ruminants including red deer, roe deer, chamois, and ibex, as well as wild boar, hare, pheasant, and partridge (Onderscheka et al. 1982, 1986; Tataruch et al. 1984).

We try to obtain samples representing the normal distribution of sex and age, habitat and season. Usually, other samples including e.g. liver tissue, rumen contents, urine, ribs, and hair, are collected and analysed too. This permits the detection of correlation between many parameters and yields as much information as possible.

Blood sampling in wildlife species encounters several difficulties. The catching of free-ranging animals is a problem and usually causes stress in the animals involved; several blood parameters, for example glucose, are strongly affected by stress.

For penned animals, netting seems to be a practical method. Last winter, 18 penned roe deer were caught in this way at a frequency of twice a month. The pens measured 100 m x 50 m and two roe deer were kept in each pen. Both animals were caught at the same time and on average catching and sampling did not take more than 5 minutes. Animals were only lost at the first catching; this concerned two deer, one of which broke its neck while jumping at the fence, and the other, a fawn, succumbed to shock. The excitement caused in the animals by catching and handling diminished further each time and values of blood parameters became fairly constant.

In small pens (6 x 6 m) at our institute, blood samples are also drawn from physically restrained chamois and roe deer. The animals are caught by 3 or 4 persons and held very firmly while blood is collected from the jugular vein. During this handling the animal should be blindfolded to minimize excitement. That this can be done successfully is proved by the slight changes in glucose over periods of months. Sampling of 25-30 ml blood can be done once a week without provoking signs of anaemia.

Effects of drugs and nutrition

Blood samples from animals immobilized by drugs differ in several ways from samples collected from the same animal when it was being physically restrained. Drugs such as xylazine, which is one of the components of the widely used Rompun, exert a strong influence on haematological values, leading for example to decreased packed-cell volume (PCV), haemoglobin, and erythrocytes. Such changes are problably due to an increase of the plasma volume, which leads to a relative reduction of red cell mass. The same effects have also been reported for the white-tailed deer by Kocan et al.(1981). Because some blood parameters are strongly influenced by nutrition, values might differ between penned and free-ranging animals. This led us to determine normal values only in the latter, blood samples being taken after the animal had been shot.

Condition indicators

Over the past fifteen years we have succeeded in establishing normal values for various blood parameters and in detecting interrelations between these values. We now know that the level of some of these blood constituents is to some degree indicative of the animals's condition as well as of some distinct forms of malfunction or metabolic disorders. For example, the availability of normal values for roe deer helped us to identify the disease caused by the uptake of rape (Onderscheka et al. 1987). Some of these indicators are discussed in this section.

Glucose: The glucose concentration in the blood decreases with increasing severity of the animal's condition. Figure 9 illustrates this effect for chamois infected with *Sarcoptes rupicaprae*. Progression of the infection finally kills the animal.

Urea: Under conditions of persistent malnutrition, carbohydrate and fat stores are mobilized; protein degradation starts in the second stage. This leads to an increase of the urea concentration in the plasma. The various stages of a catabolic condition can be seen in chamois infected with *Sarcoptes rupicaprae* (Table 4).

Alkaline phosphatase: The effect of malnutrition on the activity of alkaline phosphatase in plasma is illustrated in Figure 10 by data from a starvation experiment.

Albumin: The albumin concentration in the serum decreases in the course of malnutrition, as can been seen in Figure 11.

Table 4. Glycogen and fat content of the liver and levels of urea and total lipid in the serum of chamois during the course of a fatal *Sarcoptes rupicaprae* infection.

	Glycogen in liver (mg/g dw)			Fat in liver (% dw)			Urea in serum (mg/100 ml)			Total lipid in serum (mg/100 ml)		
	n	x	sd	n	x	sd	n	x	sd	n	x	sd
Pre-injection	31	43.5	29.8	31	9.28	4.18	21	23.6	13.6	19	421	136
Early stage	9	29.1	17.4	9	8.53	0.63	5	29.2	20.8	5	365	162
Advanced stage	6	7.5	12.2	5	12.24	2.10	3	41.1	15.4	3	442	185
Very advanced stage	12	1.1	3.0	11	6.68	1.82	10	80.3	32.0	10	200	102

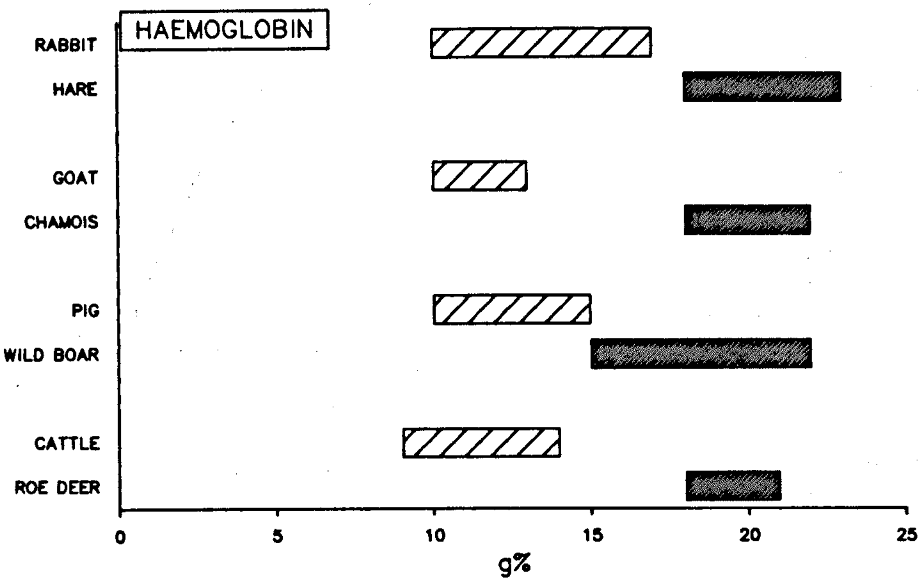


Figure 8. Haemoglobin levels in the blood of closely related animals

Other convenient methods for assessing the condition of free-ranging animals are based on analysis of tissue samples. A method we use very frequently is based on determination of the glycogen and fat contents of the liver (Tataruch et al. 1983). Glycogen represents the carbohydrates stored in the liver, which are mobilized when the organism reaches a catabolic situation. If catabolism continues and the glycogen pool is depleted, mobilization of fat reserves begins. The decrease of fat in the liver is partially compensated for by a transfer of fat from peripheral tissue to the liver, and this leads to a situation in which the fat content of the liver seems to be normal or even elevated. After the depletion of peripheral fat, the liver fat level starts to decline.

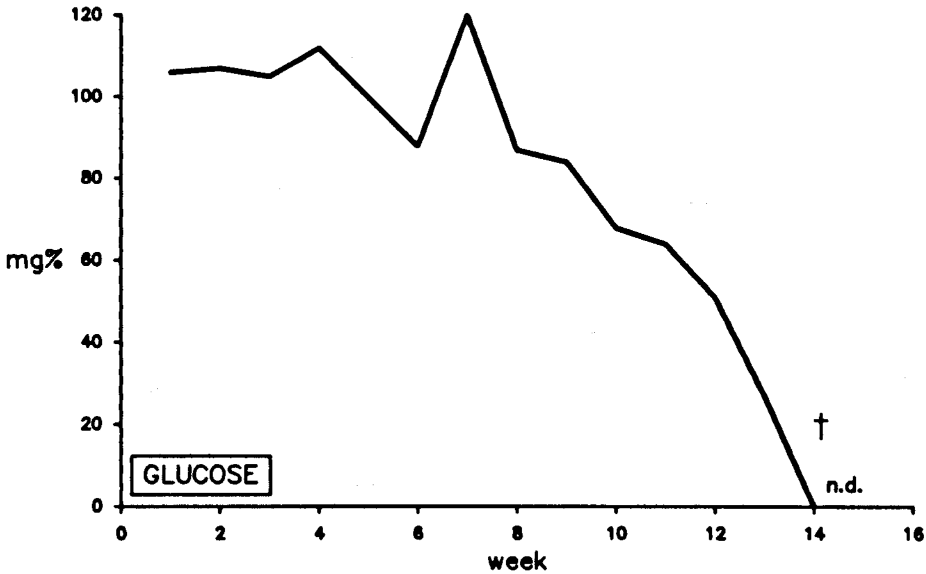


Figure 9. Course of glucose concentration during a *Sarcoptes rupicaprae* infection in chamois

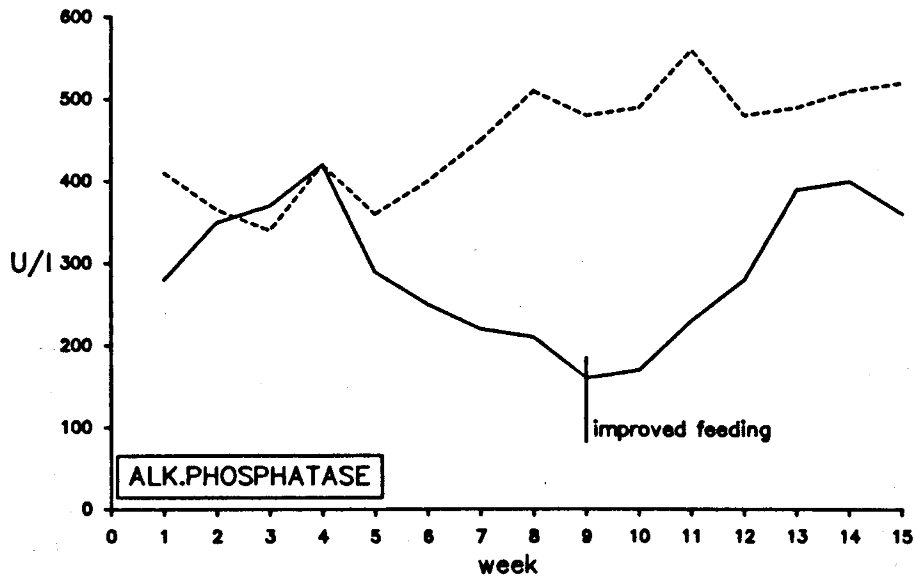


Figure 10. Effect of malnutrition on alkaline phosphatase activity in plasma of chamois........: animals given normal ration;-------: animals given one-third of the normal ration for 9 weeks, followed by normal ration

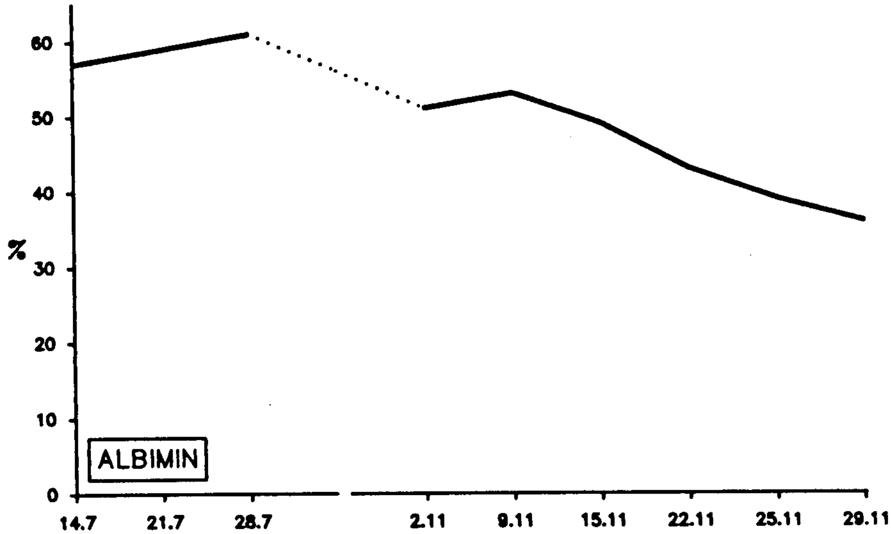


Figure 11. Course of the serum albumin concentration in chamois under conditions of malnutrition

Combination of the glycogen and fat values in the liver gives an approximation of the body's energy reserves. We can even determine the length of the period of inadequate energy supply.

After a long period of insufficient protein supply the vitamin-A stores in the liver decrease too, and this is accompanied by a decline of the vitamin-A level in the plasma.

The last method for determining the animal's condition I want to mention here is the analysis of bone marrow fat. Having compared the two methods, we think the analysis of glycogen and fat in the liver is more sensitive than that of bone marrow, especially for the detection of hunger in an early stage.

References

Kocan, A.A. et al. 1981. Effects of chemical immobilization on hematological and serum chemical values in captive white-tailed deer. J. Amer. Vet. Med. Assoc. 179: 1153-1156.

Onderscheka, K. et al. 1982. Ein Versuch zur Erstellung von Normalwerten wildlebender Tiere und die Anwendung dieser Daten in der Wildbiologie. Wr. Tierärztl. Mschr. 69: 274-279.

Onderscheka, K. & F. Tataruch 1986. Importance des normes physiologiques dans l'évaluation de la condition des animaux sauvages. Faune sauvage d'Europe, Informations Techniques des Services Vétérinaires, 31-36.

Onderscheka, K. et al. 1987. Untersuchungen über die durch Rapsaufnahme bedingten Rehwildverluste. Wr. Tierärztl. Mschr. 74: 369-379.

Tataruch, F. et al. 1983. Investigations on the metabolism in chamois suffering from Sarcoptic Mange. In: S. Lovari (ed.), The Biology and Management of Mountain Ungulates, 250-255.

Tataruch, F. & T. Steineck 1984. Hämatologische Untersuchungen beim Feldhasen (Lepus europaeus P.). Zeitschrift f. Jagdwissenschaft 30: 24-34.

XI. HOW TO DETERMINE THE CONDITION OF LARGE HERBIVORES: DISCUSSION

G.W.T.A. Groot Bruinderink, S.E. van Wieren and J. Wolkers

What is condition?

After the initial confusion about how to define the concept of condition, the following definition was generally accepted: the condition of an individual animal is the extent to which this creature can cope with a number of negative environmental factors, e.g. insufficient food supply and diseases and/or infection by parasites, which can be related to nutritional and physiological condition, respectively. This definition always applies to a relatively short period, e.g. the winter or a dry season.

Within this concept the workshop participants agreed that condition could also be defined as short-term (i.e., a few years) reproductive capacity. These three types of condition are related in the sense that in a healthy animal there is a substantial overlap and that if the condition declines, the different types perhaps decline at different rates, reproductive capacity being the last to be affected. In research papers it is advisable to specify which type of condition is concerned.

Condition indicators

One problem remains: the choice of parameters that can be used to establish condition objectively at the level of the individual in both live and dead animals.

Body weight and relative weight

The body weight, although used very frequently, is generally not considered to be a very good measure, and should always include some other quality, such as sex, age, or geographical position of the habitat. If the relative weight is taken as indicator for body condition, the body weight is related to the body frame, e.g. body length, leg length, or girth. This yields indices such as body weight/total length. This measure of fleshiness can of course be applied to both dead and live animals.

Some authors use condition scores, for example on the basis of a 1-to-5 scale derived from e.g. the pelvic curve for ponies or buffalo;

the workshop agreed that this can be done when large numbers of animals of one species present themselves to the field worker almost simultaneously. Unfortunately, this is rarely the case for red deer.

Fat indices

When dealing with dead animals, it is necessary to take into account the body's fat reserves, which might be indicative of other reserves as well. Wolkers remarked that unfortunately it does not seem possible yet to use the 'impedance meter' on hairy animals.

It was generally agreed that the reliability of the kidney-fat index as an indicator of body condition is usually overestimated due to the marked bias inherent in the sampling method and to the seasonal fluctuations of the weight of this organ, which are not correlated with the changes in total body weight.

Blood parameters

The workshop participants and the speaker disagreed about the validity of the blood-glucose parameter as a condition indicator, because of the strong dependence on stress. Unlike the speaker, the workshop was not convinced that this drawback can be overcome by sampling the blood immediately after the animal has been caught or culled.

With respect to blood urea, the speaker thought that this parameter could be a reliable indicator of the breakdown of muscle tissue in ruminants; for non-ruminants it would reflect food quality. However, Kirkpatrick et al. (1975) found a relationship between urea and food quality in ruminants too.

When asked by the participants which parameters should be measured, in a sequence of decreasing priority, to establish the condition of an animal, the speaker mentioned the glycogen and fat reserves of the liver, the blood-glucose level, and the blood concentrations of triglycerides, alkaline phosphatase, and albumin. The validity of this priority sequence was questioned by the workshop, because of the daily fluctuations and stress dependence of the liver glycogen reserves.

Minerals

Most minerals are buffered in the blood and are therefore of little practical value as condition indicators. The workshop underlined the relevance of determination of the mineral concentrations in the organs because of the correlation with body functions, e.g. a shortage of copper in relation to anaemia. The workshop concluded that there is an urgent need for investigation of not only the normal but also of the critical values of some minerals in both the organs and the food supply.

There is, however, a real risk that the wildlife ecologist could become involved in very costly and laborious physiological research. Great appreciation of the work done by the speaker was expressed and its importance repeatedly emphasized.

Reference

Kirkpatrick, R.L. et al. 1975. Energy and protein influences on blood urea nitrogen of white-tailed deer fawns. Journ. Wildl. Mgmt. 39, 4: 692-698.

One of the major problems in the assessment of mortality in a population is caused by the difficulty of finding the dead animals.

XII. BIOTELEMETRY: FEASIBILITY AND LIMITS

F. Schober

Introduction

Biotelemetry has become a widely used technique in biological and ecological research as a promising a non-reactive method to obtain representative and reliable data on the activity, behaviour, and physiology of animals. Numerous manufacturers in several countries produce a variety of biotelemetry transmitters and receiving equipment for different applications (Appendix I). Although I am aware of the continuing technical progress in biotelemetry for research on wild animals, including recent advances such as satellite tracking and single-chip computer-based transmitters, in my opinion the attention of the participants of the URF workshop should concentrate on fundamental 'real-world' applications and their feasibility.

This discussion of physiological biotelemetry, the major topic of this contribution, should be prefaced by some remarks on radio-location techniques. Radio tracking in its original meaning works very well. Radio triangulation, making use of common directional antennas and taking bearings from several receiving sites, can easily lead to erroneous results for several reasons (Schober et al. 1984).

Several strategies for collecting and analysing data on animal location and movement have been reported. These 'standardized' methods are quite useful for the comparison of published results. But, for example, if only movement data are available, there is no hope of being able to extrapolate to the social behaviour of an individual.

Nevertheless, for almost any ecological study it is important to understand the movement behaviour of free-ranging wild animals. There are two dissimilar ways to collect reliable information on movement behaviour and habitat use; the first is to install highly sophisticated and very expensive electronic equipment for fully-automatic direction and location finding (modern 'doppler'-bearing devices would be recommended), which supplies abundant data but little information about the animal's biology. The second is to use inexpensive hand-held receivers and antennas operated by mobile observers: fewer data are obtained but much is learned about the animals and their environment.

Neither of these methods can replace the other. The choice depends on the scientific question under study and on the available funds.

Transmission frequencies: VHF versus UHF

In the past the most commonly used transmission frequencies for wildlife biotelemetry were in the VHF range (2 m band/150 MHz). At present, modern components allow the design of transmitters and receivers of the same size and equal performance in the UHF range (70 cm band/430 MHz), which offers the great advantage of allowing smaller antennas, or higher gain with same antenna size, and less atmospheric and galactic noise, thus improving the detection of weak signals.

There are, of course, certain disadvantages, such as increased reflection and drop-outs in mountainous regions. Furthermore, in the UHF range there is greater loss due to surrounding tissue and therefore this range is not recommended for implanted transmitters. Finally, there is of course the practical problem of higher costs of the UHF equipment.

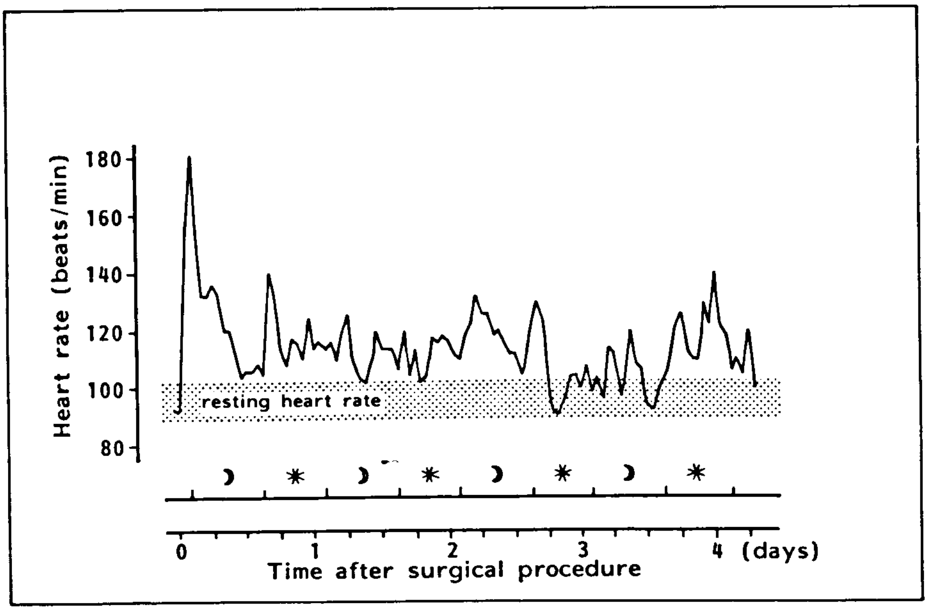


Figure 12. Course of the heart rate after transmitter implantation in a one-year-old female domestic goat

Physiological biotelemetry

In wildlife biotelemetry the most important requirements for a telemetry system are long-range and long-life transmission combined with very low power costs. Therefore, pulse-interval (PIM) and pulse-duration (PDM) modulation of carrier-frequency pulses is the preferred modulation technique. But this method can only be used for parameters where transmission deals with very low data rates, i.e., where the radio frequency pulses can be infrequent and several milliseconds long, to meet the above-mentioned requirements. Carrier frequency pulses allow narrow-band reception with very sensitive receivers of conventional radio-tracking systems. Other modulation techniques or 'storage' telemetry can be used, but for most of the purposes served by physiological transmitters, simultaneous radio location of the animal is an additional requirement.

The only satisfactory compromise for long-term studies on physiological parameters in free-ranging wild animals fitted with various sensors is the use of implanted transmitters sending the signals to a receiving station either directly or via a repeater collar. Extracorporal transmitters with external wiring or perhaps transcutaneous leads are not suitable for such applications. They can only be accepted as compromise for short-term studies. Surgical implantation is also useful for radio-tracking studies on several species for which an external transmitter is not appropriate because of their special body shape or behaviour (e.g. wild boar, red fox, badger, beaver, river otter). Additionally it is assumed that also in some cases where external transmitters are suitable in principle, a good solution for the implantation problem will lead to less constraint for the animal, reduce the probability that the transmitting equipment will influence behaviour, and provide more reliable data. The problems associated with transmitter implantation techniques are discussed in Chapter XIII.

For several species (e.g. small ruminants such as roe deer, chamois, sheep, and goats) the performance of long-range transmission can be intermediate between that of external and implanted transmitters (Schober et al. 1982). If the animal is large enough to permit use of an almost full-sized antenna, and if that antenna is matched to the animal, highly effective propagation can be achieved. Only a few physiological parameters can be measured in free-ranging wild animals without an inacceptable effort; these are the following:

Body temperature: Although body temperature is relatively easy to sense, we know from studies including circadian rhythms or hibernation that its value is limited for body energetics and metabolism because it is strongly buffered physiologically. Transmitters are available from many manufacturers.

Heart rate: With the use of passive transducers (ECG electrodes) the heart rate can be sensed without problems, and is a good indicator for stress situations (Figs. 12 and 13), energy expenditure, and metabolic rate. Transmitters are available from only a few manufacturers.

Respiration rate: This parameter is strongly correlated with heart rate, but the respiration rate is very difficult to sense and there is the additional problem that transmitters for this purpose are not commercially available.

Blood pressure: The physiological importance of this parameter is not yet fully understood. The same practical problems are encountered as for the respiration rate.

Rumen pH: Use of this parameter is restricted at present to short-term and short-range studies in which use is made of e.g. radio-labeled pills to measure the pH of rumen contents.

With respect to other parameters such as blood flow and heat flow, so little is known that methods cannot yet be developed for wildlife applications.

Receiving equipment

The use of microprocessor-based receiving and data-acquisition systems to obtain uninterrupted data records is highly recommended (Schober et al. 1987). Several manufacturers offer devices with these features.

Earlier registration methods such as chart recorders for data recording had the severe handicap that further analysis of data or transfer to the host computer had to be done 'by hand', which concealed many sources of error. Because modern data acquisition systems deliver an abundance of information, learning to interpret these data from the biological or medical point of view will demand prolonged effort.

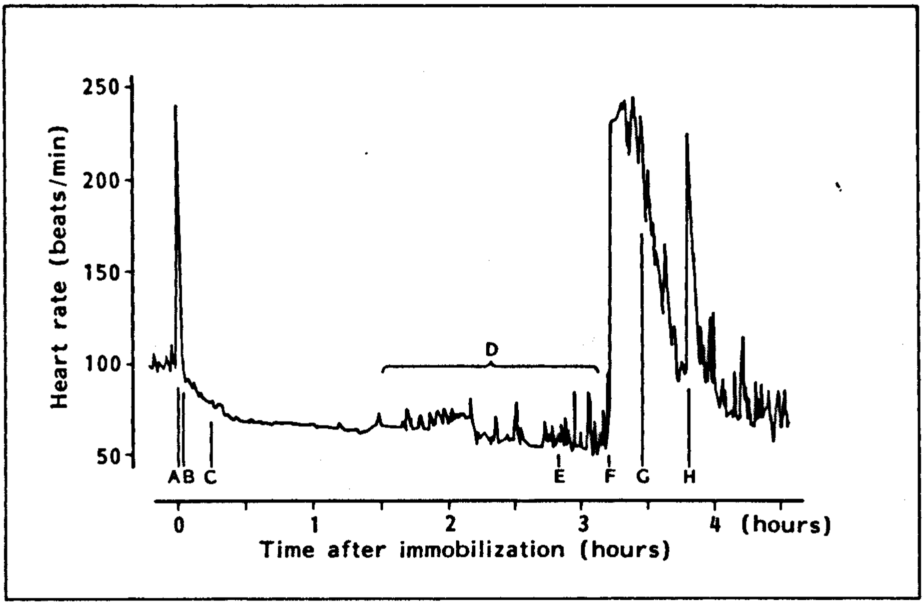


Figure 13A-H. Heart rate in relation to immobilization as assessed in a two-year-old male roe deer. A: Anaesthetic agent administered intramuscularly (i.m.) by blowpipe. B: Lying down. C: Supporting drugs given i.m. D: Unsuccessful attempts to get up. E: Caffein given i.m. F: Reversing agent given intravenously. G: Lies down. H: Disturbed by the observer, getting up, successful attempt to stand up.

References

Schober, F., W. Pasterk & F. Sommer 1982. Implantable long-range, long-life heart rate and activity transmitter for free-ranging animals. Biotelemetry VII, Proc. 7th Int. Symp. Biotel., Stanford, California; 108-111.

Schober, F., A. Marhold & F. Sommer 1984. The troublesome errors in common techniques of radio triangulation. Biotelemetry VIII: 379-382.

Schober, F. & B. Oehry 1987. Automatic RF receiving system for carrier frequency pulses. Biotelemetry IX: 351-354.

APPENDIX 1

Manufacturers of biotelemetry equipment for wildlife applications

West Germany

B + R INGENIEURGESELLSCHAFT m.b.H.
Johann-Schill-Strasse 22
D-7801 March-Buchheim

P.REICHENBACH
Weisserlenstrasse 27
D-7800 Freiburg im Breisgau

K.WAGENER
Herwarthstrasse 2
D-5000 Köln

Great Britain

BIOTRACK
Stoborough Croft
Grange Road
Wareham,Dorset

Sweden

SENSITRON AB
Sköndalsvägen 126
S-12353 Farsta

TELEVILT
Pl 5226
S-71700 Stora

U.S.A.

ADVANCED TELEMETRY SYSTEMS, INC.
470 First Ave.N.
Box 398
Isanti, Minnesota 55040

AVM INSTRUMENTS COMPANY,LTD.
2368 Research Drive
Livermore, California 94550

BARROWS CO.
13876 Skyline Blvd.
Woodside, California 94062

J.STUART ENTERPRISES
3817 Stanford Drive
Oceanside, California 92056

TELEMETRY SYSTEMS,INC.
P.O.Box 187
Mequon, Wisconsin 53092

TELONICS,INC.
932 E.Impala Avenue
Mesa, Arizona 85204-6699

ULTRASONIC TELEMETRY SYSTEMS
8315 Milliken Avenue
Whittier, California 90605

Canada

AUSTEC ELECTRONICS,LTD.
1006, 11025-82 Avenue
Edmonton, Alberta T6G 0T1

HOLOHIL SYSTEMS,LTD.
R.R. #2
Woodlawn, Ontario K0A 3M0

LOTEK ENGINEERING,INC.
34 Berczy Street
Aurora, Ontario L4G 4J9

VEMCO,LTD.
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XIII. TRANSMITTER IMPLANTATION TECHNIQUES AND RISKS FOR THE ANIMALS INVOLVED

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Introduction

As mentioned in Chapter XII, the most reliable measurements concerning animal activity and physiology are for various reasons obtained with implanted transmitters, especially in long-term studies on free-ranging animals. The surgical implantation of biotelemetry transmitters is now widely used in biological and medical research. One of the major problems encountered with this method concerns effects of rejection which, for both ethical and practical reason, must be solved, although final proof of non-reactivity can never be given.

Nevertheless, use must be made of all available indicators that might help us to check the compatibility of the method applied (e.g. changes in behaviour, inspection of experimental animals for pathologic signs).

Biocompatibility of encapsulation materials

Packaging technology for chronic implants has been fully developed in human implant surgery, but this technology is too expensive for most applications in animal biotelemetry, e.g. the welded metal cases made of titanium alloys used for pacemakers. In the early days of radio implants many kinds of surface material were used for these transmitters. The reports mention beeswax, paraffin, dental acrylic, epoxy, resins, and a wide variety of mixtures, but information about the coating material used for transmitters was sometimes no more than 'biologically inert material'.

Two materials in particular are highly recommended for use in transmitter implants for wildlife: surgical steel and silicone rubber. Surgical steel because it is an inexpensive, non-corrosive, conductive material and silicone rubber as a coating material which is very easy to handle. These two materials are widely used in human implant surgery as well.

It is generally accepted that the biocompatibility of silicone rubber and surgical steel (but not of ordinary stainless steel) is the same in animal applications as in human implant surgery. Because there are several other appropriate materials, the problem of bio-incompatibility of encapsulation materials seems to have been solved. It need hardly be said that adequate sterilization of the implant (e.g. cold sterilization with ethylene oxide or liquid sterilizing agents) is a basic requirement for successful implantation. The problem of leakage through various materials lies beyond the scope of this workshop.

The mechanical characteristics of implants

A much higher risk of rejection effects of implants than that associated with bio-incompatibility arises from improper mechanical characteristics of transmitters pertaining to e.g. size and shape, and - especially if sensors and leads are connected to the electronic package - to the elasticity and flexibility of these peripheral parts. Problems with rejection of transmitters by the organism can be reduced by adapting the shape of the implant to its site in the animal and eliminating effects of strain due to movements of the animal. The shape of the implant should be chosen to avoid local pressure on surrounding tissues. Cases of pressure necrosis in the skin covering subcutaneous implants have been reported by several authors.

We have had experience of this kind with a domestic goat provided with a subcutaneous mercury switch for the detection of activity. This device was implanted along the dorsal midline, just above the second or third cervical vertebra, the sensor passing through the skin, 2 cm lateral to the incision, which initially healed very well. When this implantation failed, we reduced the diameter of the sensor to 5 mm and applied this to goats and roe deer. We also covered the sensor with Dacron mesh, which we sutured to the subcutaneous tissue or to the underlying muscle tissue, thus distributing the pressure toward the skin over a larger area. In European roe deer the layer of subcutaneous tissue is very thin, especially in the dorsal part of the neck, which makes it difficult to find enough room even for subcutaneous sensors. The first of several implantations of this modified mercury switch was performed eleven months ago and there have been no complications so far.

Transmitter fixation

It is impossible to implant a 'free-floating' transmitter with leads to sensors or antennas in a body cavity in the same way as can be done with a transmitter for tracking purposes. Besides the shape of the transmitter, which should not give rise to mechanical irritation of the surrounding tissues, good fixation of the transmitter will insure that there is little pressure on tissues due to gravity and minimum strain on the leads and sensors. Ideally, this can be obtained by fixation of the transmitter to some part of the skeleton. We have made a series of successful implantations into the thoracic cavity of roe deer, domestic sheep, and goats (especially the left pleural cavity) and fixed the transmitter to the ribs with surgical-steel wire. In several bovid species the transmitter can be attached to the ribs in the intrathoracic part of the abdominal cavity. This method has been used in domestic goats and roe deer (Fig. 14).

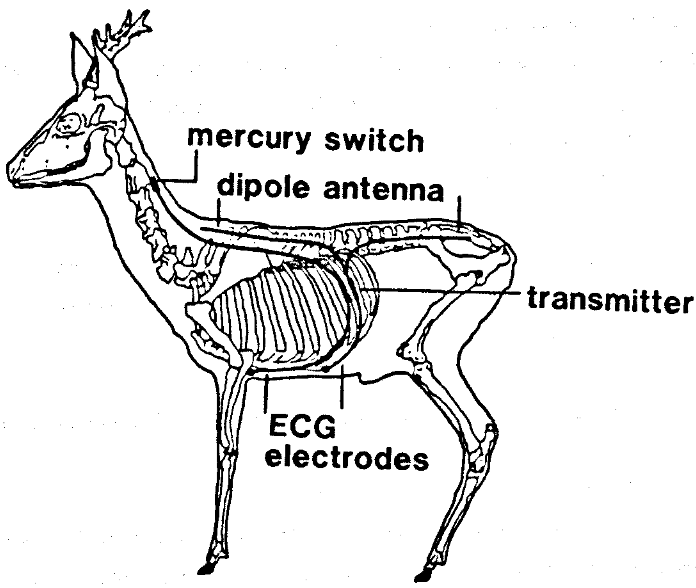

Figure 14. An example of intrathoracic implantation

In red deer and roe deer, however, the line attaching the diaphragm to the chest wall lies very close to the costal arch, which means that - in contrast to bovine species - there is simply not enough space for fixation of an implant, even one with the size of two fingers. In such animals the implant can be fixed to the muscles of the abdominal wall with loops of surgical-steel wire covered with silicone rubber tubing. Use of this transmitter site avoids the need for artificial ventilation during thoracic surgery (Fig. 15). However, this method of fixation gave

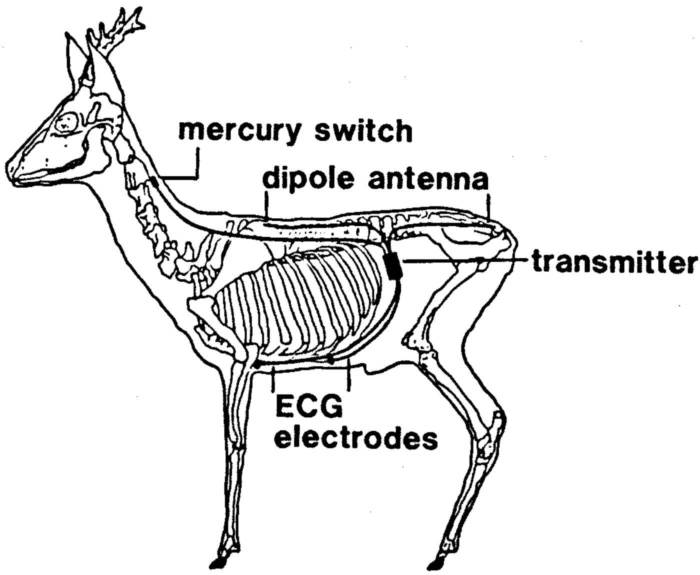

Figure 15. Intra-abdominal implantation of a heart-rate and activity transmitter

different problems. For example, some of the transmitters broke through the abdominal wall and even through the skin. But most of our transmitters stayed in place for longer periods in domestic goats and roe deer. In the latter species this was rather unexpected, because the roe deer is small in relation to other cervids and compared with them has a relatively thin abdominal wall. One of the transmitters that penetrated the animal's abdominal wall had an inappropriate shape, but we do not know whether this was responsible for the complication. Since then, the shape of the transmitters has been improved and results in several animals improved as well.

In the course of our work with implanted transmitters we have seen some cases of adhesion of the capsule to connective tissue covering both the transmitter and the rumen. Modification of the surgical technique to avoid adhesions of this kind is the subject of ongoing research (e.g. experiments with subperitoneal location of the transmitter package).

Anaesthesia

Many of the implantations being done today in animal biotelemetry go far beyond short operations and surgery of limited extent. For example, the implantation of a heart-rate and activity transmitter equipped with electrodes, antennas, and leads to the activity switch (together about 2.5 m of wire) in roe deer or other animals of that size cannot be performed under local anesthesia, because the dose of local anaesthetic agents needed for surgery of this kind would be much greater than the maximum supportable dose for an animal with a weight in the expected range.

Such cases require general anaesthesia, by preference inhalation anaesthesia with endotracheal intubation. For field application, portable equipment is required for this type of anaesthesia.

Secondary infections

It is remarkable that we have had no cases of postsurgical infection in the animals we have given an implant in the last few years. But the main complication we have encountered, i.e., sensors perforating the skin, showed that an infection associated with any part of the implant (transmitter, electrodes, antennas, activity switch) can cause heavy purulent infections leading to a rejection of the whole implant. These infections progressed along the leads, and it was only a matter of time before such an infection, if untreated, would have extended over the entire surface of the implant.

Special problems associated with wildlife biotelemetry

The applicability of surgery in free-ranging wildlife animals is limited for several reasons, two of which I want to mention here.

First: the time required for immobilization and transport must be added to the duration of anaesthesia during surgery. This is important, because the permissible anaesthesia time is in principle limited. Furthermore, animals which are captured in the field and have to be released immediately after surgery cannot be given postsurgical care.

The whole procedure will also cause much more 'mental stress' in wild than in domestic animals.

Second: since the probability of pathologic complications increases with increasing complexity of the implant from simple tracking transmitters to sophisticated multi-channel devices, increasing care is required in every surgical stage, for example sterile conditions not only during anaesthesia but also postsurgical treatment. If postsurgical treatment is not possible, the level of asepsis during the surgical procedure must be even higher than under clinical conditions.

Despite the many difficulties encountered in the development of methods for the surgical implantation of transmitters, there are reports of successful implantations. As already mentioned, we ourselves have had no cases of postsurgical infection, and have rarely seen signs of migration or of expulsion of the transmitter, including the sensors and leads. Post-mortem examination of these animals showed no evidence of degeneration of muscles of the abdominal wall and no adhesions to adjacent organs, only a perfect capsule of connective tissue with no fluid around the transmitter. One of our animals has carried an implanted transmitter for nineteen months now and is still alive without complications. But most of our unsuccessful experiments did not fail because of surgical or other medical problems but rather due to mechanical destruction of implanted leads with insufficient flexibility and bending strength. Successful implantations for tracking purpose have been reported for the beaver by Guynn et al. (1987), for the river otter by Melquist and Hornocker (1979 a,b), for the badger by Harlow et al. (1979), and for the grizzly bear by Philo, Follman and Reynolds (1981).

Folk and Copping (1972) and Folk and Folk (1980) implanted telemetry units capable of transmitting such physiological data as ECG or heart rate successfully in thirty mammal species including the polar bear, grizzly bear, black bear, wolf, arctic fox, red fox, lynx, domestic cat, domestic dog, prairie dog, arctic marmot, European hamster, domestic rabbit, raccoon, roe deer, rhesus monkey, and stumptail monkey. There are also reports of successful implantations in small rodents which are not further discussed here (see e.g. Smith and Whitley 1977).

In larger species of cervids a method for subcutaneous implantation of heart-rate or ECG transmitters ventrally at the base of the neck is widely used. This approach has been applied by Cupal, Weeks and Kaltenbach (1976) in elk, by Freddy in mule deer (1977,1979,1984), Mautz and

Fair (1980) in white-tailed deer, and Renecker, Hudson and Freddy (1982) as well as Renecker and Hudson (1985) in moose.

Finally, it seems that unlimited 'wiring-up' of an animal will never be surgically feasible. Surgical feasibility always depends on the environmental factors. The limits under laboratory conditions differ widely from those under field conditions, but in both cases high surgical standards are imperative. We suggest that the surgical implantation of a transmitter must not impair the animal in any way, either immediately or later. If there are such consequences, the search for improved or new techniques must be continued. But scientists must always weigh the value of the expected results against the risks for the animals involved.

References

Cupal, J.J., R.W. Weeks & C. Kaltenbach 1976. A heart rate-activity biotelemtry system for use on wild big game animals. Proc. 3rd Int. Symp. Biotel., Pacific Grove, California, 219-222.

Drake-Bailey, B.A. & F. Anderson 1982. Practical considerations in the long term use of totally implanted, telemetered systems in dogs. Biotelemetry VII, Proc. 7th Int. Symp. Biotel., Stanford, Calif., 93-96.

Folk, G.E. Jr. & J.R. Copping 1972. Telemetry in biometeorological studies. Telemetry in animal biometeorology, Vol. 5, Part II, Proc. 6th Int. Biometr. Congr., Noordwijk, The Netherlands, 153-170 (Suppl. to Int. J. Biometr., Vol. 16).

Folk, G.E. Jr. & M.A. Folk 1980. Physiology of large mammals by implanted radio capsules. In: C.J. Amlaner Jr. & D.W. Macdonald (eds.), A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford; 33-43.

Freddy, D.J. 1977. Snowmobile harassment of mule deer on cold winter ranges. Job. Progr. rep. W-38-R-32, State of Colorado, Division of Wildlife, 89-104.

Freddy, D.J. 1979. Measuring heart rates of mule deer using a repeater-type telemetry system. Proc. 2nd Int. Conf. Wildl. Biotel., Laramie, Wyoming; 144-155.

Freddy, D.J. 1984. Heart rates for activities of mule deer at pasture. J. Wildl. Mgmt. 48: 962-969.

Guynn, D.C. Jr., J.R. Davis & A.R. von Recum 1987. Pathological potential of intraperitoneal transmitter implants in beavers. J. Wildl.

Mgmt. 51: 605-606.

Harlow, H.J., R.W. Weeks, F.M. Long & J.M. Schrib 1979. Heart rate and body temperature of free-roaming badger. Proc. 2nd Int. Conf. Wildl. Biotel., Laramie, Wyoming; 14-20.

Korschgen, C.E., S.J. Maxson & V.B. Kuechle 1984. Evaluation of implanted radio transmitters in ducks. J. Wildl. Mgmt. 48: 982-987.

Mautz, W.W. & J. Fair 1980. Energy expenditure and heart rate for activities of white-tailed deer. J. Wildl. Mgmt. 44: 333-342.

Melquist, W.E. & M.G. Hornocker 1979a. Methods and techniques for studying and censusing river otter populations. Forest, wildlife and range experiment station, Univ. Idaho, Techn. rep. 8, Contrib. 154, 17 p.

Melquist, W.E. & M.G. Hornocker 1979b. Development and use of a telemetry technique for studying river otter. Proc. 2nd Int. Conf. Wildl. Biotel., Laramie, Wyoming; 104-114.

Philo, L.M., E.H. Follmann & H.V. Reynolds 1981. Field surgical techniques for implanting temperature-sensitive radio transmitters in grizzly bears. J. Wildl. Mgmt. 45: 772-775.

Renecker, L.A., R.J. Hudson & D.J. Freddy 1982. Heart rate as an index of energy expenditure in moose, using two telemetry systems. Proc. 7th Int. Symp. Biotel., Stanford, California; 116-119.

Renecker, L.A. & R.J. Hudson 1985. Telemetered heart rate as an index of energy expenditure in moose (Alces alces). Comp. Biochem. Physiol. 82A, 161-165.

Schober, F., W. Pasterk & F. Sommer 1982. Implantable long-range, long-life heart rate and activity transmitter for free-ranging animals. Biotelemetry VII, Proc. 7th Int. Symp. Biotel., Stanford, California; 108-111.

Schober, F. & J. Wagner 1988. Considerations on adverse effects of transmitter implants and on limits in surgical feasibility in animal biotelemetry. Biotelemetry X, Proc. 10th Int. Symp. Biotel., Fayetteville, Arkansas.

Smith, E.N. 1980. Physiological radio telemetry of vertebrates. In: C.J. Amlaner Jr. & D.W. Macdonald (eds.), A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford; 45-55.

Smith, H.R. & G.D. Whitney 1977. Intraperitoneal transmitter implants - their biological feasibility for studying small mammals. Proc. 1st Int. Conf. Wildl. Biotel., Laramie, Wyoming; 109-117.