ISSN 0308-3675

MERLEWOOD RESEARCH AND DEVELOPMENT PAPER

No 81

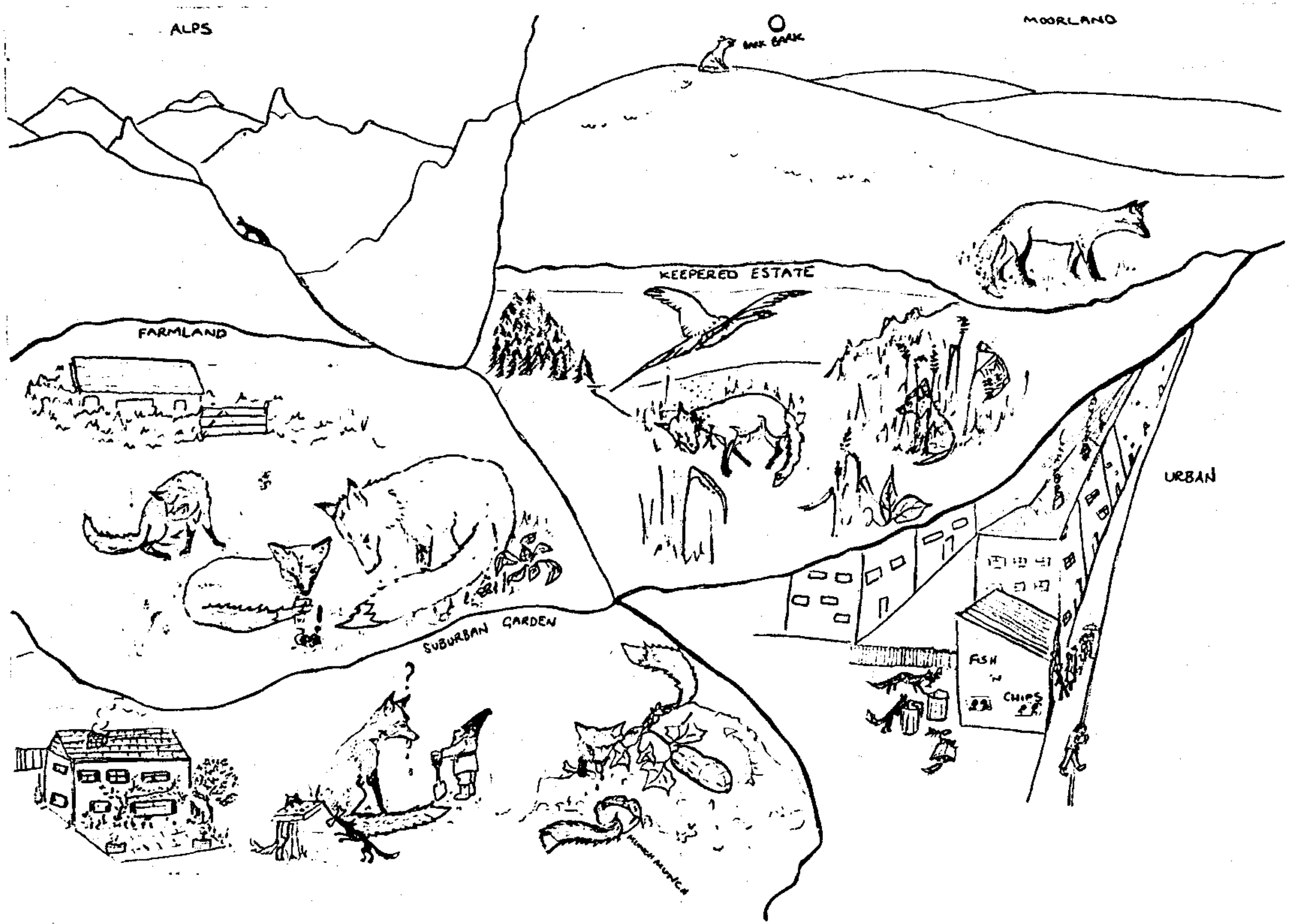
HABITAT CLASSIFICATION, FOX POPULATIONS AND RABIES SPREAD

prepared and edited by

P J BACON & D W MACDONALD

Institute of Terrestrial Ecology
Merlewood Research Station
Grange-over-Sands
Cumbria
England
LA11 6JU

March 1981


ALPS
MOORLAND
BARK BARK
KEEPERED ESTATE
FARMLAND
URBAN
SUBURBAN GARDEN
FISH 'N CHIPS
MUNCH MUNCH

HABITAT CLASSIFICATION, FOX POPULATIONS AND RABIES SPREAD

A synopsis of the meeting held in Oxford, 15-19 September, 1980.

INTRODUCTION

It has been recognised for some time that features of the landscape influence the way in which a rabies epizootic spreads. The disease may follow, for example, the course of roads and rivers. Biologists have also found that red foxes may disperse along just such features and it seems fair to assume that this partly explains the way the disease spreads. On a broader level, there are places where rabies has spread faster than in others, and it is widely believed that this may reflect differences in the population densities of foxes and hence the contact rate between them and thereby the spread of the disease. Differences in fox population densities no doubt at least partly reflect variations in the local availability of prey. The question we have tackled in organising this workshop is whether the factors which influence fox population density can be categorised broadly in terms of features of the landscape with which they may be associated. For example, if a particular habitat or combination of habitats could be identified with high fox population densities, then the distribution of that habitat, perhaps even as revealed by a simple analysis of maps, might contribute to the practical task of predicting the course of the disease.

To investigate the merit of this line of thought we have brought together experts in rabies epizootiology who may identify the habitats through which the disease has accelerated or faltered, and experts in fox biology who can provide clues as to the habitats which may favour higher fox population densities. As a catalyst to the meeting of these two, we have also asked geographers and others concerned with the classification of landscapes, and with classifications in general, to provide guidelines for both the theory and the practice of habitat characterisation. In the atmosphere of an informal workshop these people exchanged ideas and we have tried to summarise the meat of their material here. We present a summary, from our notes, for each speaker and a synopsis of the resulting discussion. In undertaking this task we inevitably run the risk that our summaries have omitted or improperly emphasised a point, Nevertheless we have tried to present the essence of each speaker's ideas and in so doing hope to provide a basis for further debate.

Philip J. Bacon
Institute of Terrestrial Ecology,
Grange over Sands,
Cumbria.

David W. Macdonald,
Department of Zoology,
South Parks Road,
Oxford.

THE PROGRAMME

HABITAT CLASSIFICATION, FOX POPULATIONS AND RABIES SPREAD

Oxford, Keble College,
15-19 September

Organisers: P.J. Bacon and D.W. Macdonald.

Legend. The diagram shows various attributes of the four entities: Environment; Habitats; Foxes; and Rabies. In the real world, these attributes interact via known cause/effect chains, eg. dotted arrows. Various disciplins of ecology investigate measured aspects of these interactions, using a sub-set ,n, of attributes, eg. thin solid arrows. Rabies could be investigated as either, or both, a function ,F, of attributes of Foxes (open arrow Fr_3,n) or as a function ,R, of Habitats and Environments (open arrow R( ) ( )). Both these procedures would be subject to measurement errors. Which errors might be larger?

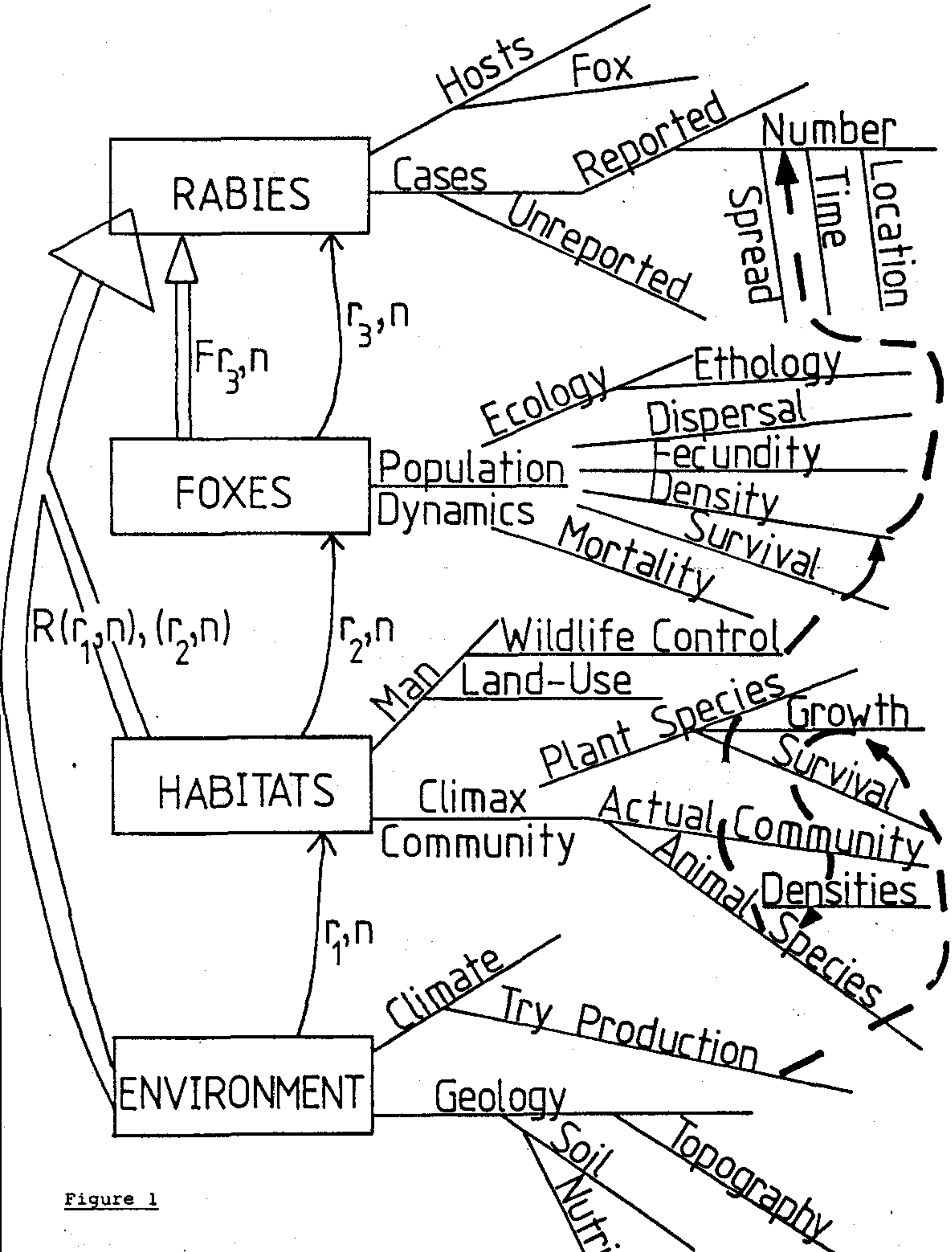


Figure 1

HABITAT CLASSIFICATION, FOX POPULATION AND RABIES SPREAD

A Synopsis

INTRODUCTORY REMARKS

Professor Peter Armitage opened the meeting by welcoming delegates to the conference and giving them a brief history of its organisation.

In 1977 Mr. J.N.R. Jeffers (Director of the Institute of Terrestrial Ecology) had suggested to the Royal Statistical Society that a working party on quantitative studies of the epidemiology of rabies would be a useful vehicle to formulate more effective control policies. Such a working party had been formed, of which Armitage was the first Chairman. The working party had held three previous meetings (e.g. Bacon and Armitage 1979). These meetings had stressed the need for quantitative studies of aspects of rabies epizootiology in Europe and it became apparent that, while WHO were collating information on rabies case occurrence ih Europe, there was not a similar comprehensive body of data concerning the distribution and density of the main host of the disease, the Red Fox (Vulpes vulpes). This information was fundamental to a quantitative understanding of rabies spread through Europe and, as it would not be possible to assess fox densities over the whole of Continental Europe on the basis of field work, it had been suggested that such estimation might be made indirectly by an analysis of habitat attributes which could be correlated to fox densities. At the same time Dr. Macdonald had attended a WHO meeting on the influence of natural barriers on the spread of rabies. This meeting had also moved towards a consideration of correlation between fox numbers and habitat characteristics and so the WHO had asked Macdonald to organise a working group to consider these issues. In view of the diverse disciplines that would be required to consider the interactions between fox rabies and habitat, it had been decided that Drs. Bacon and Macdonald would organise a meeting at which experts from a variety of different fields could contribute to this issue; this workshop was the result. Armitage expressed his thanks to the Institute of Terrestrial Ecology and to the Nuffield Foundation for providing financial support at the meeting.

Armitage then introduced Macdonald who announced the domestic arrangements for the conference, together with various minor changes to the programme. A number of people had sent apologies for their absence dur to prior commitments: Professor L. Andral, Dr. K. Bögel, Professor K. Deitz, Mr. J.N.R. Jeffers, Dr. D. Jenkins and Professor B. Sayers, who wished the meeting every success and sent greetings to their colleagues who were attending the meeting. Macdonald then introduced Bacon who spoke briefly about the aims and structure of the conference programme.

Bacon began by reminding delegates that the idea behind the conference was not new: for example, Adamovich (1978) had shown that the spread of rabies in the Soviet Union could be related to particular land forms and Sayers and colleagues (1977) had shown that the patterns of rabies spread and recurrence were also affected by landscape features. A recent paper by Kroeza and Schaeffer in the WHO Rabies Bulletin in Europe had shown that frequency of rabies cases was negatively correlated with the density of chamois (Rupicapon nipicapron) and positively correlated with the density of hares (Lepus europeans) in Austria; however, previous work had also indicated that rabies cases were more frequent in valleys and the findings in Austria could therefore not be interpreted as showing any direct involvement to the animals concerned as these might simply reflect different altitudinal zonations. Work in America had also shown that the frequency of case reporting was higher in valley bottoms. Indeed, in some cases reporting was more likely the closer one came to rabies investigation centres! Bacon showed example diagrams from the WHO Bulletin showing cases in Europe for particular quarters of the year from which it was evident that rabies cases were clustered in both time and space and basic geographical knowledge suggested that these clusterings, or the lack of them, were related to landscape features. He showed a diagram, Figure 1, which indicated four main entities of the rabies problem and attributes corresponding to these. Ecological theory suggested a causal link between features of habitats and fox population dynamics. The evidence he had referred to earlier also suggested that rabies case frequencies could be directly related to some aspects of habitat. The aim of the conference was to consider whether correlations, represented by arrows, could be established between the various attributes of the entities in his diagrams and whether such relationships could be made sufficiently precise to permit quantitative predictions, and therefore testing of hypotheses. Bacon illustrated this point with a diagram (frontice piece) which contained visual information about fox habitats; he hoped that the workshop would elucidate means whereby the subtle aspects of habitats that were important to foxes could be recorded in a manner facilitating quantitative predictions that would aid rabies prophylaxses.

Methods of land classification - A Review

Dr. G. Robinson

Land classification was a useful tool in geography in order to document changes, in particular in relation to agriculture. There was a need for information on land use and urban sprawl where the conflicting interests of industry and agriculture needed to be taken into account for planning purposes. On this basis a number of classifications had been devised to estimate the agricultural potential of the land (a method which was also used for forestry and conservation). Such assessments which have been made in the UK were generally piece-meal, but elsewhere, for example Canada, such assessments have been made on a comprehensive basis. The aim of such assessments was "to improve powers of prediction for management purposes". Classification systems had generally arisen from taxonomy which classified things on no fixed basis. More rigorous classifications needed a defined purpose and definitions of criteria to be used in those classifications. A number of distinct methods were available for example devisive classifications, monolithic classifications, and polythetic classifications. Robinson briefly described the differing assumptions behind these approaches and indicated their strengths and weaknesses.

In Britain there were three surveys which aim to assess quality of land itself; those by L.D. Stamp, the M.A.F.F. and of the Soil Survey. Stamp's survey depended heavily on existing use, not on potential use. Land was categorised into ten classes whose definitions were not particularly rigorous. This early survey had been improved upon by the Ministry of Agriculture whose surveys stressed physical limitations to agricultural productivity, and plotted the resulting land classes at a scale of 1" to a mile. The physical limitations assessed gave indications as to the range of crops which could be grown in an area, the level of yields which might be expected, the cost of obtaining those yields and the likely consistency of those yields. For example Grade 3 agricultural land is at a 100-600ft. (30.5 - 182.9m) has between 40" and 60" (101.6-152.4mm) of rain per annum and was on slopes of 1 in 8 to 1 in 7; other minor factors were also assessed. A survey by the Soil Survey produced seven classes with five subdivisions. These classes were also based on physical limitations. The main factors assessed were gradient, elevation, climate, drainage and soil characteristics. Currently an attempt was being made to amalgamate the surveys of the MAFF and the Soil Survey to produce a more comprehensive result.

Robinson then tabled the question of whether habitat could simply be considered as some division of land. As a geographer he thought this was so, and that the two aspects were mainly differences of scale; for example the divisions of land about which geographers usually talked often corresponded with the ecological divisions of ecosystems or biosystems. Such concepts have formed the basis of the Canadian-Land Inventory Survey, carried out since 1964, as "An Ecological Land Classification". The results of this survey were available at three different levels - ecosystem classification, at a scale of 1 to 1 million and based on LANDSAT imagery; soil and land for classification as a subdivision of the above at a scale of 1 to 250,000; site specific classification at a scale of 1 to 50,000 which incorporated local details of the vegetation terrain, rainfall and soils. Resulting from this survey there are maps which could indicate, for example "soil capability for wildlife". For example, maps have been prepared to show the distribution of ungulates and waterfowl in relation to conservation and hunting requirements. Robinson expressed the opinion that such approaches held promise for prediction of wildlife species densities in relation to conservarion or control purposes.

Discussion N.B. Q = question
A = answer
C = comment

Q Howard — You have made no comments or criticisms on the various methods. Do they require experience of the method on the part of the user and a pre-knowledge of the system? Could indices of various aspects be usefully constructed?

A Robinson — The British surveys do tend to be too general, farmers do not profess to use them a lot. They are perhaps too general to be of practical use. Farmers say that every field is different. The surveys are probably of more use to planners than to the farmers.

Q Macdonald — In the Canadian survey how was the suitability of land for ungulates assessed?

A Robinson — On a very ad hoc basis.

C Macdonald — So the problem remains of understanding the impact, on the key species, of those habitat variables described.

Q Bunce — Are the results of the soil survey for England and Wales as opposed to Scotland rigorously comparable, or are the criteria used slightly different?

A Robinson — Yes, there are minor differences in the methods for the regions: for example Scotland has two extra divisions at the very "low" end of the scale of usefulness. The divisions are, however, too arbitrary in any case.

C Bacon — I am glad you have raised this question of the scale of classification. In our context I believe one needs a small scale for predicting fox densities, but a higher scale is probably necessary for sufficient numbers of rabies cases to be reported to allow statistical treatment.

A Robinson — Yes, for example the subdivisions utilised in the Canadian scheme might be appropriate.

Q Zimen — The classifications you describe are based on many attributes. Has anyone summarised this information in the form of diversity indices?

A Robinson — I do not know of anybody using diversity indices but in any case I do not think statistical methods are an appropriate way of summarising such data.

C Bunce — Diversity indices are too dependent on the number of attributes used. All published diversity indices are misleading for this reason. Delegates interested in this problem should contact Ken Lakhani at the ITE Monks Wood.

A Robinson — This sounds very similar to the situation in geography where single number indices had been found of little value.

The British Land Use Survey

Dr. A. Coleman

The survey which she had undertaken required the mapping of landscape features at a resolution of 6" to a mile and results were being published at a scale of 2½" to a mile. Data were recorded such that a resolution to a size of about 10 x 10 metres was possible. The Second Land Utilisation survey of Britain could not provide maps of vegetation of all species for Britain but the survey was comprehensive, unlike those of the NCC and the ITE which were based on samples only. The scale of recording precluded the inclusion of great detail of vegetation and although they would like to provide detailed vegetation maps, the maps available would preferentially record the dominant species. Coleman considered how information from her survey might be useful to predict fox densities: she considered this in two areas, firstly in the countryside and secondly in urban areas. In rural districts vegetation was recorded by mapping the boundaries of the prominent vegetation zones. Within each zone the vegetational composition was recorded using four symbols (each symbol representing the species) which were listed in their order of abundance/dominance. In urban areas the maps show, for example, where areas of grass and scrub occurred within houses and factories. Garden boundaries and allotments were also shown. It was possible to define 250 different categories. A recent update of her survey in an area of inner London showed an increase in the amount of derelict land, due to inner City demolition. There is now a great deal of vegetation on disused land in the inner cities. The amount of disused land has increased in this borough between 1964 and 1977, and 15% of the area is currently disused. Coleman showed maps to illustrate how the distribution of bracken (Pteridium aquilinium) within Britain, as shown by her survey, had been related to the incidence of stomach cancer in people, which was caused by a carcenogenic substance in bracken which had contaminated cow's milk. She concluded by saying that she hoped to learn at the conference what aspects of habitat were important to foxes: for example in cities she imagined that railway embankments might be important and that in the countryside hedges, or the lack of them, might also affect fox densities. She asked the ecologists at the conference whether: the details on the Land Use Survey maps would be of any use to them in predicting fox densities; what other information they needed; whether the data needed to be particularly recent. She concluded that a map of the fox densities was necessary for rabies epidemiology studies and that it might be feasible to construct such a map by amalgamating maps showing aspects of the land which were favourable, or unfavourable, for the fox.

Discussion

Q Nicholson — Do your maps distinguish between individual houses?

A Coleman — Houses were not mapped because it was initially thought that planning authorities would do this every five years. The basic data on houses comes from the Ordinance Survey maps themselves.

C Zimen — Coleman had asked whether her maps would be of any use to fox ecologists: as a fox ecologist he would find them extremely useful; he regretted that in Germany such maps were not available.

Q Zimen — Had Coleman used Satellite photographs in her survey?

A Coleman — Satellite photographs were not available; she had used field survey methods.

C Zimen — She must have had a lot of volunteer helpers.

C Zimen — Coleman had asked why urban foxes occurred in Britain but not in Europe. In European cities derelict or waste land does not occur within the city boundaries. He believed this was the answer.

C Coleman — It would be possible to produce maps from my data of derelict land within the city boundaries. But the comprehensive survey is based on data for 1964 and is not therefore up to date. In Britain there are currently a number of surveys on "vacant land" being undertaken.

Q Macdonald — Are the date underlying the survey quantitative and could they be collected by relatively untrained observers?

A Coleman — The measurement method is easy and could be readily undertaken by other people. Such data define five types of land: townscape, urban fringe, farmscape, marginal scape and wildscape. These categories could be further subdivided. Coverage has been so far obtained for 95% of Britain.

Q Macdonald — Is there such a map for Oxford?

A Coleman — There is a map for Oxford held in London.

General discussions

C Armitage — Are a priori methods of classification suitable for the purposes of rabies epidemiology or fox densities? Could one use such existing data, or was a new method required?

C Emmanuelsson — (Commenting on Armitage's point) There is a lot of redundant data in vegetation maps, but there are also a lot of vegetation types which are important but which are not mapped. He believed that the vegetational, and habitat, details required would depend on the species being studied.

Habitat Analysis and Bird Populations in Northern Sweden

Dr. U. Emmanuelsson

His paper presented the results of pilot survey to assess the suitability of the "wilderness" areas of Northern Sweden and Lapland for bird species of conservation importance. The landscape was mainly birch forest and moorland. This represented some of the largest untouched wilderness areas of Europe and was currently threatened by peat extraction, hydroelectric developments and tourism; ironically the tourism largely took the form of interested naturalists visiting the area and damaging the fragile tundra vegetation by trampling. It would not be feasible to assess bird species densities over such vast areas by direct field survey techniques. Even if this were possible, it would not be adequate to visit each area only once. For example the long tailed skua (a predatory sea bird) will only be present in areas of high lemming (Lemmus lemmus), density; accordingly if suitable areas for the bird were surveyed in years of low lemming numbers it would be assumed to be absent; in fact its habitat requirement were very characteristic and field work had been shown that its presence could be predicted on the basis of these. It was similarly possible to predict the hunting areas for white-tailed Eagles, although nest sites could not be similarly predicted. The survey had been undertaken in relation to a wide range of bird species; in general the most important predictive factor which they had found was the amount of "border" between different vegetation types.

Their survey had comprised five stages:

A field survey mapping vegetational and bird species densities
A correlation analysis between the vegetational data and the bird species data for each species.
The use of vegetation maps to predict, via the above established correlations, the bird species densities in areas previously unsurveyed.
A second field survey to record the densities of bird species in the areas for which predictions were undertaken.
Correlation analyses to test the accuracy of the above predictions.

In practice, simple correlation had not been possible since many of the environmental variables were highly inter-correlated; accordingly ordination analysis had been performed on the environmental and vegetational data and regressions subsequently performed of (1) those ordinated variables in relation to (2) the known densities of particular species. Correspondence between the faunas and the floras were in general good. They had investigated which environmental variables were primarily responsible for those relationships. For example, mean altitude, and the variance of the altitude within a quadrat, were both extremely important: the distribution of many birds of prey in northern Sweden varied closely with the variance of the altitude of the quadrats which could be thought of as representing the amount of cliff-face suitable for nesting sites.

Emmanuelsson addressed the problem of predictions in more detail, as these were bedevilled by local changes. Over wide geographic regions the correlations were sometimes unstable: he therefore suggested that a sample survey should be undertaken in local areas, from which data the correlations could be re-established, providing detailed coefficients for thatarea. Predictions could then be made on a local basis, and sample areas re-surveyed to test the accuracy of those local predictions. There was an interesting statistical problem in determining the probability of finding a species in a particular quadrat and the confidence limits for this probability.

Using a trial approach they had shown that the predicted probability of finding Merlins (Falco columbarius) was closely related to the observed densities of field surveys. Predictions for many Passerine species were also good, but predictions for Ravens (Corvus corax) were poor and very variable. They believed that the poor predictions for the Raven probably resulted from the large influence of people on the distribution of that species.

Emanuelsson closed recommending the following procedures for predicting animal species densities in relation to their environment:

1. A pilot study on which environmental or topographic variables are important to the species ecology.

2. Sub-classifying areas according to those variables which are important.

3. A calibration survey of the 10% of those defined sub-areas.

4. Field survey of species densities in areas defined by the classification of three above.

5. Ordination analysis of the field survey (or map attribute) data obtained from four above.

6. Extrapolation from the relationships obtained between points 4 and 5 to predict for areas unsurveyed in point 3.

7. Field survey to test the accuracy of the predictions from point six above.

Discussion

Q	Carey	Why did you not look at vegetation structure?
A	Emanuelsson	The Alpine/Tundra area is sufficiently simple in vegetation for few species to adequately reflect the vegetations structure.
Q	Berreen	How do you test a prediction?
A	Emanuelsson	Field work was undertaken this summer; 70% of the bird species densities had been fairly well predicted particularly those for passerine species and some raptors. For some of the species poorly predicted the survey had indicated important attributes which were not present in the original data.

An Environmental Stratification Procedure for Britain

Dr. R. Bunce

Dr Bunce described an environmental stratification procedure which he had developed for Britain aimed, in part, to provide a means whereby the results of the detailed local surveys could be extrapolated to a countrywide basis. He drew an analogy between his aims and those of opinion pollsters whose work showed that attributes of large populations could be accurately predicted on the results of properly randomised sample surveys.

Such predictions required three stages:

1. Environmental classification, based on attributes of climate, topography, geology and human artifacts; these could be recorded from maps.

2. Ecological survey of the areas classified, and analyses to demonstrate correspondence between the results of the classification and the plant communities found within those land classes.

3. Projection of the correspondence analyses to predict vegetational composition in unsurveyed areas and the testing of those predictions.

The analysis was based on Indicator Species Analysis (developed by Hill; e.g. Hill 1973, Hill et al 1975) and environmental attributes recorded from maps (stage 1). The second stage of the survey involved detailed field work, in eight randomly chosen samples sites for each of the thirty two land classes defined by the above analysis. Within each of these 256 sample areas the following details were recorded:

Vegetation composition for five random plots within each quadrat; soil profile details from five pits dug at random within the quadrat; ten linear transects recording vegetation data; a complete mapping of the field boundaries and compositions.

His experience with this method, and similar previous studies, showed that considerable skill was necessary to include the appropriate data in the analysis to permit the stated objectives of the survey. He described a pilot use of his survey to predict likely fox densities for the whole of Britain, (Macdonald, Bunce and Bacon, in press). The results of this pilot study were extremely encouraging, but showed, however, that, from the point of view of the fox, his survey currently under-represented the importance of urban land. For other aspects of land use, for which his survey was much more appropriate, Bunce showed tables indicating close agreement between, for example, national acreages of crop; lengths of railway line; such predictions were often accurate to within only a few percent.

Bunce concluded by recommending that such an approach was necessary to enable the results of detailed local studies of fox populations to be applied to wider national, or continental, regions. He suggested that a suitable stratification procedure, based on aspects of the environment, the vegetation structure, and the vegetation composition could be usefully used to allow the results of local studies of fox populations to be extrapolated to a continental scale.

Discussion

Q Coleman — How many people had been involved in the survey; for how long; what did it cost?

A Bunce — The initial attribute survey took only six months and two man years were needed for the field survey, a total of about eight years in all. Taking salaries, travel expenses, etc., into account an overall costing in the region of £100,000 would be appropriate.

Q Mountford — What gain in efficiency resulted in the use of the stratification over, for example, a county system?

A Bunce — He had no budget to test this question rigorously, but would be very glad of a statistician to help with prediction problems in such surveys.

Q Armitage — On what basis was the data for the first classification collected?

A Bunce — Environmental data for a quadrat of one square kilometre.

Q Wandeler — Could European predictions be made with existing data, or would further field work be needed?

A Bunce — Both further stratification and further field data would certainly need to be done first for Europe. His experience with such procedures showed that, in general, obtaining details for more quadrats was more important than recording many attributes for fewer quadrats.

Q Coleman — Were the areas actually surveyed for environment variables and vegetation difference?

A Bunce — Yes, as the tables he showed had indicated, his predictions were tested against data obtained from entirely independent sources.

Q Carey — Were species area curves constructed from the data?

A Bunce — Yes, these were constructed by a colleague.

Q Zimen — Had the predicted fox densities been validly tested, as estimating fox densities in the field was extremely difficult?

A Bunce — The predictions were tested within the broad limits which were applicable.

C Macdonald — The spirit of the investigation of fox densities in Britain was simply to indicate whether the procedure might be useful if better data on fox habitats were available. The pilot survey had knowingly ignored two important aspects of fox habitat (1) urban land and (2) effects of human predation. There was no implication that these first predictions were accurate, but he did conclude that the principles involved were promising.

C Bunce — The results of the pilot survey had highlighted some aspects of fox habitat requirement which were currently not well known, and the survey itself could be used to aid in the selection of sites where detailed studies of fox populations would be most fruitful.

c Bacon — Such a stratification could be most useful in choosing areas in which to study foxes: time and expense of field work could be considerably reduced by choosing study areas that contained a mosaic of land classes which were close together.

Q Emanuelsson — Could a new stratification be devised from the data, which would be more applicable to foxes, by selecting from the existing data those attributes more relevant to foxes?

A Bunce — This would be possible, but the main divisions within the stratification were climatic.

Q Wandeler — Do you imagine that your estimates will closely reflect carrying capacity or actual densities?

A Macdonald — Under the conditions of our preliminary exercise the predictions are more likely to reflect carrying capacity.

C Bunce — It is hoped that the data base for this stratification will shortly be updated. For some crops, for example oil seed rape, farming practices are changing so rapidly that almost yearly surveys would be required to ensure the current data were accurate.

Estimating Fox Population Indices in France and Correlations between Fox Densities and Land

Dr. M. Artois

Most studies of fox densities were both too local and too time-consuming to be of value for rabies epidemiology. It was possible that indirect methods of estimating fox densities could be adequate based on (1) a hunting index or (2) spotlight sightings done at night. He had investigated two indirect methods: (1) a hunting index, based on the number of adult foxes shot per 10 km. x 10 km. square during the period January to June. Autumn kills were excluded because hunters do not distinguish between juvenile and adult foxes in their reports. (2) A "kilometric" index: this was based on the number of foxes observed during a 40 kilometre road journey, undertaken from a vehicle moving at 10 kilometres per hour, equipped with a Loo watt bulb spotlight. This allows foxes within a range of 50 - 300 metres of the road to be observed, but was limited to areas, or seasons, where the vegetation was not very tall.

His results, for 14 sample quadrats in Southern France, showed a hunting index which varied from 1 to 50 foxes shot per kilometre squared. There was good correspondence between the spotlight index and the hunting indices. However, Artois considered that hunting methods were insufficiently varied to be accurate. For example the intensity of hunting varied in different areas, and rabies, when it occurs, makes animals easier to shoot. No correlation was found between land type (farms, pasture, woodland) and the hunting index.

The result of his kilometric index indicated that sightings decreased in frequency before rabies reached an area. He considered the reasons for this: e.g. Enzootic rabies may have killed foxes that would otherwise have dispersed into the area.

He concluded that neither of the two proposed methods worked properly, in the sense of giving accurate measures of fox densities, although the hunting index was of practical value. He considered that three aspects were important in estimating fox population densities in his area: (1) habitat attributes; (2) rabies incidence, (3) hunting and fox population control procedures.

Discussion

Q	Carey	Are you familiar with the paper on Fox Population Indices by John Wood?
A	Artois	Yes, but it is not applicable in our circumstances.
C	Wandeler	Many of the methods developed in America have been tried in Switzerland but the results are not repeatable there, probably because of the small scale diversity of European habitats compared to those in the USA. I hope that the "radioactive" methods may work.
Q	Emanuelsson	Have you tried snow tracking methods?
A	Artois	In the South of France there is not enough snow.
C	Zimen	We have tried snow tracking in Germany, and similarly found there is not enough snow.
C	Wandeler	In Switzerland there is similarly either too little snow, or far too much!

C Zimen — I am surprised of the high incidence of human induced mortality suggested by some of your results.

A Artois — No, human induced mortality is not high, much less than 30 foxes per 100 km^2 over the 6 months January to June.

C Zimen — Then this is a very low figure (compared to Germany and Switzerland) but do you think that this level of shooting is limiting the population?

A Artois — There are two problems: (1) estimating the fox density and (2) the low frequency of reporting represented by the hunting index. In my study areas I try to get a formula to relate the hunting index to known fox densities, but the correcting factor varies between 2.5 and 10.0!

Q Wandeler — How did you assess mortality due to gassing?

A Artois — In France the gas used drives the foxes out of the dens and they are then shot.

Estimating Fox Numbers in Bristol

Dr. S. Harris

The urban study area where he works contains some 170,000 households. Within the study area he has selected two intensive zones for detailed study: an area of old Victorian housing with small gardens; contrasted with a nearby area of urban detached houses. Over a period of two years his own intensive field work has been backed up by questionnaires and surveys requesting information from members of the public on sightings of foxes; all likely areas were checked and reports from the public were double checked. The common sites for fox lairs were either under sheds and in gardens, or else under floor boards in the older houses (these latter sites were occuped less consistently, as a lair used in the house one year was generally blocked by the owners the following year). A comprehensive coverage was obtained identifying twenty fox family groups within the study area, with densities in one study area varying between 2.64 and up to 5.0 foxes per $Km.^2$; however, in the South of the town (south of the river) the density varied between 0 and 1.0 whereas in some areas north of the river densities were up to 5.0 foxes per Km^2. The number of badger sets in some areas was also extremely high. He had been unable to find correlations between fox density and either: human density; socio-economic status of the region; area of houses per unit area; or area of open land. However, data obtained from the R.S.P.C.A. on the incidence of stray dogs and cats showed that: (1) few foxes occurred in the regions where there were many dogs, with a highly significant negative correlation. (2) The density of stray cats was positively correlated to the density of dogs, but most of these cats were fed; true stray cats are a very small proportion of the pet cat population and probably do not greatly affect the fox. Stray dogs were common in the City centre and in some regions of Council housing; there was considerable variation between housing estates as to whether particular estates had a lot of, or few, dogs. The cause of death has been assessed for about 100 recovered corpses of fox cubs. Road deaths accounted for 58%; dogs for 15%; unknown causes 10% and a variety of other factors for the remainder.

Harris concluded that fox, and badger, densities in Britain were extremely high, and that these animals reacted with man, and his pets, in a complicated fashion. He would not suggest that data for Bristol were necessarily typical of other cities - the situation seems far too complex for that to be likely.

Discussion

Q	Lindsay	Were there really 91 badger sets within the study area?
A	Harris	Yes.
Q	Bunce	What is the fate of the approximate 100 fox cubs born each year in your study area?
A	Harris	Most of these disperse; an unknown proportion are killed by snaring for fox pelts.
Q	Berreen	In Birmingham there are fewer dogs than in Bristol but there are great differences in the densities of dogs depending on ethnic class and the status of those ethnic groups.
A	Harris	I investigated such relations using previous census data, but did not find good correlations.
Q	Zimen	What did this enormous density of foxes find to feed on?
A	Harris	A lot of them are hand fed by successions of people! People in Bristol like foxes. Pet rabbits, guinea pigs etc., also provide such food.
C	Zimen	The density of urban foxes reported was exceptionally high. In Saarbruken they had tried a similar questionnaire and hoped to get an idea of fox distribution; they had had only one report for the whole city over the entire year!
C	Bunce	There would seem to be an analogy with the Robin: in Britain it was a popular, tame, garden bird whereas on the Continent it was scarce, shy, woodland species.
Q	Bacon	I was surprised your figures discounted cats as predators on fox cubs. While rearing a young fox cub in an urban area this spring I found its presence was largely ignored by local dogs, but that it was stalked by most of the local cats. Do you think there could be a bias in your data underestimating the effects of cat predation?
A	Harris	There might be a small bias, but I doubt it would affect the overall picture.
C	Macdonald	The parallel studies in Oxford and Bristol are showing very significant differences in the fox densities of the two cities, and indicate that the blanket term of "urban" habitat is too simple to be very useful.
Q	Van Aarde	Why don't dogs kill cats?
A	Harris	Cats can escape much more readily than foxes, and are extremely vicious.
C	Van Aarde	There seems to be an important factor missing in relation to the relative densities of dogs, cats and foxes.
Q	Van Aarde	Were the road deaths uniform?
A	Harris	Yes, they are a lot more frequent on city boundaries.

Q <u>Meredith</u> Are there historical records of fox spread into urban areas?

A <u>Harris</u> Yes, but the patterns and details of such records vary a lot from city to city.

C <u>Bunce</u> In Continental cities is there not much less waste land that is suitable for foxes?

C <u>Zimen</u> I agree; in German cities there is no garbage, no birds, there is nothing for foxes!

A <u>Harris</u> I agree.

C <u>Berreen</u> It sounds as if there may be cultural effects within fox populations within cities; learning between foxes could be important, accounting for poor correspondence between different cities.

C <u>Bacon</u> There might be useful analogy here with cultural learning demonstrated in birds: for example cultural learning in Blue Tits (<u>Parus caeruleus</u>) feeding from milk bottles and of Siskins (<u>Carduelis spinus</u>) taking peanuts from a new type of plastic container from bird tables.

C <u>Berreen</u> I think the word "stray" is inappropriate for dogs in urban areas; most of these do have a locus of operation if not an actual home and are more accurately termed 'loose'. Conversely many of the cats found in cities are genuinely roaming and feral and for these the term "stray" would be appropriate.

A <u>Harris</u> Yes, the term "loose" would be more appropriate for many urban dogs.

<u>Wednesday 17th September</u>

<u>Statistical Considerations in Land Classification</u>

P. Howard.

Howard was presenting a review of statistical considerations of aspects of land classification that were relevant to prediction of animal densities. A full version of this review, with extensive references, was available from him on request.

<u>Classification</u> was a technique intended to emphasise the similarity between objects, and classes of objects. Historically there were two basic approaches: monothetic classification, using single criteria for each division, and running the risk of serious misclassification of an object which was abberant in one character; polythetic classification was based on the overall similarity of the many attributes but, while all members of a particular class of a monothetic classification would share many attributes, there would not, necessarily, be any one attribute which was common to all of them. Techniques of multivariate statistics had recently been applied to classification problems: generally these aim to identify discontinuities, or low densities of points, in the multivariate space that is representing the object under study. Kendall and Steward had used such a definition for classification, and argued that it was only appropriate for sets of data where such discontinuities exist. Conversely, the technique of dissection can be applied to any set of data and would also group the data items into classes; however such a grouping might not necessarily be useful.

The major problem in classification was which properties of the objects under study should be used to achieve the classification? Practical grounds demanded selection of a sub-set of properties in order to achieve the classification, and experience showed that conscious selection of attributes more likely closely related to the end-use required for the classification were generally more economical. It had also been generally found, in multivariate studies, that if many properties were used there would be much intercorrelation between them, and accordingly included much redundance. On similar statistical ground, it had also been shown that a large matrix of data items tended to produce unstable eigenvalues in the resulting analysis. There was a considerable body of evidence suggesting that, before multivariate classification algorithms were used, an ordination technique (such as Principal Component Analysis (PCA) or Factor Analysis), to reduce the dimensions of the data set and produce orthogonal variates, were an advantage.

With respect to the basic data the initial choice of information recorded could greatly affect the type of subsequent analysis which could be validly carried out. For example discrete data, (i.e., presence/absence data), often termed "attributes" required different procedures from data recorded of continuously varying factors, usually termed "variables". Analysis of disordered multistate data (e.g. colour classes) and ordered multistate data (e.g. rare, common, abundant) was more difficult, as was analysis of meristic data, in comparison to continuous variables. Presence/absence data were also poor for identifying subtle variations; in general one should not convert continuous variables into discontinuous attributes for ease of recording, as this limited the power of subsequent analyses.

Howard mentioned some of the advantages and the disadvantages of various multivariate techniques, (detailed consideration to these is given in the full version of his paper). He considered ordination techniques, cluster analyses, principal component analyses and principal co-ordinate analyses. He suggested that if a classification, or stratification, was required to predict animal densities this should be chosen so that it statistically reduced the variance of the densities within the strata defined by the analysis; he recommended investigation of the adptation of K-means cluster analysis to such problems. This technique would produce a specified number of clusters, with minimum variance properties within the clusters; he had found that it was often an advantage to use Principal Component Analysis scores as input to the K-mean analysis, as these were orthogonal and of reduced dimensionality. The K-means technique required continuous data. He thought there might be merit in investing the use of aglomorative statistical techniquem using for example, Gower's distance measure, to provide an overall summary of disparate types of data.

Finally, Howard wished to question whether classification was necessarily the right tool for predicting fox densities. He suggested a regression formulation might be more appropriate -

$$D = f\ (e_1, e_2, \ldots\ldots e_n)$$

He cited Hirst's study of ungulate species in South African woodland savanna as an excellent, rigorous study using such an approach. Hirst had stratified the savanna woodland into 14 vegetational types, to permit efficient, representative sampling. Within these vegetation zones he had recorded both the density and distribution of ungulate species and the values of 25 habitats variables. Hirst had performed Principal Component Analysis on the habitat variables, and found that 95% of the variance of the initial 25 variables was explained on the first 10 axes. Both temporal and spatial distributions of ungulates could be related to many of these factors.

Discussion

Q Bunce — I agree with your suggested regression of approach. If the environmental variables (e_1...... e_n) are PCA scores. Do you agree that this is desirable?

A Howard — That would generally be an advantage.

Q Bunce — Would caution in interpretation be necessary if the first component explained a lot of the variance?

A Howard — Yes; but I have found this unusual with environmental data.

Q Mountford — I do not understand the efficiency you attribute to the use of PCA scores; these represent the same data, with similar errors.

A Howard — I disagree: the statistical requirements of the analysis are better met with fewer orthogonal variables.

C Berreen — Such descriptive modelling is an interesting approach but how does one interpret aspects that are important on several of the component axes?

A Howard — Because they are cross-correlated to other factors: however one cannot be sure without knowing the detailed data structure. I agree that static, descriptive models have serious limitations.

C Berreen — I am worried that initial structures within the data may be lost, or obscured, by orthogonal ordination analyses.

C Bunce — The aim of stratification was to "hold the environment constant" and look for factors that determine greater variation between classes as opposed to within them.

C Berreen — Analytical approaches are powerful, and simple to perform, but did not necessarily lead to optimal interpretation.

C Howard — The conference was addressed to the exercise of predicting fox densities: I can see no reason why these should not be predicted using standard, tried methods.

C Mollison — Even so, I do not see why these predictions cannot be made from the original data.

C Bacon — There were complex advantages and disadvantages associated with the use of PCA and similar ordination techniques; it was likely that the aims of interpretation and prediction might be better met by different methods, as opposed to a common technique. I find your suggested regression approach to estimating density, rather than using a similar value for all squares of classification, of much merit. Do you think it might be feasible to similarly estimate further aspects of fox population dynamics such as: carrying capacity; reproductive potential; mortality; dispersal; etc.?

A Howard — Yes; this might be feasible.

C Macdonald — Regarding Howard's closing remarks on a regression approach, with which I wholly agree, I can see that Phil Bacon and I may have unwittingly mistitled this meeting. We did not intend the word "classification" to indicate a particular approach to the analysis of habitat characterisation. On the contrary we used the word colloquially to indicate the quest for any method of quantifying environmental variables which would help in the understanding of fox-habitat relationships. I hope then, that delegates do not interpret this as a lack of favour for, say, regression approaches.

C Berreen — In practice, in the field, is not reproductive capacity the easiest of parameters to measure?

A Macdonald — Yes.

C Wandeler — It is possible to assess the reproductive capacity quite well in the field, but the other factors are extremely difficult.

Q Mollison — Are not density estimates adequate for rabies studies?

C Bacon — Density estimates, or simply aspects of habitat itself, might be sufficient to identify areas where rabies persists endemically. However, the scale and magnitude of population density variation, in both space and time, needed to be known for dynamic modelling.

C (unknown) — But density is easier to estimate than the factors suggested by Bacon.

A Carey — I strongly disagree with the previous comment! Assessment of reproductive potentials allows one to investigate habitat quality from the point of view of the fox.

C Berreen — Representative samples would give unbiased estimates of density; if this did not happen, then the samples were not representative. Since reproduction potential was density-dependent, it could not be accurately assessed in ignorance of an index of absolute density.

C Macdonald — Despite the detailed practical drawbacks the techniques being discussed suggested means whereby the findings of intensive studies in "similar" local habitats could be related to Continental scales.

C Carey — There has recently been a conference in the United States, "Multivariate Analyses of Wildlife Habitats" the proceedings of which (edited by Capen) will be shortly available. The feeling at this meeting was that PCA analysis was becoming discredited, and preference was now being shown for "oblique" multivariate analysis techniques.

A Howard — PCA does assume linear relations among the original variates and that the underlying factors are orthogonal. Use of oblique factor analysis was becoming much more common, but was currently insufficiently used to justify confidence in the advantages claimed for it. There were also encouraging recent developments in maximum likelihood techniques.

Rabies and Foxes in South West Gernany

Dr. E. Zimen

In the early days of the European rabies epizootic Dr. Bögel had shown a correlation between a hunting index of fox population density and the number of rabies cases. In areas where the hunting index was less than 0.315 foxes rabies was rarely, if ever, reported. Bögel concluded that the hunting indicator of fox population density (HIPD) was a function of fox population density and positively correlated to it. It had been suggested that a suitable control policy would be to reduce fox population densities to a level at which the HIPD index was so low that rabies could not persist (e.g. 0.2 foxes per km.). There had, however, been considerable public opposition to the gassing of fox earths which were undertaken to effect this reduction, and subsequent work suggested that this initial analysis was too simple.

Zimen presented a number of figures (figures 2 and 3 A - D) which supported his suggestion for complex interactions between fox and: human population density; mortality from human hunting; the percentage of land area which was afforested. Initial field work suggested that fox populations were "r" selected in fields in the rural areas, but "k" selected in forest areas. Zimen suggested that when rabies came into an area of such mixed habitats that he was studying that many deaths occurred in the "r" selected field populations, resulting in a reduction to low population levels, whereas few deaths occurred in the forest habitats, where only a moderate reduction in density was achieved. Subsequently, adults and juveniles from the forest habitats might disperse into the field zones and thereby elevate the population to levels at which rabies could persist, or re-occur. He presented data (figure 4) which indicated that such a situation might have arisen when rabies passed through his study area.

He concluded that the relation reported by Bögel might be misleading. In some cases it might be that the number of foxes shot decreased the stability of the fox population and therefore caused, for intermediate initial fox densities, more cases of rabies.

Discussion

C Bunce — Walkers prefer mixed environments; do fox hunters show a similar preference?

A Zimen — Most shooting in forests is done at the edge of fields from high seats.

Q Howard — Are there not biases in your estimates of population densities from shooting figures within your study areas because one cannot get a long line of vision, or shot, in a forest?

A Zimen — Yes; there are further biases in that a hunter in the forest is shooting deer and does not compete with foxes, whereas in fields foxes take pheasants and the hunter will of course shoot foxes to protect his game.

C Thieme — You have no estimate of the percentage of foxes shot in your different habitats. Your index is therefore as "biased" as Bögel's. Mathematical theory shows that for endemic diseases (not really valid for rabies) there is a linear relation between the number of deaths and population densities.

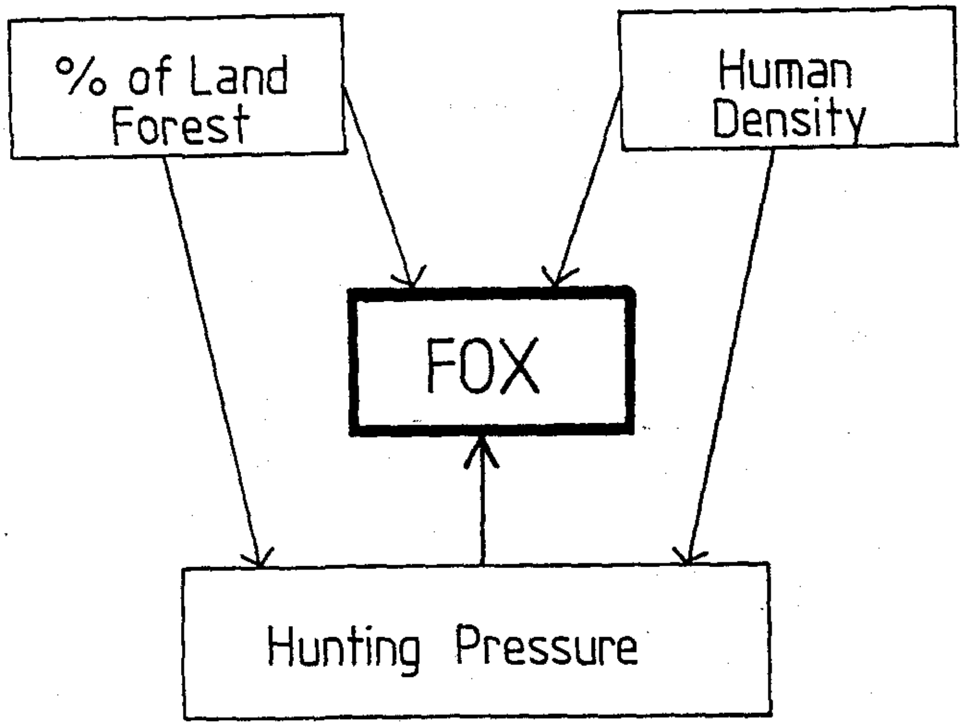


Figure 2 Diagram illustrating the main aspects of human influences on foxes in Zimen's study area.

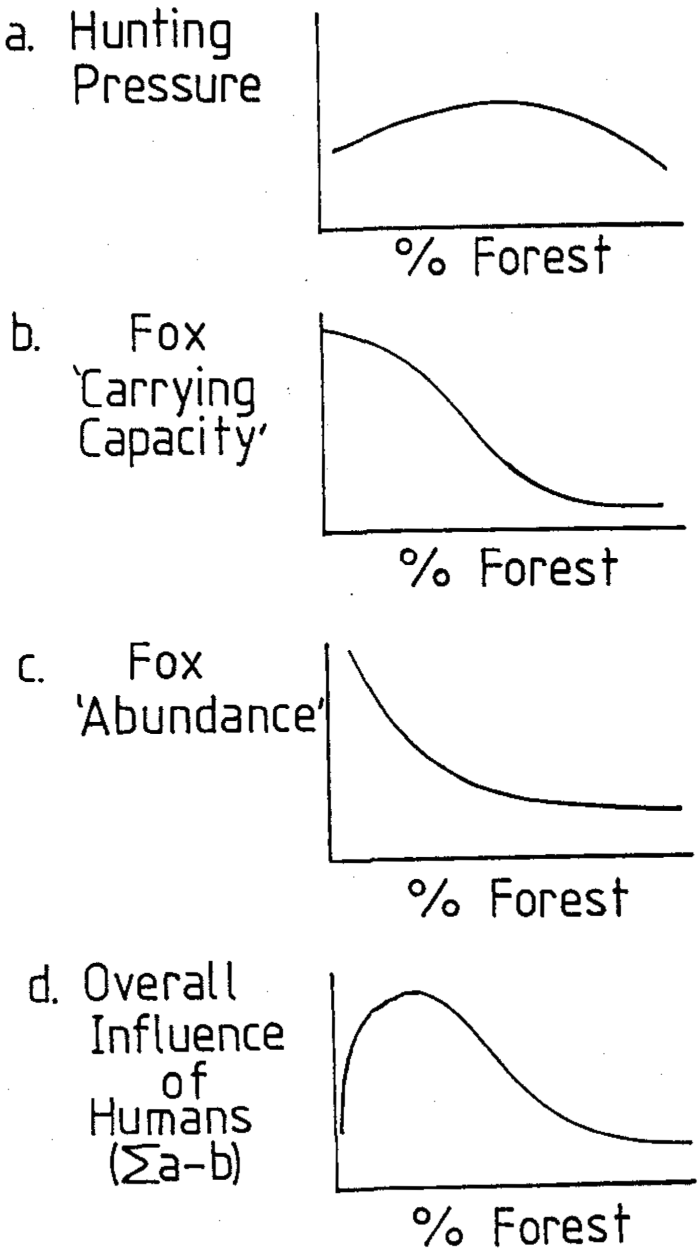


Figure 3 Possible relationships between a) aspects of human influence and b) habitats (as % Forest) in Zimen's study areas.

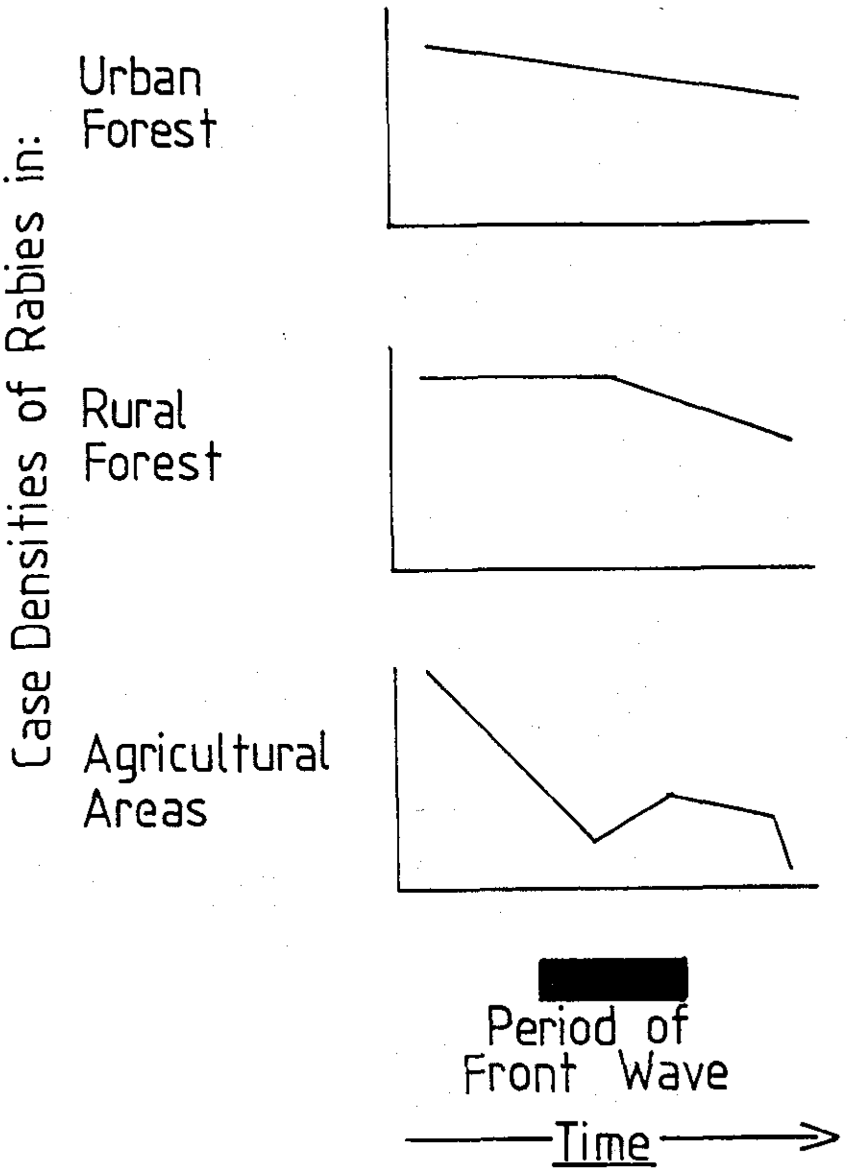


Figure 4 Possible influence of foxes emigrating from the forest areas to agricultural areas, elevating population density in the agricultural areas following deaths of rabies and aiding the persistance and reoccurance of the disease: data for Zimen's study area.

Q <u>Berreen</u> Did you find microtine species on the city fringe?

A <u>Zimen</u> No.

Q <u>Berreen</u> But the proportion of Microtus in your trapped samples was less?

A <u>Zimen</u> Yes; but the difference was made up by other rodents, mainly Apodemus.

Q <u>Thieme</u> Do you think that rodents are a limiting factor in those circumstances: could it not be rabies?

A <u>Zimen</u> Yes, it could be rabies; but the population dynamics of the fox in different areas are of importance.

Q <u>Bacon</u> Would you conclude that, in some circumstances, the disruption caused to fox population by controlled killing might enhance, rather than hinder, the spread of rabies?

A <u>Zimen</u> Yes, I would, I would suggest that one should either kill a very high proportion of the population (perhaps a higher proportion than would be feasible) or leave the population alone. However, there are some areas of North Germany where there is much hunting and no rabies.

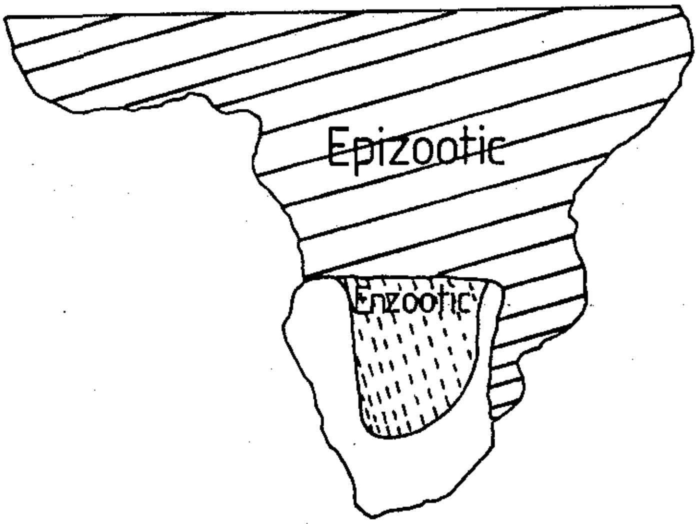
<u>Predicting the course of Wildlife Rabies from Habitat Data</u>

Dr. C. Meredith

Rabies has been known in South Africa since the nineteenth century, and may have originated then via imported dogs of the settlers. In broad terms there were two zones of rabies in Southern Africa, as shown (figure 5). In the South there was an area of enzootic rabies, where species of mongoose were the main vector and reservoir; in the north there was an area of epizootic rabies, where various species of canids (feral dogs and blackback jackal) were the main vectors and the reservoir.

Since 1950 the zone of epizootic rabies has been spreading South from the Northern region. It appeared that the extent of the Viverrid rabies might have increased since 1970, but this might just reflect better reporting since that date, In that region there were three main vegetation zones: grassvelt, corresponding to montane temperate vegetations; bushvelt, representing thorn bush (arbitrary) transition boundaries. Mongoose species, particularly the yellow mongoose which is a prime host of rabies, favours the grassvelt zone; these species and enzootic rabies accordingly show a distribution which is limited by altitude. A similar association could be found between the genet (<u>Genetta genetta</u>) (which burrows) and the bushvelt vegetation. In general, species with high habitat specificity were important as rabies vectors only over a small part of their range. Conversely, animals with less habitat specificity were associated with rabies over a higher proportion of their range.

In South Africa most of man's (unintended) activities actually favour the increase of rabies cases! Apart from direct alteration of habitat, favouring enzootic rabies, men also destroy predators which hold the small carnivores in check; for example black eagles. Suricates and wild cats all prey on mongoose species. There was also a considerable problem from feral dogs and domestic hunting dogs; hunting dogs are illegal and accordingly even pre-exposure immunisation clinics for dogs were no answer to the problem because the owners of hunting dogs were afraid to request immunisation of an animal for which they had no licence. Most human exposure in South Africa is through feral and hunting dogs.



<u>Figure 5</u> Regions of enzootic and epizootic rabies in southern Africa.

There were some aspects of human activity, such as cereal monoculture, which decreased the overall number of animals, and hence of carnivores. Also desertification which on the Western border of South Africa might be advancing at a rate of as much as ten kilometres per year also decreased animal densities and therefore carnivore species.

Meredith concluded that concepts of habitats were of practical value in South Africa where they were used to assess, qualitatively, likely risk of rabies arising. Current data were, however, quite inadequate for scientific determination of likely problem areas.

Discussion

Q Crowley — Whey are there no cases of rabies near the coast?

A Meredith — The coastal region is inhabited by the Banded Mongoose which is not presently infected with rabies. However, this species is likely to become infected soon, via a recent epizootic of canine rabies.

Q Mollison — How much does the level of rabies fluctuate; does it fluctuate in the enzootic regions?

A Meredith — In the enzootic area there is a much lower incidence of rabies in the wet season but a very high incidence during drought or the dry season. There is also a high incidence of rabies in August and September, when the kits of the yellow mongoose are driven out of parental territories; this season also corresponds to the drought period in the year.

Q Mollison — Are any spatial effects manifest?

A Meredith — There may be two to three years waves of incidence in local areas, but no extremely high mortalities occur. They could probably demonstrate spatial, and temporal patterns, if their data were on computer.

Q Carey — Was there any seralogical data on the wild animals?

A Meredith — Regrettably, there was none at all. He hoped to do a seriological study the following year. Some cases of rabies had just been reported in fruit bats near a city (Durban). The control schemes being used in South Africa were not designed for cities and would not work there. He believed it was most important to establish whether or not a carrier state for rabies existed in the yellow mongoose, and other mongoose species.

Q Zimen — You mentioned that there had been nine cases of rabies in humans; how many people were treated?

A Meredith — About 100.

C Zimen — That ratio is very surprising; in Germany 4,000 people are treated annually, and less than one case is reported in humans annually.

C Carey — 90% of treatments for rabies in the USA are almost certainly quite unnecessary.

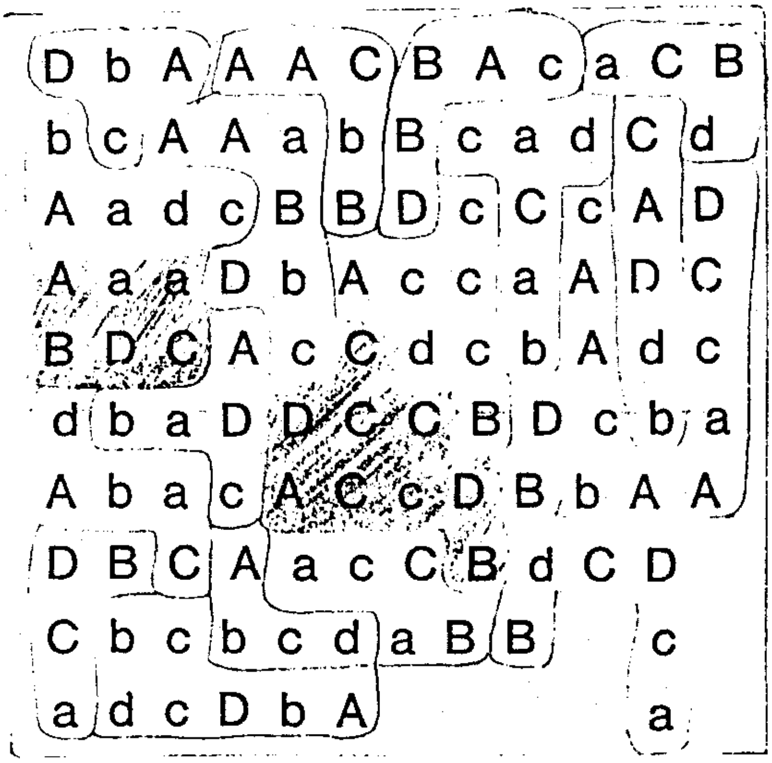
Figure 6 Variations of (i) territory size and (ii) group size under Macdonald's hypothesis depending on:

I seasonally available foods (A-D)

at II varying densities (A-D or a-d)

The types are assigned locations at random

Adequate food in	For	2 foxes	4 foxes
Spring		a	A
Summer		b	B
Autumn		c	C
Winter		d	D



Resulting territories

Only 2 foxes throughout year

4 foxes throughout year

A <u>Meredith</u> A 100 was the number of people treated that were probably exposed. Many more people were treated who almost certainly had had no real exposure; accordingly a lot of money was unnecessarily wasted on expensive vaccine.

Q <u>Zimen</u> Was there any estimate of the number of human rabies cases in the whole of Africa?

A <u>Meredith</u> I have no idea what this number might be for all Africa. I believe that less that 50% of cases are reported in South Africa.

Q <u>Hollison</u> Did the war in Zimbabwe affect the situation, and perhaps make it worse?

A <u>Meredith</u> Yes, in South Africa attempts have been made to control rabies for over 40 years and the situation is now worse.

Q <u>Berreen</u> Are the grassland areas burnt, and if so when?

A <u>Meredith</u> There is widespread burning in late winter and early spring much of which is deliberate.

Q <u>Berreen</u> In that case do you find that the burning occurs before your peak incidences of rabies perhaps due to population disruption caused by the habitat destruction created by burning?

A <u>Meredith</u> Yes, the peak incidence of cases occurred after the burning, and your interpretation is probably correct.

<u>Fox Studies in Habitats around Oxford</u>

Dr. R.W. Macdonald, N.G. Hough and M.T. Newdick.

The home range sizes of foxes around Oxford vary widely and these ranges correspond approximately to defended territories. The number of adults in the territory also varies considerably. Individuals within a territory meet, interact amicably, and even play together frequently. Mortality and natality vary between habitats. Such fox groups have been studied both on Boars Hill, (an area of houses with large gardens on the fringe of the city) and in the city centre itself. Many foxes have been radio-tracked in the area and it has been shown that their night to night patterns of territory utilisation were similar to their overall use over several days or weeks. The data suggest that the individuals have specific patterns of use of their territory both in space and in time. These patterns and the differences between individuals within territories, suggests that foxes may "timetable" their activities in order to exploit more efficiently the food sources within their territory.

Both territory size, group size and the composition of the territories vary considerably; accordingly the habitats within the territories were classified and analyses carried out on the relative and absolute areas of each habitat within several territories. The amount of land of some habitats, such as fields and woodlands, increases as territory size increases; however absolute area of residential land and the absolute number of houses within territories on Board Hill tend to be very constant. Macdonald suggested that these sites provide the major food sources for the foxes, and hence a pair tends to have a constant number of houses within their range in order to provide food throughout the year. Depending upon the dispersion of these patches of houses (or, in principle, any other food patch) their territory size will vary in order to incorporate intervening stretches of land which may be largely under or unutilised. Macdonald suggested further that the group size of foxes within a territory depended upon the amount of extra "food" which was incorporated into the territory in patches within the intervening stretches of less favoured habitat. He developed this hypothesis to suggest that fox territory size depends upon the requirements of a pair of foxes obtaining a sufficient number of patches of seasonally available food to support them throughout the year. If this strategy results in their incorporating patches of food which are superabundant, or incidentally incorporating more type of one area than they actually require, extra foxes, usually their own offspring, can be maintained within their territory at no extra net cost to themselves. Thus territory size would depend upon the dispersion in a particular area of seasonally available patches of food sufficient to support at least one adult pair of foxes, whereas the size of the group of foxes actually living within that territory would depend upon the richness of those patches, which might be surplus to the require ments of the single pair. Macdonald illustrated this hypothesis (figure 6) with the diagram of seasonally varying food, of variable density, distributed at random; on the basis of his hypothesis he had divided this into territories sufficient to support at least one adult pair and indicated within the boundary of that territory the total number of foxes that the territory would support throughout the year. The model emphasised how group size and territory size might vary independently of each other in patchy environments.

Discussion

Q Berreen — Was there any sequential consistency in patch visitation?

A Macdonald — Yes, but not an inevitable sequence. It may have been simply a consequence of the shortest route between the most frequently used patches.

Q Berreen — Did some individuals consistently use places not visited by others within their group?

A Macdonald — Within a range some (better?) patches may be used predominantly by individuals of a particular status.

Q Hewson — Did patch use vary seasonally?

A Macdonald — We think so, but have been unable to analyse the data fully as ye

Q Zimen — Have you tried experimentally manipulating the food supply, to test your hypotheses?

A Macdonald — This had been done almost accidentally and seemed to have the predicted effects; however there might be time delays in the alteration of range boundaries. Such experimental manipulation would not have been expected to have a rapid effect.

C Zimen — We have found foxes will find new food sources very quickly though it appears to take as much as six months before they will use them regularly.

C Bacon — The irregular visits to the less favoured patches sounds similar to the "two-armed bandit problem" investigated by Kacelnik (1979 this would suggest that the foxes are visiting the other areas occasionally, in order to monitor whether or not food has happene to become plentiful there.

A Macdonald — Yes that is possible, as with Royama's study of Great Tits.

Q Howard — You seem to have enough data to try out the type of analysis used by Hirst.

A Macdonald Yes but so far we have not had time. I have mentioned only provisional analyses of a long-term project.

C Carey Your findings support the suggestion of Storm that a range may be a series of pathways connecting high use areas.

Q Howard Is there more interaction at boundaries in high use areas?

A Macdonald The data do not yet suggest that, but it seems plausible.

Q Howard It might be interesting to work out "minimum spanning tree distances" between patches.

A Macdonald That sounds an interesting approach, but it might be difficult to incorporate suitability of "patch" in such a method.

Rabies Spread and European Map Attributes

H. Jackson reported the results of M.Sc. thesis study on the incidence of rabies cases in different habitats within Europe. The rabies case data had been taken from maps provided by the WHO centre in Tubingen; the habitat information resulted from an environmental, climatic and land use attributes classification following the procedure described by Bunce. As large scale maps, drawn to a common projection were difficult to obtain it had been necessary, in the time available, to assess habitat at a coarse scale (20 x 20 km quadrats) which put some restraint on the subsequent analysis. Similarly, in the time available, it had not been possible to try and account for the different reporting strategies of different European countries. The analysis had identified a number of zones in Europe, based largely on topographic features, and overall density of rabies cases varied significantly between these.

Discussion

Q Zimen Could you give us more details on the type of area where there was the most rabies?

A Jackson Generally broken country had more rabies than uniform areas.

Q Mountford What was your null hypothesis for testing the frequency of rabies cases?

A Jackson That it would be independent of the land class.

C Zimen Heterogenous habitats are believed to have more foxes and often have more people.

Q Zimen Why do you think the incidence of rabies was higher in the Alps?

A Jackson It could be simply a greater surface area in broken land.

C Zimen During 1977 to 1979, the period for which you assessed case incidence, some parts of Austria had rabies for the first time, so reporting frequencies would have been higher there.

C Wandeler The WHO centre will never get data accurately enough to show such effects, at least from Switzerland. The densest sampling of cases would be in Austria.

Q Ross — A coarse resolution was necessary due to the short time of your study. What resolution would you think best?

A Jackson — A square of about five kilometres side.

Q Ross — Why did you not use LANDSAT imagery?

A Bunce — The time and expense of LANDSAT photographs made them unsuitable for Helen's study.

C Howard — LANDSAT imagery was successfully used for habitat analysis in Alaska.

C Bunce — Yes, such imagery can be used in varied habitat.

C Emanuelsson — A good study of land classes in Italy was done from LANDSAT photographs.

C Ball — How good is the resolution of the rabies data?

A Jackson — Generally poor, usually within five kilometres, but occasionally less.

Q Mountford — Your study did not seem to account for spatial auto-correlation between neighbouring squares?

A Jackson — No, it did not and that would be desirable. However, I believe in this case it was accurate within the resolution of the data.

C Ball — Since your results were based on a 1 in 4 sample of the squares then effects due to spatial-auto-correlation would be very much less important.

C Bacon — Assessing spatial auto-correlation would be difficult: neighbouring squares of the same class should be more highly correlated than the neighbouring squares of different classes.

Q Richards — How did you assess habitat heterogeneity?

A Jackson — Squares having a low percentage of many attributes versus a high percentage of a few.

C Howard — Part of that effect might be imposed by the Indicator Species Analysis which you used.

C Zimen — We have found in our study areas that rabies seems more frequent where there are both people and areas of forest.

C Bacon — Different habitats almost certainly have different biases in reporting probability; ideally one needs data on foxes, habitats and rabies for such studies, but this is rarely available.

C Zimen — There has been indigenous rabies in areas around Hessen for over twenty years.

C Bunce — Some comments in the above discussion emphasised the need to stratify habitat before analysing rabies frequency within them.

Rabies Spread and Habitat in France

F. Ball

As part of his doctoral study on mathematical aspects of rabies epidemiology Ball had recently investigated spatial case history data of rabies cases in France. He wished to investigate three aspects of the data; how does the front wave behaviour vary with habitat; are nearest neighbour, or dispersing fox, models closer to the observed behaviour; would knowledge of habitat effects increase one's facilities to predict the likely spread in succeeding months or years.

The rabies case data has been kindly made available by Professor L. Andral. Ball had summarised this into case incidences per unit time within a 30 x 30 grid covering France, the grid squares having sides of 20 km. It was necessary to bear in mind that there were complicating "edge" effects in the data due to (1) the French political border on the East, and (2) the regions where the front wave of rabies was not yet complete. The front wave phenomenon has been investigated preferentially as reporting probabilities are believed to be in higher in such circumstances.

Ball had approached the problem by considering a front wave (figure 7a) advancing through a region, represented on his grid, and fitting a quadratic equation to the contours of the wave;

$$t = a + bx + cy + dx^2 + exy + fy^2$$

From the above formula, for any given point, the direction of advance can be be obtained as

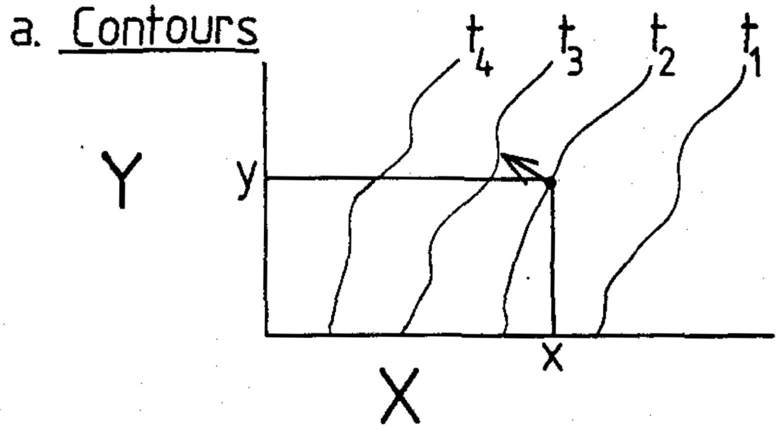
angle; $\theta = \tan -1(c/t)$

and the velocity as $V = 1/ \quad b^2 + c^2$

In fact because of the orthogonality of such a least squares approach a plane fit is equivalent to the quadratic. For each square of his grid therefore, Ball had fitted an optimal plane through the eight surrounding points and the centre point. Plotting the vectors of these planes showed that they seemed to cluster in both time and space.

In collaboration with Bacon he had obtained habitat data for the appropriate area of France, (on the same scale grid); he had used both the original data and a habitat analysis following the ISA method of Bunce to investigate the effect of habitat on his estimated velocities. An initial one way analysis of the variance between the velocity estimates of different land classes has suggested that there was a significant effect of land class; this effect however became just insignificant if spatial auto-correlation between his velocity estimates (due to the method of estimating those velocities) was accounted for. Regression on attributes of the initial habitat data suggested that the significant effects on velocity were accounted for by attributes of: altitude; railway line presence; aspects of geology; presence of fruit trees or vines.

Ball had performed further sophisticated analyses to assess the effects of spacial auto-correlation, which might have been due to the method or seasonal factors. He could find no indication of a seasonal aspect, though on the 20km grid scale he had been obliged to use this might not be expected, since rabies spreads at about 30km a year so annual effects might well be "ironed out". His final analysis attributed significant effects in predicting



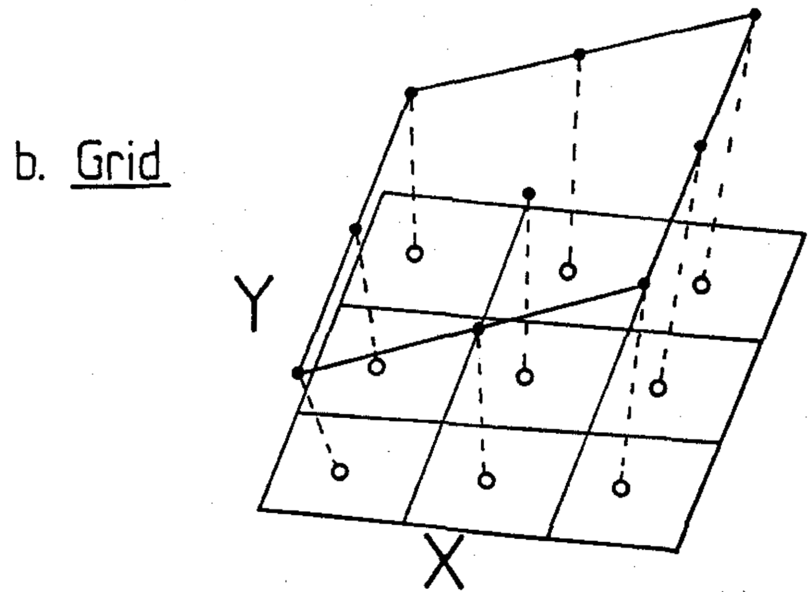


Figure 7 Velocity estimates for a front wave. In (a) a vector arrow is shown at the point (x,y,) giving the direction and rate of spread relative to contours of, eg, % incidence. In (b) this vector is approximated by having (x,y) at the middle of the central grid square: fitting a plane to the % incidence points for this and surrounding squares gives a maximal slope for the fitted plane which can be resolved into its direction and rate component vectors.

the front wave velocity to five habitat variables (though some of these might be inter-correlated) and also showed the significant effects due to spatial auto-correlation imposed by the method, which must be accounted for. The overall pattern of spread suggested by the analysis favoured a "nearest neighbour" model of spread, similar to that suggested by Toma and Andral (1977).

Ball tentatively concluded that:

1. Nearest neighbour models on rabies spread between fox territories are more likely.

2. Habitat type is clearly important in determining rate of spread.

3. Map attributes explain significant amounts of the variance in front wave velocity, and may have predictive value.

4. Analysis could be improved by accounting for: covariance structure of the data; other factors of rabies spread, for example persistence; the removal of "outliners" which might bias the effects of velocity estimates in a few extreme cases; altering the size of the grid to account for small scale habitat variation (five kilometre side).

Ball felt that such approaches held promise for predicting a likely course of future rabies outbreaks in France. He further drew attention to the suggestion that spread was largely between neighbouring fox territories, made from the results of his analysis. He briefly mentioned a model of rabies spread which he had developed for which one needed to know: (1) home range size; (2) fox group size; (3) probability of infection spreading between one group and another. Depending on the values of these three factors, the required "control depths" or number of average territories, that a control programme would need as a buffer zone, varied appreciably. He believed that map attributes might be useful in estimating these factors.

Discussion

C Crowley — I would like to congratulate Frant on an interesting and sophisticated analysis. In relation to possible rabies outbreaks in Britain the Ministry of Agriculture have contingency plans allowing for a wide control zone about any identified outbreak. We are however interested to learn of new developments which allow us to modify these plans depending upon detailed local circumstances.

Q Richards — Were the effects of roads and rivers in altering the velocity manifest in your data? Was the velocity perpendicular to, or parallel to, those roads and rivers?

A Ball — As you suggest one would expect the effects of roads and rivers to act by slowing the velocity or changing its direction; so far I have not had time to investigate this aspect.

Q Bunce — Did you try regression using the principal component axes scores produced by the ISA analysis?

A Ball — I have not yet been able to do this.

C Bunce — I think it is most important that you should try this, since those values are independent of each other, as is required by regression analysis.

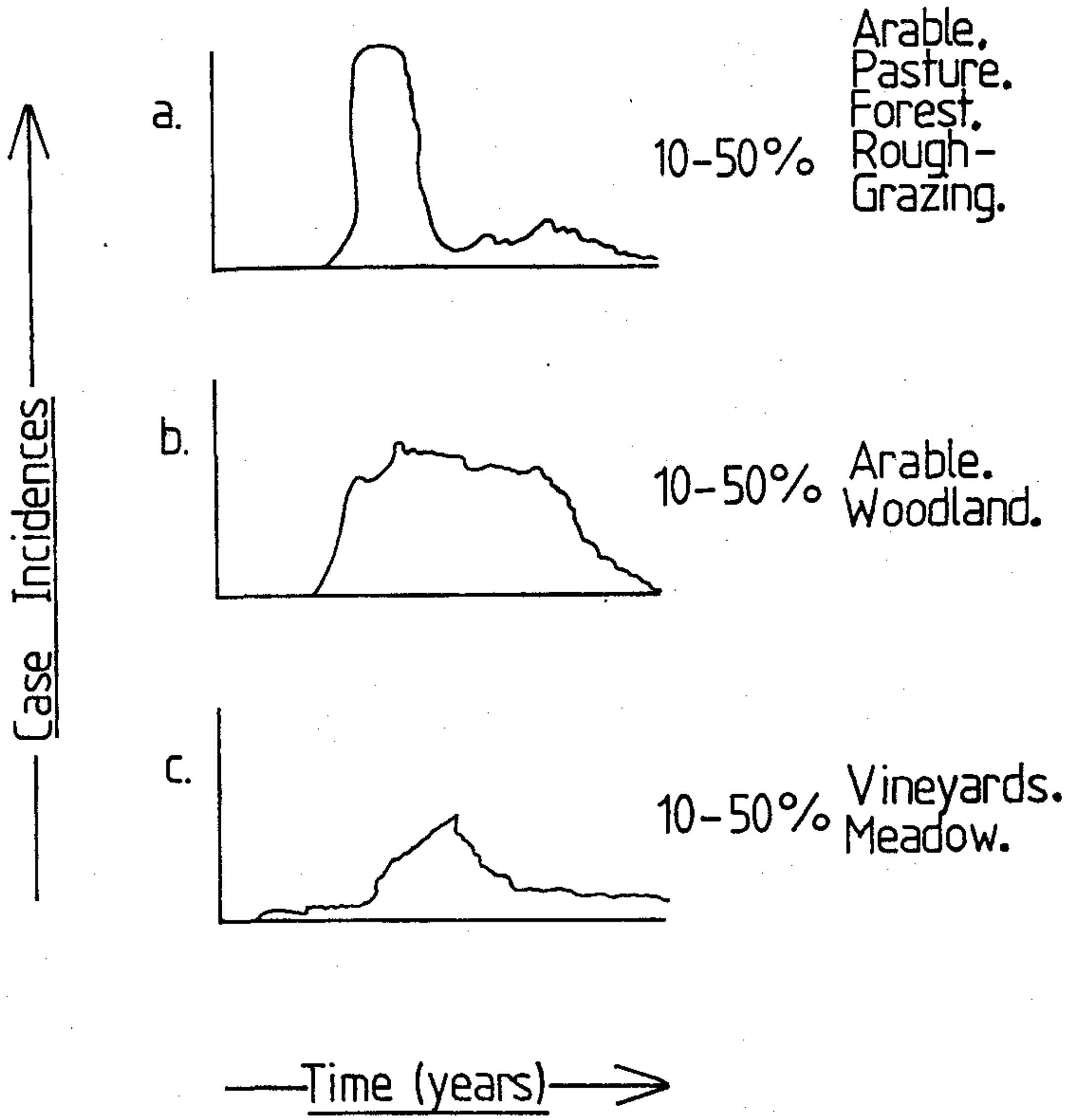


Figure 8 Differing temporal patterns of rabies typical of various Land-Classes. The strikingly different patterns of temporal spread were evident during the period of study (a,b,&c): broadly speaking, the Land-classes showing pattern (a) are diverse, mixed habitats (containing 10-50% of the 4 land-use types shown) while (b) and (c) are more uniform (10-50% of only two land-use types), with (b) probably being more suitable for a dense fox population than (c).

A Ball — That is probably true for detailed interpretation, but I am not sure that it is necessary for simple predictions.

C Howard — The original attributes will be highly inter-correlated; I would prefer to veer on the side of orthogonal data.

C Mountford — The value of Ball's study is presumably in its predictive approach, and the overall amount of variance explained.

C Richards — Ball's approach not using PCA scores does have the advantage of being less biased to "human" concepts.

Q Wandeler — The velocities suggested by your analysis are rather high. Can you suggest why this might be so?

A Ball — It might be an effect of reporting bias, for example if it is reported in one town and known to be moving westwards, the inhabitants of the next town may be looking for it harder and therefore detect it sooner.

Pattern Analysis of Rabies Spread in France in relation to Land Classes

Dr. J. Ross

Ross had investigated the spread of rabies across France using a modification of the method pioneered by Sayers (Sayers et al.1974) and data supplied by Professor Andral. She had initially investigated effects of a number of different mathematical techniques to 'correct' the density of reported cases, to produce optimal contours of the expected distribution of the disease in space and time (time being a three month period). From a succession of such analyses for different quarterly periods of succeeding years she was able to plot the trajectories of (a) peaks of rabies incidence and (b) the contour boundaries enclosing a certain proportion of the reported cases (e.g. 60% of cases). The number of cases on which this analysis was based was around 50 to 300 reports per quarter-year period.

Ross showed slides of the progression of these trajectories of peak cases, and of the movement of the contours, across France. When these slides were superimposed on topographic maps of France it became evident that rivers and a motorway had functioned to deflect, and retard, the spread of disease. Ross also showed the trajectories superimposed upon a geological map of France, from which it was apparent that the preponderance of cases was found in a belt of limestone running South West across France; a similar effect was manifest when the trajectories were shown superimposed on a LANDSAT photograph, although in this case the association between a trajectory and a particular density of shading on the photograph could not be interpreted. Ross suggested that preponderance of cases in a particular zone were due to habitat effects, probably in part resulting from the rich soil of the limestone regions, affecting fox density, population dynamics and hence rabies spread. She had further investigated the possibility of habitat features being important by using the habitat data collected by Bacon and Ball (see above). She showed a photograph of her calculated trajectories superimposed upon the land classes defined by the ISA analysis of Bacon and Ball's data. This photograph did not show a striking overall corresondence between the trajectories and the land classes, although there were some interesting details. Accordingly Ross had investigated the temporal pattern of rabies within each of the 20 x 20 km squares which formed the basis of the habitat information; she showed a further slide showing the spatial distribution of the land classes and within each grid square an inset graph showing the frequency distribution of rabies cases in that square against time. It was apparent that there were two, possibly three, distinct patterns of temporal spread (figures 8a and 8b) and that these patterns were much more consistent within land classes than between them. Grid squares showing the patterns of a high initial peak case followed by a rapid decline (8a consistently contained a mixture of arable land, pasture forest and rough grazing land. Quadrats showing more uniform temporal patterns (8b) showed somewhat less consistency in composition, but were typified by arable land, forest, with some vineyards and meadows.

Ross's analysis showed detail of the propagation of rabies epizootic in France in both space and time. She concluded that qualitative aspects of the rabies epizootic were clearly related to qualitative aspects of the habitat through which the epizootic passed. Her work suggested some ways in which this relationship could be investigated in quantitative terms, and the remaining problem was to identify means whereby such relationships could be rigorously investigated in a quantitative fashion.

Discussion

Q Zimen — What was the distinction between meadows and pasture in your habitat data?

A Bacon — The precise definition can be found in the agricultural atlas from which the data were taken. Broadly speaking 'pasture' represents lowland areas of rich permanent grassland whereas 'meadow' represents areas of poor upland grazing.

C Howard — It would seem important to me for us to establish how foxes respond to these different categories.

C Zimen — I agree with Howard.

C Bunce — I disagree that we need to know how foxes respond to those identified catogories. As Howard says, foxes probably respond tc mixtures of these. The analysis therefore already shows that they are responding to complexes of identified categories.

C Carey — It has been shown that prey species of fox do respond to structural aspects of the vegetation of an area from the physiogeographic features.

C Bunce — The association Carey suggests has recently been challenged by a large study of agricultural factors. A few simple parameters are not sufficient to predict vegetational details.

C Carey — The restriction Bunce mentions would also be expected from experience in the environmental management.

Q Zimen — You only told us about the land types corresponding with two types of the curve shown. Wasn't there a third (type (c)).

A Ross — Yes, a third pattern is evident, though not obviously associated with particular habitat features as far as I have been able to investigate at the moment.

C Wandeler — Did you take any account of the different reporting frequencies due to changes in administration procedure in France over the period of your study?

A Ross — No, I used the complete data.

The Chairman asked Dr. M. Artois for his opinion on the consistency of the French data during the period of Ross's study.

C Artois — The data from 1968 to 1975 are homogeneous for the whole of France; however, since 1975 there will be different patterns of reporting for areas in front of, and behind, the front wave. He noted that there was one area of France which had only been seriously affected in the second wave but not the first and it would be interesting to establish why this was so. He believed that it would be more useful to investigate the relation: habitat-fox-rabies, rather than to go directly for the relation between habitat-rabies; he asked if Alex Wandeler agreed with this suggestion.

C Wandeler — Probably! However in Switzerland in areas where rabies spread was studied extremely intensively, only two cases per Km^2 were reported each year; in other areas not so intensively studied, the case incidence was even lower. There would accordingly be severe statistical variation in the data if Artois's suggestions were adopted.

C Bunce — Vegetational studies have shown that the initial establishment of tropical forest is at random, but that subsequent effects are dominated by ecological factors; could this also be true for rabies?

A Ross — Yes. The pattern of secondary outbreaks are quite distinct from those of the primary wave.

C Wandeler — This could be expected anyway, as cases are always reported in much more details for the primary wave.

C Carey — Primary wave cases were also more intensively reported in the United States. In the United States one detailed study of habitat factors affecting the case frequency has only been able to attribute significant effects to the distance between the reporting site and the laboratory at which the case was analysed!

C Artois — Would it not be possible to use "surveillance quadrats" identified by such a stratification procedure the study the spread of rabies in detail?

C Wandeler — I agree with Artois in principle; however, in practice, such study areas would be too small for accurate data to be obtainable from them.

The Chairman asked the veterinary authorities present at the conference whether the types of analysis shown by Ball and Ross would be of value to them in formulating their control policies.

A Crowley — The analyses presented were most interesting; however in practice, animals and viruses always seem to do the unexpected. If the basic factors identified by the analyses of Ball and Ross were of dominating influence he believed that they would have been identified previously. He thought therefore that, in the British context, it would be more prudent to adopt a "worse case" 'policy which might take little account of the sophisticated variations proposed by such analyses.

A Watson — The information presented by Ball and Ross was most interesting; however, the initial data seemed quite inadequate as a basis for formulating detailed control policies. He thought therefore that detailed policies were better formulated from common sense, rather than detailed past histories.

A Wandeler — The basic data about rabies spread are valid but one needs to know much more about foxes and viruses. Previous information on rabies spread was of value in formulating control policies; these would be quite different if one believed that rabies spread in a similar manner to flu!

C Lindsay — Previous information does show us which control policies have not worked.

C Macdonald — Nobody is claiming to have a definitive answer to the way habitats affect fox densities and virus spread, but we do hope such approaches might help us to find one. One thing which does seem to emerge from these discussions is that the case incidence data seems so weak as to be almost useless for further sophisticated analysis. This seems to me to endorse Artois's suggestion that future attention is focussed on the habitat-fox-rabies link, and not just on the rabies-habitat element of that relationship.

C Zimen — I believe more can be learned from past mistakes.

C Crowley — We hope, in Britain, to benefit from past mistakes. For example, as Bacon and Macdonald say in their article in New Scientist, it is extremely important to act as quickly and decisively as is possible. In Britain, if an isolated outbreak is quickly identified there are good chances of containing and eradicating it.

C Berreen — Containment would be extremely difficult in cities, where rabies is more likely to start (if it ever does) in Britain, via smuggled pets.

Q Bacon — On a wider scale, a containment policy was recently advocated in Poland (Mol 1977) where it was suggested that rabies killed foxes more effectively than a control policy in areas where it had started, and hence control might be better directed at surrounding regions. Does anybody know if this policy is being followed in Poland, and if so whether it has worked?

None of the delegates knew whether the policy was being followed, or working.

C Meredith — The British authorities have indicated they would be glad of suggestions; he would, respectfully, suggest they made sure there was legislation which was completely adequate. For example the South African authorities were able to impound the dogs, but only those for which an order was signed by a state veterinarian. In the current outbreak in South Africa the official was finding it impossible to sign 10,000 orders a week!

A Crowley — The example that Meredith gave is covered by the British legislation, but I would be glad to talk over further details with him.

Q Zimen — Would it be permitted to use gas in Britain?

A Crowley — Yes, if it were absolutely necessary.

A Zimen — Continental experience shows that although it is not universally impossible to control foxes, it is impossible in some areas.

C Berreen — It also appears likely that whether or not it is possible to control foxes depends upon the habitat.

Q Mollison — In the event of a rabies outbreak in Briatin, would it be possible to impose much stricter controls on disposal of garbage which was an important food source for urban foxes in Britain.

A Crowley — Yes, if necessary.

The Chairman stated that rabies was most likely to get into Britain via a dog or a cat. He asked Wandeler how likely he thought it was that it would then spread to foxes.

A Wandeler — It is difficult to say. It might be extremely likely in Bristol, but unlikely in rural areas.

A Carey — Foxes are extremely susceptible to rabies.

C Wandeler — I agree completely with Carey.

C Bacon — As Macdonald said earlier, we are not suggesting that such approaches are, at present likely to be able to provide detailed prescriptions for rabies control policies in all areas. However, the experience on the continent has shown, that the success of control may depend upon the manpower available; for example, even in Denmark where the situation is favourable, control is not easy. We hope, therefore, that such approaches as have been used this afternoon might enable us to exploit "weaknesses" in the epidemiology of rabies in foxes, which might enable one to use available manpower more efficiently, and more effectively.

C Crowley — In addition to Bacon's points, he was personally most thankful that Britain was an island, where the probability of initial infection, and of reinfection, were exceptionally low.

Thursday, 18th September

Habitats and Badger Populations

Dr. H. Kruuk

Kruuk had studied badgers in six areas of Northeast Scotland which were very varied in so far as food supply went. However, two primary factors, human predation from gamekeepers and suitable soil in which to dig earth were extremely important aspects of the badgers' environment which would not be considered in his paper.

Analysis of droppings showed that the badgers' diet consisted of earthworm, fruit, bird remains, rodents and some rabbits. But by detailed analysis results showed that earthworm formed over 50% of the diet by volume. These worms were almost exclusively _Lumbrius terrestris_, which could only be caught on short grass or in some woodlands. Kruuk had assessed earthworm biomass, using a formalin technique, within the badgers' home ranges, and found that the available biomass varied considerably. There were also large differences in the number of animals per territory, varying between two and twelve, while the sizes of these home ranges varied between 20 and 1,500 hectares. Range size had been assessed by both radio tracking and the use of colour markers in bait, which could be identified in the faeces deposited in middens on the borders of the badgers' range. The latter technique has been extended by the use of a radioactive isotope injected into trapped badgers which could also be identified in droppings. Both between and within his study sites there was significant correlation between the square root of the home range size and the distance to the next nearest badger set.

There was however, no correlation between the size of the home range and either the number of badgers using that range, or the biomass of worms available in it. There were, however, significant positive correlations between worm biomass and both density of badgers within a range and the number of badgers using that rang This raised the question of what influenced the size of the home range used by a social group of badgers.

An important clue to this question came from the movements of badgers studied by radio tracking; these data showed that individuals tended to spend a long time in small patches, usually fields of short grass. Kruuk demonstrated that the great majority of badger groups had between three and six patches where they regularly concentrated their foraging. He further demonstrated a very close linear correlation between (a) the mean distance from five (nearest) food patches within a territory to a random point within that territory and (b) the distance between that set and the next nearest.

Kruuk concluded that a useful way to describe badger habitat requirements would be to: (1) map the density of earthworm in the study area; (2) map the distribution of fields of short grass within the area, accounting for the area of dispersion; (3) determine where soil was suitable for the digging of badge sets; (4) assess the likely impact of human induced mortality. From such data he believed it would then be possible to predict the likely frequency of contac between badgers, which would be an important pre-requisite in investigating the epizootiology of diseases, such as rabies and tuberculosis, which might largely be spread by such contacts.

Discussion

C Zimen — You mentioned that badgers are not important in the course of rabies epizootics, but the badger has declined drastically, even after gassing has stopped. Vets now think that badgers are very susceptible to rabies, but rarely found dead from it.

A Kruuk — No, I believe that German fields are not so regularly grazed by cattle, so that the grass is too long for them to find earthworms and badgers are accordingly much rarer on the Continent.

C Zimen — There are many short grass fields in my study area, but very few badgers.

C Wandeler — Badgers are certainly recorded dying from rabies, but only 30% o badgers submitted actually have rabies, whereas 96% of foxes have When badgers are diagnosed with rabies, there are often two or three individuals reported from precisely the same location; cases of badger rabies cluster much more closely than cases of fox rabies.

Q Richards — Should not the amount of short grass in an area relate to the area of total grass?

A Kruuk — No, it is the spatial distribution of suitable patches that is important.

Q Richards — Do you have some areas with many small ranges and few animals as opposed to areas with larger ranges and many animals; if so how might this influence disease transmission?

A Kruuk Contact between animals might be more frequent than for foxes but it is not possible to say definitely.

Q Richards Do you have fertility estimates for the groups?

A Kruuk Usually only one female breeds per group, and they have similar numbers of cubs. Group size depends upon the number leaving the territory, not the number born.

Q Lindsay You show that the distribution of various food patches is important to the badgers; do you know how many patches they require?

A Kruuk No, five was merely a convenient, not magic, number.

Q Macdonald Patch size varies: is there any relation between patch size and the distance between patches; does this affect the number of required patches?

A Kruuk The required number of patches appears to depend more on the grazing rotation of the fields, which provides the short grass.

Q Zimen How do badgers survive in summer, when the grass is long?

A Kruuk There is always more than 18% of the area of "short" grass.

Q Macdonald Do the badgers then always have two, three or more patches available at any one time?

A Kruuk I have not looked at that; I doubt it matters.

Q Zimen Why is short grass so important for their success at catching earthworms?

A Kruuk I don't know; experiments show that if grass is more than 5 cm tall the success drops off immediately.

Q Macdonald How many badgers feed on a patch at one time?

A Kruuk Up to eight.

Q Wandeler What bait have you used as a vehicle for the radio isotope marker, and what was the legality of using radio isotopes in the field in Britain?

A Kruuk The bait had been peanuts. Permission was relatively easy to obtain as the isotope had a very short half life and was only required in extremely low doses.

Urban Dog Population and Disease Risk

Mr. J. Berreen

Rabies was most likely to enter into the United Kingdom via a smuggled "pet"; it was therefore pertinent to investigate under what circumstances such pets might meet other pets, feral dogs and cats and wild foxes. An undergraduate student of Berreen's had done a short project the previous summer to investigate the different densities of dogs and cats in various regions of Birmingham as a preliminary to assessing circumstances in which interactions between dogs, cats and foxes were most likely.

They had hoped initially to use a stratified sampling system depending on available information to indicate areas which might have widely differing densities of pets. They found, however, that the available information was so sparse that this was not possible: for example dogs in Britain are required by law to be licenced, but they eventually discovered that in a city of 2½ milli people (Birmingham) only 36 dog licences had been sold the previous year; the city had one "dog warden" who collects about 900 "stray" dogs a year, but his records depend upon calls from the public who are complaining about "nuisance" dogs, and hence might not be representative. Within the city, habitats varied f green belt, suburb, shopping centre precincts, factories and derelict land; wit these areas there were further significant subdivisions depending upon social, ethnic, and historical factors. Accordingly, the student had done simple transe counts round a border of a sector of the city at dawn, midday and dusk; intensi studies suggested that this sampling regime was reasonable for dogs but not for cats, as the latter tended to use the roads, or be visible from roads, much less frequently. In general, there were very few true stray dogs in Birmingham; ther were many "loose" dogs, but most of these had a locus of operation and were fed regularly by somebody somewhere. This was not true for cats, of which there wer large numbers of truly feral cats in some locations. Loose dogs tended to be on the streets during the middle of the day, and interactions between them were infrequent; cats were observed on the streets more frequently during the night, therefore reducing the overall interaction between dogs and cats. The number of loose dogs on the street at any given time of day appeared to depend much more on the behaviour of their owners (determining when the dogs were let out or shut up) rather than any natural behaviour patterns from the dogs themselves. It appeared that, in Birmingham, the sociology of people was more important in determining the numbers of dogs available as potential "disease transmitters" th the behaviour of the animals themselves.

Discussion

Q Hall — In view of the behaviour changes shown by rabid dogs, which of yo groups of dogs would be most at risk?

A Berreen — For loose dogs; we have rather little data on how these interact with foxes and cats. Foxes and cats certainly interact. In this respect cities vary enormously; Bristol and Birmingham and Oxfor are very different from the point of view of their "loose" carniv populations.

Q Hough — How did the reports of the dog warden compare to your own finding

A Berreen — They were broadly similar.

Q Macdonald — You mention some groups of dogs; did members of these groups have the same "tentative" owners?

B Berreen — The student was unable to establish this.

The Ecology of Red Foxes, Grey Foxes and Rabies in the Eastern United States

Dr. A. Carey

Dr Carey had prepared a written version of his paper which would be availab from him on request.

Enzootic fox rabies is concentrated in the mountainous regions of Kentucky, Tennessee, Virginia and West Virginia; in addition epizootics of fox rabies have commonly occurred in the Gulf Coast states. Racoon's rabies predomonates in Florida, Georgia and Alabama and rabies in striped skunks predominates in the mid-west and west.

The region of fox rabies is coincident with the east coast farming belt, characterised by limestone and shale with low slopes. Rabies appears more prevalent in grey foxes and is enzootic in the western part of this region, but sporadic in the middle and eastern regions. The Blue Ridge Mountain chain acts as a physiogeographic barrier to enzootic rabies. Grey foxes are found at approximately similar densities in woodlands and farmlands, whereas 85% of red foxes occur in agricultural land, mainly pasture. Because of these preferences the ratio of red to grey foxes in an area is proportional to the afforestation of that area.

Seralogical studies show that antibody prevalence varied from 0% to 29%, and antibody was more frequent in grey foxes.

The distribution of foxes seems dependent on discontinuities between habitat types, and the dispersion of different patches. Carey suggested that rabies spread and prevalence was a function of both the population densities of the foxes and of habitat factors, determining their habitat preferences and dispersion. He suggested that useful variables to investigate this relationship quantitatively would be, for example, the mean and variance of "patch sizes" of defined habitats. Seasonal effects on the fox populations were important, as was dispersal and the "turnover" rate of the population; he believed that the turnover was so high that approaches to rabies prophylaxes using most chemo-sterilants or vaccines would need to be used on an annual basis. Such control measures, and killing, would probably need to remove between 70 and 80% of the susceptible population per year, in order to actually affect the density.

Discussion

Q Anderson — How large was the sample in which 29% were found seralogically positive?

A Carey — Quite small, about 100.

C Anderson — Such a high frequency of immunity has major implications regarding control measures.

A Carey — Yes, there is an even higher percentage of immune animals for racoons and skunks. Since rabies control measures often start late in the development of an epizootic I believe they may often make the situation worse, by removing animals which are already immune!

Q Anderson — Is there an elevated proportion of immune animals in the enzotic region?

A Carey — This is not generally thought to be so, but surveys have not been made immediately following epizootics. Reporting and diagnosis policies are too poor to allow testing of this hypothesis. If one or two foxes are found to be rabid then the rest are assumed to be so, and often no subsequent diagnoses will be made.

Q Zimen — I am extremely surprised at the proportion of immune animals you report, as Johnston in Canada, and the European data, do not show this.

A Carey — Studies in the United States show that grey foxes in enzootic areas have a high frequency of immunity to rabies, and strongly suggest the situation is being impaired by control efforts.

C Anderson — On theoretical grounds I find the proportion of immune animals reported from the United States more believable than the data for Europe.

A Carey — I agree; but rabies has been enzootic in the United States for years. 2% to 3% of Mexican free-tailed bats in the United States have antibody and very few of these die from rabies.

Q Wandeler — With regard to the serology; red foxes in Canada and Europe have been extensively surveyed for antibody immediately following epizootics and it is not present. I would like to know what titres of antibodies were reported in your foxes?

A Carey — I do not have the exact figures with me.

C Wandeler — It is extremely important to know what the titres were. In Europe titres between 1 and 20 can be found in foxes, from RABIES FREE areas, but experimental innoculations produce foxes with antibody titres between 1,000 and 2,000.

A Carey — Although I cannot remember the values of the titres I know they were sufficiently high to convince expert virologists that the foxe were immune. The situation in Europe is probably different, with a highly virulent virus in an unadapted population.

C Wandeler — I would suggest that great caution should be used in assessing the importance of low levels of antibody.

C Anderson — But selection will act in favour of immune individuals.

C Wandeler — Not necessarily; it could favour a lower turnover rate.

C Anderson — That argument requires group selection.

A Wandeler — Not at all; it could easily be explained through individual selection.

C Carey — In the United States farmers have hunting dogs that kill foxes; there is always a high turnover.

C Zimen — I disagree that rabies will impose new limitations on reproductive strategy; populations in different habitats give evidence of both r and K selection.

C Carey — I agree that foxes have an adaptable breeding strategy, but their dispersal strategy suggests r selection.

C Zimen — I disagree; dispersal can be typical of K strategies also.

C Nicholson — I would support the caution advocated by Wandeler; recovery of fo from rabies can occur, but I suggest you interpret your results with caution. I am very suspicious of such high proportions of apparent immunity.

A Carey — My own sample is too small for certainty, but several studies by the Centre of Disease Control have confirmed similar levels.

The Chairman asked for further discussion to continue during the coffee brea

A Model of Fox Population Dynamics in Heterogeneous Habitats

Dr H. Thieme

Dr. Thieme presented a preliminary formulation of a mathematical model of fo populations in a hetrogeneous environment. His model envisaged a lifetime scenar for a fox of: birth, dispersal; home range establishment; sedentary reproducti

The model environment consisted of patches of heterogeneous habitat, in which survival, mortality and other parameters varied between habitats. The model was deteministic, and births and dispersals were idealised to take place at single instants of time in Spring and Autumn respectively. Dispersing animals had higher mortality than predatory animals, their probability of becoming sedentary was inversely related to the density of sedentary animals in the area through which they were dispersing. Dr. Thieme showed slides giving the main variables and formulae for his model, and invited comments on its usefulness and realism.

Discussion

C Howard — I believe your model to be too deterministic, as stochastic effects are very important in population dynamics.

A Thieme — Your criticism is valid in some cases, however, deterministic models on average give the same results as stochastic ones; stochastic models are much harder to analyse mathematically.

C Bacon — Deterministic models will give good approximations when the number of individuals is large, however, stochastic effects would surely be very important in the small patches of habitat that your model envisages, and it is not obvious that these would average to zero.

C Anderson — Such a model might still approximate the mean answer of the stochastic formulation.

C Thieme — I am not sure that it would approximate the mean result of a stochastic formulation.

C Mollison — I agree, the numbers of foxes involved would be very small, so the stochastic effect, and hence errors, would be very large.

C Anderson — With respect to rabies, stochastic effects are important, but the three to four yearly cycle is deterministic.

C Mollison — I am not sure that the explanation of cycles is so simple.

C Carey — The model would not be applicable in the United States, where foxes do not defend territories.

C Marshall — Much of the evidence I have heard from North America suggests that foxes do occupy territories there, at least it seems that neighbouring animals utilise home ranges which are not randomly distributed, even if they do overlap slightly.

Grazing of Wild Cattle in Relation to Vegetation Classification of their Habitat

Dr. S. Hall.

Dr. Hall had studied the feeding ecoolgy and habitat utilisation of a herd of wild cattle, which were kept within the confines of Chillingham Park. There is no culling of the herd or direct interference, although they are fed a supplement of hay in winter. The bulls have well defined ranges, but the cows wander freely over the whole of the park. His study was initiated due to the concern of the owners when 22 of the 65 cattle died, due to magnesium deficiency, in a period of poor autumn feeding. The cattle were individually identifiable, by their natural markings, and Dr. Hall had compiled daily records of their movements, to investigate their habitat preferences.

After compiling a plant species list, he had undertaken a detailed botanical survey of the whole of the park, using a quadrat size of a few hundred metres (approximately the resolution with which you could plot the positio of the cattle). Within these quadrats he had recorded the abundance of all plant species, and these data had been analysed using the ISA analysis described by Bunce. Relating this classification to his sightings of cattle grazings, he was able to show that only 120 acres out of the 331 comprising the park were of any value for the grazing cattle. A two way analysis of variance showed both seasonal and habitat factors were important in determining where the cattle would feed. Overall, the cattle avoid land classes 9, 10 and 12; they were indifferent to land classes 6, 7, 8, 13 and 16; and preferred grazing in land classes 1, 2, 3, 4 and 11. Within this broad framework there were distinct seasonal preferences.

Discussion

Q Berreen — Was the grid size that you chose appropriate?

A Hall — The park is very patchy. I could not record the position of the cattle more accurately, however the vegetation does show finer divisions than the grid could resolve.

Q Kruuk — What effect did the cattle have on the vegetation?

A Hall — We do not know, and cannot experiment. Fragments are not identifiable from the droppings.

Methods of Estimating Fox Numbers

D. Gueter

Mr. Gueter presented some provisional findings from attempts to test various methods of estimating fox numbers. Almost all had so far met with only limited success. He was moderately optimistic about an index of relative numbers based on the up-take of food baits.

Q Kruuk — Does not the time taken for bait up-take vary with, for example, season?

A Zimen — I don't think so.

Q Macdonald — Do you not think that certain foxes are likely to become 'professional' bait takers, learning to follow your train and loot the bait?

A Zimen — We have no evidence of that happening.

Q Wandeler — How far apart were the bait stations? I ask because foxes certainly did follow our tracks from one station to the next when we tried this technique.

A Zimen — 1 km. apart.

Q Ross — How comparable were the results from different techniques?

A Zimen — We have not yet made detailed comparisons; these are only provisional and relative figures, but different methods did show similar trends.

Hunters and Foxes

Dr. A. Wandeler

There were many precedents in ecological literature for the use of hunting figures as indices of animal population densities. A well known example of this was the 8 to 10 year cycles of lynx and hare densities provided by the records of the Hudson Bay Company in Canada. There had been many (perhaps too many) detailed analyses of these figures, and a recent investigator had been able to argue convincingly that the hares were eating the lynxes!

It is undoubted that rabies kills a lot of foxes. Hunting figures provide an estimate of where foxes are, but before using these as a basis for deciding control strategies, it was pertinent to ask: Do hunting records allow an estimation of fox density? Do hunting records allow one to identify areas of preferred fox habitat, or of differing epidemiology?

It seems unlikely that hunters would give representative samples in different areas where, for example, foxes use different forms of cover, such as dug burrows, caves, ~~boulder scree~~, etc. Although the true age structures of fox population are not known, the indications are that hunters do obtain biased samples, and that adults are harder to kill than juveniles.

Wandeler presented sociological evidence to show that hunting reports were unlikely to be representative in either, or both, location and season. In Switzerland, five different types of hunting licence are available; for example, licence 1, which is expensive, permits the shooting of chamois and foxes in late September; licence 2 which is cheaper permits the shooting of fox and duck in September and roe deer, hare and fox in October and November; licence 5, the cheapest, permits the shooting of fox from November to February inclusive. The hunting records reflect these restrictions; In September foxes are shot in the high alps, when hunters are out for chamois; later in the year, alternative game species are found in the lowlands, and the majority of fox kills come from such areas.

Hunting methods also vary seasonally, and with area. For example bolting from dens, using terriers, is only done in certain places and at certain times; patterns of hunting were different in the lowlands, and a detailed examination of the frequency of fox kills clearly reflected the strategy of shooting foxes at bait sites on snow during a full moon!

Hunter efficiency also varied considerably with 'farmers' being most efficient, but the proportion of hunters who farm varied regionally between 1% and 50%. It was also impossible to adjust figures to represent "catch per unit effort" since hunting was a form of relaxation, and hunters often spent much of their time in the field sitting round a log fire smoking their pipes!

Discussion

Q Van Aarde — What proportion of observed foxes did the hunters kill?

A Wandeler — This is not known.

C Van Aarde — In feral cats, only 30% of those observed are killed.

Q Bunce — So you have no estimates of the percentage that are killed?

A Wandeler — We can guess; between 20 and 70%. The only accurate records could come from fox drives, when hunters are fined for missing!

Q Bunce — Does fox ecology also vary between the regions?

A Wandeler Probably similarly, but we don't know.

Q Kruuk Do you think there are real relations between fox numbers - foxes shot - rabid foxes?

A Wandeler More are shot where there are more foxes, but the data cannot be treated quantitatively,

Q Zimen You have tried marking fox cubs, were any of those marked returned by hunters?

A Wandeler Yes, but an insufficient number, only 106 out of 360 over five years.

Vole Numbers and Fox Populations

R. Hewson

Hewson reported a study of the fox and vole numbers in areas of both West and East Scotland. On the West coast foxes ate mainly rodents, but on the East coast mainly rabbit and hare. The number of fox droppings found on transect walks closely mirrored the number of foxes killed by hunters in the same area, and seemed to give a good indication of density.

On the West coast Hewson showed that the litter size of foxes was proportional to the percentage of voles in their diet. It seemed likely that foxes were limited by the scarcity of live prey in this area, due to overgrazing by sheep, and that this was responsible for the foxes feeding on sheep carrion.

There was good evidence that the stages of growth of pine plantations could be used to predict vole numbers; the number of foxes killed within an area of plantation was proportional to the size of the plantation and indicated that, in early years, foxes moved in to feed on the supply of voles.

Hewson concluded that foxes responded to vole numbers.

Discussion

Q Macdonald Could you give us further detail on how you used a dog to assess vole numbers?

A Hewson I used a trained Pointer.

Q Zimen Are not voles usually found in tunnels in long grass?

A Hewson There were only clumps of vegetation in the area in which I worked.

Q Hall Plantations are worked on a four year cycle; could this cause cycles in the voles?

A Hewson Perhaps, but this would not explain the close synchrony of cycles in different areas.

Rabbit Numbers and Foxes

H.G. Lloyd

The fox is an indigenous British animal, the rabbit was introduced by the French in the eleventh century. It rapidly colonised coastal islands and dunes, but was slow to spread into agricultural land; the rabbit became much commoner after 1750, probably due to the habitat change following the Enclosures

Acts when fields were surrounded by hedgerows. Fox numbers also increased after 1750, perhaps linked with the above, or perhaps by coincidence. Rabbits reached peak abundancy in the late 1800's and early 1900's, but during this period foxes became less numerous in some areas, possibly due to a nationwide anti-fox campaign from 1885 to 1900.

During the late 1950's the rabbit population crashed due to the disease myxomatosis which killed 99.9% of all rabbits in nearly all areas. During that period foxes may have actually outnumbered rabbits, due to a peak availability of voles after the decline in the rabbit population.

In rabbits each female bears about 20 to 25 young per year, but only around 1.3 of these survive to become juveniles; i.e. recruitment to the adult population is low. Rabbits, as well as voles, form an important part of the fox's diet in many areas; Lloyd presented evidence to show that rabbits' habitat requirements were fairly simple, and suggested that these might be predictable from map data.

Discussion

Q Kruuk — I believe you did some work tracking foxes in the snow. Did you find that fox movement is clustered into areas of high rabbit density?

A Lloyd — No.

Q Lindsay — What is the dynamics of the rabbit population on the island of Skokholm where there is no myxomatosis?

A Lloyd — Overall production is lower, but seasonal patterns are similar.

Aerial Photography as a Data Source for Habitat Analysis

Dr. J. Nichol

Dr. Nichol gave a short illustrated lecture on the use of air photographs in habitat analysis. She illustrated her talks with a series of air photographs of the new town Milton Keynes and Gairloch National Nature Reserve. She described various types of quantitative measurement, such as altitude and tree height, which could be obtained from stereoscopic photographs and showed slides to demonstrate how identifiable patches of habitat, with vegetational composition that could be subsequently determined by a brief field survey, could be readily mapped.

Discussion

Q Zimen — How did you obtain the species diversity data?

A Nichol — The average number of plants within known survey areas related to the photographs.

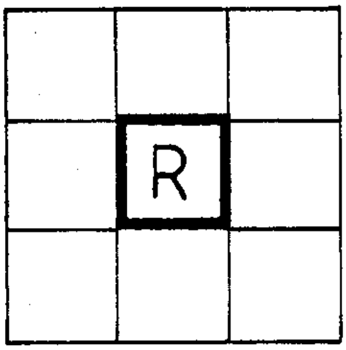
C Hall — The method seemed to be very economical.

Q Macdonald — Is there a National library of air photographs?

A Nichol — Yes, at the Department of Environment in London.

C Carey — Air photographs are a very useful data source; one can estimate tree and vegetation heights, and even tree species if one obtains photographs taken at different times of year.

C Emanuelsson — We have found air photographs very useful in Sweden, but have found it useful, if not necessary, to re-evaluate the photographs



<u>Figure 9</u> A simple stochastic model of rabies spread; the probability of spread from a square with rabies,R, to surrounding squares would depend on (i) fox densities (ii) land-form / habitat (iii) dispersal of cubs.

in the light of detailed surveys on the ground. If such approaches are used, it is often possible to identify more subtle differences in the vegetation than are obvious from an uninformed examination of the same photograph.

Q Bacon — How easy is it to make photogrametric measurements?

A Nichol — Quite simple, but it needs expensive equipment and some experience, and more photographs are needed to obtain adequate stereo coverage.

Q Howard — Could such photogrametric work be sub-contracted?

A Nichol — Yes; our unit has a photogrametric course for undergraduate students, whose measurements are quite accurate after a few weeks of training.

General Discussion of the whole Conference Topic

C Howard — I think that land classification would be a useful method whereby to stratify habitats before undertaking detailed investigations into fox densities and rabies epidemiology, but with the recommendation that such a classification should have minimum variance properties. I would, however, question whether one can predict simply on the basis of the classification. I think that a classification should be used simply to stratify, so that one can then collect standard data from within those strata, which would be used for prediction. With regard to the scale of these quadrats, if the size increases so will the number of different types it incorporates. I would suggest a square of size less than 10 kilometres would be appropriate. I would further recommend that the variables to be measured within these quadrats should be chosen carefully, with a view to excluding irrelevant information and avoiding the complexity of unnecessary cross-correlations. Finally, I would suggest a simple model for rabies propagation; if one considers rabies to be present in the centre square of a lattice (figure 9) then the rate, or probability, of spread into the surrounding squares could be assumed to depend on -

- fox density within the square
- the habitat type of the square, and surrounding squares
- dispersal of cubs from one square to another.

C Macdonald — The conference has revealed two different approaches among foxologists to the problem of habitat classification, and it is not clear to me which of those are generally thought to be better. The "Oxford" school started with many very small units of habitat classified into many types, and although some of these may be irrelevant they can presumably be lumped together later if this should be shown to be true. Other ecologists have suggested, however, that one should look to simpler measures, for example the amount of woodland. The latter approach involves less initial work, but if it were shown to be inadequate, one would have to start again from scratch.

C Zimen — I agree with Macdonald that it is desirable to collect as much data as possible initially.

C Carey — I would suggest a good rule is to choose a quadrat of small elements relative to the daily movement of the animals involved.

C Zimen — A paper by Tester on radio tracked foxes shows that the use of space depends on season, food supply and also on individual foxes.

C Bacon — It appeared that a programme of successive sub-sampling would be appropriate; if it were shown that the information contained in the smaller quadrats of the sub-sampling programme were unnecessary they could be bulked to provide estimates for the larger quadrats within which they were taken, and also as an estimate of the variance of that attribute within the larger quadr`ts.

C Mollison — I think much more data is needed on foxes and particularly the movement of rabid foxes. I think the beginning of radio tracking of rabid foxes shown in Artois's poster is extremely important.

C Carey — A rabid skunk that has been radio tracked in the United States had shown apparently normal movement behaviour. We would caution that the mild innoculation used by Artois might not give symptoms typical of naturally affected animals.

C Artois — He had simulated a natural infection in every respect possible and laboratory experiments showed their course to be closely similar to natural infections.

C Mollison — In addition to moving and contacting other individuals it was necessary to know whether the rabid individual made contacts within its own group.

C Crowley — I agree that it is most important to know the movements of rabid foxes, but there is a practical problem. Does one trap foxes, mark them, and hope that after some time they will become rabid, or else innoculate them and then release them. I would like to know if the meeting feels that the latter procedure is morally justifiable, as it involves releasing an animal in circumstances in which it could potentially infect people,

C Carey — I would question whether such experimentally innoculated animals would, in any case, show symptoms typical of natural infections.

C Meredith — I would support the caution expressed by Carey. However I believe the data on the movement of rabid foxes to be extremely important to the problem, and would suggest that "one should risk a sprat to catch a mackerel".

C Bacon — Crowley asked for opinions as to whether or not it would be morally justifiable to release foxes infected with rabies; rabies is a foul disease and I would be personally loath to inflict it on any animal without an extremely good reason. However, the French study was undertaken, and envisaged in, an area where rabies is already present. In these circumstances we know that:- 60% - 80% of foxes are likely to die from rabies naturally; the number of people infected by naturally infected rabid foxes is extremely low (perhaps even lower for one whose movements were being monitored in detail?); the vital information which might be obtained from such a study could well help to devise control policies which limit the spread of the disease, thereby saving many animals and people from exposure to the disease, a number which would be enormous in comparison to the few animals that might be experimentally infected. Under these circumstances it would seem clear to me that, while such an experiment is morally distasteful, it is easily justifiable.

C Meredith — I would support Bacon's view, with a proviso that the intensity of surveillance of the experimental rabid foxes is extremely high.

Closure of the Meeting

Professor P. Armitage.

Armitage expressed support for Howard's views on the use of classification, supplemented with regression methods for prediction.

The meeting had further confirmed that an interdisciplinary approach was necessary for the investigation of rabies epizootiology. There had been a number of instances where it seemed that sociological aspects were important, if not dominating; the density and movement of pet dogs; hunting practices within Switzerland; the price of fox pelts in Bristol.

The meeting had addressed the question as to whether aspects of habitat could be usefully used to explain aspects of rabies epidemiology. There was general agreement that such approaches might well prove fruitful, but no real concensus as to the precise methods which might best be used. It is hoped that the ideas generated at the conference would be discussed subsequently by the delegates, and that the uncertainties would be ironed out.

Lastly, he wished to thank Bacon and Macdonald for organising the conference programme and making the domestic arrangements.

SOME CONCLUSIONS

After the meeting we tried to summarise the main themes which had emerged and on that basis prepared the following report, which appeared in Nature:

An international workshop on rabies, habitat classification and fox populations was held in Oxford recently. The idea behind the workshop was that since the behaviour of vectors of rabies, most notably the red fox, Vulpes vulpes, is known to be affected by their habitat and since the epizootiology of rabies appears to be affected by landscapes on both a fine and a gross level, a meeting of zoologists, epidemiologists and geographers could spark off new approaches to understanding and combatting a disease which has so far thwarted most attempts at control. The workshop involved a coalition of various elements of the rabies-establishment, including members of the Royal Statistical Society's Working Party on Quantitative Studies in Rabies Epidemiology, and representatives of the World Health Organisation.

The three-day programme began with a series of papers, some strictly quantitative and others more descriptive, on the way in which geographers think about and classify habitats. A consistent and robust methodology for describing landscapes is necessary not only for understanding the way foxes and rabies behave in differing habitats, but also for extrapolating from small study areas to the continental scale at which disease control must work. Discussions of these points continued after each of a series of papers by speakers of 11 nationalities and from three continents.

Dr. R.G.H. Bunce of the Institute of Terrestrial Ecology presented a paper on a method of land classification that he had developed for Britain which was intended, in part, to serve as a system of stratification whereby the findings of detailed ecological studies at specified sites could be generalised to give results applicable to the whole of Britain. He presented data to show that this method had high predictive ability, predicting accurately, for example, the acreages of various crops and estimates of primary productivity, and he closed with a description of an initial attempt to use his stratification to produce a map of potential (i.e., 'carrying-capacity') fox densities for the whole of Britain. P.J.A. Howard, also from the Institute of Terrestrial Ecology, gave a detailed statistical review paper on methods of classification (i.e. categories concerned with natural divisions within the data) and dissection (i.e. categories not necessarily concerned with natural divisions) that were appropriate to habitat description; he concluded that while a suitable stratification into some type of category was most desirable to permit efficient sampling of habitats, the aim of prediction might be better served by regression approaches using the original data on variates shown to be important to the aspects being predicted. Thus he would have advocated, for example, comparing fox densities to measures of the landscape (e.g. percentage of farmland) rather than to ordinal categories into which the landscape had been classified. The aspirations of the workshop were well illustrated by two papers investigating quantitative relations between landscapes and parameters of rabies spread. Using data made available by Professor L. Andrall, F. Ball had investigated relations between the velocity of the front wave of rabies cases in France to a set of data (collected by himself and P.J. Bacon) describing the habitats in which those cases occurred. Ball had posed three questions, a) how does the behaviour of the front wave of rabies epizootic vary with habitat, b) are nearest neighbour, or dispersing fox, models more likely to imitate the observed spread of the disease and c) would a knowledge of habitat effects increase one's ability to predict the likely spread of the disease? Using preliminary methods to account for spatial-auto correlations between his velocity estimates, Ball demonostrated significant explanation of variations in front wave velocity by certain variates of the landscape data. Altitude, railway lines and vineyards were amongst the factors affecting the spread of rabies. Ball was able to conclude that habitat type had been important in determining the rate of rabies spread through France, and that map attributes could be used to explain a significant amount of the variance in front wave velocity, and thus may have predictive value. Dr. J. Ross presented the results of her extension of Professor Sayer's approach to the analysis of rabies cases when applied to the French data supplied by Professor Andral. She demonstrated an elegant piece of work showing the effects of rivers and motorways in diverting the path of the epizootic and the association of a preponderance of cases with a ridge of limestone running SW across France. Using the case-incidence data, Ross used statistical techniques to draw trajectories of the disease front as it spread across France month by month. When these trajectories were superimposed upon a geological map it was evident that the disease had followed a belt of limestone running south west across France. It seemed plausible that the rich soil of this limestone country was mirrored, through high primary productivity, in high fox populations.

Considerable debate revolved around the extent to which such sophisticated analyses could be usefully extended considering the foibles of data on the incidence of rabid foxes. It became clear that the theory and practice of rabies surveillance were quite different, with the reporting of cases being much more efficient along the epizootic front than in enzootic districts where familiarity soon breeds contempts and negligence. Rather dismaying disclosures about the consistency of the data on which statisticians must work were endorsed by a devastating analysis by Dr. A. Wandeller from Switzerland who considered the biases in hunting figures which are frequently employed as indirect indicators of fox numbers. It was widely agreed that every effort should be made to standardise the recording of rabies incidence, even if only in sample districts.

Students of fox ecology were not the only biologists present, since the principles underlying analyses of habitat utilisation are widely applicable. Papers included studies of factors affecting the distribution of birds in Sweden to an analysis of the movements of feral cattle in Gillingham Park. Dr. H. Kruuk presented a convincing analysis of how the dispersion of habitat patches (and hence available food in the form of earthworms) determined the size of badger (Meles meles) territories and hence their local population density. Earthworms are only available to badgers for capture on those nights when the microclimate is sufficiently warm and humid to tempt the worms from their burrows and onto the surface. From night to night, say with shifting wind direction, different fields may become temporarily bountiful foraging sites. Kruuk argued that badger territories must comprise sufficient potential foraging sites that at least one will yield worms irrespective of changes in the wind. Territory size, and ultimately population density, was thus a function of the dispersion of potential earthworm patches and to some extent this could be predicted from maps. When the meeting learnt from Dr. Wandeller that badgers had been more involved than previously thought in rabies spread in Switzerland it was realised that these findings were of practical as well as theoretical importance. Kruuk's findings in Scotland could be compared with those of I. Lindsay and D. Macdonald near Oxford and S. Harris's in Bristol where urban-dwelling badgers live at extraordinarily high densities.

Indeed, the participants collectively blanched at the prospect of rabies control in urban areas.

Two schools of thought began to emerge from the discussions of the most useful way to proceed: one argument ran that fox population dynamics were so complicated that effort might be more profitably directed to seeking broad relationships between general features of the landscape and rabies spread. Another view was that the data on rabies spread were so coarse and inconsistent that direct and detailed study of foxes was more likely to yield better understanding of the factors affecting the pattern of rabies spread. In either case, concensus was reached that the most crippling obstacle was our ignorance of the behaviour of rabid foxes and the extent to which it differs from that of healthy animals.

P. J. Bacon and D. W. Macdonald
(Conference Organizers)

Institute of Terrestrial Ecology,
Merlewood Research Station,
Grange-over-Sands,
Cumbria LA11 6JU

Department of Zoology, ABRG,
South Parks Road,
Oxford OX1 3PS

Rabies in Colombia

Dr. Alfonso Gomez Orozco attended the meeting and had prepared a paper, but since only a few participants understood Spanish, the paper was not delivered. Consequently, we have prepared a translation which is given in full here.

Republic of Colombia

Ministry of Public Health

Canine and Bovine Rabies in Colombia

1980

Resumé of a paper presented to the Conference on Habitat Classification, Fox Population and Rabies Spread, organised by P.J. Bacon and D.W. Macdonald, in Oxford, 15th to 19th September 1980.

Alfonso Gomez Orozco
Medical Veterinarian for Public Health

Canine Rabies in Colombia

COLOMBIA:	Land area	1,138,914 km^2
	Human population in 1980	26,892,950
	Capital - Bogotá	5,304,300 inhabitants
	Canine Population	2,689,295
	Feline population	537,859

Background

Rabies has been the main zoonosis known to affect health in Colombia since 1970, when 32 human cases were diagnosed, which represents approximately 0.15×10^5 of the population. This figure may be an underestimate due to the lack of laboratory resources, the deficiency of communications in some regions and inadequate reporting of case-incidence.

In the light of these circumstances, the government via the Ministry of Public Health increased the department's budget to fight rabies and design and execute programmes to put into operation a large and efficient campaign.

The History of Dog Vaccination: from 1970 the percentage of vaccination increased from 7.0 to 45.9 in 1974. This resulted in a decrease in the number of cases of rabies, thus:

> Since 1970 when rabies occurred at 139.3 per 100,000 this figure has been reduced to 49.67 per 100,000 (see graph 1). But since 1974 the handling of the programme has deteriorated. The size of the control operation was underestimated, the department's budget for the countryside was decreased and consequently the vaccination programme began to decline between 1973 and 1977. This was the reason why since 1976, when the frequency of rabies cases was 28.2/100,000, it has risen to over 61.8/100,000 in 1978 (see graph 1).

Human Vaccination: Graph 2 shows that, from a comparison of human and canine vaccination, the necessity to vaccinate people was reduced between 1970-1976. After 1974, due to the financial cutbacks for anti-rabic programmes, and the decreased effort put into canine vaccination, the numbers vaccinated then fell from 45.86 to 17.2 per 100,000 in 1977. At the same time human vaccination fell to a total of 2.55 per 100,000. However, in 1978 when new and serious outbreaks of rabies appeared, as often in dogs as in cattle, it was necessary to increase the vaccination (from 17.2 to 35.3 per 100,000) and hence human vaccination also increased (see graph 2). Graph 3 is a comparison of the cases of canine rabies with the cases of human rabies, and shows that as the one diminishes so does the other (1970-1977) but when the number of cases of canine rabies increased again so did the incidence of cases of human rabies

Our findings indicate that in countries like Colombia a constant programme has to be maintained to ensure continuing levels of immunity, and to increase year by year the efforts to erradicate rabies. This is very important in urban situations. Concerning wildlife rabies in Columbia, little or nothing has been done.

Thus with the gravity of the problem, the Minister of Public Health has recently established some specific objectives for the control of rabies and they are:

1. To maintain a level of immunity of 80% by means of vaccination of 25% of the urban dog population (new-born; i.e. of puppies).

2. To reach a level of 80% vaccination in the canine population, in the Sectional Health services that are still critical.

3. To maintain a minimum level of immunity with the vaccination, of 50% of the accessible rural canine population and 25% of those newly introduced.

4. To submit to clinical observation 80% of dogs and other domestic animals that come into contact with humans during suspected rabies cases.

5. To obtain diagnosed confirmation, from the laboratory of 100% of animals that die during clinical observation.

6. To lean towards closer liaison between those concerned with the clinical observation and diagnosis of rabies in suspect animals and those faced with the task of prescribing rational treatments for humans that have been exposed to infection.

7. To submit for clinical observation wild animals which have been captured and which are suspected of having rabies.

8. To maintain vigilant epidemiological activities by means of opportune notification of cases and control of foci of the disease.

National Programme of Rabies Control

Budget Appropriation
Colombia 1970-79

year	Investment in Colombian $
1970	-
1971	6,400,000
1972	6,400,000
1973	8,900,000
1974	8,150,000
1975	5,500,000
1976	8,000,000
1977	3,700,000
1978	3,000,000
1979	10,500,000
1980	11,000,000

National Programme of Rabies Control

Accomplished Human Anti-Rabies Treatments

Colombia 1970-79

(amount 1,100,000)

Year	number	Amount 10^5
1970	24,293	117.0
1971	24,574	114.9
1972	20,544	93.4
1973	15,739	69.6
1974	11,413	49.04
1975	7,436	33.76
1976	7,762	28.51
1977	6,503	25.9
1978	10,543	40.38
1979	10,534	339.17

Cases of Canine Rabies and Canine Vaccinations

Colombia 1970-79

(amount 1,100,000)

Year	Cases of canine rabies	Canine Vaccination
1970	139.3	7.0
1971	126.3	18.4
1972	96.9	25.8
1973	75.0	36.6
1974	49.67	45.9
1975	32.09	34.0
1976	28.2	28.5
1977	32.5	17.2
1978	61.8	29.08
1979	48.89	35.32

Anti-rabies Vaccination: Canine and Human

Colombia 1970-1979

(amount 110,000)

Year	Human Vaccination	Canine Vaccination
1970	11.50	7.0
1971	11.34	18.4
1972	8.30	25.8
1973	5.46	36.6
1974	5.18	45.9
1975	3.10	34.0
1976	3.10	28.5
1977	2.55	17.2
1978	1.04	29.08
1979	3.92	35.32

Cases of Canine and Human Rabies with positive laboratory diagnosis

Colombia 1970-1979

(amount 1,100,000)

Year		
1970	139.3	0.15
1971	126.3	0.15
1972	96.9	0.10
1973	75.0	0.060
1974	49.67	0.030
1975	17.76	0.0125
1976	17.74	0.0048
1977	33.0	0.0119
1978	61.8	0.028
1979	48.89	0.029

Rabies transmitted by Mountain Fox bites:

Six genera of canid are found in South America, of which four species occur in Colombia and they are:

1. Dusicyon culpaeus
2. Atelocynus microtis
3. Cerdocyon thous
4. Speothos venaticus

Cerdocyon thous: This fox lives in the woods and open praires of South America, from the meridional parts of Brazil to the south-west of Bolivia and Paraguay; in the northern parts of Argentina and Uraguay. It is the most common fox in Colombia.

The length of its body from head to tail is 60-70 cm, and its neck measures about 30 cm. Individuals vary in colour between light brown to chestnut, often with yellowish limbs. Its ears are dark. This species differs from other South American canids in the characteristics of its cranium, teeth and paws.

This fox (Cerdocyon thous) may develop rabies in Colombia. It is the most abundant fox in our landscape, and makes contact with hunting dogs, and at times attacks the bovine livestock of open farms in zones silvatic rabies. The abundance of foxes has prompted the recent establishment of work camps and laboratories to demonstrate the communicability of the virus to dogs and cattle. In 1979 four cases of the virus were isolated in foxes at the Diagnostic Centre I.C.A., Monteria, Colombia.

In the department of Antioquia, in the Bagne region, in July 1977 there was a case of canine rabies in a dog that had been bitten by a fox. It was said that the dog bit many others. On this occasion, 18 people had been bitten, 54 human anti-rabies treatments were given, and all the specimens of canine cerebra sent to the laboratory showed positive rabid results, by the methods of Seller

In 1979, in the same department of Antioquia, but in a region where rabies is endemic and largely uncontrollable, 18 of the cerebra examined were positive (11 dogs and 7 cows).

Bovine Rabies:

The losses to Latin-American cattle stock, especially by bovine rabies, are incalculable. It is transmitted by the bites of haematophagus bats and of mountain foxes. Rabies in bats is only of interest in the Americas, and rabies in haematophagus (vampire) bats is a problem limited to Latin America. The infection has been proven in the three species: Desmodus robundus, Diphylla ecaudata, and Diaemus youngi; but only the first has epidemiological importance.

Desmodus is responsible for appreciable losses in Latin American livestock, especially for bovine rabies. It has been estimated that the approximate annual mortality is 500,000 head of cattle, which signifies the loss of some 50 million Colombian dollars a year.

Since 1929, when it was observed for the first time that human rabies could be transmitted by bats, more than 170 cases have been recorded in Latin America. In South America, only Chile and Uruguay have not recorded cases of rabies transmitted by vampires.

Bovine rabies is an epidemic illness in Colombia, limited to certain geographical areas, principally within the regions (departments) of Guajira, Ce Antioquia, Sucre and Cordoba. Epidemological studies in epidemic areas, have shown that the incidence of bovine rabies in these regions is directly proportioned to the appearance of skin bites caused by haematophagus bats.

There are secondary problems arising from the bites of vampires, such as anemia by the loss of blood (each vampire can such up to 20 cc of blood and this also causes additional haemorrhaging because the wounds continue bleeding after the bat has fed itself), and the secondary infection of the wounds. We have taken special care to vaccinate those people who are exposed to risk, in the majority of regions where these outbreaks have occurred and when possible we follow up the case histories of people who are vaccinated.

For this reason, with the aim of avoiding the loss of human life and Colombian livestock, the Minister of Public Health, through its Sectional Health Services, the division of animal health of the Colombian Agricultural Institute I.C.A. with the technical aid of the vertebrate control programme of the world life agency of Denver Colorado, and the Agricultural secretaries of some departments, has planned a campaign for the control of bovine rabies in the affected areas. For the development of the campaign against bovine rabies the following parameters have been taken into account.

1. Objects and justification.

2. Plan of attack:
   - identification of the problem district in the epidemic areas.
   - diagnosis and laboratory findings.
   - training of personnel.
   - health education.
   - epidemiological vigilance.
   - investigation.
   - control of quality, distribution and management of vaccination.
   - vaccination and control of vampires.

3. Information about the development of the campaign:
   - availability of teams and biologists.
   - devolution elements.
   - elements of consumption.
   - biologists.

According to epidemiological studies the following areas of endemic rabies have been outlined.

Area 1: South of the Guajira, Cesar and Magdalena: consists of the Municipals of San Juan de Cesar, Villanueva and Fonseca, Uramita, Valledupar, Codazzi, Los Corazones, Riohacha and Sanat Marta.

Area 2: Uraba, Antioqueno and Choco: consists of the municipalities of Apartado, Chigorodo, Mutata, Dabeiba, Neocodli, Turbo and Arboletes and A Candy.

Area 3: Sucre: consists of the municipalities of Corozal, los Palmitos, Sincelejo, Tolu and Betulia.

Area 4: Cundinamarca, Boyaca and Casanare: in the municipalities of Caqueza, San Luis de Gaceno, Tamara, Gacheta and the corregedor of La Aguada.

Area 5: Narino: Region southwest of the Department (Municipality of Tambo and el penol).

In the Department of Choco, municipality of Acandy, there was a large outbreak of bovine rabies in May 1979, attributed to bites of haematophagus bats (Desmodus rotundus). This resulted from a huge migration of bats from the Pacific Ocean in September 1974, invading the northern zone of Choco and part of the Caribbean coast. On this occasion 76 cattle and 3 horses died, but it was also necessary to vaccinate 20,000 head of cattle and 10 people, who had had direct contact with the infected animals. Blood was taken from these people later to examine for antibody titre.

Other cases have been detected in the following departments:

Date	Department	Municipality
September 1979	Cesar	Valledupar
	Guajira	Riohacha
	Magdalena	Santa Marta
	Santander	Bucaramanga
	Sucre	Sincelejo
October 1979	Meta	Villavicencio
January 1980	Choco	Acandy
February 1980	Sucre	Betulia
March 1980	Choco	Acandy
	Cesar	Valledupar
	Guajira	Riohacha
April 1980	Cesar	Codazzi
	Cesar	Villanueva
May 1980	Antioquia	Arboletes
	Guajira	Villanueva
	Cesar	Valledupar
	Cordoba	Monteria
June 1980	Antioquia	Arboletes

Activities carried out for Bovine Rabies in the year 1979

Number of areas with foci of bovine rabies	83
Number of cows vaccinated	73,370
Number of animals treated	6,500
Number of bovine samples received in the laboratory	63
Number of positive samples	40
Number of sick cows	235
Number of dead bovines	235

Bibliography

This list of references contains only those papers cited in the text and discussion of this document, plus Lloyd 1980, Macdonald 1980 and Zimen 1980, which together contain reference lists giving a comprehensive background to the topic. For further details to topics mentioned in this report, refer to the microfilmed document of the authors' own summaries.

ADAMOVICH, V.L. 1978

Landscape-ecological foundations of the local foci of rabic infection. Zool. Zh. 57(2): 260-71, in Russian.
British Lending Library translation RTS 11781.

BACON, P.J. & ARMITAGE, P 1979

The epizootiology of rabies.
Merlewood R & D paper No. 76. Merlewood Research Station, Grange over Sands, LA11 6JU, England.

BACON, P.J. & Macdonald, D.W. 1980

To control rabies: vaccinate foxes.
New Sci. 87(1216): 640-645.

CAPEN, D.E. (Editor) 1980

The use of multivariate statistics in studies of wildlife habitats.
Univ. Vermont publications, USA.

HILL, M.O. 1973

Reciprocal averaging: an eigenvector method of ordination.
J. Ecol. 61: 273-249.

HILL, M.O., BUNCE, R.G.H. & SHAW, N.W. 1975

Indicator Species Analysis: a divisive polythetic method of classification. J. Ecol. 63: 597-613.

HIRST, S.M. 1975

Ungulate-habitat relationships in a South African Woodland/Savanna ecosystem. Wildl. Monographs No. 44: 66 pp.

HOWARD, P.J.A. in press

Statistical considerations in Land and Habitat classification.
Merlewood R & D paper, Merlewood Research Station, Grange over Sands, LA11 6JU, England

JACKSON, H. 1979

A contribution to the study of fox rabies in relation to habitat in Europe. M.Sc. thesis report, Imperial College, London.

KACELNIK, A. 1979

Studies of foraging behaviour and time budgeting in the Great Tit (Parus major). D.Phil. thesis, University of Oxford.

KENDALL, M.G. & STEWART, A. 1968

The advanced theory of statistics; Vol.3.
London; Griffin, 557 pp.

LLOYD, H.G. 1980

The Red Fox. Blandfords Press.

MACDONALD, D.W. 1980

Rabies and Wildlife; a biologists's perspective.
Oxford, OUP. ISBN 0 19 857576 9

MACDONALD, D.W., BUNCE, R.G.H. & BACON, P.J. in press

Fox populations, habitat characterisation and rabies control
J. Biogeography.

MOL, H. 1977

Rabies in animals as related to changes in the natural environment.
Przeglad Epidemiologiczny 31(2); 195-205, in Polish.
British Lending Library translation RTS 11961.

SAYERS, B.McN., MANSOURIAN, B.G., PHAN TAN, T. & BOGAL, K. 1977

A pattern analysis study of a wildlife rabies epizootic.
Med. Inform. 1: 11-34

STORM, G.L. 1965

Movements and activities of foxes as determined by radio-tracking.
J. Wildl. Mgmnt. 29: 1-13.

TOMA, B. & ANDRAL, L. 1977

Epidemiology of fox rabies.
Adv. in virus Res. 21: 1-36.

ZIMEN, E. (Editor) 1980

The Red fox: symposium on behaviour and ecology.
The Hague; W. Junk. ISBN 90 6103 X

Participants

Dr. R. ANDERSON
Centre for Environmental Technology
Imperial College
London SW7 2AZ

Professor P. ARMITAGE
Department of Biomathematics
Pusey Street
Oxford OX1 3PS

M. ARTOIS
Centre d'etudes sur la rage
Domaine de Pixerecourt
B.P. No. 9
54220 Malzeville
France

Dr. P.J. BACON
I.T.E.
Merlewood Research Station
Grange over Sands
Cumbria LA11 6JU

Mr. F.G. BALL
School of Mathematics
University of Sussex
Falmer, Brighton BN1 9RH
Sussex

Professor Dr. J. BERGER
Institut fur Mathematik und
Datenverarbeitung in der Medizin
Abt. Mathematik in der Medizin
Universitats-Krankenhaus Eppendorf
Martinistrasse 52
2000, Germany

Mr. J.M. BERREEN
Department of Zoology
University of Birmingham
P.O. Box 363
Birmingham B15 2TT

Dr. R.G.H. BUNCE
I.T.E.
Merlewood Research Station
Grange over Sands
Cumbria LA11 6JU

Dr. A. Carey
U.S. Department of Agriculture;
N.E. Forest Experimental Station
180 Canfield Street
Morgantown, W. Va. 26505
USA

Dr. Alice COLEMAN
Department of Geography
King's College
Strand, London WC2R 2LS

J.W.H. CONROY
I.T.E. Monks Wood Research Station
Abbots Ripton
Huntingdon, PE17 2LS

Mr. A.J. CROLEY
Ministry of Agriculture, Fisheries
and Food
Hook Rise South
Tolworth, Surbiton, Surrey KT6 7NF

Dr. U. EMANUELSSON
Vaxtekologiskarnst
O Vallgaten 14
22361 Lund
Sweden

D. GUETHER
Biogeographie
Universitat des Saarlandes
Saarlandes
66 Saarbrucken im Stadtwold
Federal Republic of Germany

Dr. S. HALL
c/o The Post Office
Chillingham
Nr. Alnwick
Northumberland

Mr. S. HARRIS
Department of Zoology
University of Bristol
Woodland Road
Bristol BS8 1UG

Mr. T.D. HEALING
Department of Microbiology
University of Reading
London Road
Reading RG1 5AQ

Dr. R. HEWSON
I.T.E.
Hill of Brathens
Glassel
Banchory AB3 4BY

P.J.A. HOWARD
I.T.E.
Merlewood Research Station
Grange over Sands
Cumbria LA11 6JU

Miss Helen JACKSON
W.H.O. Collaborating Centre for
Rabies Surveillance and Research
Federal Institute for Animal
Virus Diseases
D 74 Tubingen
Postfach 1149
Federal Republic of Germany

Professor C. KAPLAN
Department of Microbiology
University of Reading
London Road
Reading, RG1 5AQ

Dr. H. KRUUK
I.T.E.
Banchory Research Station
Hill of Brathens
Glassel, Banchory
Kincardineshire AB3 4BY

Mr. H.G. LLOYD
A.D.A.S.
Ministry of Agriculture, Fisheries
and Food
Haethorden Temple Street
Llandindrod Wells

Dr. D.W. MACDONALD
A.B.R.G.
Department of Zoology
South Parks Road
Oxford OX1 3PS

Miss F. MCALISTER
Centre for Environmental Technology
Imperial College
48 Prince's Gardens
London SW7

Mr. C.D. MEREDITH
Department of Health
National Institute for Virology
Private Bag X4
Sandringham 2131
Republic of South Africa

Mr. D. MOLLISON
Department of Acturial Mathematics
and Statistics
Heriot-Watt University
Riccarton
Currie, Edinburgh EH14 4AS

Mr. M.D. MOUNTFORD
I.T.E.
68 Hills Road
Cambridge CB2 1LA

Dr. J. NICHOL
Department of Civil Engineering
University of Aston
Gosta Green
Birmingham B4 7ET

Dr. K. NICHOLSON
Division of Communicable Diseases
Clinical Research Centre
Watford Road
Harrow, Middx HA1 3UJ

Senõr A.L. OROZCO
Medico Veterinario de Salud Publica
Apartado Aereo 50-646
Medellin
Colombia

Mr. M. RAND
E.G.I.
Department of Zoology
South Parks Road
Oxford OX1 3PS

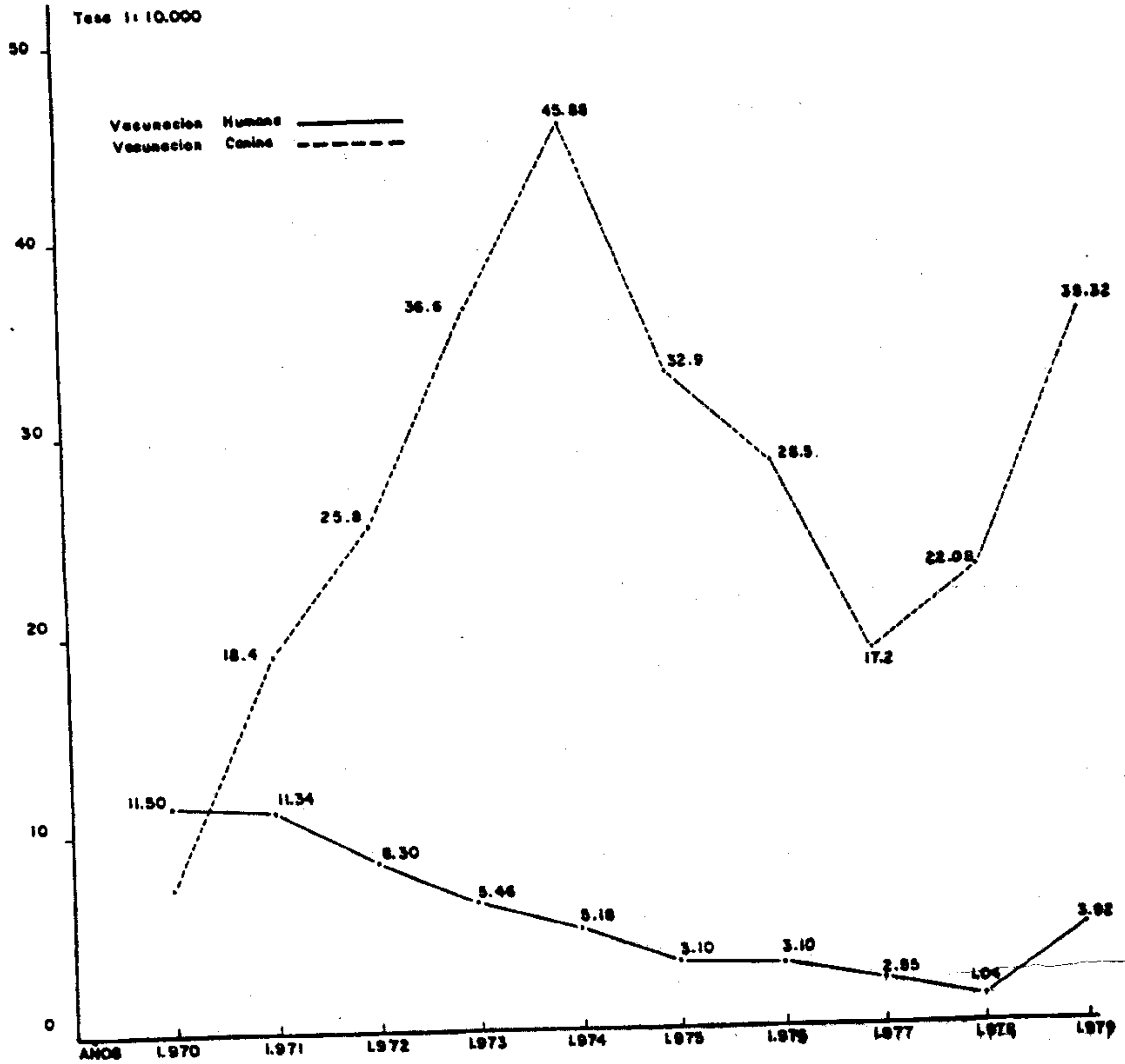

OCEANO ATLANTICO
ZONAS ENDEMICAS DE RABIA BOVINA
PANAMA
VENEZUELA
OCEANO PACIFICO
ECUADOR
BRASIL
PERU
CORDOBA
SUCRE
BOLIVAR
NORTE DE SANTANDER
ANTIOQUIA
SANTANDER
ARAUCA
CHOCO
CALDAS
RISARALDA
QUINDIO
TOLIMA
CUNDINAMARCA
VICHADA
VALLE
HUILA
CAUCA
NARIÑO
PUTUMAYO
CAQUETA
VAUPES
GUAINIA
AMAZONAS
Convenciones:
Area No. 1
Area No. 2
Area No. 3
Area No. 4
Area No. 5

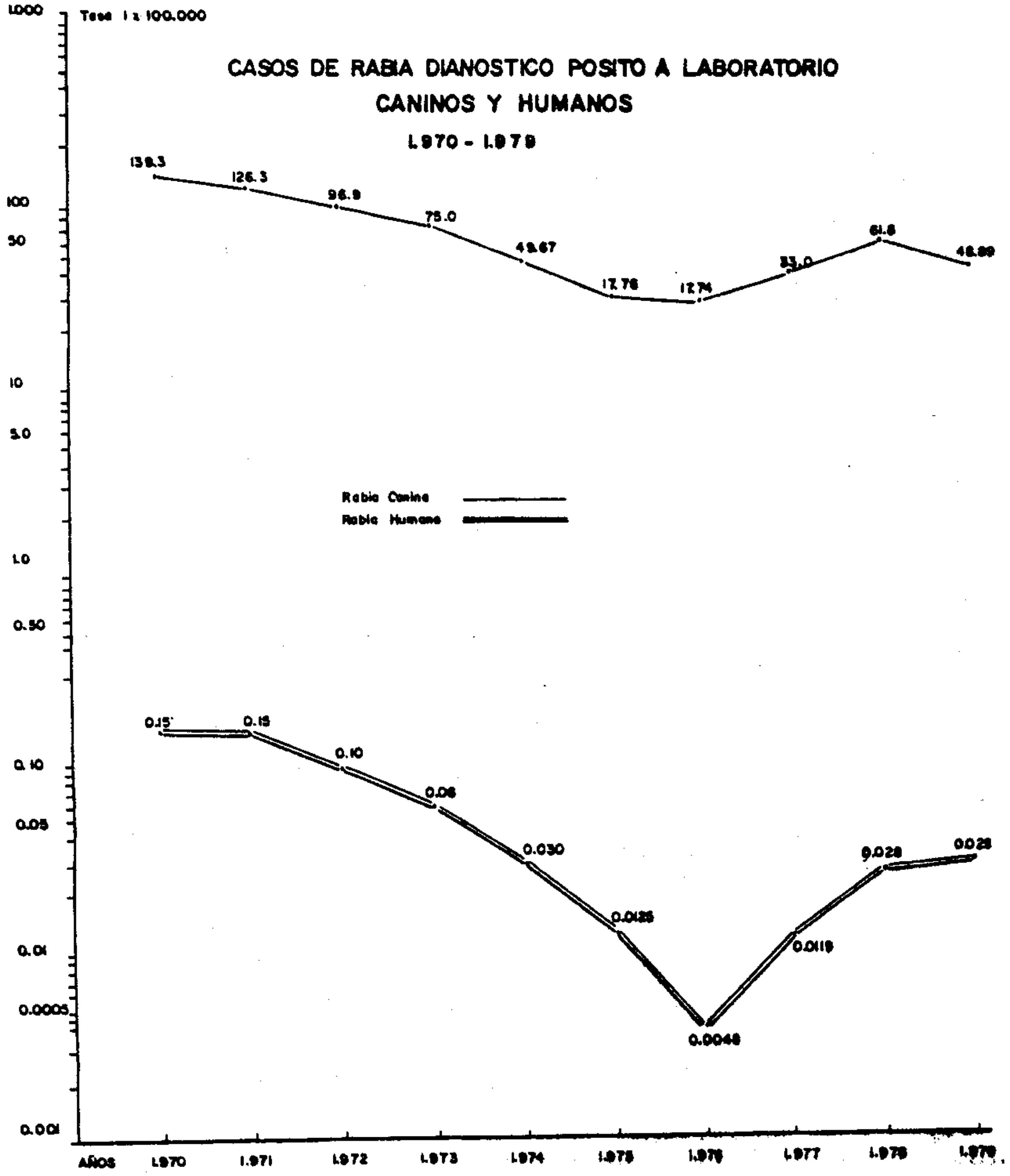
Figura No. 1

PROGRAMA NACIONAL DE CONTROL DE RABIA
VACUNACION ANTIRRABICA CANINA

INMUNOPROFILAXIS HUMANA

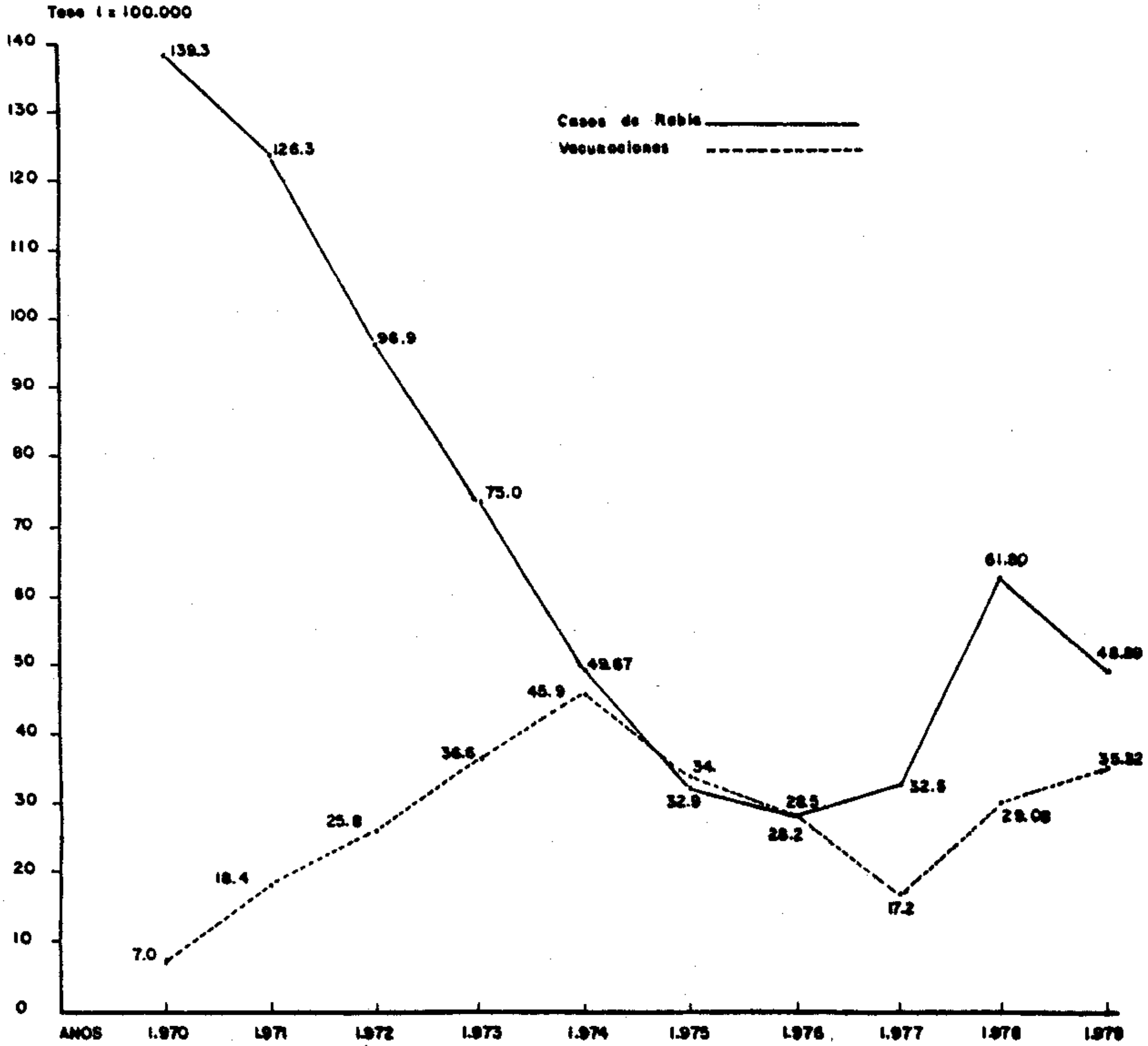
Colombia 1.970 - 1.979





CASOS DE RABIA DIANOSTICO POSITO A LABORATORIO
CANINOS Y HUMANOS
1.970 - 1.979
Tasa 1 x 100.000
1.000
100
50
10
5.0
1.0
0.50
0.10
0.05
0.01
0.0005
0.001
139.3
126.3
96.9
75.0
49.67
17.76
12.74
33.0
61.8
48.89
Rabia Canina
Rabia Humana
0.15
0.15
0.10
0.06
0.030
0.0125
0.0048
0.0119
0.028
0.028
AÑOS
1.970
1.971
1.972
1.973
1.974
1.975
1.976
1.977
1.978
1.979

PROGRAMA NACIONAL DE CONTROL DE RABIA
CASOS DE RABIA CANINA Y VACUNACIONES CANINAS - COLOMBIA
1.970 - 1.979



Mr. M.S. RICHARDS
Epidemiology Unit
Central Veterinary Laboratory
Ministry of Agriculture, Fisheries and Food
Weybridge
Surrey

Dr. G.M. ROBINSON
Department of Geography
University of Edinburgh
High School Yards
Edinburgh EH1 1NR

Dr. Jane ROSS
Department of Electrical Engineering
Imperial College
London SW7 2BT

Mr. A.D.M. SMITH
Department of Zoology
Imperial College
Prince Consort Road
London SW7 2BB

Dr. Horst THIEME
S.F.B. 123
Im Neuenheimer Feld 193
6900 Heidelberg
West Germany

Mr. R. van AARDE
Mammal Research Institute
Department of Zoology
University of Pretoria
Pretoria
South Africa

Dr. A. WANDELER
Vet.-Bakterillogisches Institut
Universitat Bern
Langgass Strasse 112
Postfach 2735
3001 Bern
Switzerland

Dr. W.A. WATSON
Ministry of Agriculture, Fisheries and Food
Hook Rise South
Tolworth
Surbiton, Surrey KT6 7NF

Miss V.E. WOOD
E.G.I.
Department of Zoology
South Parks Road
Oxford OX1 3PS

Dr. E. ZIMEN
Biogeographie
Universitat des Saarlandes
Saarlandes
66 Saarbrucken in Stadtwold
Federal Republic of Germany