

**CHARACTERISTICS OF BREEDING PASSERINE COMMUNITIES
AT EARLSHALLMUIR AND TENTSMUIR, NORTH-EAST FIFE**

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**A Thesis Submitted for the Degree of PhD
at the
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1986

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Characteristics of Breeding Passerine Communities

at Earlshallmuir and Tentsmuir, North-east Fife

by

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Thesis presented for Degree of

Philosophiae Doctor,

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ABSTRACT

The literature pertaining to a variety of methods for estimating the abundances of songbirds is reviewed, and the use of two of the main methods - mapping and transects - is described and discussed. The mapping method is found to be the most efficient and reliable in the context of the present study, and work elsewhere in the British Isles suggests that the method has wide applicability in the region.

Various methods for describing the habitats in which birds occur are discussed. In the present study the method chosen involved measuring various parameters of the vegetation within a limited area at each of several sampling points in five study plots in North-east Fife. It proved a useful method in the habitats studied - dune grassland, commercial and semi-natural coniferous woodlands, and deciduous scrub and mature woodland - and results of the vegetation sampling are discussed in terms of habitat structure and succession, and in the relationship of this structure to the breeding bird communities.

The composition of these communities in the study plots is described, as are the changes over the three breeding seasons 1979-1981, which followed on from a meteorologically "hard" winter. Over the study period there was an overall increase in the populations of all five study plots, and this increase was greatest in the poorest habitat - the dune grassland - and least in the richest habitat - the mature deciduous woodland. Using indices to compare the study plots a major difference was found between the grassland plot and all four woodland plots, amongst which the two coniferous ones were most similar.

Of the more abundant bird species, Robin, Song Thrush and Coal Tit were more prevalent in coniferous habitats; Willow Warbler and Blue Tit were more prevalent in the deciduous habitats. In relation to habitat structure, the more diverse bird communities were found in the more complex habitats, and there was evidence of succession in the bird communities concomitant with habitat succession.

The present study is one of very few in Europe involving woodland habitats especially of a commercial nature near sea-level, and it was found that the four woodland study plots were rich in terms of the diversities and densities of their passerine breeding populations when compared with other European studies.

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- (c) I was admitted as a research student under Ordinance No 12 on 1st October 1978 and as a candidate for the degree of Ph.D. on 1st October 1979; the higher study for which this is a record was carried out in the University of St. Andrews between 1978 and 1981.

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PREFACE

In June 1977, for my undergraduate thesis, I investigated the effects of afforestation on the avifauna of a hill area in southern Scotland. The bird census method I adopted was a hybrid between a simple line transect and a point-count: the fieldwork employing the line transect, and the analysis using an adaptation of the data interpretation invoked for the point-count method.

This led to an interest in the methodologies of censusing breeding "songbirds" – mainly passerines, but also those groups such as some waders, owls and woodpeckers which establish and maintain large breeding ranges by vocal and behavioural displays.

In 1978 I obtained a postgraduate studentship from the University of St Andrews to compare songbird census methodologies in the field, choosing as my study area the nearby Earlshallmuir/Tentsmuir complex of consolidated dune grassland with associated natural, semi-natural and commercial woodland areas.

However, on searching the relevant literature and contacting workers in the same field of study, it became obvious that much work had already been done on the efficiency of various census techniques and that many comparative studies had already taken place to which there was little I could add. I therefore decided to undertake an exhaustive review of the literature on songbird census methodologies up to the end of 1981 (my final fieldwork season), while at the same time carrying out a study of the breeding bird communities of my chosen study areas for its own sake, and also to see if it would shed more light on some of the problems already revealed by the literature.

This thesis presents the results of my investigation, which must be termed "preliminary" or "acquisitive", since three years of study can only begin to unravel the complexity of relationships between the birds of one species, between the species in a community, and between the communities and the

habitats they occupy; and can only begin to draw attention to areas requiring further investigation.

The first chapter of the thesis describes the principal means of estimating breeding populations of birds, particularly of passerines; it discusses the problems inherent in each of the methods; and it presents the results of comparative studies involving the three main methodologies currently in use: mapping, transects and spot-counts.

Chapter Two reviews the methods of describing and classifying habitats, especially in relation to studies of organisms dependent on the habitats; it introduces the census plots studied during the present investigation; and it presents a detailed habitat description of each, derived from extensive fieldwork carried out in 1979.

The third chapter presents the results of the breeding bird censuses which took place in each of the seasons 1979-81, while the fourth chapter draws on the previous two and examines the relationships between the bird species in each community and also at the relationships between each community and the habitats it occupies. Conclusions are arrived at regarding the methods available to census breeding passerines and those methods to describe quantitatively the habitats in which they occur. In the light of the results from the present study of breeding passerine communities and their habitats, recommendations are made for future work in both fields.

Fruitful fieldwork has been conducted throughout Europe and the results of some of it were presented and discussed at the International Bird Census Committee/European Ornithological Atlas Committee Conference in Buckinghamshire in September 1983 (proceedings in press) where it was also revealed that an exhaustive investigation of census methodologies had been commissioned and was nearing publication. Publication by the British Trust for Ornithology of its revised "Common Birds Census: Instructions to Recorders" now means that there is a powerful triumvirate of texts to herald a new era of more precise estimation of bird populations - it is gratifying to have played a small part in the dawning of this era.

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1.1 INTRODUCTION

The first question to be considered before carrying out any investigation is "Why do it?" - once a reason has been found, then the investigator can ponder "How to do it?".

Why then should people want to count breeding songbirds? There are perhaps three main levels of reasoning behind this desire:

- (1) to find out how many birds there are in a given area;
- (2) to find out why they are there;
- (3) to find out how to keep them there.

At the simplest level of enquiry an interested European ornithologist can be dealing with a patch of under 100 hectares near his home base, while at the highest level his sphere of enquiry can extend to tens or thousands of kilometres in Africa, since it is there that many of "his" breeding birds will spend the winter. It is there, too, just as much as in Europe that their lives can be threatened by environmental changes (either natural or man-made) - changes which may have important repercussions for human life. Bird populations have often been described as barometers or early warning systems of environmental perturbations, and to increase the sensitivity of this machinery it is necessary to get increasingly accurate data on its components - the communities which make up the populations - and censuses of breeding songbirds play an important role in this.

Birds have doubtlessly been counted since man first took an interest in them, but objective methods of counting birds were not developed until the present century (Kendeigh, 1944) and then mostly since the mid-1950s when birds began to be investigated in a more scientific manner than previously, and by a growing number of people, since bird-

watching was becoming a popular pursuit, especially in Europe and North America (Allen, 1978). Songbird censuses reflect these developments, from the early mapping attempts of the Alexanders (1909), the transects of Breckenridge (1935) and the point counts of Krzanowski (1964) to the more advanced Common Birds Census (B.T.O. 1977, 1983), the Finnish line transect models of Järvinen and Väisänen (1973 et seq) and the French "Indice Ponctuel d'Abondance" of Blondel et al (1970 et seq).

There is thus a choice of census methods available to the investigator - the one he chooses should depend partly on the type of results he wants, whether it be to assess absolutely or relatively the numbers of birds of each species in his study areas. For an absolute assessment it is necessary to conduct an accurate census of the bird populations of a given area of small dimensions - the mapping method will do this. For a relative assessment of the bird populations of a large area a sampling procedure is needed such as one of the line transect methods or one of the spot count methods. Ralph (1981) provides a useful list of the terminology used in estimating numbers of birds, in an attempt to clarify the situation and to introduce some standardisation.

Each of the main types of census is discussed in the following sections which review their development, describe their current states and investigate their problems and limitations.

1.2 THE MAPPING METHOD

In 1907 and 1908 C.J. and H.G. Alexander (1909) marked, on a six inch to one mile (1:10560) O.S. map, the positions of the summer migrants in the vicinity of Tonbridge Wells, Kent. Thus was created the prototype mapping method for censusing breeding songbirds. Not only did the Alexanders develop the basic principles involved in the method, that is plotting the positions of singing males, of females and of nests, but they also drew attention to some of the problems involved, such as variations in singing activity related to the stages of breeding of a pair of birds; variations both within and between species in their singing activity; the presence of transient birds singing briefly before continuing their migrations to breeding areas elsewhere; and the relationship between singing activity and weather (although they did not clarify this); they did not, however, describe how they conducted their censuses or the number of visits made. From their two year study they arrived at estimates of the breeding populations in each of the two years and were able to look at differences between the two years.

Little came of this exploration into the realms of objective mapping of breeding songbirds until the 1930s when, on the other side of the Atlantic, Williams (1936) in his investigation of a beech-maple climax community throughout the year, carried out weekly surveys during which he plotted on base-maps the positions of all birds encountered, giving rise to maps of the winter distributions and summer breeding territories of the community's birds. Williams too noticed that weather conditions affected bird behaviour and that his counts were adversely affected by high winds and heavy precipitation. He also noted that behavioural changes were reflected in the conspicuousness of birds, but this did not prevent him from comparing the average bird populations of each month even though such estimates had been affected by changes in conspicuousness of the birds he encountered.

At the same time, but in Scotland, Van Someren (1936) had been using a

mapping method to study the territories and distributional variation of woodland birds in late winter and early spring. In addition to the conspicuousness and weather problems, he was the first to describe "double-counting", that is, the danger of plotting on a base-map as two different birds the one bird which changes position undetected by the observer.

Colquhoun (1940a,b), working mainly with timed transects, also used a mapping method for a complete census of a small area, and produced a "coefficient of relative conspicuousness" for each bird species - the first attempt to quantify this problem. His coefficients (actually misnamed since they decreased as conspicuousness increased) were derived from the factors: birds per acre (mapping) , and he emphasised the need

birds per hour (transect)

to maintain a relatively constant walking speed of 0.8 - 2.0 km/hr to reduce the biases created by the faster the walking speed the fewer the birds encountered and the more disturbance created.

Although mapping work had been done irregularly in both Britain and the U.S.A., it was the latter country which took the lead in methodology with the publication by Pough (1947) of detailed instructions on "How to take a breeding bird census". These included (1) choice of study area : 8-16 ha (for amateur workers conducting the census in their spare time) wholly within one vegetation community type (to avoid the edge effect .

(2) number of visits :
at least two mornings per week with occasional evening visits throughout the breeding season and conducted in fairly noiseless conditions.
Repetition of census in subsequent years.

(3) laying out of a grid to facilitate the plotting of the positions of birds.

(4) making a habitat and field maps for the census at a scale of 1:2504.

(5) map symbols for bird activity. The symbols suggested were open squares or circles into

which a code was entered, either for the visit number or the species. Pough suggested two alternative methods of carrying out a census: either one map was used for each species, in which case many maps would have to be taken into the field on each visit; or one map was used for each visit on to which activity symbols for all bird species recorded on that visit would have to be entered. The activities represented by the symbols included simple observations of individual birds and their movements; observations of one bird singing or several birds of the same species singing at the same time; and observations of nests, their contents, and young birds.

Pough suggested that field-workers should do the censuses just for their own interest. There was no commitment at that time to a national data-base which would pool the results from many censuses across the U.S.A., but he certainly envisaged such a scheme in the future when he wrote that "these bird censuses, together with vegetation and land-use maps will ultimately provide us with an approximate figure for the bird population of each of the many different types of areas into which North America is now sub-divided." He saw the "approximate figures" as forming a base-line against which environmental changes, whether natural or man-induced, could be measured.

Edvardy (1958) presented an interim review of census studies in the U.S.A., while Enemar (1959), in his magnum opus, reviewed much of the continental European census literature since Palmgren's (1930) work, concentrating on the number of census visits needed to produce accurate and reliable results.

Enemar's own paper stands as a milestone in ornithological literature and formed the basis of all present mapping censuses in Europe. He realised that the only really reliable method for a completely accurate census of the breeding bird population of an area was to find and count all the nests, but that such a census was impracticable due to the amount of time and disturbance involved. Instead, from his work near Lund, Sweden, in the appropriately-named "Bird-song Valley" Enemar

concluded that a census concentrating on mapping the positions of what he termed "stationary singing males" would result in most of the permanently-occupied territories in an area being found. In conducting the census he suggested that 10 - 12 visits per season were necessary and that each visit should be made at a walking speed of just over 1 km/hr. On each visit a base-map was to be carried on to which would be marked the positions of all birds encountered. At the end of the season data for each species was to be transferred from all the "visit-maps" onto one map for that species - the "species-map". From the clustered distributions of registrations on each species-map, territories could be delimited and the breeding population estimated from these.

Enemar identified the main problems which could beset the final analysis as (1) including the presence of transient males which sang on passage but did not establish or maintain a breeding population;

(2) counting the same bird encountered twice on one visit as two different birds;

(3) counting as territory-holders in the study-area, regularly-visiting birds from outside the study area usually for feeding purposes;

(4) overlooking a territorial male in an area where several are present;

(5) overlooking completely a territory occupied by a pair, or territory-holding male.

From his work however, Enemar concluded that the chances of making the above errors using the mapping method were far less than with any other method, and that it was the most efficient in terms of accuracy for the man-hours involved.

Enemar expressed this efficiency in two ways: "species effectivity" and "survey effectivity", the former being the percentage of the stationary population of each species registered on the average at

each standard survey, while the latter was the percentage of the total stationary population registered on the average at each standard survey.

He identified five main factors which influenced census efficiency in the field: (1) Weather - strong wind and/or rain was found to suppress avian activity.

(2) Time of day - most registrations of birds were obtained between at least 20 minutes after dawn until noon.

(3) Date - song intensity varied with stages in the breeding cycle; and the population of stationary males changed through death and immigration.

(4) Speed of survey - too slow led to double-counting of birds; too fast led to birds being missed.

(5) Human factor - the general disposition of the census-taker affected his efficiency in the field.

This interest in the efficiency of the mapping method was to dominate bird census work in the Scandinavian countries throughout the 1960s and 1970s, and was transferred to the various line transect techniques when they became popular. It was not really until the late 1970s that British workers became involved with methodological problems (see later) after having utilised the mapping method since 1962, but especially after 1964 under the guide of Williamson of the B.T.O.

In 1961, the then Nature Conservancy (N.C.) requested the B.T.O. to carry out a breeding-bird population census, with the aim of providing basic information on population fluctuations among the commoner British birds. The first pilot survey of this census - the Common Birds Census (C.B.C.) - was carried out largely on farmland plots in 1962 and 1963, with a woodland pilot survey in 1963, and more woodland plots included from 1964 (Williamson 1964, Williamson and Homes 1964). A separate Waterways Bird Survey (W.B.S.) was begun in 1974 using the basic mapping methodology (Marchant and Hyde, 1980) and revised instructions were issued in 1982 (B.T.O., 1982).

The census method chosen by Williamson was Enemar's (1959) mapping method adapted to the British situation of smaller and more fragmented habitats than in Scandinavia, and in 1964 Williamson outlined the method to British ornithologists. B.T.O. members were encouraged to participate in the C.B.C. in areas of woodland and farmland and the results of their fieldwork were used to set up population indices for many species, allowing annual population changes to be quantified for the first time. The validity of the index was demonstrated by Taylor (1965) and since 1967 annual reports on bird population changes have been published in the B.T.O.'s journal "Bird Study" e.g. Marchant and Taylor (1981), establishing 1966 as the base year (index = 100) for most species.

The first instruction sheets for participants in the C.B.C. were distributed in 1964 and have been regularly revised (B.T.O., 1977, 1983). Analysis sheets to encourage some participants to do their own preliminary analysis were issued in 1976 (B.T.O., 1976). However, all the species-maps for each breeding season are analysed by hand by scientists at the B.T.O. headquarters. Work in progress at present may allow mechanical analysis in the future (North, 1977 et seq) but there are many problems still to be overcome.

In 1968 the international study conference on bird census methods and results was held at Hillerød, Denmark, at which was stressed the need for an international standard for a mapping method to facilitate the comparisons of results between countries. A committee - the International Bird Census Committee (I.B.C.C.) - was established and in 1969 it presented its recommendations for an international standard (I.B.C.C., 1969).

Those recommendations are set out in four main sections dealing with:

- (1) The applicability of the method;
- (2) The census aims;
- (3) The terminology to be used; and

(4) The planning of the field-work and its evaluation.

The terminology is given in full below since it will be used in later sections of this thesis, but the other sections of the recommendations are given in summary form only:

- (1) Applicability - The mapping method can normally be used only for censusing the stationary part of non-colonial passerines and other species of birds with similar dispersion mechanisms and distribution patterns in the breeding season.
- (2) Aims -
 - (i) to establish annual indices of population levels
 - (ii) to establish densities of populations
 - (iii) to investigate the species composition of a community and the relative abundance of the different species.
- (3) Terminology -

Plot: the defined area of terrain over which a census is made.

Contact: a single field record of a bird, either by sight or by sound.

Contemporary Contacts: contacts made simultaneously with more than one individual of a species, so that it is certain that they are different birds.

Registration: a record, made by the observer on a visit-map, of a contact.

Visit-map: the map, taken to the plot by the observer, for the purpose of registering contacts.

Species-map: the map, one for each species, to which all registrations are transferred from the visit-maps for cluster evaluation.

Cluster: the registrations which, on final analysis of a species-map, appear to be associated with a territory held by one male.

Surplus registration: a registration which, on final analysis of a species-map, does not appear to belong to any bird holding a

territory (that is, does not fit into any cluster) on the plot.

Stationary male: in the restricted sense of the mapping method, a male whose presence on the plot results in the formation of a cluster.

Territory: in the restricted sense of the mapping method, the area over which the registrations of a cluster are distributed.

Population: the birds of one and only one species within a defined area.

Stationary population: the particular part of a population that is censused by the mapping method.

Population density: the number of stationary males (mapped territories) per unit area.

Community: the aggregate of all the populations within a defined area.

Dominance position: the relative abundance, expressed as a percentage of the total, of the populations comprising the community.

- (4) Planning, field work and evaluation - the minimum size of the plot should be 10 - 30 ha in closed habitat and 40 - 100 ha in open habitat, and the plot should be as near as practicable to a square to reduce the amount of edge effect.

A detailed topographic, vegetation and land-use description of the plot should be made and preferably shown on a large-scale official map. A grid - 50 x 50 m in closed habitat and 100 x 100 m in open habitat - should be established on the plot to enable the observer to locate accurately his position and those of the birds. Outline maps - at scales of between 1:1250 and 1:2500 for closed habitats, and between 1:2000 and 1:5000 for open habitats - should be prepared for use as visit- and species-maps.

Census work should be planned to cover the breeding season of the species involved and each visit to the plot should occur at times when most bird song activity occurs, usually in the morning and evening. Different routes through the plot should be used and no part of the plot

should be more than 50 m away from the observer in closed habitats or more than 100 m away in open habitats. At least 10 visits in closed habitats and at least 8 in open habitats should be made throughout one season.

Abbreviated species names and standard symbols for bird activities should be used on visit-maps; new "non-standard" symbols are permissible so long as they are accurately defined.

In evaluating the field-work, all the data for each species on visit-maps is transferred to one map for each species, and territories delimited on the basis of clusters of registrations. The minimum number of registrations required before a cluster can be accepted is related to the number of valid^{*} visits made: two registrations if 5-7 visits are made, and three registrations if at least 8 visits are made; at least two registrations should have high territorial significance.

Where a group of registrations might represent one or two clusters, it is to be accepted as two if there is one pair of contemporary registrations, each supported by other observations and/or at least two pairs of non-contemporary registrations. For species with a low number of valid visits, one pair of non-contemporary registrations is enough. If the above requirements cannot be satisfied, then common-sense in conjunction with knowledge of the species' ecology should be used in the evaluation. This is the most subjective procedure of all those used in the analysis, but fortunately it rarely has to be used.

* Valid visit: a visit on which a bird of a given species could have been observed i.e. for a summer migrant like the Garden Warbler, which does not arrive on its breeding grounds until late April/May, a visit made in late March is not valid for that species, whereas a visit made when the first Garden Warblers are observed is valid; but it is possible that the birds are present but unrecorded as soon as they arrive.

Clusters which overlap the edge of the plot should be counted as belonging to the plot only if more than half of the registrations lie within the plot or on the boundary. The "edge" referred to here is different from the boundary between habitat-types where it gives rise to the "edge effect", usually manifested by an increase in the number of species and their populations. In choosing a study plot it is important to avoid the bias introduced by the edge effect, so that the study plot should ideally be a sub-area within a larger area of the same habitat. This important problem was not discussed by the I.B.C.C. (1969).

The Committee's recommendations were implemented in those European countries in which mapping was carried out, and also in Canada. In Britain the B.T.O. published instructions for participants in its Common Birds Census (B.T.O., 1977) and these were substantially the same as those of the I.B.C.C. but with some major differences, discussed later. The standard symbols used in the C.B.C. are as follows, for species X :

$X, X\sigma, X\delta, X_{uv}$: registration of the species, with age, sex and numbers if known.

\otimes : singing male.

X : alarm call.

X_{mat} : carrying nest material.

X_{food} : carrying food for a mate or young.

X^* : nest, registered once only on visit-maps.

$=X \diagup X \diagdown$: two males "fighting" (the direction of movement to or from the fight can be denoted by arrows).

$X---X$: different birds registered at the same time.

$\otimes \rightarrow \otimes$: singing bird observed to take up new position.

$\otimes \rightarrow ? \rightarrow \otimes$: probably, but not certainly the same bird moving.

$\otimes \leftarrow \otimes$: ascent and descent of a song-flight.

In the present study a distinction was drawn between an observation of a bird flying through the study plot if its point of take-off or landing was known ($X \rightarrow$, $\rightarrow X$ respectively), and an observation of a bird of unknown source or destination passing through or over the study plot

(→) so long as the species was a possible territory-holder in the plot i.e. a Swallow flying over a wood would be ignored, whereas a Carrion Crow would not. It is interesting that M. Moss (1981) independently adopted these symbols in his Welsh study. Oelke (1981a) drew attention to the effects of scale on the plotting of registration symbols on field maps. For example, at a scale of 1:2,500, a normal symbol covers a ground area of 5.0 x 7.5 m., and moving the symbol 1 mm or 5 mm or 10 mm represents ground moves of 2.5, 12.5 and 25.0 m.

The B.T.O. also listed abbreviations to be used for the names of species encountered, and instructions on how to set up mapping grids and carry out detailed habitat mapping.

In a separate document (B.T.O., 1976) guiding principles were outlined for the analysis of the species-maps of a study plot for the C.B.C. These are virtually the same as for the I.B.C.C., but with the following major differences:

(1) Maps of colonial and semi-colonial species are deemed feasible by the B.T.O. and are arrived at by either counting the number of nests in a colony where nests are obvious e.g. Swallow, House Martin, Starling; or by drawing rings on the species-map round obvious groups of registrations and taking as the number of pairs in the colony, that number of pairs substantiated on any two separate visits. The species which need to be analysed in this way are given by the B.T.O. (1977) as Swift, Sand Martin, Swallow, House Martin, Reed Warbler, Starling, House and Tree Sparrows, Greenfinch, Goldfinch and Linnet. Work since the publication of that document suggests that Woodcock, Long-tailed Tit, Siskin and Redpoll should also be treated as semi-colonial species (B.T.O. in litt; Dougall and North, 1983).

(2) Each registration of the two or three needed for a territory (2 for less than 9 visits; 3 for 9 or more) should be separated by a period of at least 10 days. In the case of crepuscular species, only two registrations (at least 10 days apart) are necessary, regardless of

the number of visits which are made.

(3) Family parties are not acceptable evidence of a territory having been occupied unless their registration has the support of at least one (with 6-8 visits) or two (at least 9 visits) other registrations, since family parties may move a considerable distance outside the study plot and conversely those from outside may wander into it.

(4) The territories at the edge of a study plot should be included in the estimation of the number of territories in the plot, so long as there is at least one territorial registration within the study plot. This is to increase the sample size of territories available to the B.T.O. analysts for their computation of the annual population index for the C.B.C.

The B.T.O. (1976) recognized that mapping does not result in a precise representation of the number of birds occupying a census plot, but that it "undoubtedly provides a closer approximation to reality than can be obtained in any other way". Attempts have recently been made to take this approximation as close to reality as it can probably get.

North (1977, 1978a, b, 1979, 1980, 1982 and with Morgan 1980, and with Wragg 1983) developed an alternative method for estimating the number of territories on a study plot. The aims of such a method were to simplify the analysis and to get complete objectivity and good agreement with B.T.O. analysis, with the possibility of the analysis becoming fully automated using a computer. North's new method utilises a simplified set of data - the only information retained from all the registrations on a species-map is the position of each registration and the number of the visit on which it was made. The reason for discarding so much useful information was to simplify the analysis to see how good estimates would be from a minimal amount of information, since it was initially felt that the B.T.O. method of analysis might use more information than was necessary simply to obtain an estimate of the number of territories. Wragg (1982) did further work to North's and devised a computer program.

The new method is based on a form of cluster analysis which groups coplanar points that are heterogeneous in the sense that they have different instants of time associated with them. Registrations are linked with their nearest neighbours among earlier registrations if they are close enough in space, relative to some defined distance: thus, for any registration from the second or later visits, reference is made to the previous registrations in its immediate vicinity, the underlying ornithological idea being that if records are repeatedly obtained in a particular region, this provides some evidence for the existence of a territory thereabouts (North, 1978b).

The new analysis method was applied to a number of species on different farmland plots over a number of years using C.B.C. data from the B.T.C. files. A series of defining distances was used, and in about half the examples the agreement between the cluster method and the B.T.C. manual method was "close", particularly for the Blackbird and also the Chaffinch, but not in every year: the agreement was "good" for the Skylark and Robin. With other years and species however, there were fairly large differences between the territory number estimates from the two methods, and more testing was obviously needed (North, 1980).

A revised clustering algorithm utilising some of the available extra information in the raw registrations produced improved results, especially when contemporary registrations of two different birds, or of one bird changing position, could be solved. Further revisions envisaged would incorporate nest data and a hierarchy of importance reflecting the strength of territorial behaviour (North, 1980). Work is in progress with these revisions, and it is also planned to test the algorithm with more species and with woodland plots - so far all the work has involved farmland plots only (North, in litt.).

The novel clustering method for estimating numbers of bird territories is a welcome innovation in the search for a more objective analysis of species-maps derived from mapping censuses, but unfortunately its widespread use by analysts is a long way off in the future; at present the

guidelines provided by the B.T.O. and I.B.C.C. remain in use. Some of the problems involved in their application have already been alluded to in this chapter - it is now appropriate to investigate them in more detail if the B.T.O./I.B.C.C. is to remain the only acceptable one at present.

Ralph (1981) has recently defined the mapping method as "a census procedure that plots individuals seen or heard on a gridded map of the area surveyed, usually over a period of days or weeks in a season; and relying on simultaneous observations, the subsequent demarcation of individual territories or home ranges by examination of the clustering of those observations" - however the inherent problems remain.

1.3 FACTORS INFLUENCING THE EFFICIENCY OF THE MAPPING METHOD, WITH COMMENTS RELEVANT TO OTHER CENSUS METHODS

Kendeigh (1944) reviewed the early work involved with this and presented some of his own results. Since most of the issues raised by him have now been studied in greater detail, the more recent work is reviewed here.

Three types of problems are associated with the mapping method (Dougall and North, 1983):

(i) "Mechanical" problems (the "extrinsic factors" of Shields, 1979) dependent on the way in which a mapping census is carried out e.g. the number of visits needed to ensure an efficient census (Svensson, 1979); the number of hours spent in the field (Enemar et al, 1976); and the use of more than one census worker per study plot (Enemar et al, 1978).

(ii) "Analytical" problems, depending on how the species-maps derived from field-work are analysed (I.B.C.C., 1969; B.T.O., 1977; North, 1977 et seq); how many analysts work on each map (Svensson, 1974; Best, 1975); and differences in the performance of one analyst (Erskine, 1974; Moss, 1976).

(iii) "Biological" problems (the "intrinsic factors" of Shields, 1979) dependent on: (a) the breeding behaviour of the species being censused, giving rise to species naturally difficult to census e.g. Sedge Warbler and Reed Warbler (Bell et al, 1968, 1973; Haukioja, 1968), Lesser Whitethroat (Da Prato, 1980) and Reed Bunting (Bell et al op. cit.; Haukioja op. cit.; Jensen, 1974). Diehl (1981) also revealed large differences in the detectability of individual birds of one species. Consequently the effectiveness of the mapping method can depend on the proportion of birds of various detectabilities in the population.

(b) variations in breeding behaviour due to pre-

vailing weather conditions (Hogstad, 1967a; Higgins, 1979; O'Connor and Hicks, 1980); the time of day (Shields, 1977) and stage in the breeding cycle (Slagsvold, 1977b).

(c) habitat "workability": different habitat types each tend to have some inherent difficulties of their own e.g. marshland (Bell et al, 1973; Jensen, 1974); farmland (Snow, 1965); and various types of forest and woodland (Enemar et al, 1976; Hogstad, 1967a).

The first two types are restricted to the mapping method, but biological problems are inherent in all songbird census methods and the discussions below of these biological problems are applicable also to transect and spot-count methods. These discussions are based on special studies set up to test the mapping method and should be regarded as additional to those of the main methodological papers of Enemar (1959), I.B.C.C. (1969) and B.T.O. (1977).

Enemar (1962) tested his observations during a mapping census against those of five other experienced ornithologists in the same area at the same time, and also investigated differences between each of the five other observers. He found a considerable variation in the total observations of the different census-takers, with full coincidence in census results not occurring for any species. He considered the causes of the deviations to have been:

- (a) the positions of the observers were not exactly the same, and could never be so;
- (b) the direction of observation of each census-taker was not the same at each separate moment;
- (c) contemporary contacts/registrations varied with each census-taker, some reporting two birds singing at the same time, whereas others interpreted that observation as one bird changing position;

(d) differences in the qualities of each census-taker.

Enemar himself deviated from the group in that he observed more species and got more maximum species totals than any of the other observers - facts which he attributed solely to his greater experience of the study plot. In looking at the number of observations common to the census-takers, there was considerable discrepancy, ranging from 13 - 39%. This led Enemar to conclude that possibly every fourth bird registered by one census-taker of two is overlooked by the other; that even a skilful census-taker is not able to make all observations, not even of all those which are accessible to him; and that, on average, only between a half and two-thirds of a stationary bird population is discovered and registered at each separate study area survey. This strongly suggests that any investigation of one study plot over the short-term by the mapping method should be made by only one census-taker, except possibly in the unusual circumstance of two field-workers being equally proficient in that habitat type, but extensive testing would be necessary to establish such a fact.

Where national schemes are involved however, such as the British C.B.C. and Swedish Breeding Birds Census, the differences between observers will tend to cancel themselves out, but this may not be so with long-term studies of one plot which may have been covered by a number of observers. Enemar et al (1978) studied observer variability in such a situation, amongst themselves. They studied the variation between themselves carrying out a 10-visit mapping census in the same plot and in the same period of time. The test was repeated in two consecutive seasons in the plot which had about 50 territorial males. The number of registered contacts provides the primary set of data for a test of observer field variability. By analysis of variance they compared the observers using the number of contacts registered during the separate visits for (a) the Willow Warbler (the dominant species), (b) all other species, (c) the whole community. No significant differences were found. They also compared the number of species for which each of two observers obtained the highest count - the expectation being that each of them scored highest

in about the same number of species: this test revealed that in none of the nine possible comparisons was there a significant difference either in the counts of evaluated territories or in the counts of contacts. Another important issue is whether the change in population size from one year to the next is registered equally well by two observers. For the three observers that counted the birds in both years, they investigated whether or not they all registered the same directions of the changes. Of the 13 species involved, the three observers agreed as to direction of change in nine; also, in none of the observers was the direction of change measured differently by using the number of contacts and the number of territories. They concluded that the observers registered the changes from one year to the next equally well both when using contacts and territories. There were differences, sometimes large, in the estimates of the magnitude of annual changes, between the observers. Enemar et al suggest that, provided a standard map evaluation procedure is followed, experienced ornithologists can replace each other in a census scheme without violating the comparability of the results.

"Experience" is one of the key-words for any census-taker - he or she must be very familiar with the species likely to occur in his/her study area and be able to identify them correctly by sight, and especially by sound, since many, if not most, contacts made in mapping censuses are of call-notes, alarm-notes and songs. Observers must also be good note-takers and familiar with the need to note events as they happen, not after some lapse of time between an event and its recording on a visit-map. Svensson (1974) recognized that there are individual differences in species recognition, in the ability to record lots of activity when it happens at the one time, and in the ability to observe and locate birds. Preston (1979) in a theoretical study, suggested that reasonably skilled observers (working at 50% efficiency) could miss 50% of objects when observing alone, but miss only 13% of objects when operating in three-person census parties; the fraction of species missed similarly falls from 15% to 5%. He does not, however, allow for the increased disturbance introduced by additional census workers who may also vary in their abilities of identification, judgement of contemporary contacts,

and estimation of distance from birds to observer (Dawson et al, 1978).

O'Connor (1981b) reported his findings on a test of 4 observers of varied census experience who conducted independent mapping censuses of a 28.7 ha scrub habitat in the Chiltern Hills during 1977 and 1978. Three trained analysts independently assessed each of the 1977 maps and showed a high degree of mutual consistency of interpretation, independent of field experience on the census plot. The four observers differed significantly as to the density of territorial clusters (all species pooled) they recorded, but the absolute range of the four estimates was only 19%. A team of two very experienced field-workers detected more birds than did a similarly-experienced observer working alone, and he in turn, detected more birds than solo observers with nil and two years previous census experience: these differences were partly explained by experienced workers spending longer on each field visit. Pairing of observer results across years eliminated the influence of these observer differences on the four estimates of the year-on-year change in bird density. The coefficient of concordance between the four observers' estimates of population changes was reported by O'Connor as 0.64, based on data for 21 different species. Thus, population changes can be assessed accurately from mapping data if the same observer is involved in both census years, and the analysts are properly trained, but the use of absolute densities requires consideration of observer field ability.

1.3 (i) "MECHANICAL" PROBLEMS

Cox (1954) was one of the first to comment on how the audibility of bird song varies with the wind strength and direction: this led, with additional observations, to Enemar (1959), I.B.C.C. (1969) and B.T.O. (1977) recommendations that census visits be made only when the wind was not strong enough to impair census efficiency.

The number of visits necessary to a study plot to get as accurate as

possible an estimate of the breeding populations was discussed by Snow (1965), Hogstad (1967a), Slagsvold (1973b), Moss (1976), Nilsson (1977), Witkowski and Ranozek (1977), Eagles and Tobias (1978), Järvinen and Lokki (1978), Svensson (1979) and Moss (1981). Snow found that on 60 - 80 ha of farmland 8 visits would reveal 60 - 70% of the territories revealed by 16 visits. Hogstad concluded that 3 - 4 visits were sufficient to determine the species-composition and total population of coniferous forest study plots, but that at least 10 were needed to estimate the stationary populations of individual species. Slagsvold showed how for one species - the Song Thrush - the number of visits should be planned to coincide with the period of song maximum of that species, but he was in agreement with Hogstad that if the mapping method is to be used for a community study, then many visits over many weeks are necessary - Nilsson suggested perhaps as many as 20 visits over two months. This requirement would be feasible for professional biologists but probably not for amateurs (whose time commitment may be divided between many interests) or those studying more than one plot. Witkowski and Ranozek, working on a small (10 ha) pine forest study plot made 40 census visits to it over a 10 week period. Taking the results of 40 visits as representing (rightly or wrongly) 100% of the community's population, then 8 visits produced 91% of the final estimate and 10 visits produced 92%. Moss (1976) suggested that in his study areas, with 8 visits as many as 15% of territories could have been missed, but with 10 visits no more than 5%. Eagles and Tobias found that doubling the number of visits to their study plot from 8 to 16 increased the number of breeding species recorded by 15 - 35% but only increased the number of territorial males found by 15%. Svensson distinguished three types of efficiency involved with the mapping method:

(a) apparent visit efficiency - the ratio between the result of a single visit and the final evaluated result of the species maps.

(b) true visit efficiency - the ratio between the result of a single visit and the true number of territories present.

(c) census efficiency - the ratio between the final evaluated result of the species maps and the true number of territories.

Accepting that three registrations are needed to validate a territory, and requiring that at least 90% of the true population to be estimated by the mapping method, then with true visit efficiencies of 30%, 20% and 10%, at least 16, 25 and 52 visits would have to be made. Svensson concluded that such numbers of visits were prohibitively high, especially if amateur workers were to be encouraged to participate in national schemes employing the mapping method, and that between five and ten visits should be aimed at by such workers. Even one visit apparently yields useful results, according to Järvinen and Lokki. They suggested that a typical (whatever that may be!) single-visit census in an area includes about 90% of the species to be found there and yields a relatively accurate estimate of species diversity. This may be so, but surely only on the best day for a census in any particular breeding season. It must be expected that the results of a single-visit census are highly susceptible to variations in the song activity and other behaviours of the birds involved due to prevailing weather conditions, the time of day and stage in the breeding cycle.

Linked to the number of visits made to a study plot is the time spent there, and linked to this is the speed of coverage of the plot. Hogstad (1967a) working in a large (112 ha) coniferous forest plot took 5.0 - 5.5 hours to complete a survey at an average walking speed of 2.2 km/hr; but he did not investigate how his general activity and alertness changed over the five hours. From rather scant evidence that pauses between bird songs last for about 3.0 - 5.5 minutes and that the average size of woodland passerine territories is 0.8 - 1.3 ha (Yapp, 1956; Enemar, 1959) Hogstad suggested that a walking speed of 1.8 - 2.4 km/hr would be the most efficient in habitats where bird abundance was not too high (Hogstad, 1967a). Luniak (1968) also commented on the effects of an observer's velocity but suggested that a closer investigation was needed. Enemar et al (1976) carried out such an investigation, comparing the results of a mapping investigation and nest-finding in a community

in subalpine birch forest in Sweden. It is virtually impossible to establish the true numbers of stationary males or territories in forest plots by mapping, and so nest-finding is the only absolute method available but it involves checking every tree, walking over every square metre of ground to flush nesting birds and following individual birds sometimes for hours. Enemar and his co-workers found that in 1972, 21.5 man-hours mapping resulted in finding 53 territories whereas 420 man-hours spent nest-hunting resulted in 57 nests being found. In 1973 the comparable figures were 20.5 man-hours for 61 territories and 300 man-hours for 62 nests. Thus the time required for mapping field-work was only 5 - 7% of that for nest-finding and even if only the most successful set of 20 hours of nest-finding was considered, this resulted in only 11 nests being found (18 - 19% of all those found). The field-work effort applied in the present study is described in Table 1.1 and Figure 1.1. In summary, for all 5 study areas in all three years, the speed of coverage ranged from 0.68 - 2.10 hrs/ha, while for the four woodland study plots only, in all three years, the range was 1.13 - 2.10 hrs/ha. (O'Connor, 1981 reported a range of 0.99 - 1.53 from four observers over two years in the same woodland area).

Combining all study plots and all years, there was a strong relationship between the total number of hours spent in the field and the resulting total number of territorial clusters for all passerines ($r = +0.59$, $p < 0.05$), but an even stronger relationship between the number of hours spent per hectare and the total number of clusters ($r = +0.85$, $p < 0.001$). For the four woodland plots only, in all years, the same relationships as above were not statistically significant ($r = +0.31$, $r = +0.53$ respectively).

Erdelen and Erdelen (1981) used a computer simulation based on field data to test the efficiency of the mapping method. Their simulation was in agreement with intuitive expectations, in that census efficiency was found to be increased using shorter distances between stops, longer listening times at each stop and using census-takers with a wide hearing range. However, in the experience of the present author, stops are made

not at regular spatial or temporal intervals, but as frequently as necessary to write notes and complete details of observations on field maps.

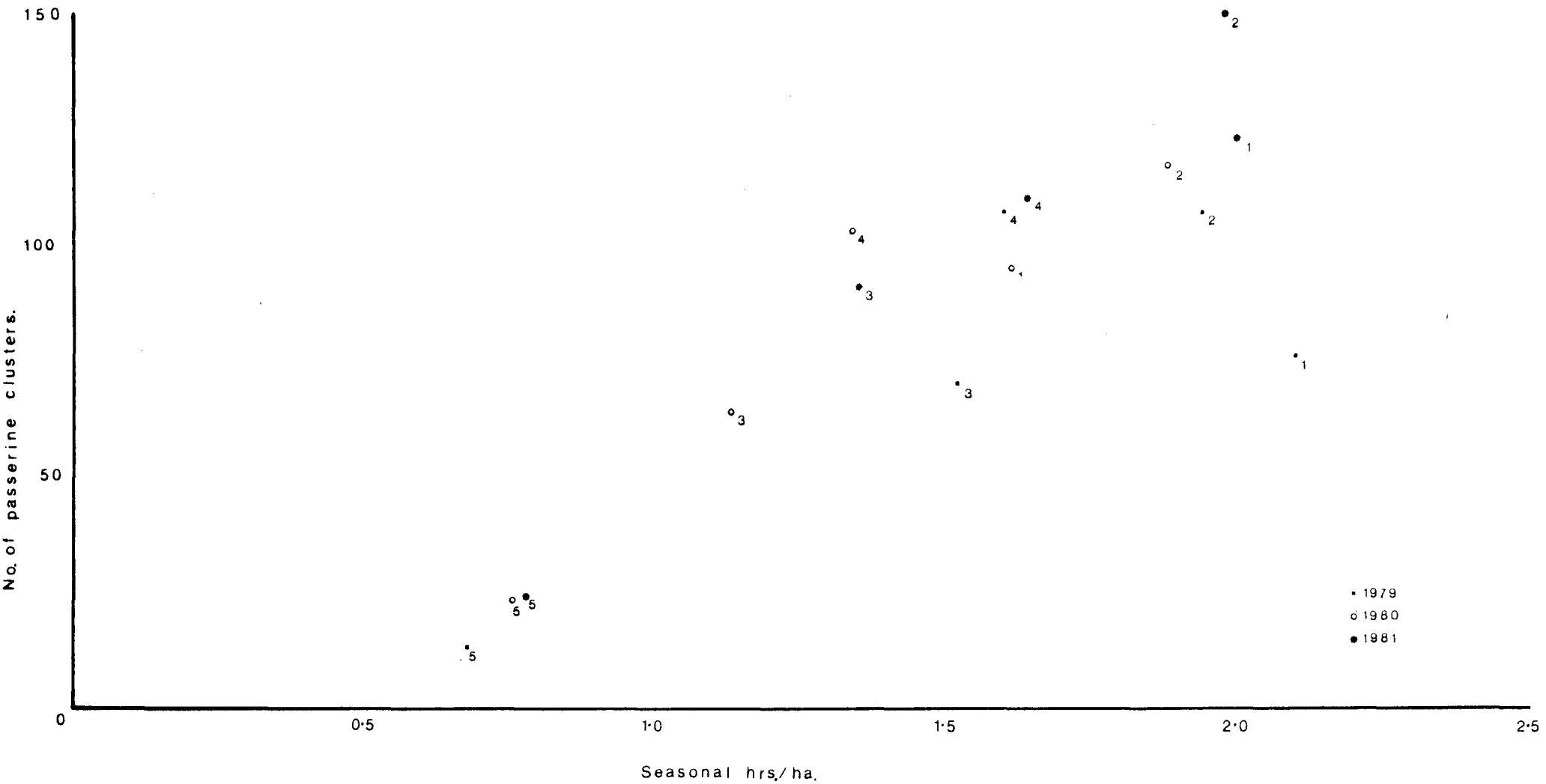
Obviously a mapping census is more efficient in terms of manpower and less disturbing to the environment than nest-finding. Efficient nest-finding also requires more than one fieldworker, especially when flushing is involved, but studies have also been carried out using more than one fieldworker in mapping censuses, as reported earlier in this section.

The above tests of the mechanics of the mapping method offer little to be added to the instructions of the I.B.C.C. and B.T.O. The present author found no mechanical problems in three seasons' fieldwork and suggests that the I.B.C.C. and B.T.O. instructions are adequate for a single census worker covering the same plots over a number of seasons and at the same general level of competence.

TABLE 1.1 : FIELD-WORK EFFORT, IN MAPPING CENSUSES CONDUCTED IN NORTH-EAST FIFE

| YEAR | STUDY PLOT | AREA (ha) | TOTAL NO. OF HOURS | HOURS PER AREA | TOTAL NO. | APPROXIMATE TOTAL OF ALL-SPECIES CLUSTERS |
|------|---------------------|-----------|--------------------|----------------|---|---|
| | | | | | OF TERRITORIAL CLUSTERS (PASSERINES ONLY) | |
| 1979 | 5 | 22.35 | 15.25 | 0.68 | 13.50 | 38.50 |
| 1980 | Open dune | 22.35 | 17.00 | 0.76 | 23.00 | 52.00 |
| 1981 | Grassland | 22.35 | 17.50 | 0.78 | 23.50 | 48.00 |
| 1979 | 3 | 19.09 | 29.00 | 1.52 | 70.00 | 91.33 |
| 1980 | Birch/Willow | 19.09 | 21.50 | 1.13 | 63.50 | 81.70 |
| 1981 | Scrub | 19.09 | 25.75 | 1.35 | 91.75 | 113.75 |
| 1979 | 4 | 11.58 | 18.50 | 1.60 | 107.50 | 128.67 |
| 1980 | Birch/Alder | 11.58 | 15.50 | 1.34 | 103.50 | 120.30 |
| 1981 | Woodland | 11.58 | 19.00 | 1.64 | 110.25 | 136.50 |
| 1979 | 1 | 19.72 | 41.50 | 2.10 | 75.50 | 95.50 |
| 1980 | Semi-natural | 19.72 | 31.75 | 1.61 | 95.50 | 122.00 |
| 1981 | Coniferous Woodland | 19.72 | 39.50 | 2.00 | 124.00 | 149.00 |
| 1979 | 2 | 20.59 | 40.00 | 1.94 | 107.50 | 138.50 |
| 1980 | Commercial | 20.59 | 38.75 | 1.88 | 117.50 | 146.50 |
| 1981 | Coniferous Forest | 20.59 | 40.75 | 1.98 | 150.00 | 181.50 |

FIG 1.1: RELATIONSHIP BETWEEN FIELDWORK EFFORT AND CLUSTERS OBTAINED.



1.3 (ii) ANALYTICAL PROBLEMS

Analytical problems in the national monitoring schemes are reduced by the fact that the same analysts operate each year and there is continuity with analysts over a number of years (B.T.O. in litt.). There is undoubtedly an element of subjectivity in species map interpretation in that no two analysts would ever arrive at exactly the same distribution of delimited territories on species maps, and this subjectivity will have to remain until North's (1977 et seq) cluster analysis is refined. It is also likely that if the same analyst were given the same species maps to evaluate but with an intervening time period, then different interpretations would result. Experience is also useful to the analyst and it is shown below how interpretations by the same analyst can change once more analytical experience is gained.

Erskine (1974) reported that in 1968-71 he carried out 21 mapping censuses on 17 different plots and analysed his results. He subsequently re-examined the field data applying both inclusive and restrictive analytical criteria and found that his "inclusive" interpretation gave about 20% more territories and about 20% more species than the restrictive one. His preferred interpretations of species-maps tended towards the "restrictive" end of the scale. Moss (1976, pp 114-6) sent a sample of his 1973 species maps to an experienced analyst at the B.T.O., and he also re-analysed his 1973 maps in 1975 after a two-year gap in which more analytical experience was gained. The results of the B.T.O. and Moss' interpretations (Table 1.2) suggest considerable divergence which was not consistently in the same direction. Moss suggested that discrepancies could have arisen from the B.T.O.'s lack of knowledge of the site and from their less precise treatment of plot boundary territories, which Moss interpreted to the nearest quarter.

/Table 1.2

**TABLE 1.2 INTRA AND INTER-ANALYST VARIABILITY IN INTERPRETATION OF
THE SAME SPECIES MAPS**

| PLOT SPECIES | A1 WREN | A2 GOLDCREST | A2 COAL TIT | S3 BLUE TIT | A4 CHAFFINCH | S1 CHAFFINCH |
|-----------------|-----------------|------------------|-----------------|-----------------|-----------------|-----------------|
| Moss 1973 | 6 | 38 | 3 $\frac{3}{4}$ | 3 $\frac{3}{4}$ | 3 $\frac{3}{4}$ | 6 $\frac{1}{2}$ |
| Moss 1975 | 6 $\frac{1}{4}$ | 34 $\frac{1}{4}$ | 4 $\frac{1}{4}$ | 3 $\frac{1}{2}$ | 4 $\frac{3}{4}$ | 5 $\frac{3}{4}$ |
| B.T.O. | 6 | 32 | 6 | 6 | 4 $\frac{1}{2}$ | 7 |

Source: Moss (1976) Table 23.

The present author in 1980 re-interpreted all his 1979 species maps and Table 1.3 presents the results of this for all passerine species having at least five territories in a study plot (adjacent plots 3 and 4 are combined).

Since the revised interpretations agreed closely with the interpretations by the more experienced B.I.C. analysts (Table 1.4), allowing for the different interpretations of boundary territories (T.W.D. included them as part of the plot only if $\geq 50\%$ of the registrations fell within the study plot, whereas the B.T.O. included them all) then the revised estimates are probably close to the actual populations in the study plots and so no revised estimates were made in subsequent years. From the directions of change between the estimates, it would appear that the present author under-estimated on his first analysis attempts: further experience led to a less cautious approach. The Coal Tit was the only species to be over-estimated on the initial interpretation (of plot 1). It was also one of four species whose population estimate on re-interpretation had changed by over 50%, the others being Blackbird, Chaffinch and Redpoll. With these three species the high under-estimates were due to overlooking several contemporary registrations, in the cases of Blackbird and Redpoll because the registrations were diffuse and referred to different birds rather than the same bird; in

the case of the Chaffinch because the contemporary registrations were "lost" in a mass of registrations on the species maps.

TABLE 1.3 : INTRA-OBSERVER VARIABILITY IN SPECIES-MAP EVALUATION*
AFTER AN INTERVAL OF ONE YEAR

| PLOT | SPECIES | TWD 1979 ORIGINAL INTERPRETATION | TWD 1979 RE-INTERPRETED 1980 | % DIFFERENCE |
|-------|-----------------|--|------------------------------------|-----------------|
| 1 | Robin | 9 | 11 | + 22 |
| | Willow Warbler | 11 | 11 | 0 |
| | Coal Tit | 10½ | 7 | - 33 |
| | Chaffinch | 29 | 33 | + 14 |
| 2 | Robin | 8½ | 10 | + 18 |
| | Blackbird | 4 | 10 | +150 |
| | Willow Warbler | 12½ | 15 | + 20 |
| | Goldcrest | 5½ | 7 | + 28 |
| | Coal Tit | 10½ | 17 | + 61 |
| | Chaffinch | 29 | 31 | + 7 |
| | Redpoll | 2½ | 6 | +140 |
| 3 + 4 | Wren | 5 | 5 | 0 |
| | Robin | 7 | 8 | + 14 |
| | Willow Warbler | 26 | 26 | 0 |
| | Long-tailed Tit | 5 | 6 | + 20 |
| | Blue Tit | 7½ | 11 | + 47 |
| | Great Tit | 6 | 7 | + 17 |
| | Starling | 48 | 49 | + 2 |
| | Chaffinch | 27½ | 43 | + 56 |
| 5 | Skylark | 8½ | 10 | + 18 |

* Estimated to nearest half territory.

TABLE 1.4 : COMPARISON OF MAP EVALUATIONS BETWEEN PRESENT AUTHOR AND
B.T.O. ANALYSTS, FOR SPECIES WITH AT LEAST FIVE TERRITORIES

| PLOT ¹ | SPECIES | TWD ² REVISED 1979 | BTO ³ 1979 | TWD ² 1980 | BTO ³ 1980 | TWD ² 1981 | BTO ³ 1981 |
|-------------------|----------------|-------------------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
| 1 | Wren | - | - | - | - | 3 | 5 |
| | Robin | 11 | 12 | 12 | 16 | 22 | 23 |
| | Blackbird | 4 | 5 | - | - | - | - |
| | Willow Warbler | 11 | 12 | 6 | 9 | 8 | 10 |
| | Goldcrest | - | - | - | - | 14 | 14 |
| | Coal Tit | 7 | 8 | 17 | 14 | 14 | 14 |
| | Chaffinch | 33 | 41 | 33 | 36 | 34 | 36 |
| | Siskin | - | - | 2½ | 9 | - | - |
| | Redpoll | - | - | 2 | 10 | 3 | 6 |
| 2 | Wren | 3 | 6 | 7 | 14 | 11½ | 16 |
| | Robin | 10 | 13 | 17 | 26 | 31 | 33 |
| | Blackbird | 10 | 10 | 3 | 9 | 5 | 11 |
| | Song Thrush | - | - | - | - | 5 | 7 |
| | Willow Warbler | 15 | 18 | 12 | 16 | 11 | 11 |
| | Goldcrest | 7 | 8 | 14 | 16 | 14 | 17 |
| | Coal Tit | 17 | 19 | 17 | 22 | 26 | 28 |
| | Chaffinch | 31 | 42 | 27 | 34 | 32 | 33 |
| | Redpoll | 6 | 7 | 2½ | 6 | 2 | 4 |
| 5 | Skylark | 10 | 12 | 15 | 14 | 15 | 22 |
| | Meadow Pipit | - | - | 7 | 6 | 7 | 8 |

- Notes:
- 1: Study plots 3 and 4 not included here because their adjacent positions and the different "boundary analyses" employed by T.W.D. and the B.T.O. precluded valid comparisons.
 - 2: To nearest half-territory.
 - 3: To nearest whole territory.
 - : Less than five territories estimated in one year, by both T.W.D. and B.T.O.

From Table 1.4 the major differences in the estimates occur in the following species: Wren, Robin, Blackbird, Chaffinch, Siskin and Redpoll. The first three can be accounted for by the inclusion of all boundary territories by the B.T.O., but the problems in the interpretations of the species-maps for Siskin and Redpoll lie elsewhere. On examination of the species-maps produced by the B.T.O. it seems that both species were treated as semi-colonial, but with the Siskin late migrants were included as part of the breeding "colony"; while with Redpoll the "colonies" were delimited on insufficient evidence and with no regard to contemporary registrations. Probably personal knowledge of the study plots by the B.T.O. analysts would have alleviated the problem, but both species appear to range widely in their song-flights over the breeding areas and it is felt that more work is needed on their breeding biology before they can be satisfactorily analysed in mapping work.

Dougall and North (1983) described the analytical problems involved with the species-maps for the Long-tailed Tit in one study area, and their Table 2 (Table 1.5 here) revealed minor differences in population estimates between three analysis: P.M.N. using his cluster algorithm, and T.W.D. and a B.T.O. analyst both applying the I.B.C.C. rules, but with T.W.D. having personal knowledge of the study plot in question.

TABLE 1.5 : ESTIMATED NUMBER OF PAIR-RANGES OF THE LONG-TAILED TIT
IN STUDY PLOT 2

| TYPE OF SPECIES MAP | NO OF PAIR-RANGES | | |
|--|-------------------|-----|-----|
| | PMN | TWD | BTO |
| 1 : Inclusion of winter flocks and/or nests | 7 | 6 | 5 |
| 2 : Inclusion of winter flocks; exclusion of nests | 6 | 6 | 5 |
| 3 : Exclusion of winter flocks; inclusion of nests | 4 | 4 | 4 |
| 4 : Exclusion of winter flocks and of nests | 4 | 4 | 4 |

Source: Dougall and North (1983) Table 2

The B.T.O.'s C.B.C. instructions (B.T.O., 1977) recommend omitting registrations of winter flocks from an analysis of species-maps. When this is complied with in the case of the Long-tailed Tits above, all three analysts are in agreement that the plot held 4 pair-ranges (the species is group-territorial). However Dougall and North's work suggests that for the Long-tailed Tit at least, the distribution of winter-flock registrations should be considered during the interpretation of species-maps since they are an important part of the species' breeding biology. The inclusion of winter-ranges in the analysis of species-maps introduces differences between analysts in their interpretations (and it is not B.T.O. policy to include these for any species) and so until this problem has been investigated further, it is suggested that the B.T.O. recommendations for winter-flock treatment be upheld, for species other than Long-tailed Tit.

More detailed work comparing different analysts has been carried out by Svensson (1974) and Best (1975). Svensson gave out 58 sets of 37 species-maps to be evaluated, and scored the results, taking into account the previous experience of the evaluators. He found that considerable variation existed between the results of different analysts and that analysts were consistent in the direction of their deviation: a person who deviated from the average was either consistently high or consistently low in his estimates and showed a variation between study plots that was fairly independent of the size and direction of deviation. Differences in evaluations between species were due to three factors: the "distinctiveness" of the clusters of a species (this seemed to be the most important, but was hard to quantify); the number and type of registrations (many song registrations made interpretation easier); the amount of simultaneous registration (the more there were, the easier the interpretation) - but relationships between these factors and the ease of interpretation were not always clear.

Surprisingly perhaps, Svensson found no significant difference in analytical ability between groups with different levels of experience, although in a shorter experiment involving conference delegates "a slight

tendency for an increase of the population estimate with increasing experience" was found. He suggested that his experiment was not conclusive and suffered from the drawbacks that the participants had no field experience of the maps they analysed; they were given no details of study plot habitats or census dates; and they had to analyse a higher number of maps with higher numbers of clusters and in a more limited time period than they were used to, and consequently they probably did not operate as carefully as they would have done under normal conditions. Svensson's findings thus suggest that in national schemes it is important to retain analysts or train them to similar levels of competence so that the annual population changes computed are real and not an artefact introduced by changing an analyst; and that there may be considerable problems in comparing census results from different plots done by different people if there are variations in their abilities to interpret maps correctly. Based on this standard,

Best (1975) working on one species on a small study plot - a Field Sparrow on 2.17 ha - gave identical completed territories to five ornithologists familiar with the mapping method. They knew the birds' behaviour. He found that inconsistency characterised the five interpretations when compared with each other and with the real territories known from observations of individually-marked birds. However, although there was uncertainty about the boundaries of the territories - and they changed over time - the "true" of territories was estimated correctly by three of the five analysts. Best identified five sources of error involved in interpretation of composite maps, as compared with the actual territories: (1) inconspicuous birds might be overlooked during mapping censuses; (2) peripheral territories with only a few registrations of registrations inside the study plot might also be overlooked or incorporated into some adjacent territories (Best's study is perhaps unrepresentative on this point since his plot was so small that the number of peripheral territories was large); (3) shifts in the boundaries of some territories due to abandonment of adjacent ones might cause problems; (4) a large territory might be split into smaller ones when, on the species-map, "false" clusters appear due to the birds

spending different periods of time in different parts of the larger territory; (5) territorial infractions could lead to confusion in interpretation since they might suggest changes in territorial configuration. Error-types 1, 2 and 4 have general application, but types 3 and 5 are probably of relevance only in intensive studies such as Best's, where a knowledge of territory boundaries is necessary.

The inconspicuousness problem mentioned by Best was also found by Colquhoun (1940a, b - see previous section) and by Davis (1965) whose work was based on counting singing males. Davis suggested that his work also revealed, for the first time, the variation in song output within a half-hour period in addition to the already-established diurnal and seasonal variations. Davis' method involved walking along a track about $\frac{3}{4}$ of a mile long, and counting the number of singing male Rufous-sided Towhees on both sides of the track. At the finishing point, Davis about-turned and walked back to the starting-point, again counting the numbers of singing males, the whole trip taking 22 - 41 minutes. During the peak song-period (19th April - 31st May 1956) he found an average of 10.64 ± 0.41 singing males on the outward trip and 6.79 ± 0.64 on the return trip; in the earlier and later stages of the census period (in March and July) he found comparable figures of 5.42 ± 0.86 and 2.33 ± 0.57 . Davis claimed this as evidence for short-term variation in song-activity, but perhaps the variation was an artefact induced by his disturbance of the birds on the outward trip, causing fewer of them to sing during his return trip. In any case his findings have little bearing on most mapping censuses (and line transects) since census-takers do not normally cover the same ground twice during a census, but in cases where they have done then any analysis would have to take into account the disturbance factor.

More detailed work on song activity by Slagsvold (1973b) revealed that the song course of forest bird communities showed approximately the same pattern in different years and in different areas, with two peaks of song activity separated by an interval of about 30 days, and with minimum values between the peaks of only about 50% of the value of the

first peak. Slagsvold's own work in a Norwegian spruce forest involved 10 censuses in each of three periods: around the first song peak, in the interval between peaks and at the second song peak. He found that the size of the population estimates from the interval and second song peak were 37% and 57% of those of the first song peak. Clearly this indicates the need to make at least once-weekly visits to a census plot throughout the season (Nilsson (1977) suggests 20 visits in 2 months for South Sweden) so that variations in song activity are accounted for, otherwise in map analysis there is the chance that only clusters of high song-activity individual birds would be accepted.

Slagsvold (1973c) is the only worker to have put into practice the theoretical treatment of inconspicuousness developed by both the Seierstads and Mysterud (1965, 1968, 1969, 1970) - the "standard check method". These latter workers defined inconspicuousness as "the phenomenon that in any animal population census, a number of individuals may remain undiscovered" and their way of tackling the inconspicuousness problem was based on the assumption that a given population may be counted several times and that it is possible to determine whether an individual revealed during one count is also discovered on other counts. The number of such rediscoveries indicates the effectiveness of the census and is used to arrive at an estimate of total population. However, even with x counts of y individuals it is possible that there are additional individuals which have remained undetected. The method can ignore the influence of transient visitors to a study plot by eliminating from consideration those individuals recorded three times or less, but only when there is no danger of confusing three different transients on three surveys with one territory-holder which has changed position between surveys. The authors suggest that the overall procedure should increase the reliability of population censuses based on only one or a few surveys (but it is suggested here that these should not be undertaken, for the reasons outlined in the previous sections above), but that their correction method would have a negligible effect when ten or eleven surveys have been undertaken. Moss (1976) suggests that corrections would be negligible with at least

eight census visits and the probability of observing a particular territory-holder as 50%.

Slagsvold (1973b) using only counts of singing male Song Thrushes compared the mapping method and the standard check method and found that the estimates by the latter were always higher than those by mapping (by up to 50%) especially if two registrations, rather than just one using mapping were used for the acceptance of a territory.* However, if observations in addition to singing males had been used in the evaluations of species maps, then the differences between the two methods would probably have been less. Slagsvold suggests that the check method should be used in preference to mapping only if the community population on a plot is small, and since the check method incorporates no spatial data it is of limited use in studies relating populations to environmental variables.

* Nilsson (1977) also suggested that higher population estimates - at least for tits, Nuthatch and Treecreeper - would result from dropping the requirement of at least two song registrations for the acceptance of a territory; and he went so far as to suggest that there should be no general and standardised rules for population estimation, but this would preclude the comparison of results between different studies. Perhaps one of the reasons Nilsson's population estimates by the mapping method were low compared with those derived from nest-finding and observations of colour-marked birds was his rather fast coverage of large woodland census plots: he states that it took him about 40 minutes per 10 hectares to cover a 70 ha plot (largely coniferous) and about 50 mins/10 ha in a 46 ha plot (largely deciduous). The present author covered his five study plots at the speeds recommended by the I.B.C.C., B.T.O. and other workers (Table 1:6 and previous discussion). Taking the average time for a census over the three-year period in each study area produces figures of 3.27 hours/19.72 ha (coniferous plot), 3.59 hours/20.59 ha (coniferous), 2.18 hours/19.09 ha (deciduous), 1.47 hours/11.58 ha (deciduous) and 1.46 hours/22.35 ha (open grassland) which are equivalent to 99 minutes/10 ha, 105 mins/10 ha, 69 mins/10 ha, 76 mins/10 ha and 39 mins/10 ha. Ignoring the last figure which refers to open grassland, the present author was working at least 38% to 52% slower than Nilsson in deciduous woodland and 148 to 163% slower than him in coniferous forest - it seems probable that such deviation from the "norm" by Nilsson influenced his results.

Svensson (1979) comments that with the standard check method, in practice census efficiency is rarely known and almost never constant and so the "check" calculation of efficiency does not produce particularly accurate estimates when only a few clusters are involved. He also draws attention to one condition that has been neglected in theoretical consideration of census efficiency: the fact that the detectability of a bird species is not independent of the detectability of other birds. Instead, the song activity and thus the detectability of a bird is dependent on, or correlated with, that of other individuals through mutual stimulation of environmental influences.

Finally in this section on analytical problems the present author found most of his interpretative difficulties in delimiting clusters on species-maps concerned diffuse registrations; diffuse registrations both within territories, and between entire plots; and lack of simultaneous registrations. These varied with species and will be discussed below, in the next section. Consequently his analytical procedure in such cases where clustering of registrations with territorial significance (for example, some were not apparent was to look at the interdistances between registrations, especially those involving movement of one bird or simultaneous observation of at least two, and to group adjacent observations within a "true" cluster bearing in mind the distances involved. This is akin to North's use of "defining distances" developed independently, and agrees closely with the procedure adopted by Moss (1976, p. 71), also developed independently: all of which lead to minimum estimates of population. For example, 8 diffuse registrations of song with no similarity might be counted as one territory when there were actually two real ones, and/or several registrations with no territorial significance could represent one or more real territories in which the birds are very not territorially-active on census visits - only personal knowledge of the study plot would help to resolve this type of problem.

TABLE 1.6 : CENSUS SPEEDS DURING THE PRESENT STUDY

| Study plot | Habitat type | 1 | 2 | 3 | 4 | 5 |
|--|--------------|---------------------|-----------------------------------|----------------|-----------------------------|-------------------|
| | | Semi-Natural | Commercial Mixed Coniferous | Birch Scrub | Birch/ Alder Woodland | Dune Grassland |
| | | Mixed Coniferous | | | | |
| A Area (ha) | | 19.72 | 20.59 | 19.09 | 11.58 | 22.35 |
| B Approx. distance walked per census (to nearest 0.25 km) | | 4.75 | 5.75 | 4.00 | 2.50 | 3.00 |
| C Total hours spent (to nearest 0.25 hr) in | 1979 | 41.30 | 40.00 | 29.00 | 18.50 | 15.25 |
| | 1980 | 31.75 | 33.75 | 21.50 | 15.50 | 17.00 |
| | 1981 | 39.50 | 30.75 | 25.75 | 19.00 | 17.50 |
| D (b) complete censuses (n) | 1979 | 10.75 (10) | 13.25 (8) | 25.75 (11) | 18.50 (12) | 15.25 (11) |
| | 1980 | 13.75 (10) | 13.75 (10) | 20.50 (10) | 15.00 (10) | 17.00 (11) |
| | 1981 | 16.50 (11) | 13.75 (12) | 25.75 (12) | 16.50 (12) | 17.50 (12) |
| E Average no. of hours spent per complete census | 1979 | 1.11 | 3.33 | 2.34 | 1.54 | 1.39 |
| | 1980 | 1.11 | 3.98 | 2.05 | 1.50 | 1.55 |
| | 1981 | 1.11 | 3.40 | 2.15 | 1.38 | 1.46 |
| F Total hours spent (to nearest 0.25 hrs), 1979-81. | | 112.75 | 119.50 | 76.25 | 53.00 | 49.75 |
| (a) in all censuses | | 98.00 (30) | 107.75 (30) | 72.00 (33) | 50.00 (34) | 49.75 (34) |
| (b) in complete censuses (n) | | | | | | |
| G Average no. of hours spent per complete census (1979-81) | | 3.77 | 3.59 | 2.18 | 1.47 | 1.46 |
| Average walking speed per complete census (km/hr) (B/E) | 1979 | 1.44 | 1.63 | 1.71 | 1.62 | 2.16 |
| | 1980 | 1.49 | 1.48 | 1.95 | 1.67 | 1.94 |
| | 1981 | 1.43 | 1.69 | 1.86 | 1.81 | 2.05 |
| (B/G) | 1979-81 | 1.45 | 1.60 | 1.83 | 1.70 | 2.05 |
| Average time (mins) taken for a complete census per 10 ha (G/A) x 600 | | 99 | 105 | 69 | 76 | 39 |

1.3 (iii) BIOLOGICAL PROBLEMS

(a) PROBLEMATICAL SPECIES

Since this thesis is concerned primarily with passerines, census methods for breeding non-passerines will not be discussed in any detail - they mainly involve counts of nests and/or young. Nevertheless some non-passerine species can be censused by methods applicable largely to passerines, especially by the mapping method, and they are indicated below in a brief review of some of the literature pertaining to those non-passerines which can be encountered during censuses of breeding passerines in woodland, heathland and moorland.

Grey Heron - most counts have been carried out at colonies in the British Isles since 1928 (Nicholson, 1929). A review of that project has been given recently by Reynolds (1979).

Wildfowl - Dzubin (1969) discusses census methods which are based mainly on counts of nests for example, Newton and Campbell (1971) and on broods of young, see Dougall (1978b). The B.T.O. (1977, 1978) includes wildfowl species in both its C.B.C. and W.B.S. work but Erskine (1974) describes how such methods may be inapplicable for some species like the mallard with a home range of 200 ha.

Hawks - usually censused by nest-counts, see Moss (1976); although methods based on "territory" ("home-range" is a preferable term) have been suggested (Jablonski, 1976), and estimates can be derived from distribution mapping (Frestt and Bell, 1966; Sharrock, 1976). A few raptorial species are encountered during C.B.C. work (B.T.O., 1977) and from the registrations it is possible to monitor nationally the population trends of Kestrel and, more recently, Sparrowhawk (Merchant, 1980).

Rails - Water Rail, Moorhen and Coot are covered by the two B.T.O. surveys and because nests are hard to find, counts of broods have

been used, for example Dougall (1978b). The Corncrake gives perhaps the most reliable census results from mapping the positions of calling males (Cadbury, 1980).

Waders - usually censused by nest and/or brood counts, see Wilson (1978), but some species' populations can be estimated from mapping (Smith, 1981 for Snipe), line transects and distribution mapping (Järvinen and Väisänen, 1978d). The Woodcock is included in the B.T.O.'s list of species which can be censused by mapping, especially of displaying males, but interpretation of such maps is considered very difficult (B.T.O. *in litt*). Tester and Watson (1973), Shorten (1974) and H irons (1980) discuss counts of displaying birds and H irons now thinks (per. comm.) that the species cannot be properly censused without radio-tracking birds equipped with a transmitter.

Gulls and terns - nest-counts of moorland colonies are given in Bourne et al (1978).

Doves - Stock Dove, Woodpigeon, Collared Dove and Turtle Dove are included in the B.T.O.'s C.B.C. species list, but the Woodpigeon does not figure in the annual index (Marchant and Taylor, 1981) since it is best censused by nest-counts (B.T.O., 1977; Tomiałojc, 1978) and in some habitats these are very difficult and time-consuming to make.

Owls - again included in the C.B.C. species list, but most study plots are smaller than the breeding territories of most species. Annual indices are produced for Little Owl and Tawny Owl (for example, Marchant and Taylor, 1981). Most population estimates are based on nest-counts (Village, 1981) but see also Prestt and Bell (1966) and Jabłonki (1976) for details of distribution- and territory-mapping over large areas.

Nightjar - can be censused satisfactorily by the mapping method (B.T.O., 1977; Berry and Bibby, 1981; Cadbury, 1981).

Woodpeckers - can also be censused by the mapping method but breeding ranges may be larger than many study plots. Amman and Baldwin (1960) in North America found that fixed plots and variable-width strips were accurate census methods.

Breeding populations of most passerine species can be estimated adequately by various census methods, notably the mapping method. However some species, because of their particular breeding biology, prove difficult to census and/or evaluate by any method other than by nest-finding. These are discussed below along with other species, not particularly difficult to census, but which have been commented on by various authors, including the present one.

Robbins and Stallcup (1981) found that the possibilities for species mis-identification based on vocalization or habitat association are high. However, they thought that the magnitude of the errors actually perpetrated is generally within an acceptable range in most types of survey work. Although their study was based on American species, it is felt here that useful comparable work could be conducted on the following species which have similar vocalizations: Blackcap and Garden Warbler (song); Goldcrest and Long-tailed Tit and Treecreeper (calls); and Great Tit and Chaffinch (calls). Robbins and Stallcup ranked census techniques investigated by them according to vulnerability to species identification error as follows, from best to worst: (1) trapping and marking, (2) mapping, (3) atlas, (4) point and variable-circle, (5) single-visit transects, (6) breeding bird survey with series of short single visits.

The species treated here are arranged in the Voous' sequence, as given in Hudson (1978). The maps are all at a scale of 1:2500 except Figures 1.2 (1:3080), 1.3 (1:3260) and 1.4a,b (1:3610).

Skylark - Delius (1965, Figure 19) working with a colour-marked population found no overlaps in 22 territories on his study area, but the present author found territorial overlap in his grassland study area, and watched birds in their song-flight fly above several territories.

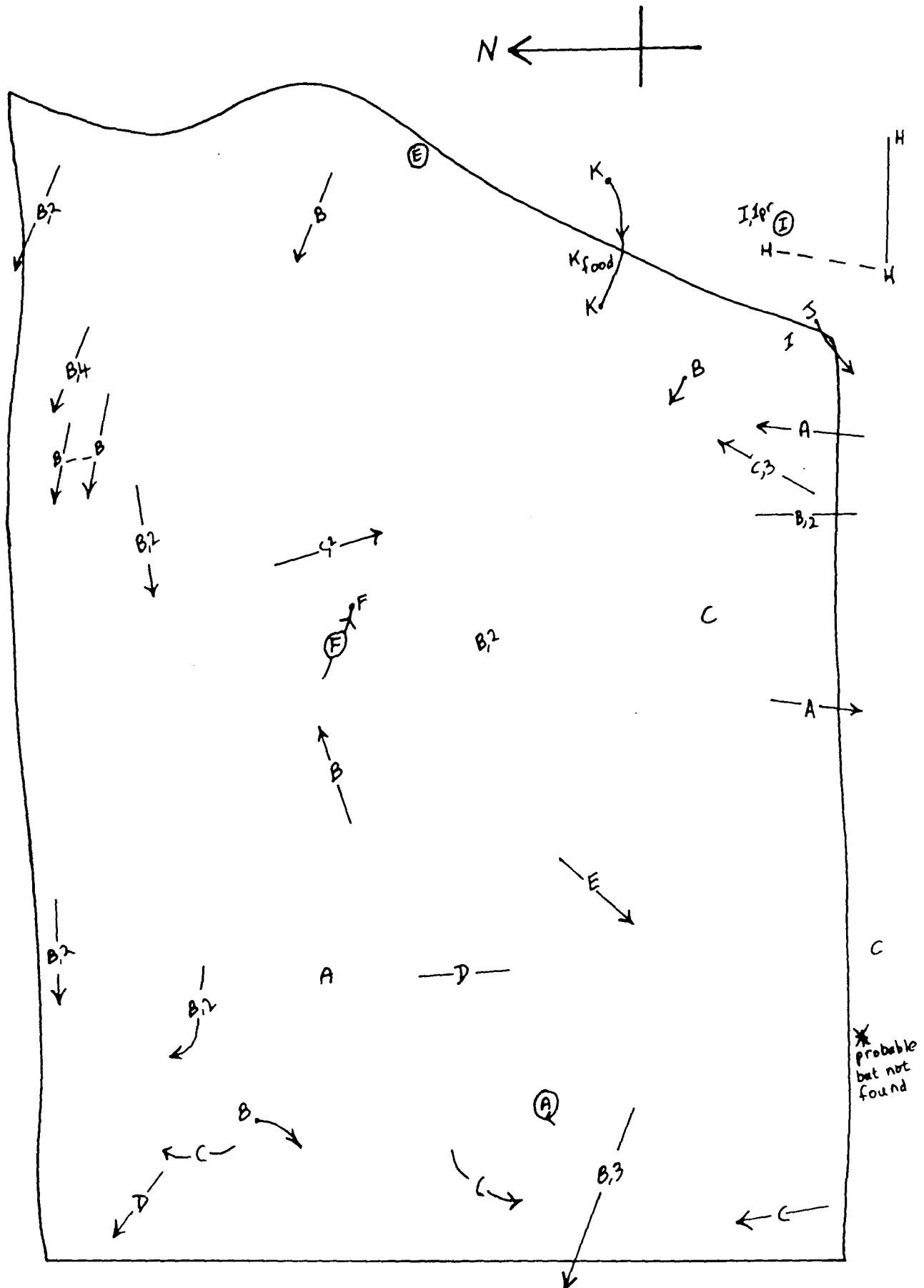
Skylarks produce many contacts and this factor, together with their sometimes wide-ranging breeding behaviour can make species-map evaluation difficult, especially at high population densities, in which case species-maps are easier to evaluate if divided into two time periods corresponding to census visits.

Meadow Pipit - (Fig 1.2). Conversely, at low densities such as occur after a hard winter, this species produces few territorial contacts, making map evaluation occasionally difficult. Also, in coastal situations a complicating factor is the spring passage of migrant birds.

Yellow Wagtail - M. Moss (pers. comm.) found the species to be semi-colonial in parts of Wales and treated its species-maps accordingly.

Dunnock - Although this species can produce good clusters and is therefore well covered by the mapping method (Snow, 1965; Williamson, 1971a) problems can arise. The species is a skulker and so will often not be seen during a census visit. Hogstad (1967a) found, in Norway, that by the middle of the breeding season and later, the ratio of visual to auditory contacts for this species was 1:10 and with a weak song which does not carry far, there is the chance that many will not be heard: many individuals show a low level of song output in marshes (Jensen, 1974). Williamson (1971a) suggested that for farmland a minimum of 10 visits which produces a minimum of 3 song registrations per territory is needed for the species; Jensen suggested 15 visits were needed when dealing with a marshland population - 5 visits in April and 10 in May and June. Snow (1965) alluded to the species having unusual social and territorial habits for a passerine and Jensen noted wide variations in territory size. Birkhead (1981) has studied the problem and his findings suggest there is often an additional male present in a breeding territory and such territories will be large in relation to others. The additional male helps the other in territorial defence against an intruder and sometimes sings with him, but about one metre apart.

Fig. 1.2 : Meadow Pipit, Area 5, 1979



There is thus the possibility that some registrations of 2 or 3 males singing in close proximity could be interpreted as representing the boundary between 3 territories, when in fact only 2 are involved. Snow and Snow (1983) have elaborated on the problem, showing that Dunnock territories are "spheres of influence" rather than the sharply-demarcated, exclusive territories typical of many song-birds: indeed the "territories" of two males can overlap completely.

Robin - This species is strongly territorial and gives rise to well-defined clusters on species-maps. When not vocalizing the species can be difficult to observe, however, and Hogstad (1967a) found a ratio for visual:auditory contacts of 1:10.

Blackbird - With the Blackbird his ratio was 1:5. Snow (1965) found this species difficult to census accurately on farmland using only song contacts, since these could result in 25% of the actual territories being overlooked. He found that the species had an erratic song output, with great individual variation. The output could be reduced at low population densities, but increased where there was a high proportion of unmated males. On open farmland the species can have large territories, and the present author found this phenomenon also in coniferous forest (Fig. 1.3). Clearly all records must be taken into account and species-maps interpreted with care.

Song thrush - Snow found that this species provided similar problems to the Blackbird but could have even larger territories; and often sight records depended on the chance flushing of birds. Hogstad's findings in woodland bear this out to only a limited extent, since he give it a visual:auditory ratio of 1:5. Slagsvold (1973b) found that the size of the male population determined was entirely dependent on the stage of the breeding cycle at which a census took place, and that it was necessary to include all contacts of the species to get an accurate population estimate. The present author found that occasionally the numbers singing at dusk were much higher than at dawn (Fig. 1.4), emphasising the need for dusk censuses.

Fig. 1.3 : Blackbird, Area 1, 1980

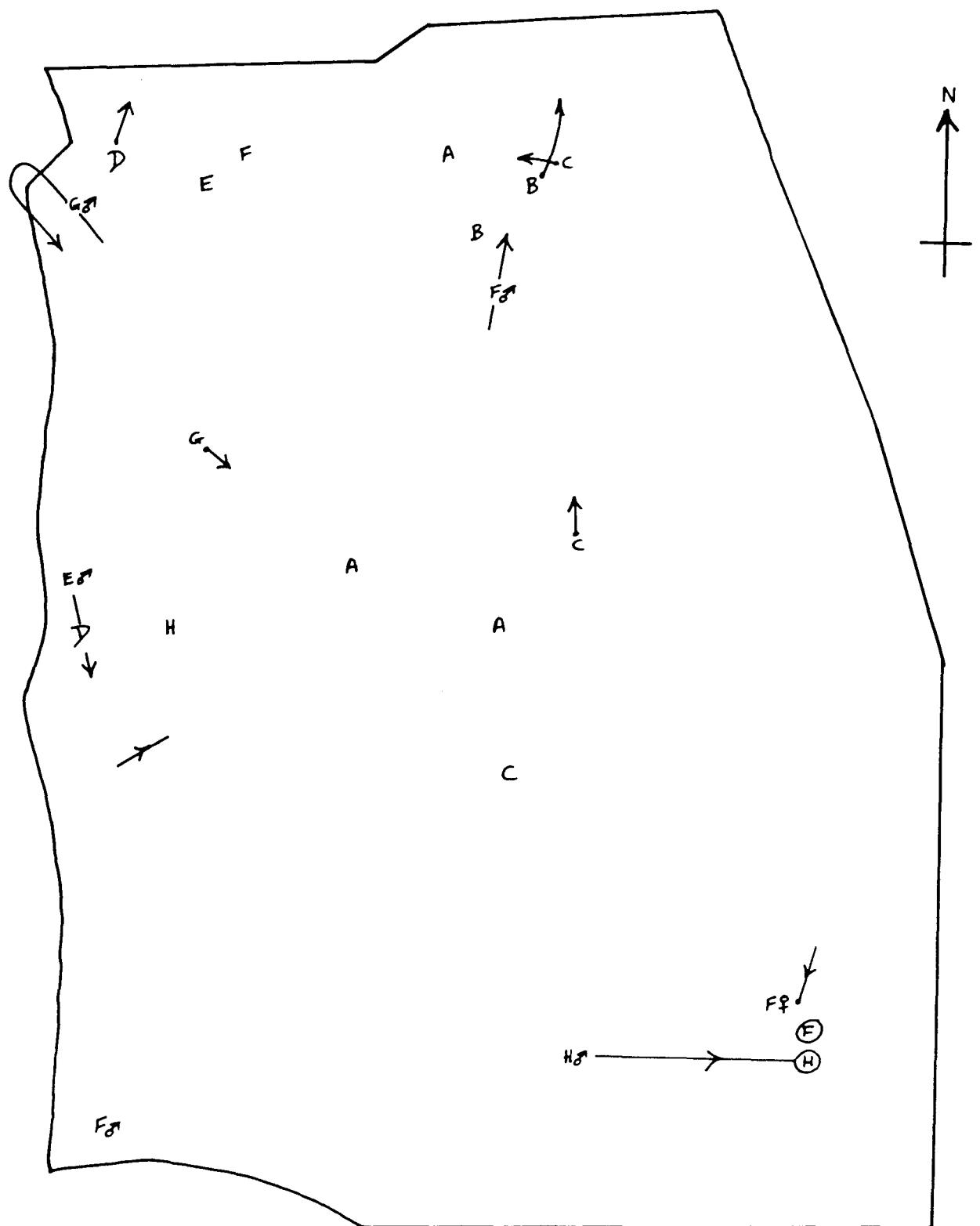


Fig. 1.4a : Song Thrush, Area 2, 1981; Excluding dusk censuses

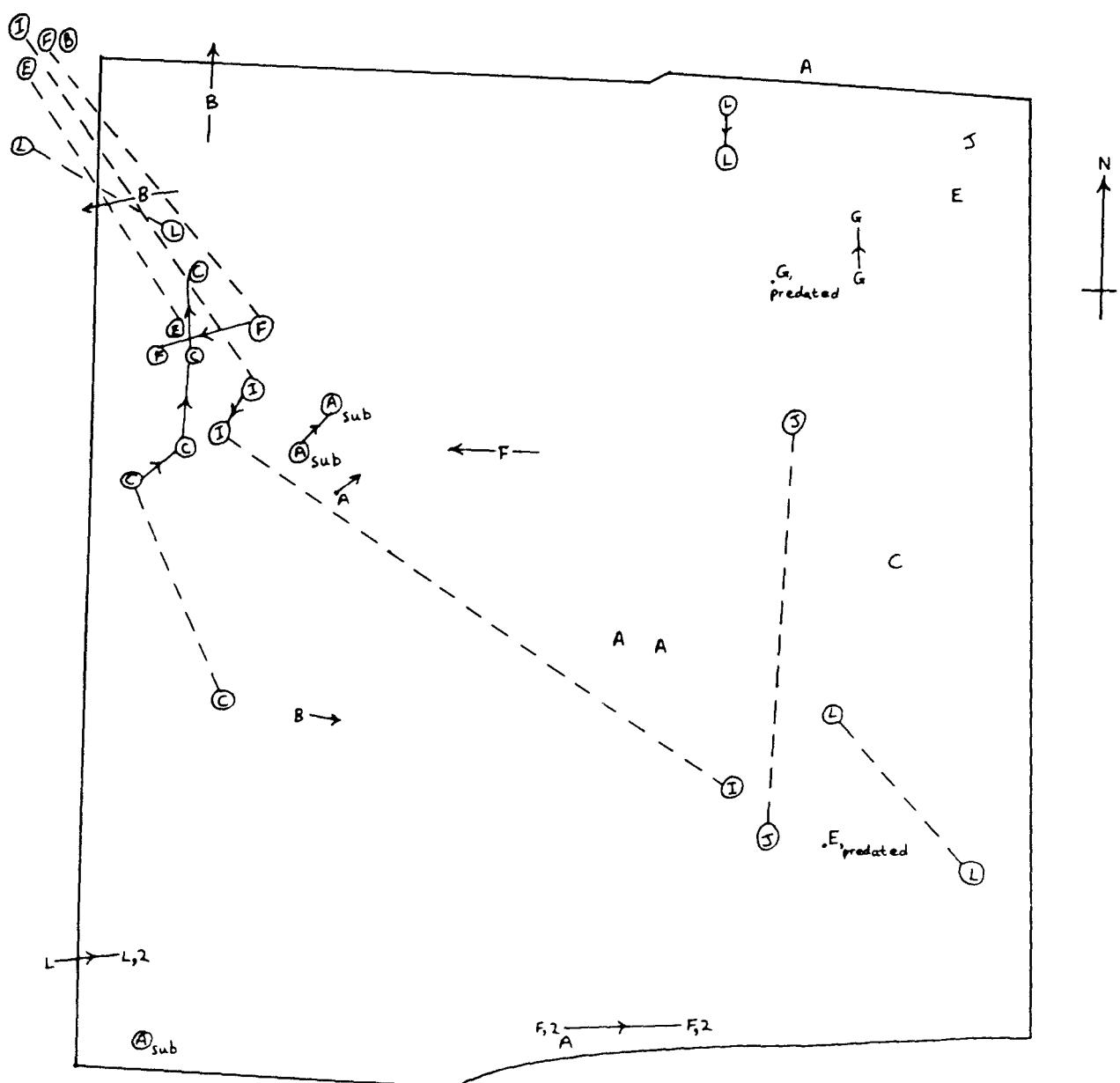
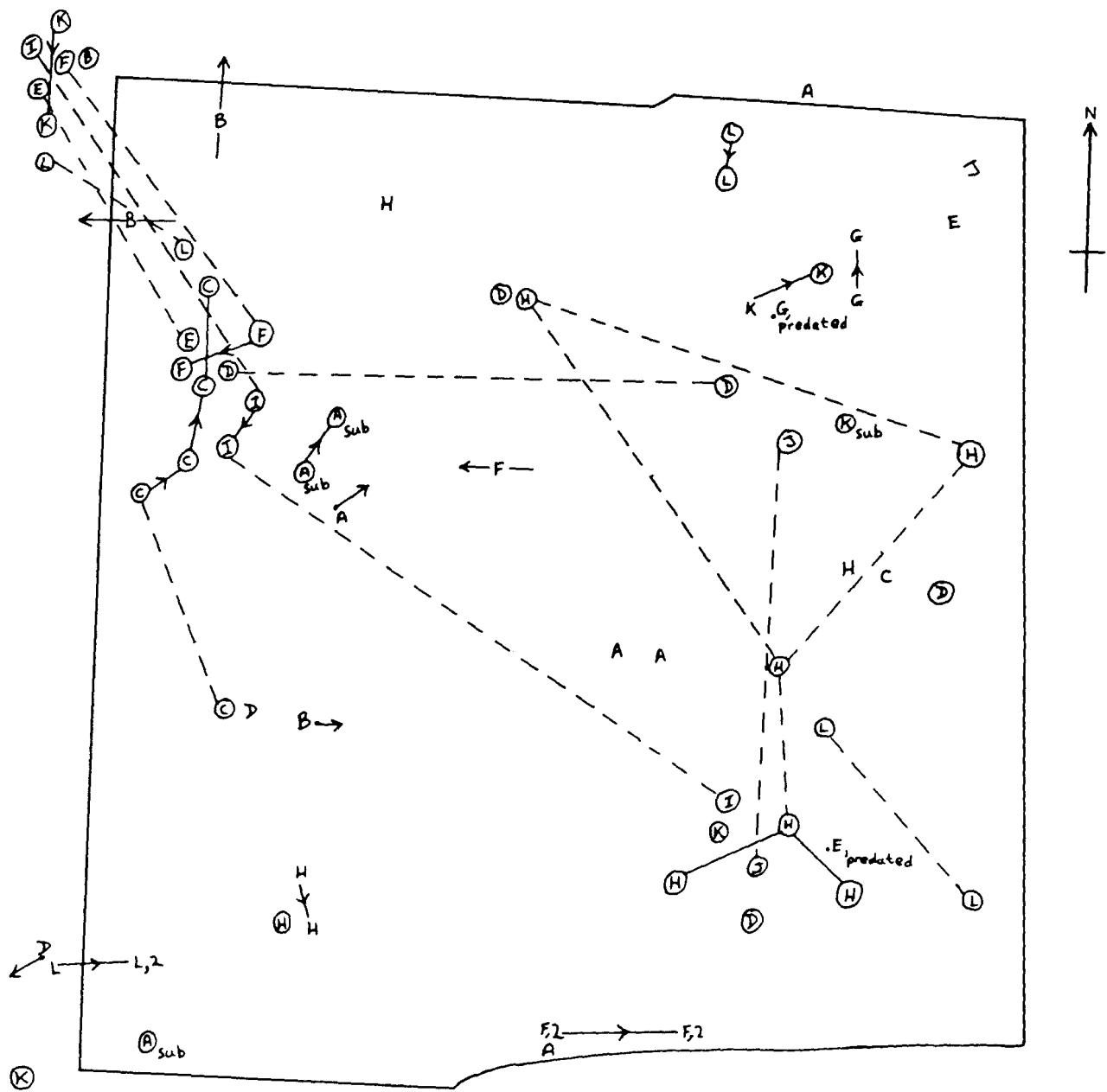


Fig. 1.4b : Song Thrush, Area 2, 1981; Including dusk censuses



Sedge Warbler and Reed Warbler - Snow found the former species easy to census (he did not comment on the latter) due to its persistent singing, and conspicuous behaviour when feeding young. Bell et al (1968, 1973) studied a population of Sedge and Reed Warblers by mapping, nest-hunting and ringing, and found that mapping underestimated the actual populations by 25% in the Sedge Warbler and by 63% in the Reed. The main problem with both species is that the males, which arrive from migration earlier than the females, decrease their diurnal song output once they have mated. There is also a tendency to shift territories during the breeding season. In addition to these problems Haukioja (1968) found individual differences in song output and conspicuity, and that some birds were "wanderers" through the established territories of other birds. It is thus imperative with these two species to carry out censuses during the period of male arrival.

Lesser Whitethroat - Like the previous two species, once mated the males reduce their song output and thus become hard to detect (Snow, 1965). Da Prato (1980) combining mapping with a ringing study found that sometimes the first indication of a breeding bird was when he netted one. In one season when 4 adults and 2 young had been caught, the species map interpreted by the B.T.O. suggested that no birds had held territory. Since the species is not common in Scotland, where his study took place, Da Prato suggested that possibly the low population density diminished the need for territorial conflict, and that singing males may in fact be transients and not territory-holders.

Whitethroat - Snow found this a difficult species to census accurately on farmland, requiring a large number of visits. Even so, some territories could still be overlooked and others defined erroneously. Jensen (1974) also described the species as difficult to census in marshland since it was often colonial, sometimes bigamous, and some males had low song output.

Garden Warbler and Blackcap - Snow found that on farmland, species-maps for these species were difficult to evaluate due to the presence

of isolated song registrations. Since other workers have not commented on these species, perhaps Snow's study area was such as to produce isolated registrations - in woodland these are probably not found.

Chiffchaff and Willow Warbler - Snow found no problems with these.

Hogstad (1967a) found them very difficult to observe other than via their vocalizations: his visual:auditory contacts ratio for them was 1:20. Enemar et al (1979) compared the actual population of Willow Warblers determined by nest-finding to that determined by mapping and found complete agreement in the numbers in his study area. However, agreement between actual territories on the ground and clusters on the map was good but not perfect, since the distribution of nests did not fully conform with that of the mapped song-posts of males, and two clusters were defined where there was only one real territory.

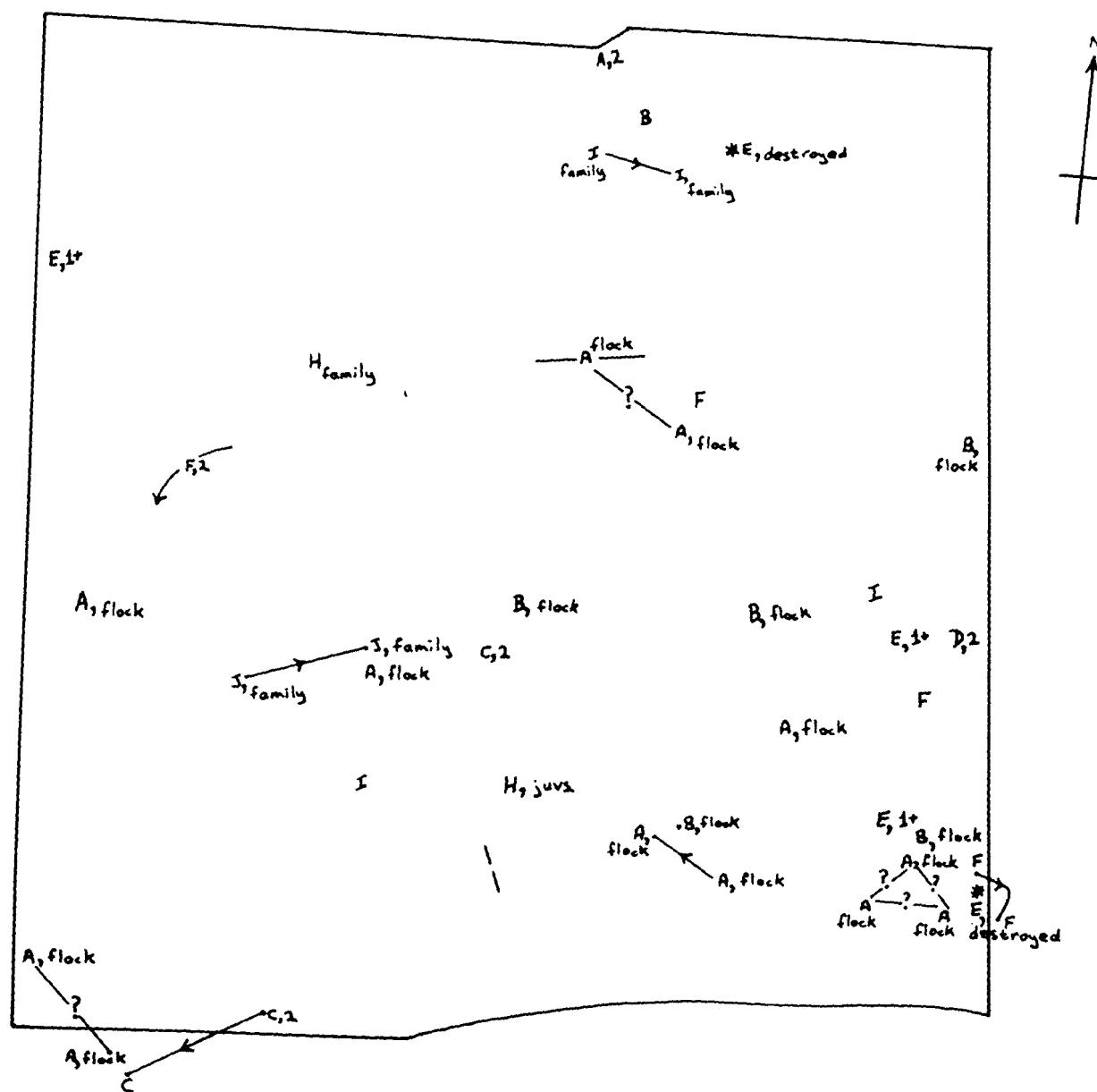
Goldcrest - This species has a quiet, high-pitched song (North and Simms, 1969) which does not carry far and is possibly overlooked on windy days with trees making background noise. Moss (1976) found the species-maps amongst the most difficult to evaluate, but the present author found no difficulty.

Spotted Flycatcher - This species' song consists of high-pitched notes strung together and is easy to overlook if the census-taker is inexperienced. In Scotland the species sometimes does not start singing until late May (this study) and consequently it may not be possible to obtain the three registrations needed to indicate occupation of a territory before the end of the census season, in late June.

Long-tailed Tit - This species has been discussed previously under "analytical problems", where preliminary work by Dougall and North (1983) suggested that it was very important to take into account registrations of winter flocks in a study area, since these were an important factor in the species' breeding biology (Fig. 1.5).

Willow Tit - Hogstad (1967a) found this species quite conspicuous, giving

Fig. 1.5 : Long-tailed Tit, Area 2, 1980



it a ratio for visual:auditory contacts of 1:5, similar to Chaffinch. Its species-maps are therefore probably relatively easy to evaluate.

Coal Tit - Moss (1976) found this, along with Goldcrest, the most difficult species to evaluate. The present author did not find any great difficulty with the species-maps, but this was the one species whose population was overestimated by him in his first series of map interpretations (see Table 1.3).

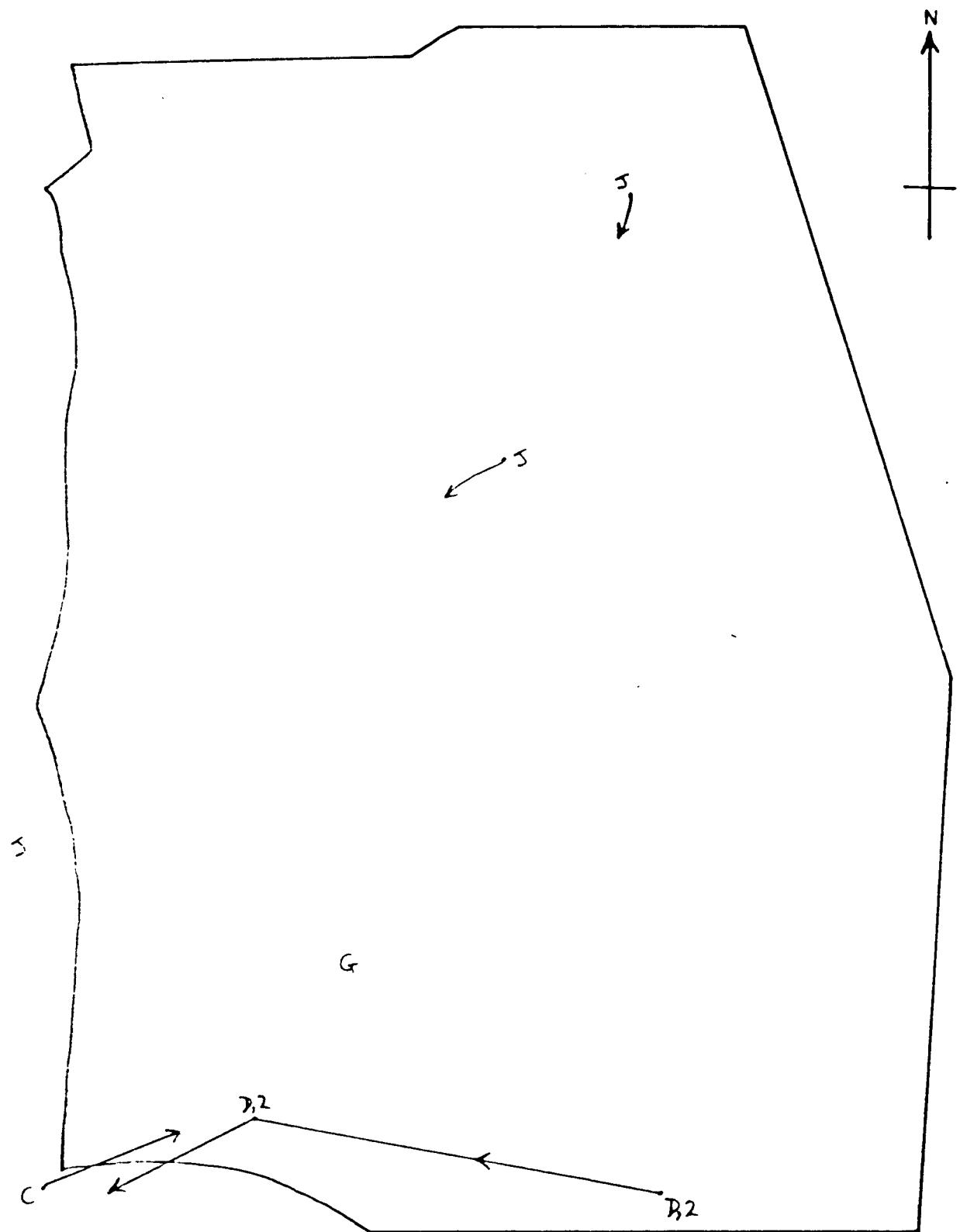
Blue Tit and Great Tit - On farmland these species produce scattered, rather than clustered, registrations, because of the linearity of habitat produced by hedgerows - consequently much subjectivity is involved in interpreting their species-maps (Snow, 1965). Nilsson (1977) in coniferous woodland, also found these species hard to evaluate accurately.

Nuthatch and Treecreeper - Nilsson found that with these two species, along with the tits above, censuses were less efficient in the second part of the breeding season (from mid-May to the end of June) probably due to reduced output of song. The present author suggests in addition that because of its high-pitched calls and song, the Treecreeper could be overlooked on "noisy" days - especially since it is hard to observe by sight. However, he found no great problems in species-map evaluation.

Jay - This is a secretive species with no song, but a distinctive rasping call. Most registrations involve records of this call and are diffuse, making map interpretation unlikely (see Fig. 1.6). The B.T.O. analysts suggest treating it as a non-colonial species.

Chaffinch - This species is a conspicuous singer whose song carries far, and the birds themselves are fairly easy to see, which is reflected in Mogstad's ratio for visual:auditory contacts of 1:5. Moss (1976) found the species-maps of the Chaffinch difficult to interpret, possibly related to population density. While the present author found that

FIG 1.6 JAY AREA 1.1980



although the species produced many registrations, often contemporary, at high population levels these were so numerous as to make cluster determination difficult.

Greenfinch, Goldfinch, Linnet - Snow found difficulty in evaluating maps for these species which are non-territorial and semi-colonial during the breeding season. These behavioural characteristics are now accounted for by the B.T.O. (1976, 1977) recommendations for interpreting colonial and semi-colonial species' maps.

Siskin, Redpoll, Crossbill - The present author considers that the breeding populations of these species are not adequately evaluated by conventional census methods since the birds range widely in song-flights over their breeding areas (Fig. 1:7; Fig. 1:8) and nest semi-colonially. The crossbill is also an early breeder (usually February to April) and may be overlooked in censuses which do not cover the early part of the breeding season (Newton, 1972; Sharrock, 1976).

Bullfinch - This is one of Hogstad's more visually-conspicuous species with a visual:auditory ratio of 1:5. It has a subdued, quiet song which was never heard during three seasons' work in Fife (this study, see Fig. 1:9), and this can lead to difficulties in map evaluation.

Reed Bunting - Several authors have commented on the problems encountered in censusing this species (Enemar and Sjöstrand, 1967; Williamson, 1967; Haukioja, 1968; Bell et al, 1968 and 1973; Jensen, 1974). These problems centre round individual variation in song output; the effect of population density on song output - which was to increase it at higher densities, probably due to a higher level of stimulation; variation in song activity with stage in the breeding cycle; bigamy in some populations; and confusion between singing spring migrants and territory-holding males. Bell et al (1968) found that mapping detected 78% of a known population; and Haukioja found the line transect method totally unsuitable for the species.

FIG. 7: SISKIN, AREA 1. 1980

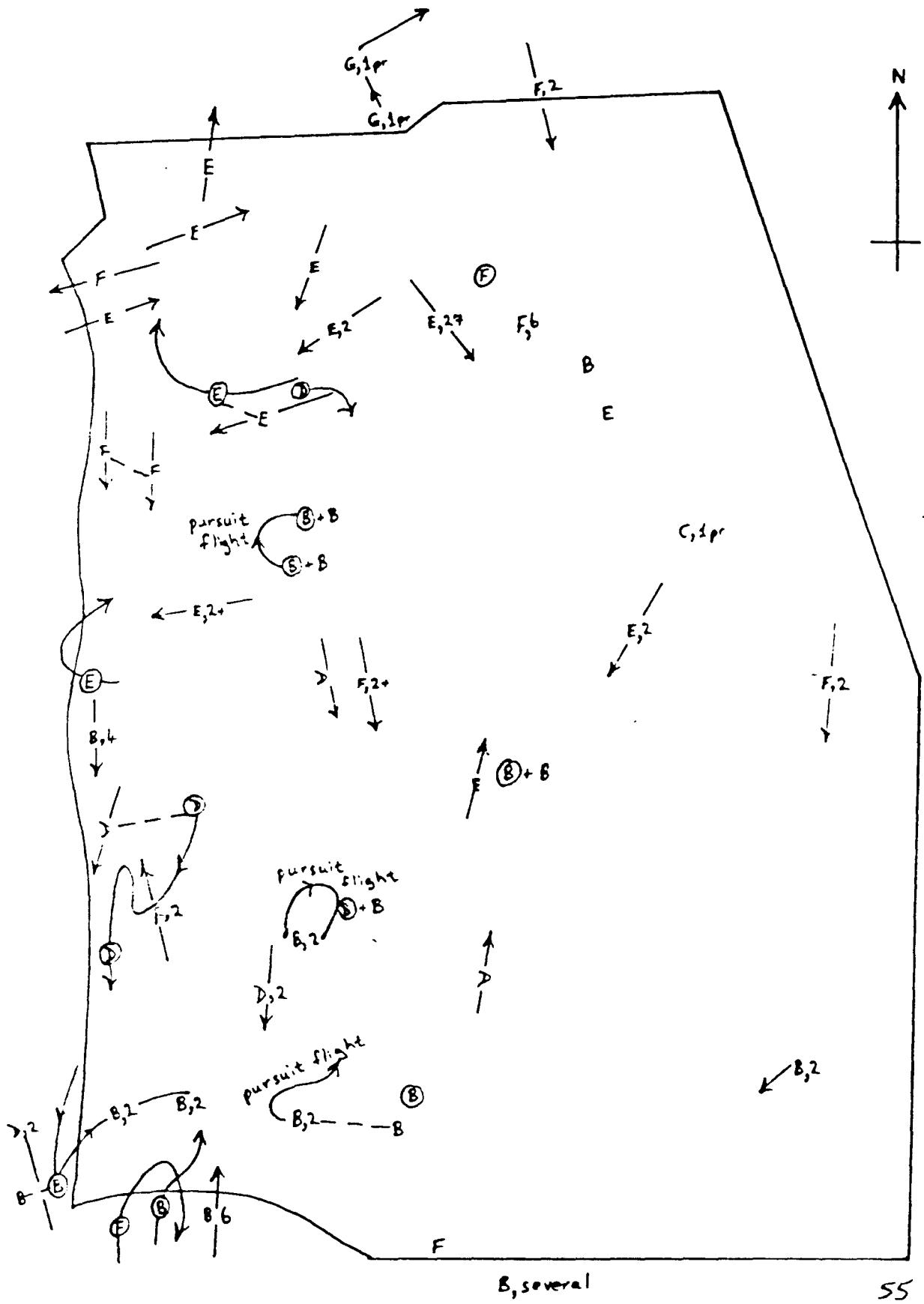


FIG 1.8: REDPOLL AREA 1. 1981

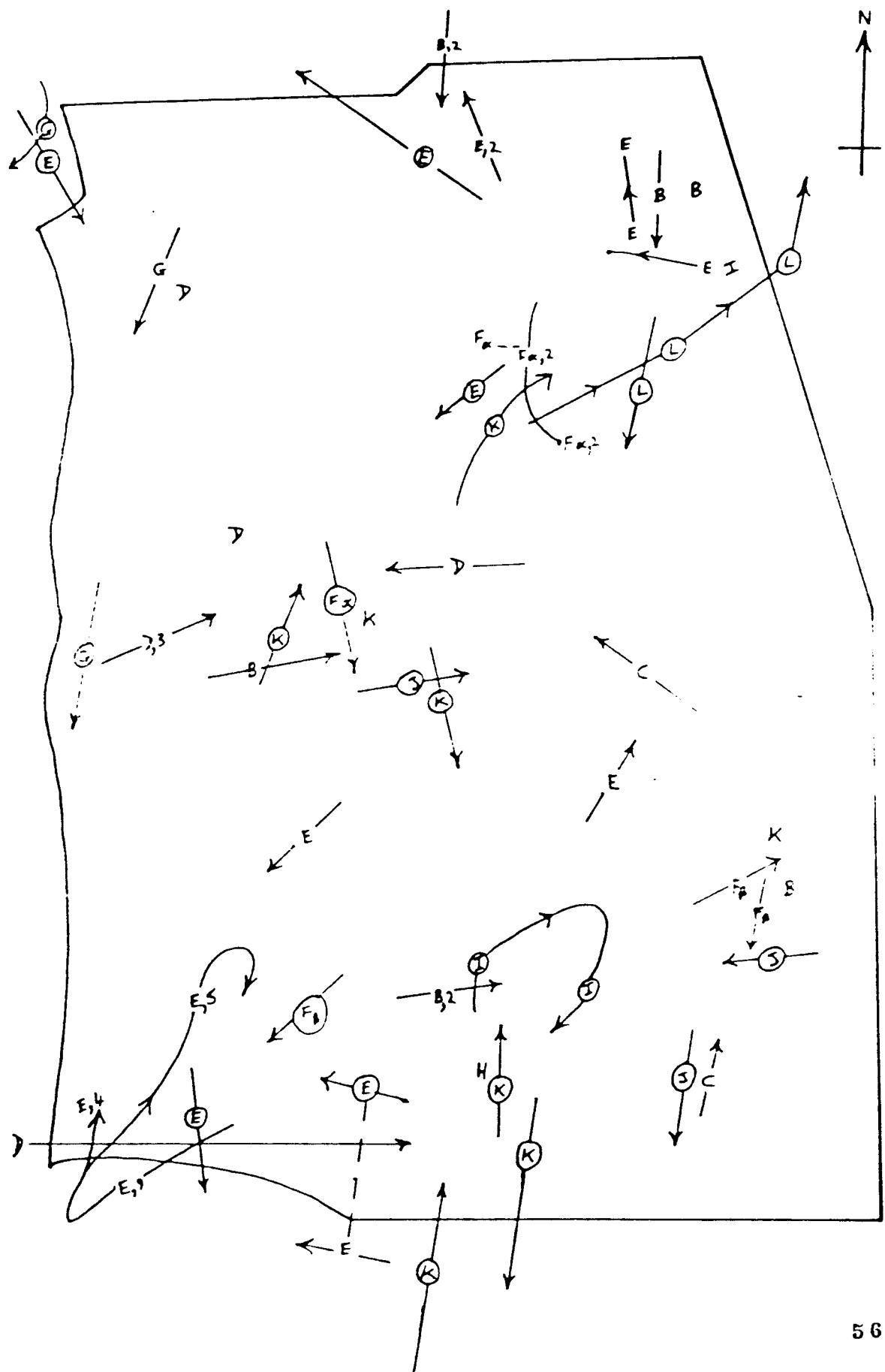
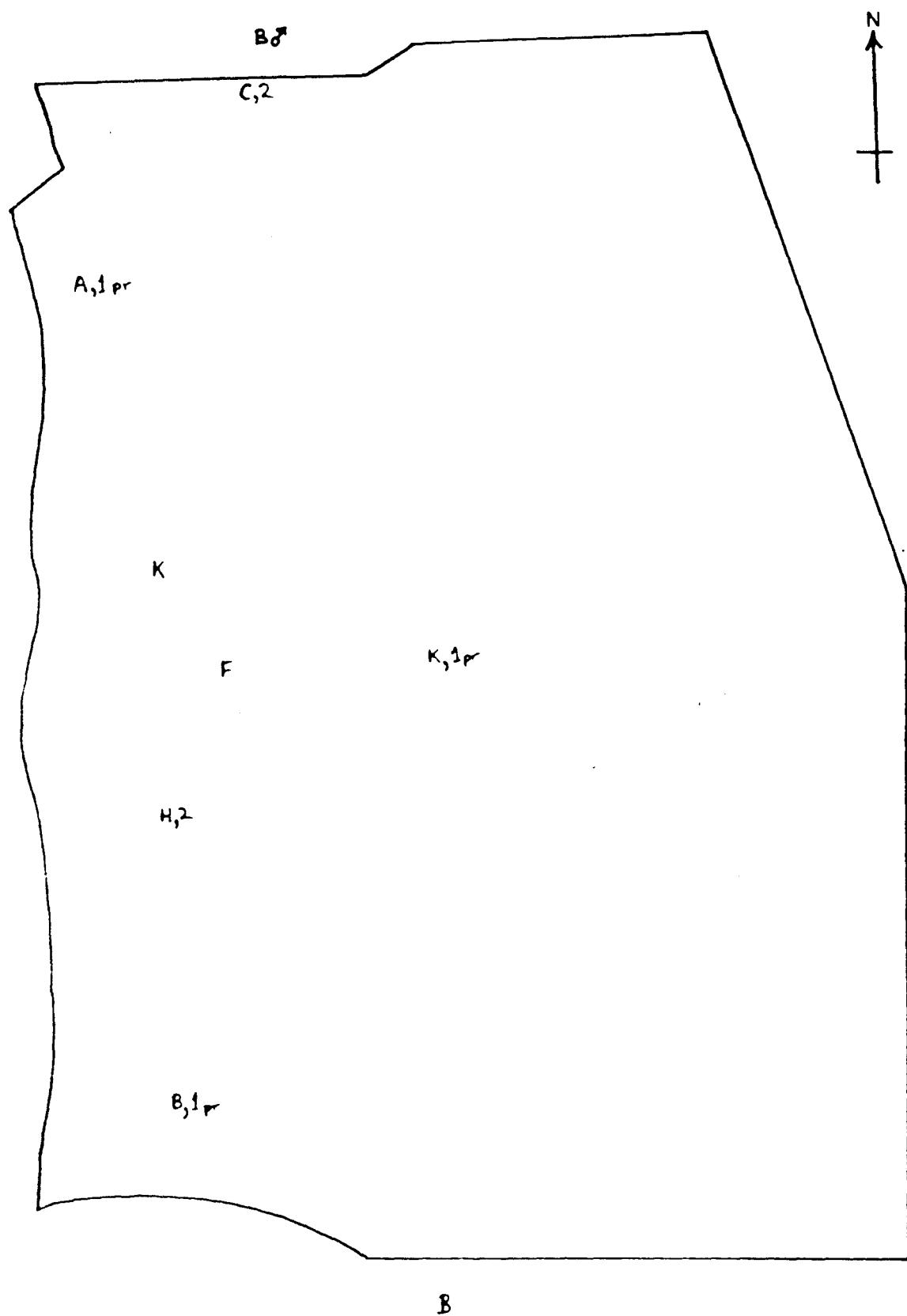


FIG. 9 BULLFINCH AREA 1. 1981



Variation in song output seems a characteristic of many passerine species, and recent studies have shown how weather types can influence such variation. There are other factors involved and the next section discusses them as well as the effects of weather.

1.3 (iii)

(b) SOME METEOROLOGICAL AND LONG- AND SHORT-TERM TEMPORAL INFLUENCES ON BREEDING BEHAVIOUR

Meteorological Influences - General

As a general rule low temperatures, high precipitation and high wind velocities reduce bird song, both individually e.g. snow or wind, and in combination e.g. a blizzard, although the precise effects of the combined factors are not known.

The Alexanders (1908, 1931) were among the first to comment on this, but in addition the source of any song which does occur will be harder to locate under conditions of strong wind (Cox, 1944). Armstrong (1963) reviewed the influences of weather on bird song and concluded that temperature was of dominant importance, though spells of sustained wind, rain or snow each had retarding effects. Hogstad (1967a) divided his census results into three groups, based on the prevailing weather conditions in which they were undertaken:

- (1) Rain with wind at force 2-4 (Beaufort): about 20 registrations per survey;
- (2) Rain clouds present and slight wind, or fair with winds of force 2-5: about 55 registrations per survey.
- (3) Slightly cloudy or cloudy with little wind (force 0-1): about 100 registrations per survey.

In addition, calm foggy days and days with light mild rain seemed to stimulate song, whereas on days with lower than normal temperatures song

was suppressed and a higher proportion of birds were audibly located by contact calls and alarms.

Slagsvold (1977) found that the first song maximum of the community he studied occurred early in "early" springs and that the dates of the maxima of species with naturally early maxima were closely correlated with the temperatures of the days preceding the maxima. He found no significant relationship between the dates of the first song maximum and precipitation. Since the second song maximum occurred at about the same time as the young in the community fledged (at a date already predetermined by the times of laying of the first clutches) it was more closely correlated with the mean temperatures preceding the first song maximum rather than with the second. Again, he found no significant relationship between the date of the second song maximum and precipitation.

O'Connor and Hicks (1980) gave some examples of how weather could affect songsters of birds: rain may make the gathering of nesting material and food easier and birds will sing less when engaged in such activities; nestlings may have to be brooded more during rain thus restricting territorial activity to the nest vicinity; low temperature rain may result in birds having to search more for food and so reduce song, but possibly increase the chance of sight records; wind may cause birds to seek cover.

Weller and Thelinge (1977) found that if days of rain and strong winds were avoided (as recommended by T.B.C.L. and B.I.C.L.) then the weather during a survey should have little effect on the counts obtained. For national-scale surveys, O'Connor and Hicks (1980) found, for the C.B.C., that although seasonality, temperature and rainfall were the most important correlates of the registration totals obtained on a census visit, especially early in the season, it was unlikely that various errors could be introduced into the C.B.C. as this by the normal pattern of weather variation during the period of British census work.

However, the more serious effects of severe weather on depressing bird populations are well-known and are becoming better-documented, with

the amalgamation of data from breeding bird censuses and ringing returns, and it may soon be possible to document the movements of birds across the country during cold weather (Lack, 1980, 1981). For details of the effects of the 1962/63 winter on British bird populations at

- (a) a national scale, see Dobinson and Richards (1964)
- (b) a local scale, see McMillan (1963) and
- (c) a community scale, see Hope-Jones (1966).

Cawthorne and Marchant (1980) have documented the population changes induced by the less severe 1978/79 winter at the national scale - see the appendix to this thesis.

Less well documented are the effects of severe weather during the breeding season, but there can be little doubt that they are sometimes great, and contrast with the normal losses during a breeding season (Tomiačkojc, 1974). Bull and Dawson (1969) described bird mortality after a severe late-spring snowfall in New Zealand, and Ojanen (1979) described the effects of similarly severe weather in late May 1968 in Finland. In the Finnish case bird mortality was related to the sudden drop in temperature, the duration of the snowfall and its depth. Northwards-migrating insectivorous species were worst affected and over 3000 birds of 42 species were found dead - this must have represented only a small fraction of the total killed, possibly several hundreds of thousands. Those birds not killed deserted their nests and formed flocks which wandered to look for food - food shortage was apparently the main cause of death. More males than females were found dead, which Ojanen attributed to males arriving from migration earlier than females, and the poorer survival rate of males in hunger experiments; he did not suggest that many females may have died on their nests or that females are less brightly-coloured than males and probably harder to find lying on the ground. In pairs of congeneric species, the species which wintered farther south appeared to be more severely affected by the severe weather, but possibly many of these had not arrived from the south. Although this meteorological incident was harmful in the short-term, it had little long-term effect with many species apparently at the normal strength in subsequent years.

Meteorological Influences - Specific

Bull and Dawson (1969) and Ojanen (1979) mentioned that the populations of some species were more susceptible to the effects of severe weather than others (usually those of smaller body size and lower weight - Cawthorne and Marchant, 1980); and evidence is now growing that the behaviour of some species is more affected than others by variations in the weather, both within and between days :-

Wren: Garson and Hunter (1979) found that for this species, the number of Wren songs per hour had the highest correlation with the minimum temperature during the preceding night, suggesting that the recent temperature regime has a great effect on the time allocated by the birds to singing behaviour, and that as the temperature rises, the amount of song increases.

Blackbird: Burkitt (1934) found that as the breeding season progressed and the weather "improved", Blackbird song periods changed from the evening to the evening plus morning, and finally to all through the day.

Song Thrush: Burkitt (1934) found that this species' song period began earlier in the season than the Blackbird's and that its song was concentrated in the evening, being especially prominent on dull evenings. Higgins (1979) studied the mid-winter morning song of the Song Thrush and found its onset was delayed by decreasing intensity of illumination and increasing wind strength; general vocal activity was positively correlated with air temperature.

Great Tit: Garson and Hunter (1979) found similarity with the Wren in the relationship between song activity and the recent temperature regime, in that the higher the minimum overnight temperature, the longer the duration of song per hour on the following day. There was also a strong positive correlation between the amount of time spent singing and time of year for the Great Tit, but not for the Wren.

Chaffinch: Burkitt (1934) found that the dusk song of this species was less dependent on the weather than the dawn song. The dusk song often stopped exactly at sunset and rarely went to fifteen minutes after it; the dawn song started fifteen minutes after sunrise in February and 27 minutes before sunrise in June - possibly related to increasing light intensity and early morning temperatures.

The next section deals with this factor in more detail, starting with an investigation into why there is a "chorus" at dawn.

The Influence of Time of Day

Henwood and Fabrick (1979) hypothesised that, since early morning songs typically were used for territorial communication or mate attraction, selection would favour the caller who could reach the greatest area with an identifiable song; they found that early morning microclimatic conditions were as optimal for sound propagation as would be present at any other time during the day or night. Depending on the environment, calls voiced in the early morning were up to twenty times more effective in area of broadcast coverage than the same amplitude signal broadcast at mid-day. Increasing height above the ground also increased the area of broadcast coverage. It is hardly surprising therefore, that many songbird species have high song outputs in the early morning, and often sing from elevated positions. Catchpole (1979) suggested that songs are specifically and individually recognisable and that males learn not only each neighbouring conspecific's song but also their normal singing locations. A sudden change in location might indicate e.g. that a neighbour was extending his territory and that such a threat would have to be resisted.

Richards (1981) indicated how such factors could affect census efficiency, much of which is based on identification of the singing bird and estimation of its location. The acoustical properties of the environment interfere with both of these, the effects dependent on habitat type. In open fields the primary sources of sound degradation are

attenuation and amplitude fluctuations. Attenuation limits the maximum range of detection, and alters the frequency composition of the sound as heard by the observer. Fluctuations are random and interfere with amplitude modulation - this can cause error in estimation of distance. In forests attenuation has a similar effect, though the exact values depend on the type of forest. Reverberation of sound is of major importance as a source of sound degradation, and virtually obliterates the fine details of songs at moderate distances, thus interfering with recognition. Sound scattered by trunks and foliage also makes estimation of the location of the singer more difficult. Adaptation by some bird species to combat the effects of song degradation by the environment may both help and hinder species identification and location estimation.

It is obvious from the above that in any census of territorial songbirds, the most efficient time to carry out the census is in the early morning when the birds are territorially active. This is recommended by the I.B.C.C. and B.T.O., but has also been commented upon by other authors.

Hogstad (1967a), following on from Enemar (1959) conducted an experiment with continuous 24-hour observations of breeding birds and found that his census efficiency was highest between 0200 - 0930 hours with a maximum at 0430 - 0700. Weber and Theberge (1977) found that most species sang less frequently as mornings progressed; Shields (1977), using line transects, registered most contacts in the early morning during the breeding season, as did Järvinen, Väisänen and Haila (1977) using a different transect type. These latter workers found some inter-specific differences, however, and called for an investigation into the daily activity patterns of different populations of a species to see if these were affected by geographic location. Indeed Slagsvold (1977) found regional variations in the Goldcrest's period of song maximum, and found that with other species there was much evening song activity during their periods of song maximum.

The Influence of Seasonality

/Slagsvold's

Slagsvold's (1977) findings are probably the most important in this respect and have been discussed above when considering the general influences of meteorological factors on dates of song maxima. It is necessary to bear in mind that increasing daylength is the most important stimulus to gonadal development in northern latitude birds, while subsidiary proximate factors (see Lack, 1954) trigger the onset of egg laying. These stimuli probably operate over a shorter time period the further north that birds breed, giving rise to sharper onsets of the breeding season there than at lower latitudes.

Järvinen, Väisänen and Haila (1977) divided the breeding season into three periods: early, middle and late, and found that their density estimates for forest censuses from the late season were 20% less than in mid-season, but there were no significant differences for field censuses.

Weber and Theberge (1977) found that time of year had a significant effect on breeding bird counts, based mainly on the timing of arrival and passage of spring migrants into and through their study areas. Their results are complicated by the fact that their methodology does not adequately distinguish between territory-holders and transients.

O'Connor (1980) in a study of simulated short-term "expedition-type" mapping censuses found no evidence of major changes in census efficiency through the season apart from the possibility of a slight decline in late June. At the species level firm conclusions about the effects of seasonality on efficiency could not be reached. It was suggested that the "expedition approach" to mapping censuses would produce the most efficient results if carried out in mid-season.

O'Connor and Hicks (1980) found a systematic trend towards seeing and hearing more bird activity in later censuses in a season, but that there was a bias which varied between species: early-breeding species having finished breeding and perhaps commencing moult by the last few census visits would become inconspicuous and yield fewer registrations

than late-breeding species still in the midst of their breeding activities. The seasonal increase in total registrations indicated either that most species were more frequently registered later in the season or that those birds numerically most abundant were registered most frequently in later visits. Whichever the case, any future analyses of the relationship between registrations or census efficiencies and seasonality, especially where measured by temperature, would have to be carefully interpreted.

The meteorological, temporal, and seasonal effects on bird census work offer a profitable area for future study, but in the meantime so long as censuses are conducted on mild, dry and rather windless days in the early morning, and extended throughout the breeding season, then the interpretation of their results will be made that much easier.

1.3 (iii)

(c) HABITAT "WORKABILITY"

Ideally when censusing birds, the nearer to the birds that the census-taker can get the better, so that they can be positively identified and their behaviours observed. In reality, however, the best that can be aimed for when using a 50 m grid in mapping censuses, or a 50 m wide transect band, is to be within 25 m of each bird. Most study plots present few problems but some habitat types can influence this "contact distance" as discussed by Oelke (1981b) and below.

Farmland: Snow (1965) and Williamson (1971a) found little difficulty in working on farmland with the mapping method, but the presence of hedgerows introduced an element of linearity into the distributions of territorial clusters for some species.

Moorland and grassland: The present author found that some birds, especially the larger non-passerines, took flight at great distances on his approach and that it was useful to plot the positions of such birds from a distance (using binoculars) before going on to the study

plot. Oelke (1981b) also listed habitats with low growing vegetation as difficult to census.

Marshland: Bell et al (1968, 1973) and Jensen (1974) found this habitat type difficult to census especially where islands, dense reedbeds and heterogeneity of vegetation were present, since these obscured birds and made observation of their behaviour and of their precise location difficult.

Ecotone: Hogstad (1967b) reviewed the little work previously conducted on this transitional habitat composed of a variety of types of vegetation and concluded that bird population densities were always higher among habitat boundaries. This could mean the overlooking of more song and behaviour due to the higher numbers present than on more homogeneous habitats. Cousins (1977) found that the mosaic of habitats and greater proportion of "edge" on farmland precluded the use of normal community measures. Marchant (1981) reported including 10 - 27% edge clusters wrongly in a census plot studied by him, leading to inflated estimates of density. He suggested that observers were biased towards including peripheral observations as within a plot to make it seem "richer".

Woodland and forest: This presents problems only at its young stage where there is thicket or scrub development, and at the mature stage when there are areas of thick undergrowth present. Particularly difficult of access are areas of thorn scrub such as Gorse, Sea Buckthorn and Hawthorn; areas of birch thicket and the thicket stages of commercial coniferous forest. Extensive work in Scandinavia (by such as Enemar et al, 1976; Järvinen, Väisänen and Enemar, 1978; Järvinen, Väisänen and Walankiewicz, 1978) using both mapping and line transects has shown that there are few difficulties with mature birch and coniferous habitats.

It has been shown in the previous subsections that the successful and efficient use of songbird techniques is far from straightforward and depends on several mechanical (for bird censusing), analytical and biological factors. These factors have been discussed in some detail,

mainly in relation to the mapping method, but the latter group - biological factors - is relevant to the other census techniques of line transects and spot-counts. This must be borne in mind in the sections below, which discuss the methodologies and associated problems of line transects and spot-counts.

1.4 LINE TRANSECTS

All forms of line transect counts ("A sampling route that bisects a surveyed area followed by an observer counting contacts over a measured distance" Ralph, 1981) represent sampling procedures, and so their analyses have a more statistical base than do mapping census analyses. Three main forms of line transects are used in bird census work: simple line transects which yield data on the relative abundance of species; and the "Emlen-type" and "Finnish-type", both of which are intended to yield data on absolute densities of bird populations through the use of correction factors.

Anderson (1981) concluded that the majority of line transect types (within the three main forms) were ad hoc in nature, that they lacked a firm foundation, and that little was known about their small-sample properties, their sampling variance estimators and other parameters of their sampling.

Eberhardt (1968) produced a classification of line transects (Fig. 1.10) which was updated by Moss (1981) (Fig. 1.11) with respect to the inclusion of the Finnish model. Smith (1979) produced simple definitions of various line transect sampling techniques and Tilghman and Rusch (1981) compared 12 variants of line transect methodology (their Table 1) but their results did not clearly reveal any one method or group of methods which produced better estimates than another.

1.4 (i) SIMPLE LINE TRANSECTS

This form of census was used in most of the surveys of breeding birds made before the publication of Enemar's paper in 1959. Lack and Venables (1939) reported on its use in a national survey of woodland birds organized by the B.T.O. The method simply required birdwatchers to record the number of birds of each species noted on woodland walks ("unlimited distance strip transects" - Ralph, 1981). The maximum

count for each species from several walks was coded and the average code number used to give an index of relative abundance between bird species and different types of woodland. Unfortunately no standard method was established and the derived index figures were largely meaningless since they suffered from variations in the number, length and duration of the walks, in addition to variations in the size of woodland and amount of "edge" habitat present.

Davis (1942) working in Cuba, counted the number of birds along a selected route representative of the habitats of the surrounding area. His sampling strips were of various widths; he thought that he would record all the birds present along his strips; and he omitted those species with "peculiar" distributions. These factors introduce great bias into his method and so his results are not very reliable.

Hayne (1949) described a transect method for counting game-birds based on flushing them. This was updated by Eberhardt (1968) who assumed (wrongly) that "chain reactions" did not occur during flushing (that is, that one bird flying off did not cause another one to do so), that there was no movement away from the transect route before flushing occurred, and that the probability of simultaneous sightings was very small. Further discussion and mathematical treatment of flushing methods can be found in Gates et al (1968), Gates (1969) and Sen, Tourigny and Smith (1974).

Yapp (1956a) provided a theoretical analysis of the variables involved in line transect methodology, based on the formula:

$$D = \frac{Z}{2R (\bar{u}^2 + \bar{w}^2)^{\frac{1}{2}}}$$

where D = density per unit area.

Z = number of encounters between observer and organism in unit time.

R = effective radius of the organism.

\bar{u} = mean speed of organism.

\bar{w} = mean speed of observer.

Skellam (1958) discussed the equation and the mathematics of it. He suggested that line transects would give best results in summer, when birds are more conspicuous and populations stable and confined to their breeding areas. He suggested values for \bar{w} of 1.6 - 3.2 km/hr, since below 1.6 not enough ground would be covered, while above 3.2 not enough attention would be paid to the job in hand. The theoretical approach of Yapp could not be put into practice because (a) two of the parameters (R and \bar{u}) cannot be measured; (b) he did not employ any lateral boundaries to his transects since he thought these would be hard to apply visually (he did not seem to consider marking them in the field); and (c) he did not specify how many transects should be carried out in a season. Yapp's paper was not well received by general birdwatchers who were upset by the use of mathematics (Norris, 1956; Welch, 1956; Suffern, 1957).

FIGURE 1.10 : A CLASSIFICATION OF TRANSECT MODELS BASED ON THE DETECTION OF OBJECTS (AFTER EBERHARDT, 1968)

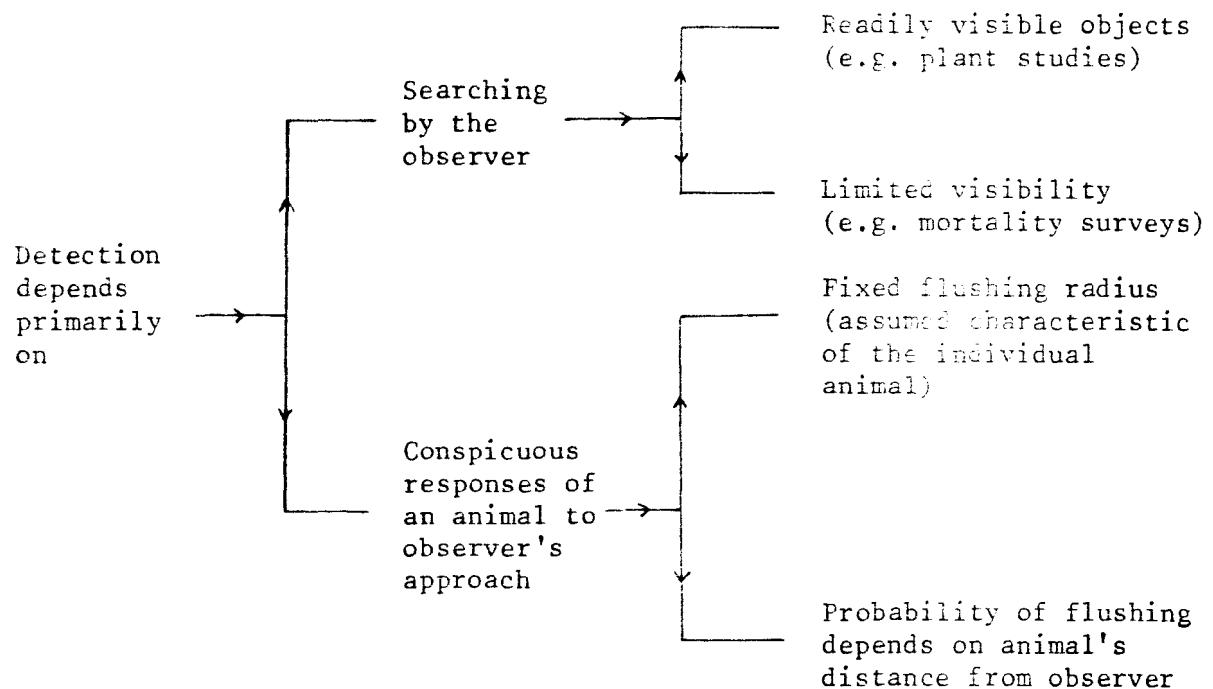
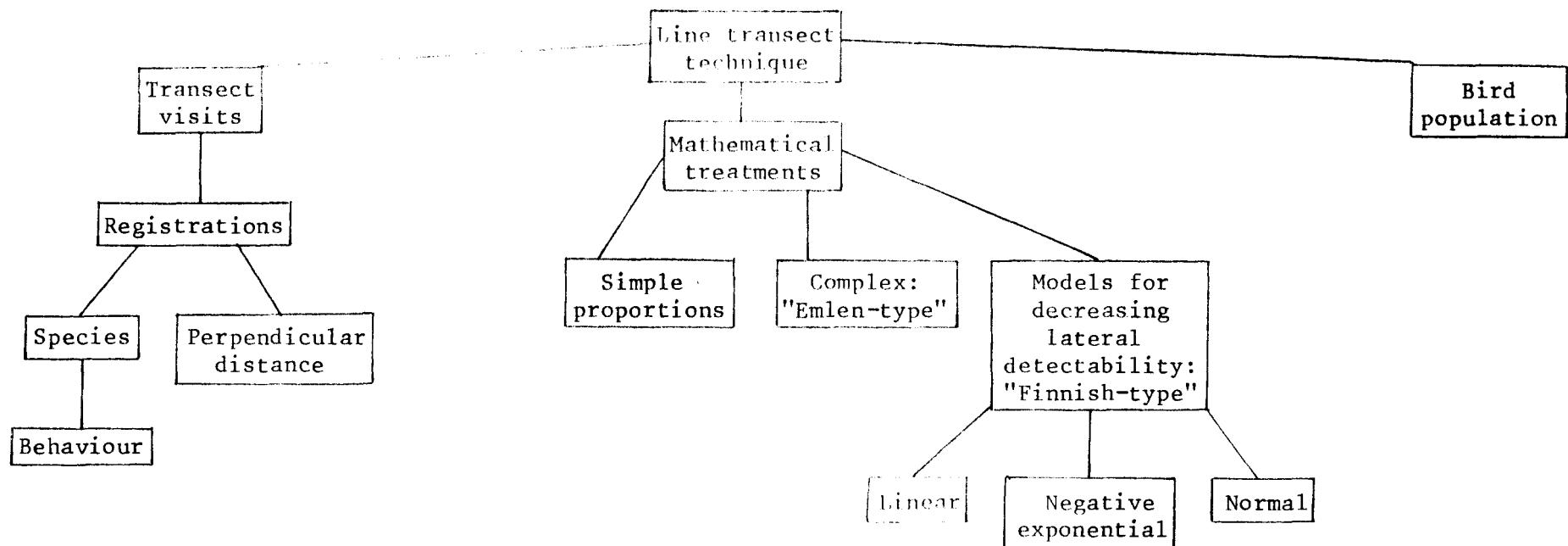


FIGURE 1.11 STRUCTURED DIAGRAM OF THE LINE TRANSECT TECHNIQUE (AFTER MOSS, 1981)



In practice Yapp (1956b, 1959, 1962, 1974) used as his census method a simple transect in which the number of contacts with members of each bird species was recorded on each visit. After all the visits had been completed the relative abundance of each species was calculated, based on percentage representation. The results take no account of the conspicuousness differences between species, and within one species but in different habitats; and again Yapp did not specify the use of lateral boundaries, so his results were influenced by habitat factors as well. They are therefore of limited value, as are those of Simms (1971) who used a basically similar method.

Watson (1969) used the simple line transect with single observers and with pairs walking in parallel, and found that even with the increase in the number of observers birds could still pass undetected or be flushed before observers reached them. No fixed lateral boundaries were used.

Moss (1981) also did not use boundaries to his simple transects ("unlimited distance transects") and found high levels of inconsistency in inter-habitat comparisons, which may have been due to this factor. It is difficult to understand why, with simple line transects, their users do not impose some lateral limits to their observations. Birds differ in their conspicuousness, as has been discussed above, and the more conspicuous (especially audibly) will be detectable at greater distances than the less conspicuous ones. Also, the wider the study area habitat, the more birds will be recorded if no limit is applied. Habitats differ in their "workability" and in their ability to screen birds from view or hearing. At least by imposing lateral limits to the recording area there would be some degree of standardisation in the census method between habitats, which might permit comparisons to be considered. The actual physical setting-up of the boundaries, either by tree markers or poles, does not take very long especially if two people work in parallel. For example, it took the present author with the help of an assistant two hours (= 4 man-hours) to mark out with thin bamboo canes at 25 m intervals, 1.15 km of transects on open grassland and three hours

(= 6 man-hours) to do the same over 1.35 km in birch scrub.

Bibby (1978) working on heathland, surveyed 1 ha squares along a 7 km transect route marked with permanent markers at 500 m intervals. In the present study three transects - evenly-spaced and orientated due magnetic north - were used in the grassland and birch scrub habitats mentioned above. Each transect was 50 km wide and the markers along its length were colour-coded in parallel. A line as close to the centre of each transect was followed and all birds within each sector (25 m x 50 m) were recorded on field sheets using a species and behaviour code. Their distances from the observer were not recorded and so the method would be termed a "strip survey" by Smith (1979). As many transects as possible were made in each season, but mapping work took precedence and if some mapping days had been lost due to bad weather, they were accounted for by foregoing transect work. At the end of each season the field data were converted into total contacts and audible contacts for each species, and relative abundancies calculated. It is not possible to calculate population densities from such data resulting from simple line transect work because no idea of territory size or distribution is available, and the transect width is rather narrow compared to territory dimensions, but if it were any wider then probably many birds would be overlooked.

1.4 (ii) EMLEN-TYPE LINE TRANSECTS

Breckenridge (1935) described a transect method in which he noted the distance of each bird recorded from his route. He found that few birds were flushed from directly on the line, but that the number flushed increased as the distance from the transect-line increased, up to 20 m, and decreased noticeably beyond 30 m. He thought from this that he had seen all the birds up to 30 m away, including those which moved away from the centre-line to either side.

This principle of Breckenridge's was largely ignored until 1971 when Emlen described his development of it. In this he counted all the birds

recorded from the transect line in 10-foot strips up to 100 feet on either side of this line, then in one strip 100 - 200 feet from the line, one strip 200 - 400 feet and one beyond 400 feet (later defined as "variable distance strip transects" by Ralph, 1981). He recommended working in study plots of about 50 acres (20 ha) of uniformity of physiognomy and vegetation, walking at 0.5 - 1.5 mph (0.8 - 2.4 km/hr) in woodland and at 1 - 2 mph (1.6 - 3.2 km/hr) on open ground. He did not record birds seen ahead of him until they were within 100 feet, and he used vocal sounds to lure hidden birds into view, thus introducing an element of bias into his method. He did not mark out lateral boundaries in the field and noted that it was difficult to judge distances accurately beyond 100 feet. It is felt here that it is not always easy to judge accurately distances less than 100 feet, especially when there are ten bands to contend with on either side of the observer. Emlen claims he tested estimated distances in the field by using a range-finder and also by pacing. These introduce other biases into his method: in the first case by stopping, he may have recorded more birds than he would have had he kept walking, or conversely he may have disturbed birds and not seen them; in the second case he certainly would have disturbed birds.

Scott et al (1981) found that under good field conditions observers were able to estimate distances to birds within \pm 10% (range of averages: -9.1% to +6.3%) and that the range of all distance estimates was a quarter to four times the measured value, with 95% falling between $4/7$ and $1\frac{1}{2}$ times. There were significant differences between observers' estimates for different species. They suggest that to reduce the bias in estimates, observers could be trained, distances could be marked in the field, range-finders could be used, and more robust analytical techniques employed: however these all add to costs in terms of time, money and enthusiasm.

Emlen himself, and De Jong (1981), acknowledged that subjective estimates of the distance to unseen singing or calling birds are a serious source of error. They proposed that measurement of the detection threshold

distance (D.T.D.) of a song (the maximum distance from which a song can be heard by an experienced observer with full hearing ability*) could provide more reliable estimates than "the elusive and highly subjective reference standards (then) in use." They hypothesized that D.T.D. values would prove sufficiently objective and uniform when obtained in a standard manner to permit the preparation of reference tables applicable for census work by competent observers in a variety of situations.

Perhaps the most objective comment on the evaluation of line transects is provided by Engel-Wilson et al (1981), using computer simulation to identify variation due to random fluctuation of density estimates inherent in the technique. Effects of transect length (457 - 1828 m), number of censuses (up to 15) and density value (4/40 ha to 201/40 ha) were tested. For moderately abundant species (35-37 birds/ha), between 6 and 9 surveys at least 914 m in length were sufficient to obtain accurate and consistent estimates. At least 15 surveys were needed for shorter transects.

From the distribution of the birds within the lateral strips of his transects, Emlen calculated "coefficients of detectability (C.D.)" for each species - comparable to Yapp's (1956a) "effective radius of the organism". Emlen treated song and non-song registrations separately, counting one pair for each singing bird and a half pair for the others; for density estimates he took the larger of the two values. He calculated his C.D. values from histograms (where a plateau width was estimated), which represented detection of constant numbers of birds) as did Moss (1976); and Moss (1981) showed that this could be done from tables (Figure 1.12). "Uncorrected densities" resulted from the use of the C.D.s; "corrected densities" were obtained by Emlen also calculating

* Ramsey and Scott (1981) tested the hearing of 274 participants at the Asilomar conference (Ralph and Scott, 1981), the results of which tests indicated large differences in the hearing ability of active birders. Simulation of the detectability of birds for observers with hearing thresholds of 10, 20, 30 and 40 dB indicated differences in the area effectively surveyed as large as an order of magnitude.

an "incompleteness factor (I.F.)" for each species, based on a comparison between the population estimates derived from his transect method and a mapping study. The parameters C.D. and I.F. are thus two parts of the conspicuousness of a species: the C.D. when multiplied by the transect strip width represented approximately the average range over which a species was detectable, whereas the ratio 1:I.F. represented the ratio of individuals close to the route which were detected.

Moss (1976) used a modified form of the Emlen line transect type, in which he counted one pair for each singing bird and a half pair for other registrations, and calculated a C.D. value based on all observations, which maximised the sample sizes. Moss also calculated a separate set of densities from song observations only, giving rise to C.D. values based solely on song. "Song densities" were always greater, for all species, than the non-song densities calculated from all contacts. Moss also tested a value of 0.8 pairs (rather than 0.5) for each non-song registration, to take account of the greater conspicuousness of males relative to females. This modification increased uncorrected densities, lowered incompleteness factors and made little change to the variability of the results.

Moss (1981) progressed with his brother's work and found that C.D.s in his Welsh study areas varied considerably, due to small sample sizes, daily variation in song-activity, and longer-term variations influenced by the stage of breeding. He concluded from his results that the C.D. was not a reliable factor upon which to base population estimates and that Emlen's statement that species appeared to have characteristic C.D. values varying within limits and in a predictable manner with the type of vegetation was untenable. In addition, he found that if a sufficient number of visits were to be carried out on a census site to reduce the variability of the C.D. estimates to an acceptable level, then as much time would be spent as in the mapping method. This, coupled with the need to use a mapping census to allow calculation of incompleteness factors, rather defeats the object of using complex line transects to save time in censusing birds.

FIGURE 1.12 A WORKED EXAMPLE OF THE NUMBER OF TERRITORIES ESTIMATED
BY EMLEN'S (1971) LINE TRANSECT METHOD (AFTER MOSS, 1981)

| | Distance (m) from transect route, 3600 m long | | | | | | | | | Total |
|---------------------|---|------|-------|-------|-------|-------|--------|------------|----|-------|
| | 0-5 | 5-10 | 10-15 | 15-20 | 20-25 | 25-50 | 50-100 | ≥ 100 | | |
| Singing males | 3 | 4 | 2 | 5 | 0 | 6 | 1 | 0 | 21 | |
| Other registrations | 6 | 2 | 4 | 6 | 1 | 5 | 0 | 0 | 24 | |
| Total | 9 | 6 | 6 | 11 | 1 | 11 | 1 | 0 | 45 | |

(A) 1 singing male = 1 territory; 1 other registration = 0 territories

$$\text{No. of territories} = (21 \times 1) + (24 \times 0) = 21$$

Plateau width = 20 m

$$\text{Projected number of registrations to } 100 \text{ m} = 14 \times \frac{100}{20} = 70$$

Actual number of registrations to 100 m = 21

$$\text{C.D.} = \frac{21}{70} = 0.30$$

$$\text{density} = \frac{21}{0.72} = 97 \text{ territories/km}^2$$

(B) 1 singing male = 1 territory; 1 other registration = 0.5 territories

$$\text{No. of territories} = (21 \times 1) + (24 \times 0.5) = 33$$

Plateau width = 20 m

$$\begin{aligned} \text{Projected number of registrations to } 100 \text{ m} &= 5((14 \times 1) + (18 \times 0.5)) \\ &= 115 \end{aligned}$$

Actual number of registrations to 100 m = 33

$$\text{C.D.} = \frac{33}{115} = 0.287$$

$$\text{density} = \frac{115}{0.72} = 160 \text{ territories/km}^2$$

/Continued

FIGURE 1.12 continued

(C) 1 singing male = 1 territory; 1 other registration = 0.8 territories

$$\text{No. of territories} = (21 \times 1) + (24 \times 0.8) = 40.2$$

Plateau width = 20 m

$$\begin{aligned}\text{Projected number of registrations to } 100 \text{ m} &= 5((14 \times 1) + (18 \times 0.8)) \\ &= 142\end{aligned}$$

Actual number of registrations to 100 m = 40.2

$$\text{C.D.} = \frac{40.2}{142} = 0.283$$

$$\text{density} = \frac{142}{0.72} = 197 \text{ territories/km}^2$$

Notes

$$(1) \text{ C.D.} = \frac{\text{Actual number of registrations to } 100 \text{ m}}{\text{Projected no. of registrations to } 100 \text{ m}}$$

$$(2) \text{ Density} = \frac{\text{No. of registrations}}{\text{C.D.}} \times \frac{1}{\text{Area covered by transect}}$$

In the above examples, there were no registrations at over 100 m

$$\text{so density} = \frac{\text{Projected no. of registrations to } 100 \text{ m}}{\text{Area covered by transect}}$$

Robinette et al (1974) suggested that the Emlen transect method might be suitable for single-species studies e.g. with grouse, but as soon as more than one species were to be investigated, problems would arise with observing all the birds and with estimating perpendicular distances to them. In studies of habitat selection Dawson (1981) suggested that small or variable cut-off distances would be needed so that the birds encountered would be associated with the "correct" habitat.

In 1977 Emlen presented a revision of his 1971 model, with modifications for recording detections, establishing specific strip widths, bypassing the calculation of C.D.s, requiring a measurement of song frequency, and calculating densities. Emlen admitted that his method presented density estimates for birds present at a particular time rather than for those wholly or partially resident during a season, and that his 1971 method was largely unsatisfactory for breeding season studies since many individual birds would not have been detected, even at close range e.g. nesting females which remain silent. Emlen's revision was based mainly on the two variables affecting the relation between the number of registrations obtained along a transect and the absolute density of birds represented by that number:

- (1) cue attenuation with lateral distance from the transect
- (2) the frequency with which birds produce visual or auditory cues detectable by an observer at any range.

He outlined new field procedures for each of three seasons: the non-breeding season, the breeding season, and the two transitional seasons between total breeding and total non-breeding. For breeding season studies - those relevant to this thesis - Emlen suggested using only song registrations and making adjustments for undetected males and females based on indices of song frequency, but again a form of mapping census is needed to derive song frequencies. In addition the ranges over which songs can be heard vary between species, giving rise to species-specific song-boundaries which introduces a large element of bias, further complicated by study area size and habitat size. All in all, neither of Emlen's line transect methods seems suitable for use in studies of breeding songbird populations.

Later work on the Emlen-type method by Franzreb (1981) and by Hutto and Mosconi (1981) involved, in the former case, using "all observations" and pooling them into smaller distance increments than those recommended by Emlen. For fixed-strip transects, Franzreb suggested that species could be assigned belts of different widths, depending on their detectability characteristics.

Hutto and Mosconi (1981) tested the Emlen-type transect using multiple observers, comparing a 1 km transect covered by 1 observer 4 times and by 2 observers working together 4 times. They found that the addition of a second observer (a) increased the number of individual birds detected for most species present; (b) increased the number of detections significantly more for rare than for common species (but was the second observer perhaps biased towards rarer species?); and (c) increased the number of detections significantly more at farther than at closer lateral distances. Therefore, considering the problems involved in estimating true lateral detectability profiles, the results suggest that multiple observers might be better for dealing with detectability differences than using detectability profiles.

1.4 (iii) FINNISH-TYPE LINE TRANSECTS

Merikallio (1946, 1958) and Haapanen (1965, 1966) used transects in their studies of Finnish forest birds, the former using them to derive population estimates for the whole of Finland; the latter to obtain estimates for populations in various stages of forest succession. All singing males and females feeding young were taken as representing pairs and were counted within a strip extending to 25 m on either side of the transect line ("grundstreife"), and beyond this lateral distance ("hörestreife"). Merikallio (1946) suggested that using the grundstreife, the general numbers and distributions of the commoner species were recorded, while use of the hörestreife provided both counts of the rarer species and enlarged the sample area. Densities were calculated directly from the transect data, with no corrections for differences in species conspicuousness or variations in activity due to weather conditions and

stage of the breeding cycle.

Järvinen and Väisänen (1973) made use of Merikallio's data in addition to their own and renamed the transect strips the "main belt" (to 25 m either side of the observer), the "supplementary belt" (beyond 25 m) and the two in combination the "survey belt" ("fixed-distance strip transect" - Ralph, 1981). The authors were working at the national scale and suggested that their main belt transect sampling should cover 28 km per 10,000 km² (= 0.014%); using the whole survey belt they recommended 16 km/10,000 km². The basic unit being measured was the breeding pair which they saw as represented by a nest or a singing male or a single male or a single female. This is only one of several sources of bias in their method, the others being that the 25 m lateral boundaries were not marked out in the field; no account was taken of transient birds of either sex; no distinction was drawn between each sex in a pair; no account was taken of variations in conspicuousness of the birds; only one transect per season was used; and it used data gathered by several workers over a 30-year time period. Järvinen and Väisänen were aware of the limitations of their method, noting however that "it provides a valuable supplement to the mapping method" - which they saw as the most accurate way to census breeding songbirds.

In 1975, in the first of a long series of papers, Järvinen and Väisänen outlined what is termed here the "Finnish-type" line transect method. This utilises three models to account for decreasing lateral detectability - linear, negative exponential, and normal, based on the relationship between the number of registrations in the main belt and in the survey belt. Again the idea was to get population data for vast areas in Finland, and the models permitted the calculation of relative densities. However, the relative density estimates from the three models varied considerably, possibly influenced by variability in the results from using the same model for different species, and by the variability in the results from using different models for the same species. Each model apparently gave better density estimates for different species in different sites, and so it is concluded here, and

also by Moss (1981) that the method does not give very dependable results. In their 1976b paper, the authors hinted at the possibility of density-dependent errors in the estimation of the width of the main belt - a factor which would totally invalidate results derived from their method. Such errors could arise from (a) census-takers extending the estimated width of the main-belt where there were high densities of birds and (b) more time being spent censusing the high densities in the main belt at the expense of the supplementary belt.

Nevertheless this possibility did not prevent the authors from recommending that their method be used to estimate breeding bird populations in large areas, and in their papers outlining the field-work needed (e.g. 1977c) they did not suggest that the 25 m lateral boundaries be marked in the field. In addition to use in Finland (e.g. Järvinen, Kuusela and Väisänen, 1977; Järvinen and Väisänen, 1977a, 1978a, b, c) the method has also been used in large forests in Poland (Järvinen and Väisänen and Walankiewicz, 1978). It is unlikely that the method, even if improved upon, could be used in the British Isles (apart from possibly in huge commercial forests) due to the smaller and more fragmented areas of habitat, their heterogeneous nature, and the longer duration of the breeding season. As latitude increases the duration of the breeding season decreases, so there is a high degree of synchrony in the peak periods of song activity (Slagsvold, 1973b) and most species would be detectable in full song on a few transects only, rather than on a larger number of transects during the more protracted breeding season at lower latitudes. Indeed Järvinen and Väisänen recommend that in Finland transects should be conducted between 1st and 20th June in the south and between 10th and 30th June in the north. A recent review of the Finnish method (Hildén, 1981) revealed that its efficiency in estimating a known population size ranged from 33 - 67%, averaging 48%. Using repeated surveys of the same transect did not improve the efficiency, but rather showed how estimates varied greatly from survey to survey. He concluded that much of the published material on densities, biomass and energy flows must be considered unreliable and seriously underestimates.

1.4 (iv) ADDITIONAL FACTORS INFLUENCING THE EFFICIENCY OF THE THREE MAIN LINE TRANSECT TYPES

Several of the problems inherent in the three line transect methods described above have been discussed there in the relevant sections; the purpose of this section is to investigate other factors affecting the efficiency of their use.

Moss (1981) was apparently the first worker to test all three methods concurrently. He found serious errors with each and concluded that none was a reliable alternative to mapping and was no more efficient in terms of time spent obtaining the results. Little investigation of efficiency has been carried out at the species level, unlike studies using mapping; and all birds observed during transect work are recorded even though they may not breed on a study plot.

With the simple line transect, Yapp's (1956b) "provisional theoretical conclusion is that, for the larger species and perhaps for most of them, the total error may be of the order of 50%." Haukioja (1968) found the line transect virtually useless for censusing Sedge Warblers and Reed Buntings due to the breeding biologies of the species. Enemar and Sjöstrand (1967, 1970) found the main drawback of the simple line transect its inability to provide data on densities; they produced an index, "derived density", which they found useful for following population fluctuations, but it was no real substitute for absolute density which was obtained from mapping work. They also saw the dependence on audible contacts in transects as a problem, since bird vocalizing could vary too much, and was sometimes due to transients which did not form a part of the stable breeding population.

With Emlen-type transects Moss (1976) found marked fluctuations in density estimates based on individual transects on different days, which he attributed to:-

- (1) variation in the proportion of birds active and likely to be

detected at different stages of the breeding cycle.

- (2) variation in the intensity of the bird's activity from day to day.
- (3) observer error, particularly due to difficulties in estimating distances, heightened in poor weather.
- (4) smallness of the individual samples on which the transect results were based.

(1) caused a fluctuating value of the incompleteness factor (I.F.), which could not be accounted for without a detailed study of song activity; (2) and (3) caused variations in the observed coefficients of detectability (C.D.); and (4) affected both the individual I.F. and C.D. values. Moss concluded that the method was unreliable and just as time-consuming as mapping.

Since few other workers have adopted the Finnish-type line transect, the only tests of its efficiency are by the originators of the method - Järvinen and Väistönen and their co-workers, and so it is not possible to present any comments on independent tests of it other than those already discussed by Moss (1981). Recently O'Meara (1981) reported his findings on a comparison of the Euler-type and Finnish-type transects, where he found that similar density estimates could be obtained by both methods. However he found the latter method easier to use since it requires only the determination of whether detected birds are within a specified distance, not the actual distance. Järvinen and Väistönen suggested that 25 km (about 20 hours of fieldwork) of a Finnish-type transect would reveal about 60% of the bird species in south Finland but only about 40% in north Finland, due to a lower density of birds in the north. However, this suggests that the transects could be a rapid way of producing species lists for faunal areas in Finland. Järvinen, Väistönen and Haila (1977) found that, as with mapping censuses, their method was most efficient when conducted in the early morning, and for community studies it should be carried out throughout the breeding period, and so "one-off" transects are of little use. Järvinen, Väistönen and Enemar (1978) found similar results from censusing an area of mountain birch forest in Sweden by both the Finnish-type transects and

mapping, and suggested that the transect census using the linear model for correction could, in optimal conditions, result in a density value of around 2/3 to 5/6 that derived from mapping. However, they pointed out that the similarity in results could have been an artefact due to the short census period during optimal weather conditions used for transects (middle of breeding season), the narrow census area (25 m on either side of observer), the inclusion of transients in the estimates based on transects, and the use of species correction coefficients derived from work in Finland on birds in Sweden. Järvinen (1978) discussed further the species-specific census efficiencies in line-transect work and distinguished two forms of detectability: "lateral detectability" which decreased with increasing distance of the bird from the observer; and "basal detectability" which is always less than 100%, even at zero distance from the observer. In transect work main belt efficiency is exclusively determined by lateral detectability, while in mapping work basal detectability determines census efficiency.

Outside Scandinavia, Järvinen, Väisänen and Walankiewicz (1978) tested the Finnish-type transect in Polish forests using mapping as a baseline. They found that the overall efficiency of the transects compared with mapping was 93.3% for main belt data and 104.7% for survey belt data. Taking individual transects the efficiency of the main belt ranged from 86 - 98%, and for the survey belt from 93 - 127%. Again however, they were using correction coefficients resulting from work in Finland.

Finally, transects have been carried out from trains in the British Isles (Southern, 1944) and by car in Bulgaria (Nankinov, 1977), New Zealand (Gill, 1977), Canada (Erskine, 1974) and in the United States where there is a national "roadside census" (Howell, 1951; Bock and Leptien, 1975). Rotenberry and Wiens (1976) reviewed the roadside census methodology, which is basically a combination of two census types - transect and spot-count. Transects of various forms have been discussed above; spot-count methodologies and their problems will now be discussed.

1.5 POINT OR SPOT-COUNTS

These have recently been defined by Ralph (1981) as "counts of contacts recorded by an observer from a fixed observation point and over a specified time interval"; with variations of this basic theme such as using a fixed radius, variable radii (species-specific) or unlimited distance.

Krzanowski (1964) described an "aural stationary" method which could be used to give an assessment of the abundance of forest avifaunas. The method involved the observer standing still for two minutes and recording all singing males heard. After two minutes the observer would move on a sufficient distance to avoid double-counting and would listen for another two minutes before moving on again. Ralph calls this method a "point transect" i.e. a transect along which point counts are made. Ten to twelve counts were needed per visit and three visits needed per season, one in each of March, April, and June. (May was avoided presumably to escape the influence of birds singing on migration.) Results were expressed in terms of relative densities, although Krzanowski hoped that future work with the method would produce correction factors to allow the calculation of absolute densities.

The methodology was both refined and redefined by French workers as the "indice ponctuel d'abondance" (I.P.A.) (Blondel et al, 1970, 1977; Ferry, 1972) which was established to replace the "indice kilometrique d'abondance" (I.K.A.) - a transect type - of Ferry and Frochot (1958). For the I.P.A. all birds seen and heard in exactly twenty minutes from one point in a study area are recorded, and the observer then moves to other points to repeat the process (the points can be chosen either randomly or systematically); two visits are needed per breeding season. At the end of the season the data are analysed to give an indication of relative abundance, as follows:- for each spot there are two lists of records, one of species and the other of numbers. For each species each count is translated into a number of pairs, one pair being

represented by a singing male or an occupied nest or a pair or a family party; and half a pair is represented by a single bird. The higher of the two figures from both counts for each species at each spot is taken as the species' I.P.A. at that spot. The data from all the points in a study area can be combined to give mean I.P.A. for each species, mean I.P.A. for the community, mean species richness per spot, total species richness for the community, and frequency of presence, that is the percentage of spots at which a species is recorded.

Each count should be carried out before and after the main period of settlement of migrants and in the early morning in good weather. Blondel et al suggested that four or five spots can be covered in a morning, leading to a seasonal total of 8 or 10. Such a small sample can only give a basic notion of the characters of a studied community; to obtain a total of at least 30 from 2 counts would mean 15 spots in one morning, involving 5 - 6 hours work, during which it is felt by the present author that bird sing activity would decrease and observer concentration wane somewhat. An additional problem is that some birds and species not breeding in the study area would be counted. Since the technique samples a relatively small area the authors recommended it as particularly suitable for studies of habitats of limited extent e.g. clumps of deciduous trees within a coniferous forest.

Nevertheless the spot-count method, either as the I.P.A. or in a modified form, has been used in breeding season investigations in France e.g. Ferry, 1974; Blondel, 1975; Cruon and Baudez, 1978; in Denmark (Laursen and Braae, 1978); in the British Isles (Moss, 1976; Moss, 1981); in Sweden (Svensson, 1977) and in New Zealand (Dawson and Bull, 1975). It has also been used to study winter bird populations in France (Cordonnier, 1975) and in Sweden (Källander et al, 1977) and seasonal changes in bird populations throughout a year e.g. Cordonnier (1971, 1976).

Little work has been done specifically on the problems involved with, or the efficiency of, the spot-count technique but it must be detrimentally affected by its inability to account for variations in

conspicuousness of species and of individual birds at different times of day and stages in the breeding cycle as well as by variations in the ranges over which songs can be heard. This would certainly preclude its use in seasonal comparisons of populations.

Of the few tests of the methodology reported in the literature, Dawson and Bull (1975) found that in New Zealand fieldworkers using their method - which involved walking 200 m, stopping and recording for 5 minutes or 10 minutes - preferred the five minutes recording period since it was apparently no less accurate than the ten minutes version; more habitat could be sampled in a given time and there was less chance of double-counting. They do not seem to have considered that five minutes would probably not produce so many birds as ten minutes. They recommend omitting birds recorded at a distance of over 200 m, and recording separately birds flying over a study area and birds only heard. Ratkowsky and Ratkowsky (1979) re-interpreted Dawson's and Bull's (op. cit) data, and from this and their own work they recommended use of a ten-minute count, since it was found to increase the number of species recorded from between 1.7 to 3.7 times that in five minutes; using 15 minute count periods produced an increase on this of a further 0.7 to 1.7 times, but was susceptible to changes in the weather during the count period.

Moss (1976) reported his use of five-minute counts to sample the abundance of songbirds within the territories of nesting Sparrowhawks. His results, which he compared with those from mapping studies encompassing the same sites, suggested that fixed-time counts were unreliable and tended to under-estimate audibly-inconspicuous species like Goldcrest, and over-estimate conspicuous ones such as Wren and Chaffinch. Moss also found that as well as varying between species, the range of song-audibility also varied with population density: where a species was numerous, individuals in the range 50 - 100 m from the observer were probably not recorded when others were within 50 m; but they were recorded when there were no individuals closer than 50 m. Any attempt to improve upon this by estimating the distance from the observer to the bird and

then finding a "plateau" radius similar to that required for Emlen-type line transects, or by restricting observations to within a certain radius would be subject to the same problems as discussed in the section on Emlen's method.

Svensson (1977) described the use of 5-minute counts to sample the bird populations in a 375 km^2 study area in Sweden. He saw as sources of variation in the counts, the following:-

- (1) sampling distance: only 36% of individual birds were observed within 100 m of the sampling-point, and the percentage varied between species.
- (2) observer variation: only when more than one observer used in censuses.
- (3) time of day: the number of species, as well as of individuals, recorded decreased during the day due to a fall-off in song activity.
- (4) time of season: the number of records declined as the season progressed, again probably due to a decrease in the song activity.
- (5) weather: counts should be made only in "good" conditions.
- (6) habitat: affects visibility and audibility.
- (7) duration of count: both the numbers of species and of individuals are affected by this. Svensson's Figure 3 shows that 62% of species recorded after a 30-minute count had already been observed in the first 5 minutes and 75% within the first 10 minutes. He suggested from this that counts should be at least of 5 minutes duration.

Cruon and Baudez (1978) also listed seven variables which they saw as influencing spot-counts: cloud-cover, wind, rain, background noise, time of day, date, and observer's abilities. Most of these have been discussed above and the only new finding they provided was that data for the cuckoo had to be treated with caution since the species could be heard at a great distance and could be liable to double-counting from a number of spots.

Bournaud and Corbillé (1979) investigated the effect of the number and distribution of counting spots on the number of resident species detected in a 20-minute count at each spot during the breeding season. They took

212 randomly distributed spots over a grid with lines 1.6 km apart, and detected 84 species. They compared this with the results from 10-minute counts at each of 23 and 24 count-spots distributed at random on a grid with lines 5.0 and 5.6 km apart in the same study area. From the 23 spots, 56 species were detected, while from the 24 spots 52 species were detected. They concluded that using 150 spots with 20 minute counts, 95% of the resident bird species could be detected.

Moss (1981) compared the results of spot-counts of five minutes and ten minutes duration, and found that the ten minute counts revealed 25% more species than did those of five minutes in Welsh woodland habitats. This contrasted with a difference of 12% on Danish farmland (Jørgensen, 1974). However, one problem with Moss' results is that they are from counts made around mid-day, which is commonly identified as a poor period for censusing songbirds.

Clearly there is need for a standard count duration in censuses using the spot-count technique. The literature describes the use of 5, 10, 20 and 30-minute counts and the problems involved in interpreting the results from such counts. Until there is a standard it is not possible to compare the results from different areas, habitats and seasons; and really all that can be gleaned from spot-counts, as used so far, are a rough indication of the species-richness on a site and a qualitative estimate of bird abundance, with both pieces of information being more reliable in breeding season studies than in those from other seasons.

So far it would seem that the mapping method, even with its problems, is the most reliable and efficient in terms of results for labour and time input. To test this further, section 1.6 below discusses the results of comparative studies using mapping and/or line transects and/or spot-counts.

1.6 COMPARATIVE STUDIES

There are four ways in which the three principal census methods can be compared: mapping versus line transects; mapping versus spot-counts; mapping versus line transects and spot-counts; and line transects versus spot-counts, although this latter has been encompassed by the third comparison in the published literature.

1.6 (i) MAPPING VERSUS LINE TRANSECTS

Kendeigh (1944) reviewed the methodologies and uses of these two techniques but passed no judgement as to which was the more reliable method.

Enemar and Sjöstrand (1967) described the simple line transect as "a complement to study area investigations" since it could reveal population changes of scarce species better than intensive mapping studies, but obviously the authors preferred mapping since it could exclude transient birds; was not affected so badly by variations in conspicuousness of birds; and allowed the estimation of population density of the stationary breeding populations. The same authors later suggested (1970) that since strip surveys could supply much data in a short time they obviously had their uses. To try and improve the quality of the data they produced, Enemar and Sjöstrand proposed an index - "derived density" - which combined the density results from mapping work with the relative abundance results from transect work in the same areas. Unfortunately this index was biased in an indeterminable way since it combined data from the breeding population only (from mapping) with data from the total population (breeding and transitory, from transects), and its use was confined to noting just general population fluctuations, with poor accuracy.

Kenny (1972) working on a post-breeding population, found that simple line transects used fewer man-hours per bird detected (0.022 ± 5.61 (mean \pm s.d.)) compared with mapping (0.052 ± 6.24) and deduced that they were more effective because of this, and because they required less

time to establish in the field. He did not look at "effectiveness" in terms of the accuracy of his results and admitted that they "(did) not provide substantial proof of the superiority of the accuracy of the transect method in determining absolute densities."

Franzreb (1976) compared Emlen-type transects with the mapping method proposed by Williams (1936) but ignored the caveats initially supplied by Williams, and later by Enemar, the B.T.O. and I.B.C.C. Franzreb found that mapping produced higher estimates of density but was more time-consuming, requiring at least three visits per study area per month; whereas transects needed only three visits in a season. Like Kenny (1972) she does not seem to have concerned herself with the accuracy of her results, but just the time needed to obtain them. Dickson (1978) found the Williams mapping method gave "better" results than transects, yielding higher numbers of males and of mean detections per count.

Berthold (1976) called for the cessation of use of all relative techniques since their results, although obtained more rapidly than by the absolute technique of mapping, were not so reliable.

Planterose (1978) compared Emlen-type transects with CBC work in an English study area in one April only, so he did not census several species of summer migrants, but the species he did census were probably at their most conspicuous both vocally and behaviourally. He found that even with correction factors the data resulting from the use of transects could not be converted into density values as produced by mapping. Planterose recommended that "the use of transect data might therefore be best confined to the provision of indices of abundance rather than for subsequent application of correction factors based on mapping results", but that "where observers and/or time are limited, a consideration of this factor alone may favour the use of transects," since he had found in his study area that a mapping census took twice as long as transects to cover an area. In addition, for woodland studies, he recommended that transects be used only in the interiors since they were greatly biased by any "edge

effects"; and that transect routes should encompass all the main habitats in a wood in the ratio:-

$$\frac{\text{Transect length in a "micro" habitat}}{\text{Total transect length in a wood}} = \frac{\text{Area of "micro" habitat}}{\text{Area of wood}}$$

From this Planterose suggested that Emlen-type transects at least could not be used satisfactorily in the British Isles due to the relatively small areas and fragmentary nature of woodland, much of which is heterogeneous in character.

1.6 (ii) MAPPING VERSUS SPOT-COUNTS

There has been practically no comparative study of these two methods in the same study areas, which must cast some doubt on the validity of the spot-count method until there has been further testing.

The findings of Moss (1976) and Moss (1981) will be discussed in the next subsection. Only two other comparisons in the English literature are available. Frochot et al (1977) claimed "very similar" results in density estimates in their oak forest study area by mapping (49.9 prs/10 ha) and I.P.A. (47.0 prs/10 ha), although some of the count spots used in the latter were outwith the area used for mapping, and there was no consistency in the direction of density estimates for individual species - in their Table 2, of the twelve species listed, four gave higher estimates from mapping and eight from I.P.A. During the season studied censusing took ten hours by I.P.A. and 43 by mapping.

Walankiewicz (1977), working in a variety of deciduous woodlands and one area of coniferous woodland, found that of 102 comparisons of results between mapping and I.P.A. involving 11 species in 5 plots, 64% of the comparisons showed statistically significant differences between the two methods. Walankiewicz also dismissed the advantage of the low time expenditure of I.P.A. censuses compared with mapping, and claimed that on a 10 ha plot 25 - 30 hours fieldwork would be needed for

mapping and 24 hours for 30 point-counts. He concluded that "in forest habitats the I.P.A. method has no clear advantages over the mapping method", and according to his results it gave much less accurate evaluations of numbers.

1.6 (iii) MAPPING VERSUS LINE TRANSECTS VERSUS SPOT-COUNTS

In his comparisons of mapping, simple and Emlen-type transects, and spot-counts, Moss (1981) found that simple line transects and spot-counts were useful only for obtaining species-lists from study areas since neither method took account of the "conspicuousness problem". Complex (= Emlen-type) line transects were able to accommodate differences in conspicuousness but were susceptible to day-to-day variations in birds' activities, and to longer-term variations according to the stage of the breeding cycle. The reliability of the method might have been improved by increasing the length of each transect to at least 16 km, as recommended by Emlen. Moss had no hesitancy in claiming the mapping method as the most reliable of those he tested, principally because it utilised several visits to build up a picture of the bird distributions and breeding density, whereas each transect was a complete entity, and results were based either completely on observations made on a single occasion or on a series of occasions, which became just as time-consuming (but less accurate) than mapping.

Moss (1981) tested, in addition to the four methods studied by his brother, Finnish-type line transects (as urged by Shields, 1979) but reached the same conclusion: that the mapping method was the most reliable one available for censusing breeding songbirds.

1.7 THE CURRENT STATE OF KNOWLEDGE

This review has described and discussed the main methods currently in use for counting songbirds, particularly during the breeding season. Evidence is abundant that the mapping method is the most accurate and reliable of those available, a finding mirrored at the International Monterey Bird Census Symposium (O'Connor, 1981), where Erskine (1981) synthesized much of the proceedings in statements on planning census work. He suggested that any method requiring more than one person at a time, or calls for more specialized equipment than maps or binoculars, or for knowledge over and above bird identification will be less usable than a simpler one for the following reasons:

- (1) The simpler methods suffer fewer constraints, provided they are adequately standardised.
- (2) Selection of methods for standardization must include some that can be replicated by other people, even if these must be coupled with quicker but more wide-ranging methods in most cases.
- (3) Innovation in census methods should be encouraged, but especially to supplement existing methods rather than to replace them.

In the present study, the habitats were not amenable to sampling by either the Emlen-type or Finnish-type line transects. Thus, simple line transects were undertaken as a complement to mapping, but their shortcomings were soon apparent when preliminary results showed that they provided no evidence of breeding by the birds present; they produced dominance values quite different from those obtained by mapping; and more importantly, whereas mapping revealed all the species detected by simple line transects, the converse was not true (see results and discussion in later chapters).

Therefore, for the reasons outlined in this review, the mapping method was chosen to census the breeding songbird populations in the five study areas in north-east Fife, discussed in the next chapter.

CHAPTER 2 THE HABITATS

2.1 INTRODUCTION

The habitats can be described briefly and semi-quantitatively, as in Table 2.1. Unfortunately, in much of the ornithological literature, especially pre-1955, such a description would be all that was given, if in fact any, even at this minimal detail.

However, during the late 1950s and early 1960s ornithologists (see Emlen, 1956) became much more aware of the importance of special features of habitats such as canopy height and breadth, and diversity of plant species, and structures. It was, therefore, necessary to move away from general qualitative descriptions of habitat, for example "Birch/Alder Woodland" to more precise descriptions which included details of the density of vegetative cover, and parameters of its height, structure and age; and because of the size of areas which ornithologists were seeking to describe quantitatively, sampling procedures had to be devised.

Fortunately, around the same time, there was a tremendous increase of interest in the classification and ordination of vegetational samples or units by plant ecologists (see Kershaw, 1973) and ornithologists were able to borrow from the methodologies developed in the former, but modified somewhat in order to cope not with the vegetation features *per se*, but with those features of the vegetation which seemed important to bird communities, usually during the breeding season. A major problem emerges here - how can humans decide what is important from a bird's point of view, especially when several bird species are to be considered? This is where habitat selection by birds needs to be considered and this is discussed more fully later, but basically during the breeding season, birds need food for themselves, cover in which to nest, and abundant food to enable their young to survive. In addition, some species require special features such as prominent song-posts or a particular type of nest material. These needs were succinctly summarised by Hildén (1965)

in terms of ultimate factors (those concerned with survival value) - (a) food, (b) requirements imposed by structural and functional characteristics of the species, (c) shelter from enemies and adverse weather; and proximate factors (those concerned with adaptations in physiology and behaviour) - these are characteristic stimuli of the species - special habitat, but their nature is virtually unknown - (a) landscape, (b) terrain, (c) sites for nesting, singing, feeding, drinking and predator-searching, (d) absence of other birds and animals, (e) food (in certain species) and (f) internal motivation which contributes to the release of the selection response and in some way determines the sensitivity of the bird to external stimuli.

In the following sections, there is a brief review of the literature pertaining to habitat descriptions for ornithological work, a description of the methodology adopted for the present study, and a presentation of the results with a discussion of them.

TABLE 2.1 SEMI-QUANTITATIVE DESCRIPTIONS OF STUDY PLOTS :

(a) Physical Properties

| Plot | Name | Area (ha) | Altitude (m) | Aspect | Substrate | |
|------|-------------------------------|-----------|--------------|---|--|--------------------|
| | | | | | Type ¹ | Class ² |
| 1 | Tentsmuir Point N.N.R. | 19.72 | 5 - 10 | Generally level, gently undulating | Links: Stabilised wind-blown sand | 7 |
| 2 | Tentsmuir Forest | 20.59 | 5 - 10 | " | " | 5 |
| 3 | Earlshallmuir, Birch scrub | 19.09 | 5 - 10 | " | " | 5 |
| 4 | Earlshallmuir, Fir park | 11.58 | 5 - 10 | " | " | 5 |
| 5 | Earlshallmuir, Moorland | 22.35 | 5 - 10 | " | " | 5 |

TABLE 2.1 (contd.) (a) Physical Properties (contd.)

| Plot | Name | Area of Woodland (ha) | Area Open (ha) | % Open of whole area | Total length of edge ³ (m) | Ratio ⁴ of total edge ³ : total area | Length of woodland edge ³ (m) | Ratio ⁴ of woodland ³ : woodland edge ³ area |
|------|---|-----------------------------|----------------------|-------------------------------|---|---|--|---|
| 1 | Tentsmuir Point N.N.R. | 15.71 | 4.01 | 26.36 | 1000 | 0.0051 | 1000 | 0.0064 |
| 2 | Tentsmuir Forest | 16.18 | 4.41 | 21.46 | 300 | 0.0015 | 300 | 0.0019 |
| 3 | Earlshallmuir, Birch scrub: (a) whole study area | 13.13 | 5.96 | 31.23 | 2800 | 0.0147 | | |
| | (b) woodland only | 13.13 | 0.12 | 0.95 | | | 2730 | 0.0208 |
| 4 | Earlshallmuir, Fir park: (a) whole study area | 7.20 | 4.38 | 37.90 | 850 | 0.0073 | | |
| | (b) woodland only | 7.20 | 1.86 | 25.90 | | | 750 | 0.0065 |
| 5 | Earlshallmuir, moorland | 0.00 | 22.35 | 100.00 | 600 | 0.0027 | | |

TABLE 2.1 (contd.) (b) Floristic and Faunistic Properties

| Plot | Name | Establishment of habitat (year) ⁵ | Age when censused (years) | Grazing animals ⁷ | Adjacent areas |
|------|-------------------------------|--|--|---------------------------------------|--|
| 1 | Tentsmuir Point N.N.R. | Earliest topography formed in mid/late 18th century. Western boundary present in 1862; eastern boundary formed 1912-40; south-east corner only since 1954. Deciduous trees present 1940-54; coni- ferous tree colonization from mid-1950s, associated with reduced rabbit grazing due to the effects of myxomatosis. | c. 25 | Rabbit Roe deer | Open area of stabilised dunes to north and east; habitat similar to study plot to south; commercial coniferous forest to west. |
| 2 | Tentsmuir Forest | Topography present before 18th century. Study area first planted: c.1925 and first felled : c.1955 replanted 1956-65. | 14-25 | Rabbit Roe deer | Commercial coniferous forest on all sides. |
| 3 | Earlshallmuir, Birch scrub | Topography present before 18th century. Long north-south water bodies present since at least 1792-95. No woodland in 1862; central strip of main wood present in 1912; no sign of east strip of 1924, but scattered trees in 1940. | Some parts 70-150 Others ≤50 | Rabbit Roe deer Cattle Sheep | Commercial coniferous forest to north; water- body and older birch/ alder woodland to west (study plot 4); links grassland to east; rush- dominated ⁶ moorland to south. |

/Contd.

TABLE 2.1 (contd.) **(b) Floristic and Faunistic Properties** (contd.)

| Plot | Name | Establishment of habitat (year) ⁵ | Age when censused (years) | Grazing animals ⁷ | Adjacent areas |
|-------------|----------------------------|---|---------------------------------|--|--|
| 3 contd. | | Tree colonization of western-most open areas and water body since 1940. | | | |
| 4 | Earlshallmuir, Fir Park | Topography present since before 18th century; woodland definitely on site in 1750s (possibly Scots Pines:- planted, not remnants of any natural cover). Long north-south water bodies present since at least 1792-95. Deciduous woodland present since at least 1862. | ≥230 | Rabbit Roe deer Cattle Sheep | Commercial coniferous forest to north; birch scrub to east (study plot 3); open birch/alder woodland and grassland to west; rush-dominated ⁶ moorland to south. |
| 5 | Earlshallmuir, moorland | Topography present since at least 1750s. | >250 | Rabbit Roe deer Horse Cattle Sheep | Habitat similar to study plot. |

TABLE 2.1 (contd.) **(b) Floristic and Faunistic Properties** (contd.)

| Plot | Name | Dominant ⁶ tree canopy species | Shrub layer: dominant ⁶ species (5m) | Field layer: dominant ⁶ species | Ground layer: dominant ⁶ species |
|------|-------------------------------|---|---|---|--|
| 1 | Tentsmuir Point N.N.R. | Scots Pine Corsican Pine Lodgepole Pine Birch spp. Alder Willow spp. | Sea Buckthorn Birch spp. Willow spp. | Meadowsweet Rosebay Willowherb Creeping Willow Grass + Sedge spp. | Moss spp. Lichen spp. Conifer needles |
| 2 | Tentsmuir Forest | Sitka Spruce Scots Pine Lodgepole Pine | ----- ⁹ | Fern spp. Rosebay Willowherb Rush spp. Grass + Sedge spp. Brashings | Moss spp. Lichen spp. Brashings Conifer needles |
| 3 | Earlshallmuir, Birch scrub | Birch spp. Willow spp. | Birch spp. Willow spp. | Creeping Willow Ragwort Rush spp. Woodrush Grass + Sedge spp. | Moss spp. Lichen spp. Birch leaves |
| 4 | Earlshallmuir, Fir Park | Scots Pine ⁸ Birch spp. Alder Willow spp. | Birch spp. Willow spp. | " | Moss spp. Lichen spp. |
| 5 | Earlshallmuir, moorland | ----- ⁹ | ----- ⁹ | Creeping Willow Cross-leaved Heath Ragwort Rush spp. Woodrush Grass + Sedge spp. | " |

Notes to Table 2.1

- 1: Substrate type - from Macaulay Institute for Soil Research (1968)
- 2: Substrate class - from Macaulay Institute for Soil Research (1969)
- 3: Edge (= ecotone) : Defined in text.
- 4: Ratio : expressed in $m \div 10^4 m^2$
- 5: Establishment of habitat (within recent past (c 250 years)), derived from laboratory work with published literature, maps and aerial photographs from :-

Fairey Surveys (1973, 1978); Haggart (1978); Leach, S. (1979, pers. comm.); Lockhart, W.A. (1979-81, pers. comm.); Martin, Drysdale and Johnson (1827); Ordnance Survey (1862, 1912, 1921, 1945, 1956); Ratcliffe (1977); Roy (1747, 1755); Royal Air Force (1940, 1954); Sinclair (1791-99); Thompson (1800); Wilson (1910).
- 6: Dominance - estimate of numerical abundance, by eye. Plant sequence follows Clapham, Tutin and Warburg (1962). Some plant genera and groups were not identified to the species or genus levels respectively since this is of no relevance to the avifauna.
- 7: Grazing animals : species sequence follows that in Corbet and Southern (1977) The Handbook of British Mammals Blackwell, Oxford.
- 8: Scots Pines : in Fir Park (study plot 4) these are structurally, not numerically, dominant.
- 9: ----- = absence of feature.

2.2 METHODOLOGIES OF HABITAT DESCRIPTION IN ORNITHOLOGICAL STUDIES

General Background

Useful reviews of approaches to the description and analysis of vegetation can be found in Kershaw (1964, 1973), Harrison (1971), Goldsmith and Harrison (1976) and Whittaker (1978). The methodologies outlined are those most used by botanists, foresters (see also Bråkenhielm, 1977 and Frey, 1978), and plant ecologists, although they are also of relevance to animal ecologists and entomologists engaged in intensive studies at the small scale. In general, however, such workers are interested not in vegetation per se, but as a matrix in which animals and insects live and feed and so they are more interested in vegetation structure, its degree of stratification and its diversity (Goldsmith and Harrison, 1976). Nevertheless, during the last 20 years there has been an increase of interest in the methodologies involved and modern studies have adopted a more scientific and analytical approach than the informality of Tansley (1939, 1949). Two main directions of study can be recognised in Britain according to Harrison (1971): first, a classification approach which is useful for the primary survey of a large area and which is based upon the subjective comparison of numerous, detailed, floristic samples; and secondly, a statistical approach which relies on the use of computers. This latter approach is one of two major new developments in plant ecology since the early 1960s according to Kershaw (1973), who sees the other new development as plant population studies. However, there is still a wide variety of ways in which vegetation can be described with no standard method having yet emerged - which is not surprising given the individualistic distributions of species and the continuity of communities - and Whittaker (1978) considers there to be 12 basic approaches to the classification of vegetation.

In selecting a method, Goldsmith and Harrison (1976) suggest that the primary objective should be its informativeness (that is, its ability to enable people other than the observer to build a mental picture of

the vegetation described, and to allow the comparison and ultimate classification of different units of vegetation (Kershaw, 1973); and that other criteria involved in the choice of method should be relevant to the aims of the investigation, speed, accuracy, objectivity (reproductibility) and non-destructiveness. Bearing these in mind, and the factors mentioned by Hildén (1965), the method described later in this section, was chosen.

In addition to vegetation per se, the following habitat features should also be measured - presence of open water bodies, altitude, aspect, light intensity, substrate type and soil fertility of the site.

Most of these features can be measured from published maps, but light intensity has to be measured in the field. Several papers deal with the construction and use of photometers (see e.g. Powell and Heath, 1964; Jackson and Slater, 1967; Getz, 1968; King, 1974; and Binkley and Merritt, 1977), but in the present study a light-meter was used (environmental comparator with light probe and meter module - manufactured by Walden Precision Apparatus Ltd.), since one was readily available and was suitable for the present study.

Ornithological Applications

Elton and Miller (1954) were among the first to try and formulate a standard system of classifying habitats occupied by animal communities, basing their system on structural features of the habitat. They were closely followed by Yapp (1955) and Emlen (1956). Yapp's was a system based on continuous subdivision of vegetation types, as described by Tansley (1939), which he hoped would be usable by amateur ornithologists and general birdwatchers who lacked a botanical/ecological background. His scheme was adopted in part for the B.T.O.'s nest record scheme (Mayer-Gross, 1972), and a similar system is employed in the recording of biological sites (SPNR, 1972) - but it has not seen widespread use by "lay" birdwatchers, most of whom are unfortunately, too concerned with watching birds to pay much attention to the critical factor of

habitat. Emlen realised that it was not possible to have a standard method of description of avian habitats because of the number and variety of these, but he outlined a method based on the direct measurement of the physiognomy of habitats, which he suggested, with suitable modifications, could have wider applications than in southern Africa and North America where it was developed and tested. His Table 1 - "some important measurable features of bird habitats" is a useful summary of what should be covered in a habitat study. Again, the system did not receive the acceptability it deserved.

There were no further major developments until the early 1970s when national schemes designed to census bird populations revealed that not enough was known about the effects of habitat changes on bird populations, and that more detailed descriptions of the habitats censused should be forthcoming from the census-takers.

In the U.S.A., in an attempt to increase the value of the breeding-bird census and the winter-bird population study, James and Shugart (1970) compared four methods recommended by plant ecologists for making quantitative estimates of vegetation. They found that each had its merits and problems depending on the habitats involved, but overall a method which sampled at least five 0.1 a (0.04 ha) circular plots in a study area maximised the accuracy and efficiency of measuring the features which the authors saw as important: density, basal area, size and frequency of trees; canopy height, shrub density, % ground cover and % canopy cover.

In the British Isles, the B.T.O. (1972, 1977), which organises the national bird population monitoring scheme - "the Common Birds Census" (C.B.C.) - requires its participants to compile habitat maps and descriptions of their study plots, and these descriptions are necessarily qualitative, since they are compiled by amateur ornithologists, some with a poor botanical background, but they serve to give a broad outline of the habitats studied in terms of dominant vegetation species and their densities, open or closed canopy, height of canopy, number of vegetation strata, presence of open water, grazing pressure, use of

farm chemicals etc. The B.T.O. encourages better-qualified field-workers to complete more detailed and quantitative habitat descriptions and stresses the importance of noting any changes in habitat structure between census years.

The above requirements for national schemes give a general idea of the habitat features which should be recorded in detail, and for examples of their use see e.g. Thomas, DeGraaf and Mawson (1974) (suburban context); Whitmore (1975) who also used an ordination technique in his analysis; Stocker and Gilbert,(1977), and Stocker, Gilbert and Smith (1977) working on vegetation and deer habitat relations; Cyr (1977) who found that James and Shugart (1970) used too few sampling circles; Nilsson (1977), working on small islands using 2-6 10 m diameter (0.0079 ha) sampling circles; Rice (1978) who also used 10 m diameter sampling circles; and Moss (1978) who updated the important work on foliage height diversity by MacArthur and MacArthur (1961) and MacArthur, MacArthur and Preer (1962); in addition, Moss found that the Wren took advantage of dead brash in plantations, and that this should be recorded as a habitat feature.

Several papers have emerged dealing with field techniques involved in habitat description, such as for measuring arboreal canopy cover (Emlen, 1967); foliage profile (MacArthur and Horn, 1969; Aber, 1979); and edge (Patton, 1975). Perhaps the final product has now been developed - the "stratiscope" of Blondel and Cuvillier (1977) - an instrument for field use, which "divides biological space into horizontal planes (layers of vegetation) and vertical planes for each layer" and so "permits a rapid quantification of avian habitats". The instrument performed very well in the trials described by Blondel and Cuvillier, and perhaps deserves wider application since it introduces an element of objectivity into habitat description - possibly if the paper were to be published in English, the technique would be more widely accepted and used, and perhaps the instrument could be manufactured for sale to bird population students.

2.3 THE PRESENT STUDY

2.3.A. Methodology

(i) Field

With study areas ranging from 11.58 - 22.35 ha in size, a complete habitat survey was not possible and it was obviously necessary to sample habitat features, and ideally a random sampling procedure should have been used. In the event this also was not possible because two of the five study areas were impenetrable in places, the commercial forest almost everywhere apart from along the access strips.

Therefore, since a 50 m grid had been established in each study area for the bird census work, it was decided to utilise this for the habitat sampling (Table 2.2), in the following manner:

- (1) Since no guidelines were available in the literature regarding the number of points needed to sample an area of a given size, it was decided that a minimum of 25% of all the points in each study area should be covered in this study, given the time budget, which involved all the study areas being sampled both for vegetation and light intensity between mid-May and mid-June of the one season (1979) when the trees were in full leaf, ground vegetation emergent, and birds at the peak of their breeding cycle.
- (2) For each study area, three or four (depending on the total number of sample points) grid-lines running west-east (for ease of movement) were picked so that there were lines at the north, central and south of the study areas, but not along any edge.
- (3) Every 50 m along a grid line, at a grid point, and within a 10 m radius from it at every 10° , the following vegetation parameters were measured and plotted on concentric-circle graph paper: tree species, height (measured using clinometer) and trunk diameter

at breast height (DBH) of each tree, scored as 1 for 1-10 cm, 2 for 11-20 cm etc.

On a separate sheet of paper were noted the height at which the general canopy was most widespread, the % of ground covered by the canopy and details of the field vegetation - dominant species (estimated by eye), heights and % ground covered by them, and presence of open water and dead brash. Readings of the relative amount of light reaching the ground were also taken at the same grid points but on different "standard" days - around mid-day within 10 days either side of mid-summer's day, and only on days with clear sky and bright, direct sunlight. Where tree cover was too dense to employ the above circle method, notes were made of the tree species, general height at which the canopy was most widespread; the general, maximum and minimum tree heights, general DBH and spacing of trunks, to enable the calculation of a density index. That the field method used met the criteria suggested by Goldsmith and Harrison (1976) can be witnessed by the fact that it was successfully used by several university honours students who acted as field assistants.

TABLE 2.2 Percentages of Study Plots Covered by Sampling Procedure

| Census Plot | Area (ha) | Total no. of points at 50 m spacing | No. of Sample Points ¹ | % of Plot Area Sampled | % of Points at 50m spacing, sampled |
|-------------|-----------|-------------------------------------|-----------------------------------|------------------------|-------------------------------------|
| 1 | 19.72 | 101 | 26 | 4.10 | 25.74 |
| 2 | 20.59 | 126 | 33 | 5.00 | 26.19 |
| 3 | 19.09 | 80 | 24 | 3.92 | 30.00 |
| 4 | 11.58 | 48 | 16 | 4.31 | 33.33 |
| 5 | 22.35 | 100 | 33 | 4.60 | 33.33 |

¹ A sample "point" covers an area of 314 m^2 (0.0314 ha) centred on the grid point which is sampled.

2.3.A

(ii) Laboratory

In addition to the analysis of the field data described above, laboratory work using O.S. maps and aerial photographs (colour, August 1978, by Fairey Surveys) was carried out to establish the altitude, aspect and substrate of the study areas, their approximate ages, the percentage of tree cover and of open ground in each and the amount of "edge" between them and any adjacent different habitats (the ecotone).

It is difficult to accommodate the effects of "edge" on the bird populations of a given habitat, and it is equally difficult to define what is "edge" in some habitats. In the present study, each of the four woodland plots had clearings in them and these clearings were an integral part of the woodland, but formed a sub-habitat within the main habitat. In addition, around parts of the perimeters of three of the study areas, the habitat was distinctly different, while in the fourth study area - the commercial forest plot - there was a wide track all the way along one edge. Obviously an operational definition had to be sought to distinguish the "edge" around sub-habitats from the proper "edge" or ecotone.

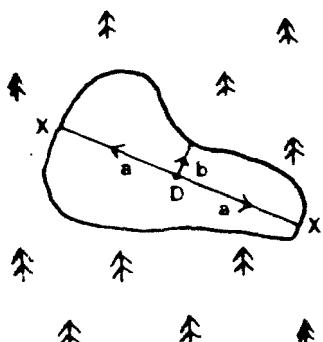
The literature revealed that ecotones usually have a greater bird population density and often contain more species than homogeneous habitats but that there has been little quantification of this edge effect (Hogstad, 1967b). Beecher (1942) showed that the population density of several bird species was proportional to the ratio of edge area to unit area. Simms (1971) devotes a chapter of his book to edges, but even so provides little quantitative data on their effect on breeding bird populations and only emphasises the points made by Hogstad (1967b). However, he does produce a preliminary classification of the birds of woodlands and woodland ecotones and sees five main types of ecotone overall: woodland/heath or open ground, parkland (trees and grassland), hedgerows and treelines or shelterbelts/fields, orchard, gardens in an urban setting. Patton (1975) introduced an index for quantifying habitat edge - the index is related to the ratio of the circumference to the area of a

circle, and undoubtedly has potential, but it would be useful only for discrete units of different habitats and it would be difficult using it, to account for small lengths of edge separating homogeneous habitats. Cousins (1977) stressed the importance to bird populations of the ecotone created by internal and boundary hedgerows on arable farms and felt it necessary in his study to compensate for such "edge effects" since he showed that boundary habitat features could be responsible for as much as 50% of the total numbers of birds found on some census areas. However, it seems that there is some confusion in his study between edges which are boundaries - which may mark off the physical limits of a study area but which may not separate different habitats (the I.B.C.C. Rules (1969) take care of this boundary problem) - and edges which are ecotones - transition zones between different habitats. This is a pit-fall to beware of. Morgan and O'Connor (1980) avoid the problem and use a modification of Beecher's method to express hedgerow density as hundreds of yards of hedgerow per acre of study plot.

This was the method employed in the study area, but before it could be used, "edge" had to be given an operational definition, to cope with the problems discussed in the second paragraph above in this section on laboratory work.

Using 1978 colour aerial photographs at a scale of 1:10,000, all open areas and edges in the study plots were mapped on 1 mm square transparent graph paper. The total open area and its proportion in each of the study areas was calculated (Table 2.1). Next, the largest open area within the main body of habitat in each study plot was found and its longest axis measured. This represented the greatest distance between adjacent areas of trees, and half the length of this axis represented the greatest possible distance within the woodland that a bird could find itself isolated from the nearest point of tree cover. (Figures 2.1, 2.2). Figure 2.3 indicates the distribution of "edge" in each of the five study plots.

FIG 2.1 MAXIMUM DISTANCE OF BIRD FROM SURROUNDING WOODLAND.

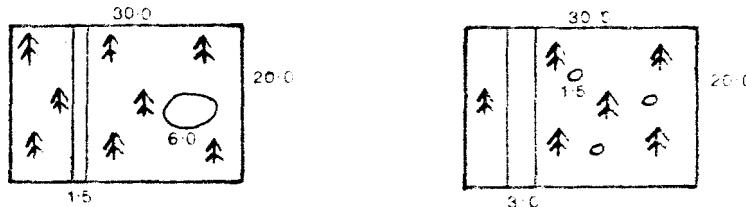


a: the greatest possible distance that a bird could be from the surrounding woodland. Even though at this "most distant" position, (D) there is a short distance (b) to the nearest piece of tree cover, the bird might not necessarily choose to move there when looking for cover if, e.g. it had a nest or young requiring to be protected or fed at X.

Therefore, except in the obvious cases where there was a distinct boundary between two adjacent habitat types, for the gap between two areas of similar habitat to be considered as forming an edge (ecotone), whether within or bounding on a study plot then half the length of the longest axis of the gap had to be greater than half of the longest axis of the largest integral open area.

Tracks are a special case, and with them, half the general width should be taken, not half the length of the longest axis. (Figure 2.2).

FIG 2.2 ECOTONE / TRACK RELATIONSHIP.



Track does not form an ecotone,
since $0.75 < 3.00$

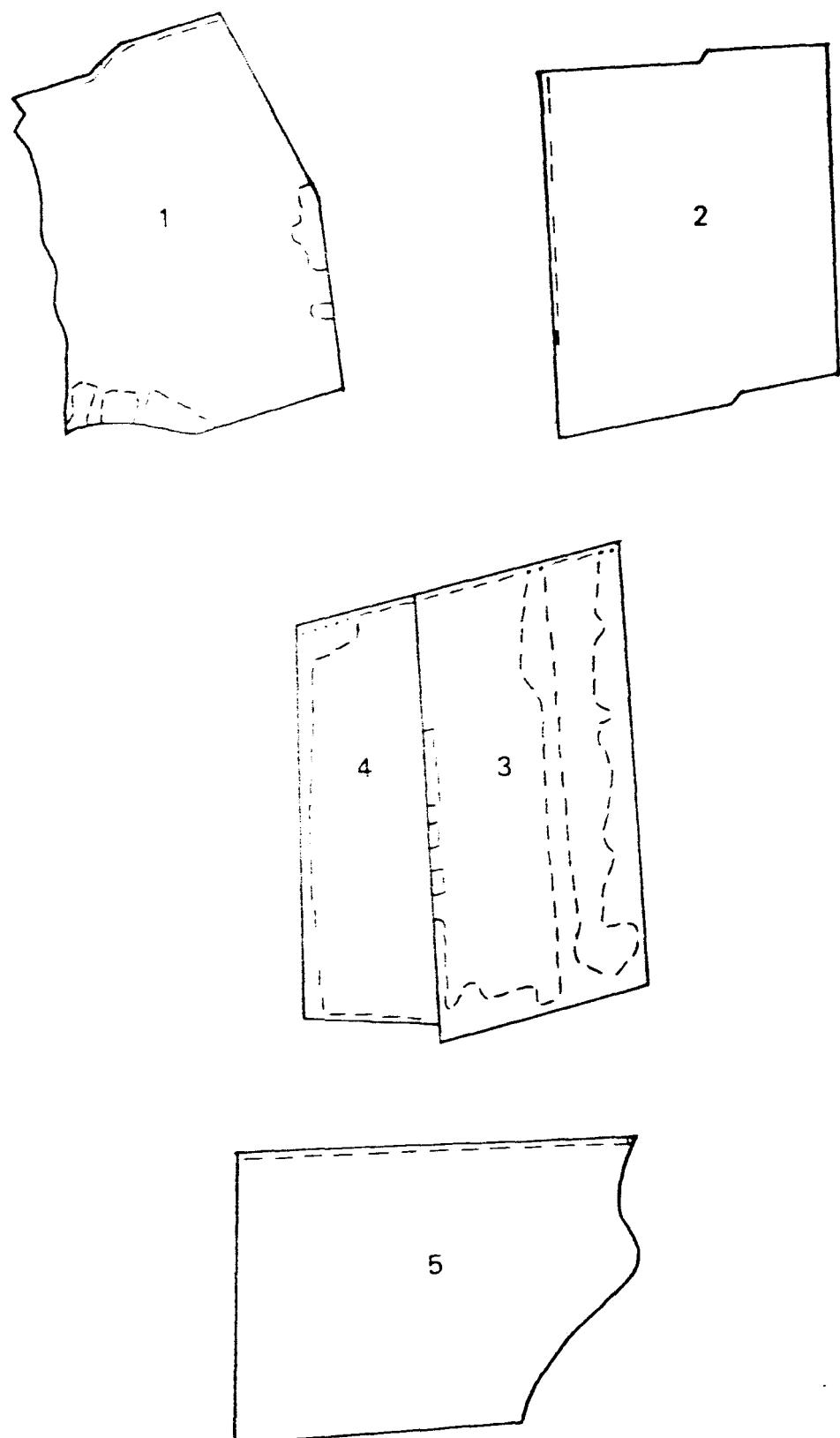
Track does form an ecotone,
since $1.50 > 0.75$

KEY

===== track

○ open area with length of longest axis
4.5

FIG23 DISTRIBUTION OF ECOTONE IN EACH STUDY PLOT.



KEY

- Study plot boundary.
- - Ecotone in relation to main habitat type in study plot.
- *** Ecotone in relation to whole study plot.

Scale
1 : 10,000



2.3.B. Results

(i) Light intensity at ground level

The amount of light reaching the ground serves as an index of the filtering effect of the vegetation (normally tree canopy) overhead and, ideally, the denser the canopy, the less light will be able to pass through it. Since it was not possible to measure canopy thickness per se in the field, surrogate measures of density of tree cover, the height at which the canopy was most widespread and the % of ground covered by it were tested (Table 2.3c).

In general, inverse relationships were involved between vegetation structure and light levels - the denser the tree cover, the lower the canopy level and the wider the canopy, the less light reached ground level. There were two exceptions to this - the density of tree cover in the commercial forest, and the % of ground covered by the canopy in the birch/alder woodland of Fir Park. It seems from the other two relationships, which are poor, that in the commercial coniferous forest it is factors other than those measured in this study which affect the amount of light penetrating to ground level. In Fir Park, the direct relationship is hard to explain, but could be a reflection of the small number of sample points involved with the absence of any "dense" areas and/or the presence of many tall mature trees with wide, but high canopies, composed of deciduous leaves and thin branches allowing much light to reach the ground below.

In the present study, the amount of light at ground level was measured using an "environmental comparator" on standard days and at the same sampling points used in the vegetation work (see methodology discussion above).

A reading made in open ground, in full sunlight, was taken as the maximum possible reading (absolute reading - RA) with no overhead interference, for a plot. This reading was converted to an index value of 100, and

the readings taken at the other sampling points expressed relative to this (R_R). An index of light intensity for the whole plot (R_p) was derived by summing the relative readings (R_R), and dividing by the potential maximum for the plot - the index value of 100 multiplied by the number of sample points ($100 \times N_{R_R}$) (Table 2.3).

TABLE 2.3 (a) Index of Light Intensity at Ground Level for each Study Plot

| Plot | No. of sampling points (N_{R_R}) | Relative Readings | | | | Light intensity index |
|------|--------------------------------------|-------------------|--------|-------|-------|-----------------------|
| | | Total | Range | Mean | S.D. | |
| 1 | 26 | 1707 | 35-100 | 65.65 | 19.52 | 0.66 |
| 2 | 33 | 1845 | 25-100 | 55.91 | 12.43 | 0.56 |
| 3 | 24 | 1813 | 45-100 | 75.54 | 19.93 | 0.76 |
| 4 | 16 | 1233 | 59-100 | 77.06 | 15.32 | 0.77 |
| 5 | 33 | 3181 | 86-100 | 96.39 | 3.69 | 0.96 |

TABLE 2.3 (b) Comparisons between Study Plots of Relative Light Intensity at Ground Level (Results of t-Test)

| Study Plot | 1 | 2 | 3 | 4 | 5 |
|------------|------------------|-------------------|-----------------|------------------|---|
| 1 | - +2.33, 57d.f.* | -1.77, 48d.f. | -1.99, 40d.f. | - 8.87, 57d.f.** | |
| 2 | | - -4.57, 55d.f.** | -5.17, 47d.f.** | -17.93, 64d.f.** | |
| 3 | | | - -0.26, 38d.f. | - 5.89, 55d.f.** | |
| 4 | | | | - 6.92, 47d.f.** | |
| 5 | | | | | - |

* = significantly different at $p < 0.05$

** = significantly different at $p < 0.001$

Study plots 1, 3 and 4 are similar in the amount of light reaching the ground; but plots 2 (commercial coniferous forest) and 5 (open grassland) are significantly different from all the other plots, and each other.

TABLE 2.3 (c) Relationships between Relative Light Intensity at
Ground Level and Vegetation Structure in Woodland
Study Plots
(Significance levels of correlation coefficients)

| Relationship | Study Plot | | | |
|--|---------------------------------|----------------------------------|----------------------------------|---------------------|
| | 1 | 2 | 3 | 4 |
| Density of tree cover ¹ and R.L.I. | -0.41, 19d.f. (0.21, 29d.f.) | 0.11, 30d.f. | -0.80, 9d.f. ** | -0.89, 7d.f. ** |
| Height at which canopy most wide- spread ² and R.L.I. | -0.54, 24d.f. ** | -0.12, 31d.f. | -0.39, 20d.f. (-0.83, 18d.f.) | -0.61, 10d.f. * |
| % ground covered by the canopy and R.L.I. | -0.59, 24d.f. ** | -0.18, 31d.f. (-0.09, 30d.f.) | -0.18, 20d.f. ** | +0.36, 10d.f. ** |

* : significant at $p < 0.05$

1 : excludes "dense" areas with no count of tree trunks

** : significant at $p < 0.01$

2 : where more than one value at a sample point, mean value used in calculation

*** : significant at $p < 0.001$

() : excludes extreme values, obvious on graphs of relationships

2.3.B. Results

(ii) Habitat Structure and Characteristics

The results of the field surveys carried out in May and June 1979 are presented in Tables 2.4 - 2.12 below.

Abbreviations used in Tables 2.4 - 2.12

| | | | |
|-------|--------------------------------|------------------------------|--|
| NS | : Norway Spruce | <i>Picea abies</i> | O : Bare ground |
| SS | : Sitka Spruce | <i>Picea sitchensis</i> | BR : Dead brash |
| L | : Larch Hybrid | <i>Larix</i> sp. | LN : Leaves + needles |
| SP | : Scots Pine | <i>Pinus sylvestris</i> | |
| CP | : Corsican Pine | <i>Pinus nigra</i> | FN : Fern spp. |
| LP | : Lodgepole Pine | <i>Pinus contorta</i> | GO : Gorse Ulex europaeus |
| SY(S) | : Sycamore (sapling) | <i>Acer pseudoplatanus</i> | CL : Clover spp. Trifolium spp. |
| WBH | : Sweet Briar | <i>Rosa rubigenosa</i> | M : Meadowsweet Filipendula ulmaria |
| H | : Hawthorn | <i>Crataegus monogyna</i> | WH : Willowherb spp. Epilobium spp. |
| R | : Rowan | <i>Sorbus aucuparia</i> | D : Dock spp. Rumex spp. |
| SB(R) | : Sea Buckthorn (regeneration) | <i>Hippophaë rhamnooides</i> | N : Nettle Urtica dioica |
| B(S) | : Birch (regeneration) | <i>Betula</i> spp. | C : Creeping Willow Salix repens |
| A | : Alder | <i>Alnus glutinosa</i> | HE : Heather Calluna vulgaris |
| W | : Willow spp. | <i>Salix</i> spp. | CH : Cross-leaved heath Erica tetralix |
| E | : Elder | <i>Sambucus nigra</i> | CB : Crowberry Empetrum nigrum |
| WR | : Woodrush | <i>Luzula campestris</i> | RA : Ragwort Senecio jacobaea |
| D | : Dense cover | | R : Rush spp. Juncus spp. |
| GS | : Grass spp. + Sedge spp. | | ML : Moss spp. + Lichen spp. |

Density of tree cover (Table 2.6) was estimated by using the number of trunks counted along each of the 36, 10 m long radial lines used to sample the vegetation in each 10 m - radius "sampling circle". In the commercial forest only an approximation could be arrived at, given the difficulties of conducting fieldwork in closely-spaced timber with thick foliage almost to ground-level in places. The approximate number of trunks at a sample point in the commercial coniferous study plot was calculated using

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$$(M_N + \frac{1}{2} DBH)(M_E + \frac{1}{2} DBH)$$

where DBH = Trunk diameter at breast height

M_E = Median value of east-west spacing

M_N = Median value of north-south spacing

This formula represents numerically: Area of 10 m radius sampling circle

Space occupied by 1 trunk

TABLE 2.4 Mean number of tree species at each sample point

| Study Plot | n | Mean | S.T. | S.E. | Range |
|------------|----|------|------|------|-------|
| 1 | 64 | 2.46 | 1.03 | 0.20 | 1 - 4 |
| 2 | 75 | 2.27 | .98 | 0.17 | 1 - 5 |
| 3 | 31 | 1.29 | 0.69 | 0.14 | 0 - 3 |
| 4 | 24 | 1.50 | 1.11 | 0.30 | 0 - 4 |

TABLE 2.5 Range of trunk diameters* at breast height in study plots

| Study Plot | NS | SS | L | SP | CP | LP | Species | | | | | | | | |
|------------|-----|-----|---|-----|-----|-----|---------|-----|---|---|----|-----|-----|-----|---|
| | | | | | | | SY | WBR | H | R | SB | B | A | W | E |
| 1 | | | | 1-2 | 1-4 | 1-4 | | | 1 | 1 | 1 | 1-4 | | 1-2 | |
| 2 | 1-4 | 1-2 | | | 1-3 | 1-3 | 1-3 | 1 | | | 1 | 1-4 | 1-2 | 1 | 1 |
| 3 | | | | | 4-5 | | | 1 | | | | 1-6 | 1 | 1-5 | |
| 4 | | | | | 4-8 | | | | | | | 1-7 | 2-7 | 1-3 | 5 |

* Code: 1 = 1-10 cm; 2 = 11-20 cm; 3 = 21-30 cm etc.

TABLE 2.6 Overall¹ density of tree cover; and mean at each sample point

| Study Plot | Σ | n | Mean | S.D. | S.E. | Range | No. of dense areas ² |
|------------|----------|----|--------|--------|-------|--------|---------------------------------|
| 1 | 657 | 26 | 25.27 | 39.90 | 7.8- | 6-215 | 6 |
| 2 | 6023 | 33 | 182.51 | 140.57 | 21.97 | 73-924 | 6 |
| 3 | 250 | 17 | 14.71 | 15.41 | 1.7- | 1- 43 | 16 |
| 4 | 155 | 16 | 9.69 | 9.94 | 1.49 | 4- 33 | 12 |

¹ : Species were not separated due to the bias introduced by the presence of dense areas.

² : Dense areas were too thick to work in, and so no numbers are available to indicate the density of tree cover in them.

TABLE 2.7 General height of tree cover, in metres

| Study Plot | Species | Σ | n | Mean | S.D. | S.E. | Range |
|------------|---------|----------|----|-------|------|------|----------|
| 1 | L | 3.5 | 1 | 3.50 | | | |
| | SP | 161.5 | 27 | 5.98 | 1.75 | 0.34 | 2.5- 9.0 |
| | CP | 35.0 | 3 | 11.67 | 9.44 | 5.43 | 3.5-22.0 |
| | LP | 5.0 | 1 | 5.00 | | | |

/Contd.

TABLE 2.7 contd. General height of tree cover, in metres

| Study Plot | Species | Σ | n | Mean | S.D. | S.E. | Range |
|--|---------|----------|-----------------|-------|------|------|----------|
| 1 (contd.) | H | 1.5 | 1 | 1.50 | | | |
| | SB | 3.0 | 1 | 3.00 | | | |
| | B | 108.5 | 17 | 6.38 | 3.31 | 0.80 | 1.5-12.0 |
| | W | 36.0 | 7 | 5.14 | 1.57 | 0.48 | 3.5- 7.5 |
| | ALL | 344.0 | 56 ¹ | 6.14 | 3.22 | 0.43 | 1.5-22.0 |
| 1 : includes two areas of SP + B combined. | | | | | | | |
| 2 | NS | 37.5 | 5 | 7.50 | 2.89 | 1.29 | 3.0-10.5 |
| | SS | 16.5 | 5 | 3.30 | 1.75 | 0.67 | 1.5- 5.0 |
| | SP | 197.0 | 30 | 6.57 | 2.49 | 0.45 | 3.0-13.0 |
| | CP | 13.0 | 2 | 6.50 | 0.71 | 0.50 | 6.0- 7.0 |
| | LP | 29.0 | 5 | 5.80 | 1.25 | 0.56 | 4.0- 7.0 |
| | SY | 5.5 | 3 | 1.83 | 1.26 | 0.73 | 0.5- 3.0 |
| | R | 8.0 | 2 | 4.00 | 2.83 | 2.01 | 2.0- 6.0 |
| | B | 133.0 | 20 | 6.65 | 2.68 | 0.60 | 3.5-13.5 |
| | A | 7.0 | 1 | 7.00 | | | |
| | W | 2.0 | 1 | 2.00 | | | |
| | E | 2.0 | 1 | 2.00 | | | |
| | ALL | 450.0 | 75 | 6.00 | 2.70 | 0.31 | 0.5-13.5 |
| 3 | SP | 15.5 | 1 | 15.50 | | | |
| | SY | 0.5 | 1 | 0.50 | | | |
| | B | 216.5 | 31 | 6.98 | 3.62 | 0.65 | 1.5-16.5 |
| | A | 7.5 | 1 | 7.50 | | | |
| | W | 38.5 | 7 | 5.50 | 1.38 | 0.52 | 4.0- 7.5 |
| | ALL | 278.5 | 41 | 6.79 | 3.65 | 0.57 | 0.5-16.5 |
| 4 | SP | 18.0 | 1 | 18.00 | | | |
| | B | 82.0 | 19 | 4.32 | 2.96 | 0.68 | 1.5-11.0 |
| | A | 47.5 | 6 | 7.92 | 1.72 | 0.70 | 6.0-10.5 |
| | W | 20.5 | 4 | 5.13 | 1.65 | 0.83 | 3.5- 7.0 |
| | E | 5.0 | 1 | 5.00 | | | |
| | ALL | 173.0 | 31 | 5.58 | 3.65 | 0.66 | 1.5-18.0 |

TABLE 2.8 Height at which canopy most widespread, in metres

| Study Plot | Species ¹ | Σ | n | Mean | S.D. | S.E. | Range |
|------------|----------------------|----------|----|-------|------|------|----------|
| 1 | ALL | 109.0 | 26 | 4.19 | 4.65 | 0.91 | 1.0- 9.5 |
| 2 | SS | 1.5 | 1 | 1.50 | | | |
| | SP | 24.5 | 5 | 4.90 | 2.58 | 1.15 | 2.0- 8.5 |
| | LP | 17.0 | 4 | 4.25 | 3.57 | 1.79 | 1.5- 9.5 |
| | B | 13.0 | 20 | 6.50 | 5.66 | 4.01 | 2.5-10.5 |
| 3 | ALL | 171.5 | 40 | 4.29 | 2.59 | 0.41 | 0.5-10.5 |
| | B, dense | 20.5 | 3 | 6.83 | 1.44 | 0.83 | 6.0- 8.5 |
| | W, dense | 13.5 | 3 | 4.50 | 0.50 | 0.29 | 4.0- 5.0 |
| 4 | ALL | 177.5 | 31 | 5.73 | 3.32 | 0.60 | 1.0-13.0 |
| | SP | 9.0 | 1 | 9.00 | | | |
| | B | 1.5 | 1 | 1.50 | | | |
| | A | 4.0 | 1 | - .00 | | | |
| | ALL | 67.5 | 18 | 3.75 | 2.55 | 0.60 | 1.0-10.0 |

1 : Species separated only where there were differences in the height at which the canopy was most widespread, between species at a sample point.

TABLE 2.9 % of ground covered by the canopy and mean at each sample point

| Study Plot | Σ | n | Mean | S.D. | S.E. | Range |
|------------|----------|----|-------|-------|------|--------|
| 1 | 1154 | 26 | 44.38 | 26.01 | 5.10 | 5- 90 |
| 2 | 2925 | 33 | 88.52 | 10.25 | 1.79 | 50-100 |
| 3 | 1250 | 22 | 56.82 | 34.66 | 7.39 | 5-100 |
| 4 | 410 | 12 | 34.17 | 14.12 | 4.08 | 10- 60 |

TABLE 2.10 General height of field components¹, in metres; and mean at each sample point

| Study Plot | Field Component | Σ | n | Mean | S.D. | S.E. | Range |
|------------|--------------------------------------|----------|----|------|------|------|---------|
| 1 | Brash + leaves/needles | 3.70 | 3 | 1.23 | 0.12 | 0.07 | 1.1-1.3 |
| | Plant spp. | 9.30 | 26 | 0.36 | 0.15 | 0.03 | 0.1-1.3 |
| 2 | Brash + leaves/needles | 17.80 | 19 | 0.94 | 0.47 | 0.11 | 0.3-1.5 |
| | Plant spp. | 11.75 | 33 | 0.36 | 0.16 | 0.03 | 0.1-1.5 |
| 3 | Dead twigs/branches + leaves/needles | 1.50 | 1 | 1.50 | | | |
| | Plant spp. | 9.31 | 17 | 0.39 | 0.17 | 0.03 | 0.1-1.5 |
| 4 | Plant spp. | 5.17 | 17 | 0.39 | 0.16 | 0.04 | 0.1-1.5 |
| 5 | Plant spp. | 9.08 | 33 | 0.28 | 0.10 | 0.02 | 0.1-1.1 |

1: separated into components where applicable.

TABLE 2.11 % Ground covered by field components, and mean at each sample point

| Study Plot | Field Component | Σ | n | Mean | S.D. | S.E. | Range |
|------------|------------------------|----------|----|-------|-------|------|--------|
| 1 | Brash + leaves/needles | 260 | 9 | 28.89 | 25.34 | 8.45 | 5- 80 |
| | Plant spp. | 2235 | 26 | 85.96 | 21.21 | 4.16 | 20-100 |
| 2 | Brash + leaves/needles | 1573 | 33 | 47.67 | 31.93 | 5.56 | 5- 95 |
| | Plant spp. | 1675 | 33 | 50.76 | 31.70 | 5.52 | 5- 95 |

/Contd.

TABLE 2.11 Contd.

| Study Plot | Field component | Σ | n | Mean | S.D. | S.E. | Range |
|------------|------------------------|----------|----|-------|-------|------|--------|
| 3 | Brash + leaves/needles | 375 | 14 | 26.79 | 20.81 | 5.37 | 5- 80 |
| | Plant spp. | | 24 | 83.13 | 19.94 | 4.07 | 20-100 |
| 4 | Leaves/needles | 70 | 3 | 23.33 | 2.89 | 1.67 | 20- 25 |
| | Plant spp. | | 16 | 95.00 | 9.31 | 2.33 | 75-100 |
| 5 | Plant spp. | 3205 | 33 | 97.12 | 4.85 | 0.84 | 80-100 |

TABLE 2.12 Mean number of plant species at each sample point

| Study Plot | Σ | n | Mean | S.D. | S.E. | Range |
|------------|----------|----|------|------|------|-------|
| 1 | 85 | 26 | 3.27 | 1.19 | 0.23 | 1-6 |
| 2 | 85 | 33 | 2.58 | 0.97 | 0.17 | 1-6 |
| 3 | 78 | 24 | 3.25 | 1.54 | 0.31 | 1-6 |
| 4 | 59 | 16 | 3.69 | 0.87 | 0.22 | 2-5 |
| 5 | 126 | 33 | 3.82 | 0.81 | 0.14 | 3-6 |

2.3.C. Discussion - Foliage Height Diversity

Foliage height diversity (F.H.D.) is an expression of the complexity of vegetation structure (Moss, 1978), and is usually a measure of the vertical distribution of leaves in woodland. Work in North America (MacArthur and MacArthur, 1961; MacArthur, MacArthur and Preer, 1962; Karr, 1968; and Cyr, 1977); in Australia (Recher, 1969); and in Europe (Cyr, 1977; Moss, 1976, 1978) indicated a close relationship between F.H.D. and the measure of complexity of songbird populations as expressed by bird species diversity (B.S.D.). The index of diversity used was the Shannon-Weaver H' (for details, see below) even though different methods of measuring the vegetation structure in the field were employed, some of which yielded data not transformable for use in diversity calculations. The Shannon-Weaver index seems to have been used with no regard to its statistical application which is appropriate only in population studies (Cormack, pers. comm.), and its use by the above authors in their descriptions of vegetation structure must therefore be regarded as suspect. Indeed the whole field of diversity study is now split between two main schools of thought - those who regard diversity indices as biologically meaningless (see e.g. Hurlbert, 1971) and those who find them a useful measure in population studies (see e.g. Järvinen and Väisänen, 1973, 1976a, 1976b et seq; Moss, 1976, 1978a, 1978b). Diversity indices have been used in the present study to facilitate comparisons between it and those by other authors.

In the present study, to enable use of the Shannon-Weaver diversity index, the data on general height of tree cover and on the general height at which the canopy is most widespread were used as surrogate measures for foliage height diversity, in the following manner, to give diversity of general height of tree cover (T.C.H.D.) and diversity of general height of canopy maximum width (C.W.H.D.):-

- (a) for each of the four woodland study plots - 1,2,3,4 - the frequency distributions of the general heights of the cover and canopy maximum width were calculated in both 0.5 and 1.0 m intervals and the dist-

ributions were expressed graphically for (i) all study plots, (ii) the coniferous plots (1,2) and (iii) the deciduous plots (3,4).

- (b) height classes were identified from the 12 graphs - these corresponded to vegetation strata.
- (c) the proportions of observations encompassed in each height class (P_i) were found, and used in $H' = \sum p_i \log_e p_i$, the Shannon-Weaver index of diversity.

The results are expressed in Table 2.13 (A,B), and their relationship to results of other studies in terms of vegetation strata (Table 2.14) are discussed.

Table 2.13A reveals that there are probably four layers of woody vegetation (in addition to a field layer of mosses and lichen) in both the coniferous and deciduous study plots, and four layers in all plots combined. There are similarities in the lowest and highest layers between the coniferous and deciduous plots, but differences in the intermediate layers, which reflect the absence of saplings, young trees, and areas of dense low scrub in the coniferous areas. The four layers correspond to sycamore saplings, scrub (low and medium), low canopy and high canopy.

Table 2.13A reveals that there are two to four layers of maximum canopy width, with 3-4 layers in coniferous plots and 2-3 layers in deciduous plots, but with close similarity in the ranges of the layers.

Table 2.13B expresses the diversity indices for each study area, using the same height classes as in Table 2.13A. Tables 2.15A and B are the same as 2.13A and B, but with the inclusion of data for brash, since this has an effect on Wren populations and so is reflected in B.S.D.

From Table 2.14, it can be seen that there are general similarities,

between the study plots in the heights of woody vegetation strata, depending on whether there are three or four involved. For three layers, the height ranges are in the order of < 1 m, < 1-4.6/7.5/9.1 m, > 4.6/7.5/9.1 m while for four layers, the ranges are in the order of:-

< 1 m, < 1 - 1.8/3.0/6.0/8.5, 1.8/3.5/6.0/9.0 - 4.6/11.5/15.0,
> 4.6/11.5/15.0

In a later chapter the relationships between bird species diversity (B.S.D.) and the vegetation diversities (T.C.H.D. and C.W.H.D.) discussed above will be investigated, and compared with the relationships found between B.S.D. and foliage height diversity (F.H.D.) by Moss in Scotland (Moss, 1976, 1978a, 1978b).

Table 2.13A Height classes, and diversity indices (H') of general heights of tree cover and of canopy maximum width

| Study | Main Tree Type | Tree cover | | | Canopy Max. Width | | |
|---------------|--|----------------------------------|-----------|-----------|----------------------------------|-----------|-----------|
| | | Height Class (m) ¹ | Frequency | Diversity | Height Class (m) ¹ | Frequency | Diversity |
| 1, 2, 3, 4 | CD ₁ C + D | <1.0 | 2 | | <1.0 | 1 | |
| | | 1.0-11.5 | 192 | 0.2364 | 1.0- 7.5 | 96 | 0.5105 |
| | | >11.5 | 9 | | 8.0-11.5 | 14 | |
| | | <1.0 | 2 | | >11.5 | 2 | |
| | | 1.0- 8.5 | 169 | 0.5830 | <1.0 | 1 | |
| | CD _{0.5} | 9.0-11.5 | 23 | | 1.0- 4.0 | 69 | |
| | | >11.5 | 9 | | 4.5- 7.5 | 27 | 1.0152 |
| | | <1.0 | 1 | | 8.0-11.5 | 14 | |
| | | 1.0- 8.5 | 111 | 0.5323 | >11.5 | 2 | |
| | | 9.0-11.5 | 15 | | <1.0 | 1 | |
| 1, 2 | Coni. ₁ | >11.5 | 4 | | 1.0- 6.5 | 56 | 0.4746 |
| | | <1.0 | 1 | | >6.5 | 9 | |
| | | 1.0- 8.0 | 109 | 0.5494 | <1.0 | 1 | |
| | | 8.5-12.0 | 18 | | 1.0- 4.5 | 49 | |
| | | >12.0 | 3 | | 5.0- 7.5 | 5 | |
| | Deci. ₁ C _{0.5} | <1.0 | 1 | | >7.5 | 5 | 0.7962 |
| | | 1.0- 3.5 | 19 | 0.8746 | 1.0- 7.5 | 39 | 0.4562 |
| | | 4.0-11.5 | 47 | | >7.5 | 5 | |
| | | >11.5 | 5 | | <1.0 | 1 | |
| | | <1.0 | 1 | | 1.0- 4.5 | 11 | |
| 3, 4 | Deci. _{0.5} | 1.0- 3.0 | 17 | 0.8473 | 3.0- 7.5 | 25 | 0.9498 |
| | | 3.5-11.0 | 49 | | >7.5 | 5 | |
| | | >11.0 | 5 | | <1.0 | 1 | |
| | | <1.0 | 1 | | 1.0- 4.5 | 11 | |

¹ : Upper set of figures are the classes resulting from grouping heights into 1.0 m intervals, C = coniferous, D = deciduous.

: Lower set of figures are the classes resulting from grouping heights into 0.5 m intervals, C = coniferous, D = deciduous.

TABLE 2.13B Diversity indices (H') for general heights of tree cover and of canopy maximum width, in each study area (1-4)

| Main Tree Type | Height Class Group | Diversity indices for general heights of | | | | | | | |
|----------------|--------------------|--|--------|--------|--------|-------------------|--------|--------|--------|
| | | Tree cover | | | | Canopy max. width | | | |
| | | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| Coni and Deci | CD_1 | 0.1541 | 0.1934 | 0.4318 | 0.1425 | 0.1630 | 0.5758 | 0.6145 | 0.3768 |
| | $CD_{0.5}$ | 0.4516 | 0.5802 | 0.7381 | 0.5225 | 0.5858 | 0.9225 | 1.1680 | 0.9003 |
| Coni | C_1 | 0.4516 | 0.5802 | | | 0.2712 | 0.5758 | | |
| | $C_{0.5}$ | 0.4969 | 0.5802 | | | 0.5858 | 0.8772 | | |
| Deci | D_1 | | | 0.8969 | 0.7785 | | | 0.4913 | 0.3768 |
| | $D_{0.5}$ | | | 0.8643 | 0.7585 | | | 0.9695 | 0.9003 |

Note: Tree types and height class groups as in Table 2.13A.

TABLE 2.14 Heights of Vegetation Strata (m) Published in Literature

| Source | Study areas | Tree type | Strata heights |
|--------------------------------|----------------------------------|--------------------------|--|
| Elton and Miller (1954) | British Isles | Coniferous and Deciduous | 0-0.15, 0.15-1.83, 1.83-4.57, >4.57 |
| MacArthur and MacArthur (1961) | Temperate North America | Coniferous and Deciduous | 0-0.61, 0.61-7.62, >7.62 0-0.91, 0.91-9.14, >9.14 |
| B.T.O. (1977) | British Isles | Coniferous and Deciduous | 0.91, 1.22-4.57, >4.57 |
| Cyr (1977) | Southern Canada and West Germany | Coniferous and Deciduous | 0-0.5, 0.5-2.0, 2-6, 6-10, >10 |
| Blondel and Cuvillier (1977) | Southern France | Deciduous | 0.25, 0.5, 1, 2, 4, 8, 16, 32 |
| Moss (1976, 1978a, b) | Scotland | Coniferous | 0-0.6, 0.6-6, 6-15, >15 |
| This study | Scotland | Coniferous | < 1.0, 1.0-8.0, 8.5-12.0, >12.0 and < 1.0, 1.0-4.5, 5.0-7.5, >7.5 |
| This study | Scotland | Deciduous | < 1.0, 1.0-3.0, 3.5-11.0, >11.0 and 1.0-2.5, 3.0-7.5, >7.5 |

TABLE 2.15A Height classes, and diversity indices (H') of general heights of tree cover, when brash¹ is included

| Study Plots | Main Tree Type | Height class ² | Frequency | Diversity Index |
|-------------|--------------------------|---------------------------|--|---------------------|
| 1, 2, 3, 4 | Coniferous and Deciduous | CD_1 | < 1.0 1.0-11.5 >11.5 | 7 210 9 |
| | | $CD_{0.5}$ | < 1.0 1.0- 8.5 9.0-11.5 >11.5 | 7 187 23 9 |
| | Coniferous | C_1 | < 1.0 1.0- 8.5 9.0-11.5 >11.5 | 6 128 15 4 |
| | | $C_{0.5}$ | < 1.0 1.0- 8.0 8.5-12.0 >12.0 | 6 126 18 3 |
| 3, 4 | Deciduous | D_1 | < 1.0 1.0- 3.5 4.0-11.5 >11.5 | 1 20 47 5 |
| | | $D_{0.5}$ | < 1.0 1.0- 3.0 3.5-11.0 >11.0 | 1 18 49 5 |

¹ : includes piles of dead branches and twigs

² : See note 1, Table 2.13A

TABLE 2.15B Diversity indices (H') for general height of tree cover
when brash¹ is included, in each study area

| Main Tree Type | Height Class Group | Diversity indices | | | |
|--------------------------|---|-------------------|--------|--------|----------------|
| | | 1 | 2 | 3 | 4 ² |
| Coniferous and Deciduous | $\left\{ \begin{array}{l} CD_1 \\ CD_{0.5} \end{array} \right.$ | 0.1480 | 0.3389 | 0.4246 | 0.1425 |
| | | 0.4352 | 0.6678 | 0.7264 | 0.5225 |
| Coniferous | $\left\{ \begin{array}{l} C_1 \\ C_{0.5} \end{array} \right.$ | 0.4352 | 0.6678 | | |
| | | 0.4803 | 0.6678 | | |
| Deciduous | $\left\{ \begin{array}{l} D_1 \\ D_{0.5} \end{array} \right.$ | | | 0.9133 | 0.7785 |
| | | | | 0.8845 | 0.7585 |

¹ : includes piles of dead branches and twigs

² : No brash in study area, therefore diversity indices same as Table 2.13B.

2.3:D Summary of the habitat characteristics of the study plots

Based on the results of the library, laboratory and field investigations outlined in this chapter, each study plot is summarised here as a prelude to the ornithological results presented in the next chapter.

Study plot 1: part of Tentsmuir Point National Nature Reserve.

The woodland on this 19.7 ha area became established as recently as the mid-1950s, and it comprises 80% of the study area. It is composed of self-seeded trees, chiefly pines - Scots, Corsican and Lodgepole - but with areas of Birch, Alder and Willow mixed in, and Sea Buckthorn thickets at the seaward edge of the plot. The plot has an edge:area ratio of 0.006, and the woodland in it is moderately open, having just over 25 trees per sampling point, with the canopy allowing a Light Intensity Index of 0.66, while covering on average 44.3% of the ground, and being most widespread at around 4.2 m above the ground. Between one and four tree species with trunks up to 40 cm in diameter were present at each sampling point and there was a variety of average heights depending on the species: 11.5 m for Corsican Pine, 6.4 m for birches, 6.0 m for Scots Pine and 5.1 m for willows, but even so, this plot had the lowest diversity index value for average heights.

Study plot 2: part of Tentsmuir Forest.

Surprisingly perhaps, given the "bad press" associated with the commercial forestry industry, this study plot had the second highest diversity index value for average tree heights, due perhaps to the greater number of species involved: 7.5 m for Norway Spruce, 7.0 m for Alder, 6.7 m for birches, 6.5 m for Scots and Corsican Pines, 5.8 m for Lodgepole, 3.3 m for Sitka Spruce and 2.0 m for willows. This variety of species led to four different average heights at which the canopy seemed most widespread: 6.5 m for birches, 4.9 m for Scots Pine, 4.3 m for Lodgepole Pine and 1.5 m for Sitka Spruce. The study plot had been densely planted - in the late 1950s to mid 1960s - with

an estimate of over 150 trees on average per sampling point, and 79% of the 20.6 ha plot was wooded. The canopy was closed, covering 89.6% of the ground on average and allowing only a Light Intensity Index of 0.56. Between one and five tree species with trunks up to 40 cm in diameter were present at the sampling point; little "edge effect" occurred, with the edge:area ratio being only 0.002.

Study plot 3: Earlshallmuir Birch/Willow scrub

There has been tree cover on this 19.1 ha site for at least 150 years, and at present 69% of the plot is covered by natural deciduous woodland, largely of birches and willows (some trees very old, up to 60 and 50 cm trunk diameter at breast height respectively) but with some remnant Scots Pines present. The birch component of the woodland tends to occupy former low dune ridges, with the willows and Alders in old slacks, and this linearity has given rise to a high proportion of edge (edge:area ratio of 0.021). The canopy is fairly open (Light Intensity Index = 0.76) and covers on average 56.8% of the ground. The trees occur at a low density (mean of 14.7 per sample point) but there are occasional dense thickets of young birches and willows. Some sample points have no trees present, but up to three species can occur. This study plot has the highest diversity index value for tree heights which are, on average, 15.5 m for the remnant Scots Pine, 7.5 m for Alders, 7.0 m for birches and 5.5 m for willows. The canopy is most widespread at an average of 6.8 m among the birches and 4.5 m among the willows.

Study plot 4: Earlshallmuir, Fir Park

From a purely subjective point of view, this area looked "good" for birds - there was a certain feel to it. More objectively, the 11.6 ha study plot was at least 230 years old, was 62% wooded, largely with birches and Alders - some very old, up to 70 cm trunk diameter - and with some big remnant Scots Pines from 40 to 80 cm in trunk diameter. The woodland was open, with an average of 9.7 trees per sampling point,

and like the birch/willow scrub, the birches occupied former dune ridges, often in dense thickets, while the Alders and willows occurred in or along former dune slacks; it had a lower (0.007) amount of edge, however. The canopy was open, allowing a Light Intensity Index of 0.77 to prevail, and it covered on average only 34.7% of the ground. Between none and four tree species were present at each sampling point, and each species had a different mean height: 180 m for Scots Pine, 7.9 m for Alder, 5.1 m for willows and 4.3 m for birches; and this gave the second lowest diversity index for average height. The canopy was most widespread at 9.0 m for the Scots Pines, 4.0m for the Alders and 1.5 m for the birches.

Study plot 5: part of Earlshallmuir.

This plot was 22.4 ha in extent and was a totally open area of undulating consolidated dune grassland, with dune slacks running north-south to its east and west, and with "blow-outs" running east-west across it; this topography had been present for at least 250 years. Given its open nature, it is not surprising that it had a Light Intensity Index of 0.96, the only shade at ground level being from the field vegetation of grasses, rushes and Ragwort, which were between 10-110 cms in height (mean 28.0 cm) and covered 97% of the ground, the remaining 3% being unvegetated sand in or around blow-outs and rabbit burrows.

CHAPTER 3RESULTS3.1 INTRODUCTION

The previous two chapters have described the study areas and the methods employed in them.

This third chapter describes the results obtained from the fieldwork spread over the three breeding seasons of 1979, 1980 and 1981. The chapter is divided into sections covering the results from the two field methods used (mapping and simple line transects) and a comparison between them; a description of the breeding bird communities in the study areas and comparisons between them; and descriptions of the communities in relation to habitat type and then of the habitats and communities along a successional gradient.

It is relevant to note here that the winter of 1978/79, which preceded the first season's fieldwork was, from a meteorological viewpoint, the most severe since that of 1962/63, and followed a series of particularly mild winters. This meant that there was high mortality of many species of resident birds, and consequently their populations were depressed to a low level at the start of the ensuing breeding season of 1979 (Cawthorne and Marchant, 1980).

Thus, in addition to acquiring basic data on the breeding populations of the study areas, the same data also revealed how the populations responded to the hard winter. In this respect the breeding communities of the study areas can be compared in relation to the magnitudes of their responses; and in a wider context the annual changes in their populations can be compared with the national changes analysed and published by the B.T.O. (Marchant and Taylor, 1981; Marchant, 1982).

3.2 RESULTS FROM THE MAPPING CENSUSES

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3.2 RESULTS FROM THE MAPPING CENSUSES

During fieldwork all bird species noted in a study area and its immediate vicinity were recorded on each visit map, and all the visit maps analysed for each species at the end of each fieldwork season. The results were presented in manuscript form, copies of which are held by the author and by the N.C.C.'s Assistant Regional Officer for Fife and Kinross (Dougall, 1980, 1981). However, since the mapping method works best for breeding passerine species, only these will be dealt with in the present thesis; but in passing it is interesting to note the proportions of non-passserine and passerine species in each study area (Tables 3.1, 3.2).

TABLE 3.1 The proportions of non-passserine (NP) and passerine (P) species in the breeding populations studied 1979-81

| Study area : | 1 | 2 | 3 | 4 | 5 | | | | | | | |
|---------------|--|------------------------------------|-----------------------|-------------------------|------------------------|----|----|-----|----|----|-----|----|
| Habitat type: | Semi-natural Coniferous Woodland | Commercial Coniferous Forest | Birch/Willow Scrub | Birch/Alder Woodland | Open dune Grassland | | | | | | | |
| % NP or P : | S | %NP | %P | S | %NP | %P | S | %NP | %P | S | %NP | %P |
| 1979 | 22 | 41 | 59 | 21 | 33 | 67 | 28 | 43 | 57 | 26 | 35 | 65 |
| 1980 | 29 | 34 | 66 | 24 | 25 | 75 | 29 | 38 | 62 | 29 | 34 | 66 |
| 1981 | 31 | 39 | 61 | 22 | 18 | 82 | 32 | 37 | 63 | 31 | 42 | 58 |
| | 11 | 55 | 45 | | | | 11 | 64 | 36 | | | |

S = number of species attempting to breed.

Three of the five areas showed an increase in the number of species attempting to breed between each of the three years studied, but this cannot be taken as evidence of a general trend due to the small sample sizes involved. Neither is there a general trend of increase or decrease in the proportions of the species which were passerine, but this proportion did not vary greatly within a study area. Overall the proportion of passerine species ranged from 31 - 82%, but for woodland only from 57 - 82%, with a further

breakdown to 59 - 82% for coniferous woodland and only 57 - 66% for deciduous woodland.

Little work has been done on the ratios of non-passserine to passerine species in breeding habitats, but the apparently low variation would suggest that this might be an area of fruitful further investigation (Faaborg, 1977; Fuller, 1982).

Fuller (1982, p 186 and Table 55) has documented the non-passserine:passerine ratio for a variety of general habitat types. For woodland during the breeding season he found that the ratio of mean number of non-passserine to passerine species on 240 sites was 0.29 - this reflects the general dominance of the smaller, more active, and behaviourally more flexible passserines in woodland and scrub habitats. Table 3.2 documents the ratio for the four woodlands in the present study, and except for Area 2 in 1981, all values are above those of Fuller, which may be a genuine difference or an artefact of the small sample size.

TABLE 3.2 The numbers of non-passserine (NP) and passerine (P) species in four woodland study areas 1979-81

| Study area Species | 1 | | | 2 | | | 3 | | | 4 | | | Mean All areas | | |
|------------------------|----|----|------|----|-----|------|----|-----|------|----|----|------|-------------------|-----|------|
| | N | P | N/P | N | P | N/P | N | P | N/P | N | P | N/P | N | P | N/P |
| 1979 | 9 | 13 | 0.69 | 7 | 14 | 0.50 | 12 | 16 | 0.75 | 9 | 17 | 0.53 | 37 | 60 | 0.62 |
| 1980 | 10 | 19 | 0.53 | 6 | 18 | 0.33 | 11 | 18 | 0.61 | 10 | 19 | 0.53 | 37 | 74 | 0.50 |
| 1981 | 12 | 19 | 0.63 | 4 | 18 | 0.22 | 12 | 20 | 0.60 | 13 | 18 | 0.72 | 41 | 75 | 0.55 |
| Mean coniferous (1,2) | | | | N | P | N/P | | | | | | | | | |
| Mean deciduous (3,4) | | | | 48 | 101 | 0.48 | | | | | | | | | |
| Overall mean (1,2,3,4) | | | | | | | N | P | N/P | | | | N | P | N/P |
| | | | | | | | 67 | 108 | 0.62 | | | | 115 | 209 | 0.55 |

In the analysis of the species maps resulting from a season's fieldwork the following corrections were made to the basic data, to arrive at a "minimum" total of territories for each species in a study area: territories were classed as "complete", "proportional ≥ 0.5 ", and "partial". A "complete" territory had all of its registrations within a study area; a "proportional ≥ 0.5 " territory had at least half of its registrations within a study area; and a "partial" territory was one with a known number of registrations occurring within a study area but with an unknown number occurring outside it, usually the case with large territories belonging to non-passerines. The total number of "paper territories" (estimated territories rather than precisely delimited ones) held by a species in a study plot was estimated as follows:-

$$\frac{\text{No. of "complete" + "proportional } \geq 0.5 \text{ territories} + \text{No. of "partial" territories}}{2}$$

From these totals were calculated the populations, population densities, diversity indices and between-year changes documented later in this chapter.

In the following tables the species are arranged in Voous sequence (Hudson, 1978) and the study areas are arranged in a successional sequence from dune grassland (5) through birch scrub (3) to birch/alder mature woodland (4) and coniferous woodland (semi-natural, with its own succession across the dunes:1, and commercial:2).

In the tables a ✓ represents a species holding territory only on the edge of a study plot but with less than 50% of its registrations within the plot; and a () indicates the corrected figures resulting from the omission of the Starling colony in study area 4 from calculations of overall population density and diversity indices for that study area.

Table 3.3 presents the actual population figures for the study areas in terms of the estimated numbers of territories held by each species; while

Table 4 corrects for variations in the sizes of the study areas by expressing the data in terms of territories per unit area, in this case territories per square kilometre (territories/km²). In Table 4 there is also an expression of the diversity - in terms of both species richness and relative abundances - of the breeding population in each study area. The index used is that of Shannon and Weaver (1949): $H = -\sum p_i \log_e p_i$, where p_i = proportion of the total population represented by the i th species, and the sum taken over all species. Section D of Table 3.4 takes an overall view of the populations over the three-year study period in terms of the ranges of the population densities - the use of mean density was not practicable due to the small sample size (three years) and the varying rates of change in the population densities between study areas.

From Table 3.4 it can be seen that the highest total population densities were of the mature birch/alder woodland plot (4), followed by the commercial coniferous woodland plot (2), the semi-natural coniferous plot(1), the birch/willow scrub (3) and finally the open grassland (5); this ranking was consistent over the three years. The maturity of the woodland in study plot 4 meant that there were several dead and dying trees present with their attendant holes, cracks and fissures due either to processes of decay or woodpecker activity or a combination of both. In addition several of the live birches and alders were holed, all of which allowed the development and maintenance of a Starling colony of 35-47 nests. If this colony is omitted from calculations of population density then in two of the three years (1979 and 1980) the density figures for the birch/alder woodland and commercial coniferous woodland were equal highest while in the third year the latter habitat held the highest population density. This could indicate population expansion in, and saturation of, the preferred habitat of many species (birch/alder woodland) followed by overspill into a less preferred habitat (commercial coniferous woodland) - see discussion later (Glas, 1960; Williamson, 1969; Dougall, 1983). However, a caveat to bear in mind is that observed densities may not necessarily bear a close relationship to habitat variables if "source and sink" structuring is involved (Wiens and Rotenberry, 1981) - in such

cases a surplus over the carrying-capacity of one habitat (the "source") may move into another habitat with spare capacity (the "sink").

The diversity indices (taking account of the Starling colony in study plot 4) showed no consistency between the study plots except that the grassland plot always had the lowest values. The birch/willow scrub had the highest index value for the first year, to be overtaken by the commercial coniferous woodland in the second year, and the semi-natural coniferous woodland in the third year. Omitting the influence of the Starling colony in the mature birch/alder woodland makes no difference to the ranking of diversity indices in 1981, but improves the ranking of it from third to second highest in 1979 and from third highest to highest in 1980.

Table 3.5 describes the annual population changes in the study plots in terms of the % differences between years (Table 3.5A), the overall difference over the three year period (Table 3.5B) and the annual changes for all four woodland plots combined and compared with the national changes computed by the B.T.O. for all of its C.B.C. woodland plots (Table 3.5C) (Marchant and Taylor, 1981; Marchant, 1982).

Upton and Lampitt (1981), Mountford (1982) and North (1982) have each proposed mathematical models to compare annual population changes for species, based on the national samples of C.B.C. plots held by the B.T.O. Each of the studies revealed complicating factors, but hopefully there will be a concensus of views in the near future; in any case the findings are not of direct relevance to the present study which was conducted at the local, rather than the national scale.

TABLE 3.3 The breeding populations of each study plot 1979-81

| Study plot (area) | 5 (22.35 ha) | | | | 3 (19.09 ha) | | | | |
|---------------------------------|--------------|------|------|------|--------------|------|------|-------|--------|
| | Year | 1979 | 1980 | 1981 | Total | 1979 | 1980 | 1981 | Total |
| Skylark | | 10.0 | 15.0 | 15.0 | 40.0 | | | | |
| Meadow Pipit | | 1.0 | 7.0 | 7.0 | 15.0 | | | | |
| Pied Wagtail | | | | | | ✓ | | | ✓ |
| Wren | | | | | | 1.0 | 3.0 | 8.0 | 12.0 |
| Dunnock | | | | | | | | | |
| Robin | | | | | | 5.0 | 9.0 | 11.0 | 25.0 |
| Wheatear | | 1.0 | 1.0 | | 2.0 | | | | |
| Blackbird | | | | | | 1.0 | 1.0 | 1.0 | 3.0 |
| Song Thrush | | | | | | | 0.5 | 1.0 | 0.5 |
| Mistle Thrush | | | | | | | | 0.5 | 0.5 |
| Sedge Warbler | | | | | | | | | |
| Willow Warbler | | | | | | 15.5 | 15.0 | 19.0 | 49.5 |
| Goldcrest | | | | | | | | | |
| Spotted Flycatcher | | | | | | | | | |
| Long-tailed Tit | | | | | | 3.0 | 2.0 | | 5.0 |
| Coal Tit | | | | | | 3.0 | 3.0 | 3.0 | 9.0 |
| Blue Tit | | | | | | 5.0 | 6.0 | 9.0 | 20.0 |
| Great Tit | | | | | | 4.0 | 3.0 | 3.0 | 10.0 |
| Treecreeper | | | | | | 2.0 | 1.0 | 2.0 | 5.0 |
| Jay | | | | | | 1.0 | | 1.0 | 2.0 |
| Jackdaw | | | | | | | | ✓ | |
| Carrion Crow | | 0.5 | | 0.5 | 1.0 | 0.5 | 1.0 | 1.0 | 2.5 |
| Starling | | | | | | 2.0 | 1.0 | 4.0 | 7.0 |
| Chaffinch | | | | | | 22.0 | 14.0 | 23.0 | 59.0 |
| Siskin | | | | | | | | 0.25 | 0.25 |
| Linnet | | | | | | 1.0 | | 1.0 | 2.0 |
| Redpoll | | | | | | 3.0 | 2.0 | 2.5 | 7.5 |
| Crossbill | | | | | | | 2.0 | | 2.0 |
| Bullfinch | | | | | | | | 1.5 | 1.5 |
| Yellowhammer | | | | | | 1.0 | | | 1.0 |
| Reed Bunting | | 1.0 | ✓ | 1.0 | 2.0 | | ✓ | | ✓ |
| Total | | 13.5 | 23.0 | 23.5 | 60.0 | 70.0 | 63.5 | 91.75 | 225.25 |
| No. of species (excludes ✓) | | 5 | 3 | 4 | 5 | 16 | 15 | 19 | 22 |

TABLE 3.3 Continued

| Year | Study plot (area) | | | | 4 (11.58 ha) | | | | 1 (19.72 ha) | | | |
|---------------------------------|-------------------|-------|--------|--------|--------------|------|-------|-------|--------------|------|------|-------|
| | 1979 | 1980 | 1981 | Total | 1979 | 1980 | 1981 | Total | 1979 | 1980 | 1981 | Total |
| Skylark | | | | | | | | | | | | |
| Meadow Pipit | | | | | | | | | | | | 1.0 |
| Pied Wagtail | | | | | | | | | | | | 1.0 |
| Wren | 4.0 | 6.0 | 12.0 | 22.0 | | | | | ✓ | 3.0 | 3.0 | 3.0 |
| Dunnock | | | 1.0 | 1.0 | | | | | 2.0 | 1.0 | 3.0 | 3.0 |
| Robin | 2.0 | 5.0 | 8.0 | 15.0 | 11.0 | 12.0 | 22.0 | 45.0 | | | | |
| Wheatear | | | | | | | | | | | | |
| Blackbird | 1.0 | 2.0 | 1.0 | 4.0 | 4.0 | 1.0 | 3.0 | 8.0 | | | | |
| Song Thrush | 1.0 | 0.5 | | 1.5 | 2.0 | 2.0 | 3.0 | 7.0 | | | | |
| Mistle Thrush | | | 0.5 | 0.5 | | | | | | | | |
| Sedge Warbler | 1.0 | 1.0 | 1.0 | 3.0 | | | | | | | | |
| Willow Warbler | 10.5 | 10.0 | 11.0 | 31.5 | 11.0 | 6.0 | 8.0 | 25.0 | | | | |
| Goldcrest | | | | | ✓ | 5.0 | 14.0 | 19.0 | | | | |
| Spotted Flycatcher | 1.0 | 1.0 | | 2.0 | | | | | | | | |
| Long-tailed Tit | 3.0 | 2.0 | | 5.0 | 1.0 | 3.0 | 2.0 | 6.0 | | | | |
| Coal Tit | 1.5 | 5.0 | 4.0 | 10.5 | 7.0 | 17.0 | 14.0 | 38.0 | | | | |
| Blue Tit | 6.0 | 7.0 | 6.0 | 19.0 | | 2.0 | 2.5 | 4.5 | | | | |
| Great Tit | 3.0 | 4.0 | 5.0 | 12.0 | 2.0 | 1.0 | 3.0 | 6.0 | | | | |
| Treecreeper | 1.0 | 4.0 | 2.0 | 7.0 | 2.0 | 2.0 | 3.0 | 7.0 | | | | |
| Jay | | | | | ✓ | 1.0 | 1.0 | 2.0 | | | | |
| Jackdaw | | | | | ✓ | ✓ | | | | | | |
| Carrion Crow | 0.5 | 1.0 | 1.0 | 2.5 | 0.5 | 1.0 | 1.5 | 3.0 | | | | |
| Starling | 47.0 | 37.0 | 35.0 | 119.0 | | | | | | | | |
| Chaffinch | 21.0 | 15.0 | 20.0 | 56.0 | 33.0 | 33.0 | 34.0 | 100.0 | | | | |
| Siskin | | ✓ | 0.25 | 0.25 | | 2.5 | 3.0 | 5.5 | | | | |
| Linnet | | | | | | | | | | | | |
| Redpoll | 3.0 | 2.0 | 2.0 | 7.0 | 2.0 | 2.0 | 3.0 | 7.0 | | | | |
| Crossbill | | | | | | | 2.0 | 2.0 | | | | |
| Bullfinch | | | | 0.5 | 0.5 | | 1.0 | 2.0 | | | | |
| Yellowhammer | 1.0 | | | 1.0 | 2.0 | | | | | | | |
| Reed Bunting | | ✓ | | | ✓ | | | | | | | |
| Total | 107.5 | 103.5 | 110.25 | 321.25 | 75.5 | 95.5 | 124.0 | 295.0 | | | | |
| No. of species (excludes ✓) | 17 | 17 | 16 | 21 | 11 | 18 | 19 | 20 | | | | |

TABLE 3.3 Continued

| Study plot (area) | 2 (20.59 ha) | | | |
|---------------------------------|--------------|--------------|--------------|--------------|
| Year | 1979 | 1980 | 1981 | Total |
| Skylark | | | | |
| Meadow Pipit | | | | |
| Pied Wagtail | | | | |
| Wren | 3.0 | 7.0 | 11.5 | 21.5 |
| Dunnock | 2.0 | 3.0 | 3.0 | 8.0 |
| Robin | 10.0 | 17.0 | 31.0 | 58.0 |
| Wheatear | | | | |
| Blackbird | 10.0 | 3.0 | 5.0 | 18.0 |
| Song Thrush | 1.0 | 3.0 | 5.0 | 9.0 |
| Mistle Thrush | | | | |
| Sedge Warbler | | | | |
| Willow Warbler | 15.0 | 12.0 | 11.0 | 38.0 |
| Goldcrest | 7.0 | 14.0 | 14.0 | 35.0 |
| Spotted Flycatcher | | | | |
| Long-tailed Tit | 2.0 | 4.0 | 1.0 | 7.0 |
| Coal Tit | 17.0 | 17.0 | 26.0 | 60.0 |
| Blue Tit | 1.0 | 2.0 | 1.0 | 4.0 |
| Great Tit | | 1.0 | 2.0 | 3.0 |
| Treecreeper | 2.0 | 2.0 | 3.0 | 7.0 |
| Jay | 0.5 | 0.5 | ✓ | 1.0 |
| Jackdaw | | | | |
| Carrion Crow | | | | |
| Starling | | | | |
| Chaffinch | 31.0 | 27.0 | 32.0 | 90.0 |
| Siskin | | 1.5 | 1.0 | 2.5 |
| Linnet | | | | |
| Redpoll | 6.0 | 2.5 | 2.0 | 10.5 |
| Crossbill | | ✓ | 0.5 | 0.5 |
| Bullfinch | | 1.0 | 1.0 | 2.0 |
| Yellowhammer | | | | |
| Reed Bunting | | | | |
| Total | 107.5 | 117.5 | 150.0 | 375.0 |
| No. of species (excludes ✓) | 14 | 17 | 17 | 18 |

TABLE 3.4 The densities of the breeding populations of each study plot (territories/km²)

A: 1979

| Study plot | 5 | 3 | 4 | 1 | 2 |
|--------------------|--------|--------|----------|--------|--------|
| Skylark | 44.70 | | | | |
| Meadow Pipit | 4.47 | | | | |
| Pied Wagtail | | | | | |
| Wren | | 5.24 | 34.56 | | 14.58 |
| Dunnock | | | | | 9.72 |
| Robin | | 26.20 | 17.28 | 55.77 | 48.60 |
| Wheatear | 4.47 | | | | |
| Blackbird | | 5.24 | 8.64 | 20.28 | 48.60 |
| Song Thrush | | | 8.64 | 10.14 | 4.86 |
| Mistle Thrush | | | | | |
| Sedge Warbler | | | 8.64 | | |
| Willow Warbler | | 81.22 | 90.72 | 55.77 | 72.90 |
| Goldcrest | | | | | 34.02 |
| Spotted Flycatcher | | | 8.64 | | |
| Long-tailed Tit | | 15.72 | 25.92 | 5.07 | 9.72 |
| Coal Tit | | 15.72 | 12.96 | 35.49 | 82.62 |
| Blue Tit | | 26.20 | 51.84 | | 4.86 |
| Great Tit | | 20.96 | 25.92 | 10.14 | |
| Treecreeper | | 10.48 | 8.64 | 10.14 | 9.72 |
| Jay | | 5.24 | | | 2.43 |
| Jackdaw | | | | | |
| Carrion Crow | 2.24 | 2.62 | 4.32 | 2.54 | |
| Starling | | 10.48 | 406.08 | | |
| Chaffinch | | 115.28 | 181.44 | 167.31 | 150.66 |
| Siskin | | | | | |
| Linnet | | 5.24 | | | |
| Redpoll | | 15.72 | 25.92 | 10.14 | 29.16 |
| Crossbill | | | | | |
| Bullfinch | | | | | |
| Yellowhammer | | 5.24 | 8.64 | | |
| Reed Bunting | 4.47 | | | | |
| Total | 60.35 | 366.80 | 928.80 | 382.79 | 522.45 |
| | | | (522.72) | | |
| Diversity Index | 0.9229 | 2.1851 | 1.9109 | 1.7745 | 2.1401 |
| | | | (2.1778) | | |

() = with Starling colony omitted

TABLE 3.4 Continued

B: 1980

| Study plot | 5 | 3 | 4 | 1 | 2 |
|--------------------|--------|--------|----------|--------|--------|
| Skylark | 67.05 | | | | |
| Meadow Pipit | 31.29 | | | | |
| Pied Wagtail | | | | | |
| Wren | 15.72 | 51.84 | | 34.02 | |
| Dunnock | | 8.64 | 10.14 | 14.58 | |
| Robin | 47.16 | 43.20 | 60.84 | 82.62 | |
| Wheatear | 4.47 | | | | |
| Blackbird | 5.24 | 17.28 | 5.07 | 14.58 | |
| Song Thrush | 2.62 | 4.32 | 10.14 | 14.58 | |
| Mistle Thrush | | | | | |
| Sedge Warbler | | 8.64 | | | |
| Willow Warbler | 78.60 | 86.40 | 30.42 | 58.32 | |
| Goldcrest | | | 25.35 | 68.04 | |
| Spotted Flycatcher | | 8.64 | | | |
| Long-tailed Tit | 10.48 | 17.28 | 15.21 | 19.44 | |
| Coal Tit | 15.72 | 43.20 | 86.19 | 82.62 | |
| Blue Tit | 31.44 | 60.48 | 10.14 | 9.72 | |
| Great Tit | 15.72 | 34.56 | 5.07 | 4.86 | |
| Tree creeper | 5.24 | 34.56 | 10.14 | 9.72 | |
| Jay | | | 5.07 | 2.43 | |
| Jackdaw | | | | | |
| Carriion Crow | 5.24 | 8.64 | 5.07 | | |
| Starling | 5.24 | 319.68 | | | |
| Chaffinch | 73.36 | 129.60 | 167.31 | 131.22 | |
| Siskin | | | 12.68 | 7.29 | |
| Linnet | | | | | |
| Redpoll | 10.48 | 17.28 | 10.14 | 12.15 | |
| Crossbill | 10.48 | | 10.14 | | |
| Bullfinch | | | 5.07 | 4.86 | |
| Yellowhammer | | | | | |
| Reed Bunting | | | | | |
| Total | 102.81 | 332.74 | 894.24 | 484.19 | 571.05 |
| | | | (574.56) | | |
| Diversity Index | 0.7771 | 2.2330 | 2.1988 | 2.1919 | 2.3285 |
| | | | (2.7908) | | |

TABLE 3.4 Continued

C: 1981

| Study plot | 5 | 3 | 4 | 1 | 2 |
|--------------------|--------|--------|----------|--------|--------|
| Skylark | 67.05 | | | | |
| Meadow Pipit | 31.29 | 2.62 | | 5.07 | |
| Pied Wagtail | | | | | |
| Wren | | 41.92 | 103.68 | 15.21 | 55.89 |
| Dunnock | | | | 5.07 | 14.58 |
| Robin | | 57.64 | 69.12 | 111.54 | 150.66 |
| Wheatear | | | | | |
| Blackbird | | 5.24 | 8.64 | 15.21 | 24.30 |
| Song Thrush | | 5.24 | | 15.21 | 24.30 |
| Mistle Thrush | | 2.62 | 4.32 | | |
| Sedge Warbler | | | 8.64 | | |
| Willow Warbler | | 99.56 | 95.04 | 40.56 | 53.46 |
| Goldcrest | | | | 70.98 | 68.04 |
| Spotted Flycatcher | | | | | |
| Long-tailed Tit | | | | 10.14 | 4.86 |
| Coal Tit | | 15.72 | 34.56 | 70.98 | 126.36 |
| Blue Tit | | 47.16 | 51.84 | 12.68 | 4.86 |
| Great Tit | | 15.72 | 43.20 | 15.21 | 9.72 |
| Treecreeper | | 16.48 | 17.28 | 15.21 | 14.58 |
| Jay | | 5.24 | | 5.07 | |
| Jackdaw | | | | | |
| Carrion Crow | 2.24 | 5.24 | 8.64 | 7.61 | |
| Starling | | 20.96 | 302.40 | | |
| Chaffinch | | 120.52 | 172.80 | 172.38 | 155.52 |
| Siskin | | 1.31 | 2.16 | 7.61 | 4.86 |
| Linnet | | 5.24 | | | |
| Redpoll | | 13.10 | 17.28 | 7.61 | 9.72 |
| Crossbill | | | | | 2.43 |
| Bullfinch | | 7.86 | 4.32 | 10.14 | 4.86 |
| Yellowhammer | | | 8.64 | | |
| Reed Bunting | | 4.47 | | | |
| Total | 105.05 | 480.77 | 952.56 | 613.47 | 729.00 |
| | | | (650.16) | | |
| Diversity Index | 0.8636 | 2.2960 | 2.1335 | 2.3016 | 2.2200 |
| | | | (2.2102) | | |

TABLE 3.4 Continued

D: Ranges of Population Densities and Diversity Indices 1979-81

(n) = no. of years' data, if < 3, or where figure identical for 2 or 3 years.

| Study plot | 5 | 3 | 4 |
|--------------------|---------------|-----------------|-----------------|
| Skylark | 44.70- 67.05 | | |
| Meadow Pipit | 4.47- 31.29 | 2.62(1) | |
| Pied Wagtail | | | |
| Wren | | 5.24- 41.92 | 34.56-103.68 |
| Dunnock | | | 8.64(1) |
| Robin | | 26.20- 57.64 | 17.28- 69.12 |
| Wheatear | 4.47(2) | | |
| Blackbird | | 5.24(3) | 8.64- 17.28 |
| Song Thrush | | 2.62- 5.24(2) | 4.32- 8.64(2) |
| Mistle Thrush | | 2.62(1) | 4.32(1) |
| Sedge Warbler | | | 8.64(3) |
| Willow Warbler | | 78.60- 99.56 | 86.40- 95.04 |
| Goldcrest | | | |
| Spotted Flycatcher | | | 8.64(2) |
| Long-tailed Tit | | 10.48- 15.72(2) | 17.28- 25.92(2) |
| Coal Tit | | 15.72(3) | 12.96- 43.20 |
| Blue Tit | | 26.20- 47.16 | 51.84- 60.48 |
| Great Tit | | 15.72- 20.96 | 25.92- 43.20 |
| Treecreeper | | 5.24- 16.48 | 8.64- 34.56 |
| Jay | | 5.24(2) | |
| Jackdaw | | | |
| Carrion Crow | 2.24(2) | 2.62- 5.24 | 4.32- 8.64 |
| Starling | | 10.48- 20.96 | 302.40-406.08 |
| Chaffinch | | 73.36-120.52 | 129.60-181.44 |
| Siskin | | 1.31(1) | 2.16(1) |
| Linnet | | 5.24(2) | |
| Redpoll | | 10.48- 15.72 | 17.28- 25.92 |
| Crossbill | | 10.48(1) | |
| Bullfinch | | 7.86(1) | 4.32(1) |
| Yellowhammer | | 5.24(1) | 8.64(2) |
| Reed Bunting | 4.47(2) | 4.47(2) | |
| Total | 60.35-105.05 | 332.74-480.77 | 894.24-952.56 |
| | | | (522.72-650.16) |
| Diversity Index | 0.7771-0.9229 | 2.1851-2.2960 | 1.9109-2.1988 |
| | | | (2.1778-2.7908) |

TABLE 3.4 Continued

D Continued

(n), as before.

| Study plot | 1 | 2 |
|--------------------|-----------------|---------------|
| Skylark | | |
| Meadow Pipit | 5.07(1) | |
| Pied Wagtail | | |
| Wren | 15.21(1) | 14.58- 55.89 |
| Dunnock | 5.07- 10.14(2) | 9.72- 14.58 |
| Robin | 55.77-111.54 | 48.60-150.66 |
| Wheatear | | |
| Blackbird | 5.07- 20.28 | 14.58- 48.60 |
| Song Thrush | 10.14- 15.21 | 4.86- 24.30 |
| Mistle Thrush | | |
| Sedge Warbler | | |
| Willow Warbler | 30.42- 55.77 | 53.46- 72.90 |
| Goldcrest | 25.35- 70.98(2) | 34.02- 68.04 |
| Spotted Flycatcher | | |
| Long-tailed Tit | 5.07- 15.21 | 4.86- 19.44 |
| Coal Tit | 35.49- 86.19 | 82.62-126.36 |
| Blue Tit | 10.14- 12.68(2) | 4.86- 9.72 |
| Great Tit | 5.07- 15.21 | 4.86- 9.72(2) |
| Treecreeper | 10.14- 15.21 | 9.72- 14.58 |
| Jay | 5.07(2) | 2.43(2) |
| Jackdaw | | |
| Carrion Crow | 2.54- 7.61 | |
| Starling | | |
| Chaffinch | 167.31-172.38 | 131.22-155.52 |
| Siskin | 7.61- 12.68(2) | 4.86- 7.29(2) |
| Linnet | | |
| Redpoll | 7.61- 10.14 | 9.72- 29.16 |
| Crossbill | 10.14(1) | 2.43(1) |
| Bullfinch | 5.07- 10.14(2) | 4.86(2) |
| Yellowhammer | | |
| Reed Bunting | | |
| Total | 382.79-613.47 | 522.45-729.00 |
| Diversity Index | 1.7745-2.3016 | 2.1401-2.3285 |

TABLE 3.4 Continued

E: "Total" 3-year densities (terrs/km²)

| Study plot | 5 | 3 | 4 | 1 | 2 |
|----------------------|--------|---------|------------|---------|---------|
| Skylark | 178.80 | | | | |
| Meadow Pipit | 67.05 | 2.62 | | 5.07 | |
| Pied Wagtail | | | | | |
| Wren | | 62.88 | 190.08 | 15.21 | 104.49 |
| Dunnock | | | 8.64 | 15.21 | 38.88 |
| Robin | | 131.00 | 129.60 | 228.15 | 281.88 |
| Wheatear | 8.94 | | | | |
| Blackbird | | 15.72 | 34.56 | 40.56 | 87.48 |
| Song Thrush | | 2.62 | 12.96 | 35.49 | 43.74 |
| Mistle Thrush | | 2.62 | 4.32 | | |
| Sedge Warbler | | | 25.92 | | |
| Willow Warbler | | 259.38 | 272.16 | 126.75 | 184.68 |
| Goldcrest | | | | 96.33 | 170.10 |
| Spotted Flycatcher | | | 17.28 | | |
| Long-tailed Tit | | 26.20 | 43.20 | 30.42 | 34.02 |
| Coal Tit | | 47.16 | 90.72 | 192.66 | 291.60 |
| Blue Tit | | 104.80 | 164.16 | 22.82 | 19.44 |
| Great Tit | | 52.40 | 103.68 | 30.42 | 14.58 |
| Treecreeper | | 26.20 | 60.48 | 35.49 | 34.02 |
| Jay | | 10.48 | | 10.14 | 4.86 |
| Jackdaw | | | | | |
| Carrion Crow | 4.47 | 13.10 | 21.60 | 15.21 | |
| Starling | | 36.68 | 1028.16 | | |
| Chaffinch | | 309.16 | 483.84 | 570.00 | 437.40 |
| Siskin | | 1.31 | 2.16 | 27.89 | 12.15 |
| Linnet | | 10.48 | | | |
| Redpoll | | 39.30 | 60.48 | 35.49 | 51.03 |
| Crossbill | | 10.48 | | 10.14 | 2.43 |
| Bullfinch | | 7.86 | 4.32 | 15.21 | 9.72 |
| Yellowhammer | | 5.24 | 17.28 | | |
| Reed Bunting | 8.94 | | | | |
| Total* | 268.20 | 1180.31 | 2775.60 | 1495.65 | 1822.50 |
| Species: | 5 | 22 | 21 | 20 | 18 |
| * omitting Starling: | | | 1747.44;20 | | |

The 103 woodland census plots used in the national comparisons for 1979-80 had a mean area of 21.6 ha (Fife plots 17.75 ha), and were subdivided into true woodland (78% of plots, mean area of plot 19.8 ha), parkland (13% of plots, mean area 26.8 ha) and heathland with scrub (10% of plots, mean area 29.2 ha). Only 12% of all woodland plots were in Scotland (85% in England, 2% in Northern Ireland, 1% in Wales) so the four studied here are of great interest (Marchant and Taylor, 1981 and in litt.).

In the 1980-81 comparisons the 100 woodland census plots had a mean area of 20.7 ha and were divided into true woodland, parkland, heathland with scrub in the following proportions and mean areas: 80%, 11%, 9%; 19.2 ha, 24.4 ha and 30.1 ha. In all respects the comparisons of the national figures for 1979-80 and 1980-81 can be justified from the similarities of the parameters of the study plot types. The importance, in a Scottish context, of the four Fife plots studied here is again evident from the fact that only 6 others were under scrutiny in Scotland, compared with totals of 88 in England and one in each of Northern Ireland and Wales (Marchant, 1982 and in litt.).

Below is a key to Table 3.5:-

For parts A, B and C: % population change =
$$\frac{\text{population in year } (x + 1) - \text{population in year } x}{\text{population in year } x}$$

= species with ≥ 5 territories in at least one of the years being compared (for parts A,B) and with ≥ 10 territories for part C.
 $(\frac{5}{10}) \approx 10\%$ of max. total for a species)

+ = increase in population, but % size unknown due to zero figure in year x.

- = decrease in population, but % size unknown due either to presence of species in a non-territorial capacity in year $(x + 1)$ but with population figures for year x e.g. 5, ✓; or presence of species in a non-territorial capacity in year x and absence of the species in the following year $(x + 1)$ e.g. ✓, 0.

For part C only: n = number of study plots in sample; see text for further details.

Footnote 1: the national changes are presented in tabular form as % change with 95% confidence limits.

Footnote *: the statistical significance refers to this change within its confidence limits.

TABLE 3.5 A % change in populations 1979-80, 1980-81

| Study area Years | 5 | | 3 | | 4 | |
|---------------------|----------|---------|---------|----------|----------|----------|
| | 1979-80 | 1980-81 | 1979-80 | 1980-81 | 1979-80 | 1980-81 |
| Skylark | +50.00* | 0* | | | | |
| Meadow Pipit | +600.00* | 0* | | | | |
| Pied Wagtail | | | + | - | | |
| Wren | | | +200.00 | +166.67* | +50.00* | +100.00* |
| Dunnock | | | | | + | -100.00 |
| Robin | | | +80.00* | +22.22* | +150.00 | +60.00* |
| Wheatear | 0 | -100.00 | | | | |
| Blackbird | | | 0 | 0 | +100.00 | -50.00 |
| Song Thrush | | | + | +100.00 | -50.00 | -100.00 |
| Mistle Thrush | | | | + | | |
| Sedge Warbler | | | | | 0 | 0 |
| Willow Warbler | | -3.23 | +26.67* | | -4.76 | +10.00* |
| Goldcrest | | | | | | |
| Spotted Flycatcher | | | | | 0 | -100.00 |
| Long-tailed Tit | | | -33.33 | -100.00 | -33.33 | -100.00 |
| Coal Tit | | | 0 | 0 | +233.33* | -20.00* |
| Blue Tit | | | +20.00* | +50.00 | +16.67* | -14.29* |
| Great Tit | | | -25.00 | 0 | +33.33 | +25.00* |
| Treecreeper | | | -50.00 | +100.00 | +300.00 | -50.00 |
| Jay | | | -100.00 | + | | |
| Jackdaw | | | | + | | + |
| Carrion Crow | -100.00 | + | +100.00 | 0 | +100.00 | 0 |
| Starling | | | -50.00 | +300.00 | -21.28* | -5.41* |
| Chaffinch | | | -31.82* | +64.29* | -28.57* | +33.33* |
| Siskin | | | + | -50.00 | + | + |
| Linnet | | | -100.00 | + | | |
| Redpoll | | | -33.33 | +25.00 | -33.33 | 0 |
| Crossbill | | | + | -100.00 | | |
| Bullfinch | | | | + | | + |
| Yellowhammer | | | -100.00 | | -100.00 | + |
| Reed Bunting | - | + | + | - | + | 0 |
| Total | +70.37 | +2.17 | -9.29 | +44.49 | -3.72 | +6.52 |

TABLE 3.5 A Continued

| Study area Years | 1 | | 2 | |
|---------------------|----------|----------|----------|----------|
| | 1979-80 | 1980-81 | 1979-80 | 1980-81 |
| Skylark | | | | |
| Meadow Pipit | | + | | |
| Pied Wagtail | | | | |
| Wren | | + | +133.33* | +164.29* |
| Dunnock | | -50.00 | +50.00 | 0 |
| Robin | +9.09* | +83.33* | +70.00* | +82.35* |
| Wheatear | | | | |
| Blackbird | -75.00 | +200.00 | -70.00* | +66.67* |
| Song Thrush | 0 | +50.00 | +200.00 | +66.67* |
| Mistle Thrush | | | | |
| Sedge Warbler | | | | |
| Willow Warbler | -45.45* | +33.33* | -20.00* | -8.33* |
| Goldcrest | +* | +180.00* | +100.00* | 0* |
| Spotted Flycatcher | | | | |
| Long-tailed Tit | +200.00 | -33.33* | +100.00 | -75.00 |
| Coal Tit | +142.85* | -17.65* | 0* | +52.94* |
| Blue Tit | + | +25.00 | +100.00 | -50.00 |
| Great Tit | -50.00 | +200.00 | + | +100.00 |
| Treecreeper | 0 | +50.00 | 0 | +50.00 |
| Jay | + | 0 | 0 | - |
| Jackdaw | | | | |
| Carrion Crow | +100.00 | +50.00 | | |
| Starling | | | | |
| Chaffinch | 0* | +3.03* | -12.90* | +18.52* |
| Siskin | + | -40.00 | + | -33.33 |
| Linnet | | | | |
| Redpoll | 0 | -25.00 | -58.33* | -20.00 |
| Crossbill | + | -100.00 | + | + |
| Bullfinch | + | +100.00 | + | 0 |
| Yellowhammer | | | | |
| Reed Bunting | | | | |
| Total | +26.49 | +26.70 | +9.30 | +27.66 |

TABLE 3.5 B % change between the populations of 1979 and 1981

| Study area | 5 | 3 | 4 | 1 | 2 |
|--------------------|----------------------|----------------------|----------------------|----------------------|----------------------|
| Skylark | +50.00 [#] | | | | |
| Meadow Pipit | +600.00 [#] | + | | + | |
| Pied Wagtail | | | | | |
| Wren | | +700.00 [#] | +200.00 [#] | + | +283.33 [#] |
| Dunnock | | | | + | +50.00 |
| Robin | | +120.00 [#] | +300.00 [#] | +100.00 [#] | +210.00 [#] |
| Wheatear | -100.00 | | | | |
| Blackbird | | 0 | 0 | -25.00 | -50.00 [#] |
| Song Thrush | | + | -100.00 | +50.00 | +400.00 [#] |
| Mistle Thrush | | + | + | | |
| Sedge Warbler | | | 0 | | |
| Willow Warbler | +22.58 [#] | +4.76 [#] | -27.27 [#] | | -26.67 [#] |
| Goldcrest | | | | + [#] | +100.00 [#] |
| Spotted Flycatcher | | | -100.00 | | |
| Long-tailed Tit | -100.00 | -100.00 [#] | +100.00 [#] | | -50.00 [#] |
| Coal Tit | 0 | +166.67 [#] | +100.00 [#] | | +52.94 [#] |
| Blue Tit | +80.00 [#] | 0 [#] | + | | 0 |
| Great Tit | -25.00 | +66.67 [#] | +50.00 | | + |
| Treecreeper | 0 | +100.00 | +50.00 | | +50.00 |
| Jay | 0 | | | + | - |
| Jackdaw | | | + | | |
| Carrion Crow | 0 | +100.00 | +100.00 [#] | +200.00 | |
| Starling | | +100.00 [#] | -25.53 [#] | | |
| Chaffinch | | +4.55 [#] | -5.00 [#] | +3.03 [#] | +3.23 [#] |
| Siskin | + | + | + | | + |
| Linnet | 0 | | | | |
| Redpoll | | -16.67 | -33.33 | +50.00 | -66.67 [#] |
| Crossbill | | | | | + |
| Bullfinch | | + | + | + | + |
| Yellowhammer | | -100.00 | 0 | | |
| Reed Bunting | 0 | | | | |
| Total | +74.07 | +31.07 | +2.56 | +64.24 | +39.53 |

TABLE 3.5 C % change in total populations in all four woodland study areas between 1979-80 and 1980-81 and comparisons with the national¹ figures for the same periods

| | Study areas (n=4) 1979-80 | National (n=103) | Study areas (n=4) | National (n=106) 1980-81 |
|--------------------|---------------------------------|---------------------|--------------------------|--------------------------------|
| Skylark | | | | |
| Meadow Pipit | | | | + (1) |
| Pied Wagtail | | | | |
| Wren | +100.00 [*] (3) | +57 (102)* | +115.63 [*] (4) | +18 (100)* |
| Dunnock | +200.00 (2) | -1 (94) | -33.33 (3) | +8 (91) |
| Robin | +48.28 [*] (4) | +14 (103)* | +67.44 [*] (4) | +15 (99)* |
| Wheatear | | | | |
| Blackbird | -56.25 [*] (4) | +6 (103)* | +42.86 [*] (4) | +4 (99) |
| Song Thrush | +50.00 (4) | +3 (101) | +50.00 [*] (4) | +13 (98)* |
| Mistle Thrush | | +7 (80) | + | +10 (87) |
| Sedge Warbler | 0 (1) | | 0 (2) | |
| Willow Warbler | -13.46 [*] (4) | +16 (98)* | +8.89 [*] (4) | +9 (95)* |
| Goldcrest | +171.43 [*] (2) | +60 (63)* | +47.37 [*] (2) | +12 (70) |
| Spotted Flycatcher | 0 (1) | +5 (48) | -100.00 [*] (1) | -3 (47) |
| Long-tailed Tit | +22.22 [*] (4) | +44 (80)* | -72.73 [*] (4) | -12 (83) |
| Coal Tit | +50.88 [*] (4) | +14 (86)* | +9.30 [*] (4) | +6 (89) |
| Blue Tit | +41.67 [*] (4) | +10 (102)* | +8.82 [*] (4) | +3 (98) |
| Great Tit | 0 (4) | +7 (103)* | +44.44 [*] (4) | +14 (99)* |
| Treecreeper | +28.57 (4) | +6 (65) | +11.11 [*] (4) | -2 (68) |
| Jay | 0 (3) | +2 (77) | +33.33 (3) | +14 (78)* |
| Jackdaw | | | + | (2) |
| Carrion Crow | +100.00 (3) | +12 (83) | +16.67 (3) | -1 (82) |
| Starling | -22.45 [*] (2) | +16 (75) | +2.63 [*] (2) | -10 (60) |
| Chaffinch | -16.36 [*] (4) | +4 (101) | +21.79 [*] (4) | +1 (98) |
| Siskin | + (4) | | -25.00 (4) | |
| Linnet | -100.00 (1) | -8 (44) | + | (1) |
| Redpoll | -39.29 [*] (4) | | +5.88 (4) | |
| Crossbill | + (3) | | -87.50 (3) | |
| Bullfinch | + (2) | +17 (85)* | +150.00 (4) | -9 (84) |
| Yellowhammer | -100.00 (2) | +15 (56)* | + | (1) |
| Reed Bunting | + (2) | | + | (2) |

+8.69

+22.76

Notes: ¹: From Marchant and Taylor (1981) and Marchant (1982)

*: Changes significant at p < 0.05

From Table 3.5A the greatest change in total population for a study area was of 70% between 1979 and 1980 on the open grassland, and this was followed in 1980-81 by the smallest increase recorded (2%) possibly reflecting the population reaching near saturation in just one year. It is of interest that both the deciduous plots recorded decreases in population (the only decreases noted) between 1979-80 when increases might have been expected as populations recovered from the "hard" winter of 1978-79. The decreases in the total populations were due largely to decreases in the populations of Starling and Chaffinch, the former did not nest in either of the other two study plots (both coniferous) and the latter showed a population decrease in the commercial forestry plot and no change in the semi-natural coniferous plot.

Between the breeding seasons of 1980 and 1981, all woodland populations showed increases, lowest (6.5%) in the mature birch/alder woodland, of similar intermediate values (27% and 28%) for the two coniferous plots, and highest (44%) for the birch/willow scrub. This suggests that the populations may have declined least or recovered faster in the most mature (and diverse in terms of tree species, vegetation strata and presence of holes) and probably preferred habitat, while there was still room for population expansion and increase in the less preferred habitats. However, this is by no means clear, given the inter-plot differences within species which occurred (see later discussion).

Over the three-year period the balance of population in 1981 over that in 1979 was positive in each study area (Table 3.5B), being highest on the grassland plot where the value was 74%. The next highest increase was in the semi-natural coniferous woodland (64%) with the lowest in the mature birch/alder woodland (2.5%), again suggesting that either the population level was not so depressed by the 1978/79 winter in the latter, with a consequently smaller recovery rate; or that the population level was at least equally depressed but that recovery proceeded faster and more completely.

At the species level there is much of interest in the annual population

changes but to increase the reliability of the results, only those species holding at least 5 territories in any study plot in any year are considered below.

The Meadow Pipit showed the highest recorded change (+600% 1979-80) followed by no change 1980-81. This was mirrored by the Skylark on the same study plot, with increases of 50% 1979-80 and no change 1980-81. This offers evidence that both species were able quickly to recover their population levels on the study plot and that the Meadow Pipit was perhaps the harder hit of the two species by the winter of 1978-79. However, this was not reflected in the national figures where the farmland Skylark population dropped by 14% (significant at $p < 0.05$) 1978-79 but the Meadow Pipit only by 7% (not significant). This difference could be an artefact due to the larger sample size of Skylark territories nationally (around three times that of Meadow Pipit), the small size of the present study sample, but possibly also due to the fact that in the present study, the plot censused is classed by the B.T.O. as "special" i.e. neither woodland nor farmland, while the B.T.O. data for Skylark and Meadow Pipit come from farmland study plots (Marchant and Hyde, 1980). The recovery in national population 1979-80 was 12% (significant at $p < 0.05$) for Skylark and 10% (significant at $p < 0.05$) for Meadow Pipit (Marchant and Taylor, 1981).

The Wren and Robin each showed high increases in population in each of the four woodland study plots with the highest increases for Wren in the two "scrubby" sites - the birch/willow scrub and the commercial coniferous woodland, with its ground layer of brashings. In addition the Wren was absent as a territory-holding species from the semi-natural coniferous woodland in 1979 and 1980, but in 1981 three territories were occupied, coincident with both an increase in the species' population generally and the appearance of clumps of brashed timber as a result of tree clearance during the winter of 1980-81 (Dougall, 1983). The national census figures for Wren suggest that between 1978 and 1979 the woodland population fell by around 47% (significant at $p < 0.05$) and the farmland population fell by around 43% (significant at $p < 0.05$). The recoveries in the woodland population were +57% 1979-80, +18% 1980-81 and in the farmland population

+51% 1979-80 and +20% 1980-81. For Robin the comparable national figures for woodland are +14% and +15% (Fife +48%, +67%) and for farmland +15% and +12% (all significant at $p < 0.05$) (Marchant and Hyde, 1980; Marchant and Taylor, 1981; Marchant, 1982).

The Fife study areas presented inconclusive figures for Blackbird and Song Thrush, possibly due to small sample sizes. With Willow Warbler, the four Fife woodlands studied each showed a population decrease 1979-80, which was not reflected nationally, but three of the four plots echoed the national increase 1980-81. The three tit species with at least five territories in the Fife woodlands present a confused picture of increases and decreases, with a continued increase being noted only for the Blue Tit in birch/willow scrub. However, the combined populations for the four Fife woodlands for Coal, Blue and Great Tits reflected the national trend of increase, although always larger at the local scale. The Long-tailed Tit at the local scale showed population increase between 1979 and 1980 and decrease between 1980 and 1981, both revealed at the national scale.

The only other species with at least five territories in any one of the Fife woodland study areas were Starling (birch/alder plot), Chaffinch (all four plots) and Redpoll (commercial coniferous plot). The Starling colony showed signs of a decrease (partly reflected in national figures); the Chaffinch populations of the study plots showed a general decrease between 1979 and 1980 followed by a recovery in 1980-81, the size of the recovery reflecting the size of the preceding decrease (Table 3.6), but this was not confirmed nationally. The data for Redpoll are inconclusive, probably due to small sample size.

TABLE 3.6 % changes in populations of Chaffinch in the study plots

| 1979-1980 | 1980-1981 | Study plot |
|-----------|-----------|------------|
| - 31.82 | + 64.29 | 3 |
| - 28.57 | + 33.33 | 4 |
| - 12.90 | + 18.52 | 2 |
| 0 | + 3.03 | 1 |

Of the generally less abundant species (i.e. those with only 5 territories on study plots) or those scarce in one habitat type, the Meadow Pipit began to occupy or re-occupy open ground along the edges of woodland in 1981; the Wren, Mistle Thrush, Jackdaw and Bullfinch all started to appear or re-appear in certain woodland plots; while Wheatear, Spotted Flycatcher and Long-tailed Tits disappeared in 1981 as territory-holding species from all or some of the plots they occupied in 1979 and 1980. Nationally the latter two species showed population decreases in woodland plots of 3% and 12% respectively but increases on farmland plots of 23% and 29% (neither statistically significant) where the sample sizes of territories occupied were smaller (no data available for Wheatear due to inadequate sample sizes). The Fife data for Yellowhammer and Reed Bunting are inconclusive, which partly mirrors the national picture e.g. an 8% increase in Yellowhammer populations on farmland 1980-81, but an 8% decrease in the woodland populations of the same species in the same period (Marchant, 1982).

3.3 RESULTS FROM TRANSECT SAMPLING

Simple line transect surveys were conducted on two study plots - plot 3, the birch/willow scrub and plot 5, the open dune grassland. The results from these surveys are presented in Tables 3.8 and 3.9, which respectively deal with all contacts, or territorial contacts only, the latter being records of song and territorial behaviour etc.

Each bird contacted during a survey was recorded as one contact and its direction of movement noted where possible to avoid double registration of the same bird. Lateral limits for recording were physically imposed in the field by the use of thin bamboo canes at 25 m on each side of the centre-line of the transect. The transects were always the same length - 1.35 km in the scrub and 1.15 km on the grassland. To achieve this length of transect in each of the two study areas, the total transect was composed of three parallel sections running north-south through the study plots. Although each section in each plot was some distance from the edges of the plot and its neighbour (78 m in plot 3 and 95 m in plot 5) to try and avoid the double registering of a bird moving from one section to another, it is probable that this was not achieved in practice, especially with such wide-ranging species as Redpoll in the scrub and Skylark on the grassland. This is an important factor against the use of sectioned line transects, but if the line transect method is to be used in the British context of rather small discrete areas of habitat then to obtain a reasonable sample length, sections may be the only feasible way of attaining this.

More than with mapping work, the amount of time spent on a transect survey is an important factor in interpreting the results, since the longer the period of a survey the more contacts can be made, or conversely the more disturbance created and the fewer contacts made. (In mapping work it is not so much the number of contacts but rather their "quality" in terms of territorial information which is the important factor). Table 3.7 presents details of the time spent on fieldwork using simple line transects. Clearly it took longer on average to complete a transect in the scrub

than on the grassland, even allowing for the greater distance walked (overall average speed of coverage was 1.39 km/hr in scrub and 1.64 km/hr on grassland). This is probably a reflection of the higher bird population although the slightly more difficult underfoot terrain may also have been partly responsible.

TABLE 3.7 Parameters of time expenditure on simple line transects fieldwork

| Census plot (transect length) | | Birch/Willow Scrub | | |
|--------------------------------|-----------|--------------------|-----------|-----------|
| Year | | 1979 | 1980 | 1981 |
| Total time per season (hours) | | 10.25 | 4.49 | 6.66 |
| No. of visits | | 9 | 5 | 8 |
| Mean time per visit (hours) | | 1.14 | 0.90 | 0.83 |
| Range of times per visit (hrs) | 0.92-1.33 | 0.83-1.00 | 0.75-1.00 | 0.75-1.33 |
| 1979-1981 | | | | |

| Census plot (transect length) | | Dune Grassland | | |
|--------------------------------|-----------|----------------|-----------|-----------|
| Year | | 1979 | 1980 | 1981 |
| Total time per season (hours) | | 7.02 | 3.12 | 5.26 |
| No. of visits | | 9 | 5 | 8 |
| Mean time per visit (hours) | | 0.78 | 0.62 | 0.66 |
| Range of times per visit (hrs) | 0.67-1.00 | 0.62-0.67 | 0.58-0.75 | 0.58-1.00 |
| 1979-1981 | | | | |

* Mean time spent per transect over three years.

Based on the mean number of contacts per visit, the most frequently contacted bird species during line transect work in the birch/willow scrub were (in decreasing order): Chaffinch (1st in all three years), Willow Warbler (2nd in all three years), Blue Tit (3rd in two years,

5th in one year), Carrion Crow (3rd in one year, 5th in one year), Robin, Long-tailed Tit, Coal Tit and Great Tit (each 4th in one year). On the grassland plot only four species were contacted: Skylark, Meadow Pipit, Wheatear and Reed Bunting and they were generally in this order of frequency of contact. As is to be expected from this, the scrub plot always had the highest diversity index values (Shannon-Weaver H') and the indices over the three years on the two study plots showed little range in value (2.1940 to 2.2384 in the scrub and 0.9439 to 1.0077 on the grassland).

TABLE 3.8 Numbers of contacts of birds, derived from simple line transects

A Study plot 3: Birch/willow scrub

| Year (No. of visits) | Total number of contacts per season | | | Mean number of contacts per visit | | |
|----------------------|-------------------------------------|----------|----------|-----------------------------------|-------|-------|
| | 1979 (9) | 1980 (5) | 1981 (8) | 1979 | 1980 | 1981 |
| Skylark | | | | | | |
| Meadow Pipit | | | | | | |
| Pied Wagtail | | 1 | 1 | 0.20 | 0.13 | |
| Wren | 1 | | 2 | 0.11 | | 0.25 |
| Dunnock | | 1 | | | 0.20 | |
| Robin | 2 | 9 | 12 | 0.22 | 1.80 | 1.50 |
| Wheatear | | | | | | |
| Blackbird | 3 | 2 | 6 | 0.33 | 0.40 | 0.75 |
| Song Thrush | 2 | 1 | | 0.22 | 0.20 | |
| Mistle Thrush | | | | | | |
| Sedge Warbler | | | | | | |
| Willow Warbler | 41 | 19 | 33 | 4.56 | 3.80 | 4.13 |
| Goldcrest | | | 3 | | | 0.38 |
| Spotted Flycatcher | | | | | | |
| Long-tailed Tit | 29 | 7 | | 3.22 | 1.40 | |
| Coal Tit | 5 | 9 | 8 | 0.56 | 1.80 | 1.00 |
| Blue Tit | 13 | 12 | 28 | 1.44 | 2.40 | 3.50 |
| Great Tit | 12 | 5 | 23 | 1.33 | 1.00 | 2.88 |
| Treecreeper | 7 | 1 | 1 | 0.78 | 0.20 | 0.13 |
| Jay | 3 | | | 0.33 | | |
| Jackdaw | | | | | | |
| Carrion Crow | 36 | 7 | 15 | 4.00 | 1.40 | 1.88 |
| Starling | 3 | | 4 | 0.33 | | 0.50 |
| Chaffinch | 72 | 36 | 53 | 8.00 | 7.20 | 6.63 |
| Goldfinch | 1 | | | 0.11 | | |
| Siskin | | | | | | |
| Linnet | 2 | | 1 | 0.22 | | 0.13 |
| Redpoll | 12 | 8 | 4 | 1.33 | 1.60 | 0.50 |
| Crossbill | | | | | | |
| Bullfinch | | | 3 | | | 0.38 |
| Yellowhammer | 2 | 1 | | 0.22 | 0.20 | |
| Reed Bunting | 1 | | 6 | 0.11 | | 0.75 |
| Total | 247 | 119 | 203 | 27.44 | 23.80 | 25.38 |
| Diversity Index | 2.2020 | 2.1940 | 2.2384 | | | |

TABLE 3.8 Continued

B Study plot 5: Dune grassland

| Year (No. of visits) | Total number of contacts per season | | | Mean number of contacts per visit | | |
|----------------------|-------------------------------------|----------|----------|-----------------------------------|-------|-------|
| | 1979 (9) | 1980 (5) | 1981 (8) | 1979 | 1980 | 1981 |
| Skylark | 47 | 33 | 54 | 5.22 | 6.60 | 6.75 |
| Meadow Pipit | 14 | 20 | 32 | 1.56 | 4.00 | 4.00 |
| Pied Wagtail | | | | | | |
| Wren | | | | | | |
| Dunnock | | | | | | |
| Robin | | | | | | |
| Wheatear | 8 | 11 | 1 | 0.89 | 2.20 | 0.13 |
| Blackbird | | | | | | |
| Song Thrush | | | | | | |
| Mistle Thrush | | | | | | |
| Sedge Warbler | | | | | | |
| Willow Warbler | | | | | | |
| Goldcrest | | | | | | |
| Spotted Flycatcher | | | | | | |
| Long-tailed Tit | | | | | | |
| Coal Tit | | | | | | |
| Blue Tit | | | | | | |
| Great Tit | | | | | | |
| Tree creeper | | | | | | |
| Jay | | | | | | |
| Jackdaw | | | | | | |
| Carrion Crow | | | | | | |
| Starling | | | | | | |
| Chaffinch | | | | | | |
| Siskin | | | | | | |
| Linnet | | | | | | |
| Redpoll | | | | | | |
| Crossbill | | | | | | |
| Bullfinch | | | | | | |
| Yellowhammer | | | | | | |
| Reed Bunting | 4 | | 8 | 0.44 | | 1.00 |
| Total | 73 | 64 | 95 | 8.11 | 12.80 | 11.88 |
| Diversity Index | 1.0016 | 1.0077 | 0.9439 | | | |

TABLE 3.9 Numbers of territorial contacts of birds, derived from simple line transects

A Study plot 3: Birch/willow scrub

| Year (No. of visits) | Total no. of contacts* per season | | | Mean no. of contacts* per visit | | |
|----------------------|-----------------------------------|----------|----------|---------------------------------|-------|-------|
| | 1979 (9) | 1980 (5) | 1981 (8) | 1979 | 1980 | 1981 |
| Skylark | | | | | | |
| Meadow Pipit | | | | | | |
| Pied Wagtail | | | | | | |
| Wren | | | 2 | | | 0.25 |
| Dunnock | | 1 | | | | 0.20 |
| Robin | 2 | 8 | 11 | 0.22 | 1.60 | 1.38 |
| Wheatear | | | | | | |
| Blackbird | 2 | 2 | 1 | 0.22 | 0.40 | 0.13 |
| Song Thrush | | | | | | |
| Mistle Thrush | | | | | | |
| Sedge Warbler | | | | | | |
| Willow Warbler | 35 | 19 | 32 | 3.89 | 3.80 | 4.00 |
| Goldcrest | | | 1 | | | |
| Spotted Flycatcher | | | | | | |
| Long-tailed Tit | 16 | 2 | | 1.78 | 0.40 | |
| Coal Tit | 2 | 2 | 2 | 0.22 | 0.40 | 0.25 |
| Blue Tit | | 4 | 3 | | 0.80 | 0.38 |
| Great Tit | 4 | | 4 | 0.44 | | 0.50 |
| Treecreeper | 2 | | | 0.22 | | |
| Jay | | | | | | |
| Jackdaw | | | | | | |
| Carriion Crow | | 2 | 2 | | 0.20 | 0.25 |
| Starling | 2 | | 1 | 0.22 | | 0.13 |
| Chaffinch | 28 | 11 | 26 | 3.11 | 2.20 | 3.25 |
| Siskin | | | | | | |
| Linnet | | | | | | |
| Redpoll | 6 | 3 | 2 | 0.67 | 0.60 | 0.25 |
| Crossbill | | | | | | |
| Bullfinch | | | | | | |
| Yellowhammer | 1 | 1 | | 0.11 | 0.20 | |
| Reed Bunting | | | | | | |
| Total | 100 | 55 | 87 | 11.11 | 11.00 | 10.88 |
| Diversity Index | 1.7519 | 1.9466 | 1.7489 | | | |

* "Contact" here means "territorial contact".

TABLE 3.9 Continued

B Study plot 5: Dune grassland

| Year (No. of visits) | Total no. of contacts* per season | | | Mean no. of contacts* per visit | | |
|----------------------|-----------------------------------|----------|----------|---------------------------------|------|------|
| | 1979 (9) | 1980 (5) | 1981 (8) | 1979 | 1980 | 1981 |
| Skylark | 21 | 17 | 23 | 2.33 | 3.40 | 2.88 |
| Meadow Pipit | 2 | 1 | 5 | 0.22 | 0.20 | 0.63 |
| Pied Wagtail | | | | | | |
| Wren | | | | | | |
| Dunnock | | | | | | |
| Robin | | | | | | |
| Wheatear | 1 | 4 | | 0.11 | 0.80 | |
| Blackbird | | | | | | |
| Song Thrush | | | | | | |
| Mistle Thrush | | | | | | |
| Sedge Warbler | | | | | | |
| Willow Warbler | | | | | | |
| Goldcrest | | | | | | |
| Spotted Flycatcher | | | | | | |
| Long-tailed Tit | | | | | | |
| Coal Tit | | | | | | |
| Blue Tit | | | | | | |
| Great Tit | | | | | | |
| Tree creeper | | | | | | |
| Jay | | | | | | |
| Jackdaw | | | | | | |
| Carrion Crow | | | | | | |
| Starling | | | | | | |
| Chaffinch | | | | | | |
| Siskin | | | | | | |
| Linnnet | | | | | | |
| Redpoll | | | | | | |
| Crossbill | | | | | | |
| Bullfinch | | | | | | |
| Yellowhammer | | | | | | |
| Reed Bunting | 1 | | | 0.11 | | |
| Total | 25 | 22 | 28 | 2.78 | 4.40 | 3.50 |
| Diversity Index | 0.6060 | 0.6497 | 0.4692 | | | |

* "Contact" here means "territorial contact".

Due to the open nature of the dune grassland, relatively more contacts of each species would be expected than in the scrub since the birds were more visible and their locations along the transect route easier to find - however there were no species common to both plots to test this assumption. In the scrub plot the line transect work tended to overestimate (compared with the more reliable mapping results) the abundance of the more conspicuous species such as Carrion Crow, although it is encouraging to find that species normally regarded as inconspicuous, such as Long-tailed Tit, were also recorded.

Estimating the abundance of birds in the two study plots by means of all contacts reveals little about the territorial status of the individuals concerned; using territorial contacts only, produces a different ordering of the most frequently-contacted species: Willow Warbler (1st in all three years), Chaffinch (2nd in all three years), Robin (3rd in two years), Long-tailed Tit (3rd in one year), Blue Tit, Great Tit and Redpoll (each having been 4th and 5th in one year at least) in the scrub; and Skylark (1st in all three years), Meadow Pipit (2nd in two years, 3rd in one year) and Wheatear (2nd and 3rd in each of two years). However, even the use of territorial contacts - which, in line transect work usually means song registration - introduces problems since (a) it is not possible to identify transient birds e.g. Willow Warblers singing while on migration through a study plot; and (b) it is not possible to identify satisfactorily a stationary male singing on two or more visits, whereas repeated mapping visits would reveal continual occupancy of a certain area. Using territorial contacts also changes the value of the diversity indices but does not affect the finding of them always being higher for the scrub than for the grassland.

Given the drawbacks to the results obtained by the simple line transect work, can they in fact be of any value? If the transect work is conducted with some degree of consistency between two different breeding seasons then, as with the data derived from mapping fieldwork, it might be possible to look at annual changes in population. However, there are three major problems, two of which cannot be overcome (2 and 3):

- (1) The small sample sizes of visits and the variations in their durations make it difficult to decide on the level of consistency of field effort between seasons.
- (2) The narrow sampling area is not sensitive to small changes in territory size and location between seasons e.g. a territory which may only just touch one of the lateral boundaries in year n could, by only being moved a few metres, be outside the recording area contained within the lateral boundaries the following year (n + 1).
- (3) The arrival and size of passage of summer migrants is not constant and a "good" passage year with many singing transients or early arrivals of summer visitors could influence the numbers of contacts made, with no regard to the actual breeding population (Riddiford and Findley, 1981).

Nevertheless, it may prove constructive to investigate the annual changes in the numbers of contacts made during line transect surveys, and Table 3.10 presents these results using the mean number of contacts for all species having at least a mean of 1.00 in at least one of the two years being compared.

The small numerical values of the means and the apparently large variations in the % changes between years (Table 3.10) suggest that simple line transect work does not provide a suitable measure of annual population fluctuations, at least in the two habitats studied here.

This, together with the drawbacks involved in the data presented in Tables 3.7 and 3.8, emphasizes the arguments developed in the earlier methodological discussion, that simple line transects can at best produce only a species list, largely of conspicuous birds present in a study area with an estimate of their relative abundances, from repeated surveys over at least one season. At worst - with only a single survey - line transects can produce very little of any value except an indication of some of the species present in a study plot at one point in time.

A comparison of the data derived from the mapping censuses and line transect sampling surveys in the same Fife study plots is presented in the next section; but on a more subjective and personal level, it is perhaps pertinent to add that the present author found the mapping field-work much more enjoyable, interesting and satisfying than the line transect work. This is not an unimportant factor (even though highly subjective in nature) since enthusiasm and a feeling of achievement might well affect fieldworking efficiency, and if a project depends on the co-operation of a large number of volunteer fieldworkers this should be borne in mind since they are more likely to carry out the work if the end results are meaningful and of a relatively high degree of accuracy - such as the B.T.O.'s Common Birds Census using the mapping method.

**TABLE 3.10 Annual percentage changes in mean numbers of contacts,
1979-1980, 1980-1981**

| Study plot | Birch/willow Scrub | | Dune grassland | |
|---------------------------------|--------------------|-----------|----------------|-----------|
| | 3 | | 5 | |
| Years | 1979-1980 | 1980-1981 | 1979-1980 | 1980-1981 |
| Skylark | | | +26.44 | +2.27 |
| Meadow Pipit | | | +156.41 | 0 |
| Pied Wagtail | | | | |
| Wren | | | | |
| Dunnock | | | | |
| Robin | +718.18 | -16.67 | | |
| Wheatear | | | +147.19 | -48.64 |
| Blackbird | | | | |
| Song Thrush | | | | |
| Mistle Thrush | | | | |
| Sedge Warbler | | | | |
| Willow Warbler | -16.67 | +8.68 | | |
| Goldcrest | | | | |
| Spotted Flycatcher | | | | |
| Long-tailed Tit | -56.52 | -100.00 | | |
| Coal Tit | +221.43 | -44.44 | | |
| Blue Tit | +66.67 | +45.83 | | |
| Great Tit | -24.81 | +188.00 | | |
| Treecreeper | | | | |
| Jay | | | | |
| Jackdaw | | | | |
| Carrion Crow | -65.00 | +34.29 | | |
| Starling | | | | |
| Chaffinch | -10.00 | -7.92 | | |
| Siskin | | | | |
| Linnet | | | | |
| Redpoll | +20.30 | -68.78 | | |
| Crossbill | | | | |
| Bullfinch | | | | |
| Yellowhammer | | | | |
| Reed Bunting | | | | |
| Total (including species <1.00) | -13.27 | 6.64 | +57.83 | -7.19 |

3.4 COMPARISONS OF THE RESULTS FROM MAPPING CENSUSES AND LINE TRANSECT SAMPLING SURVEYS IN THE FIFE STUDY PLOTS

The two sets of results - from mapping and from transects - can be compared from two viewpoints: from that of numbers and from that of species. Numerical comparisons can be drawn firstly between the numbers of territories estimated by mapping and the total or mean numbers of contacts resulting from transect sampling; and secondly between the annual percentage changes in the numbers of territories (from mapping) and the numbers of contacts (from transect sampling). From the species' viewpoint, comparisons can be drawn between the species-lists and the detection of species colonising or abandoning the study plots over the three-year study period.

To facilitate the comparison of estimated "populations" for each species, data are expressed as percentages of the total numbers of territories in a season and as percentages of the total numbers of contacts in a season (density figures and mean number of contacts could also have been used, but there would be no difference in the resulting figures since all three sets are proportional in nature). This corresponds to the "relative abundances" described by Yapp (1962, 1974) - Table 3.11.

In Table 3.11, the "number of species" in the transect column records all those species contacted within or immediately over the study plot and which could have bred in it. This excludes e.g. gull species flying over the scrub and Swallows flying over the grassland. Since the transect work gives no indication of the territorial status of a species while the mapping work does, it is necessary (for the sake of consistency) to include within the "number of species" in the mapping column those which were potential breeders in a study plot and were recorded in it but did not hold territory - the species indicated by "✓" in Table 3.3. Such species are not included in calculations of relative abundance, since there are no figures for them.

Table 3.12 directly compares the relative abundances obtained by both methods, in terms of a conspicuousness index value for each species:

**TABLE 3.11 Comparisons of relative abundances determined by simple
line transect (T) and mapping (M)**

A Study plot 3: Birch/willow scrub

| Year | 1979 | | 1980 | | 1981 | |
|--------------------|--------|--------|--------|--------|--------|--------|
| Method | M | T | M | T | M | T |
| Skylark | | | | | | |
| Meadow Pipit | | | | | 0.54 | |
| Pied Wagtail | | | ✓ | 0.84 | | 0.49 |
| Wren | 1.43 | 0.40 | 4.72 | | 8.72 | 0.99 |
| Dunnock | | | | 0.84 | | |
| Robin | 7.14 | 0.81 | 14.17 | 7.56 | 11.99 | 5.91 |
| Wheatear | | | | | | |
| Blackbird | 1.43 | 1.21 | 1.57 | 1.68 | 1.09 | 2.96 |
| Song Thrush | | 0.81 | 0.79 | 0.84 | 1.09 | |
| Mistle Thrush | | | | | 0.54 | |
| Sedge Warbler | | | | | | |
| Willow Warbler | 22.14 | 16.60 | 23.62 | 15.97 | 20.71 | 16.26 |
| Goldcrest | | | | | | 1.48 |
| Spotted Flycatcher | | | | | | |
| Long-tailed Tit | 4.29 | 11.74 | 3.15 | 5.88 | | |
| Coal Tit | 4.29 | 2.02 | 4.72 | 7.56 | 3.27 | 3.94 |
| Blue Tit | 7.14 | 5.26 | 9.45 | 10.08 | 9.81 | 13.79 |
| Great Tit | 5.71 | 4.86 | 4.72 | 4.20 | 3.27 | 11.33 |
| Treecreeper | 2.86 | 2.83 | 1.57 | 0.84 | 2.18 | 0.49 |
| Jay | 1.43 | 1.21 | | | 1.09 | |
| Jackdaw | | | | | ✓ | |
| Carrion Crow | 0.71 | 14.57 | 1.57 | 5.88 | 1.09 | 7.39 |
| Starling | 2.86 | 1.21 | 1.57 | | 4.36 | 1.97 |
| Chaffinch | 31.43 | 29.15 | 22.05 | 30.25 | 25.07 | 26.11 |
| Goldfinch | | 0.40 | | | | |
| Siskin | | | | | 0.27 | |
| Linnet | 1.43 | 0.81 | | | 1.09 | 0.49 |
| Redpoll | 4.29 | 4.86 | 3.15 | 6.72 | 2.72 | 1.97 |
| Crossbill | | | 3.15 | | | |
| Bullfinch | | | | | 1.63 | 1.48 |
| Yellowhammer | 1.43 | 0.81 | | 0.84 | | |
| Reed Bunting | | 0.40 | ✓ | | | 2.96 |
| Total | 100.01 | 99.96 | 99.97 | 99.98 | 100.53 | 100.01 |
| Diversity Index | 2.1851 | 2.2020 | 2.2330 | 2.1940 | 2.2960 | 2.2384 |
| No. of species | 16 | 19 | 17 | 15 | 20 | 17 |

TABLE 3.11 Continued

B Study plot 5; Dune grassland

| Year | 1979 | | 1980 | | 1981 | |
|--------------------|--------|--------|--------|--------|--------|--------|
| Method | M | T | M | T | M | T |
| Skylark | 74.07 | 64.38 | 65.22 | 51.56 | 63.83 | 56.84 |
| Meadow Pipit | 7.41 | 19.18 | 30.43 | 31.25 | 29.79 | 33.68 |
| Pied Wagtail | | | | | | |
| Wren | | | | | | |
| Dunnock | | | | | | |
| Robin | | | | | | |
| Wheatear | 7.41 | 10.96 | 4.35 | 17.19 | | 1.05 |
| Blackbird | | | | | | |
| Song Thrush | | | | | | |
| Mistle Thrush | | | | | | |
| Sedge Warbler | | | | | | |
| Willow Warbler | | | | | | |
| Goldcrest | | | | | | |
| Spotted Flycatcher | | | | | | |
| Long-tailed Tit | | | | | | |
| Coal Tit | | | | | | |
| Blue Tit | | | | | | |
| Great Tit | | | | | | |
| Tree creeper | | | | | | |
| Jay | | | | | | |
| Jackdaw | | | | | | |
| Carrion Crow | 3.70 | | | | 2.13 | |
| Starling | | | | | | |
| Chaffinch | | | | | | |
| Siskin | | | | | | |
| Linnet | | | | | | |
| Redpoll | | | | | | |
| Crossbill | | | | | | |
| Bullfinch | | | | | | |
| Yellowhammer | | | | | | |
| Reed Bunting | 7.41 | 5.48 | ✓ | | 4.26 | 8.42 |
| Total | 100.00 | 100.00 | 100.00 | 100.00 | 100.01 | 99.99 |
| Diversity Index | 0.9229 | 1.0016 | 0.7771 | 1.0077 | 0.8636 | 0.9439 |
| No. of species | 5 | 4 | 4 | 3 | 4 | 4 |

$$\text{Index of Conspicuousness} = \frac{\% \text{ representation in transects}}{\% \text{ representation in mapping}} \times \frac{100}{1}$$

Thus, a value of 100.00 would represent consistency between the methods; over 100.00 over-representation on transects; less than 100.00 under-representation on transects (Moss, 1976).

The two methods did not appear to be very consistent in their estimates of relative abundance (Table 3.12). Only in seven occurrences did the conspicuousness index fall within 10% of 100, and only one species - the Chaffinch - had more than one index value within the range 90-110. Between years there was much variation in index values, and only two species maintained low ranges of variation: Skylark 79.06 - 89.05 and Willow Warbler 67.61 - 78.51. Figure 3.1 illustrates the relationship between population size and conspicuousness index for species with R.A. values of 1.00 in each year with no clear trend emerging. Only three species (of those with three years' data) showed any relationship - Meadow Pipit (negative), Blue Tit and Willow Warbler (both positive). Thus, as the Meadow Pipit population increased, the consistency between the two methods increased (conspicuousness indices decreasing to around 100.00), as it did also for the Willow Warbler (conspicuousness indices increasing to around 100.00); but for the Blue Tit, as its population increased the conspicuousness increased to around 100.00 but continued beyond this, indicating a decrease in consistency between the two methods. However, with only three data points for each of these species, little significance can be attached to the results.

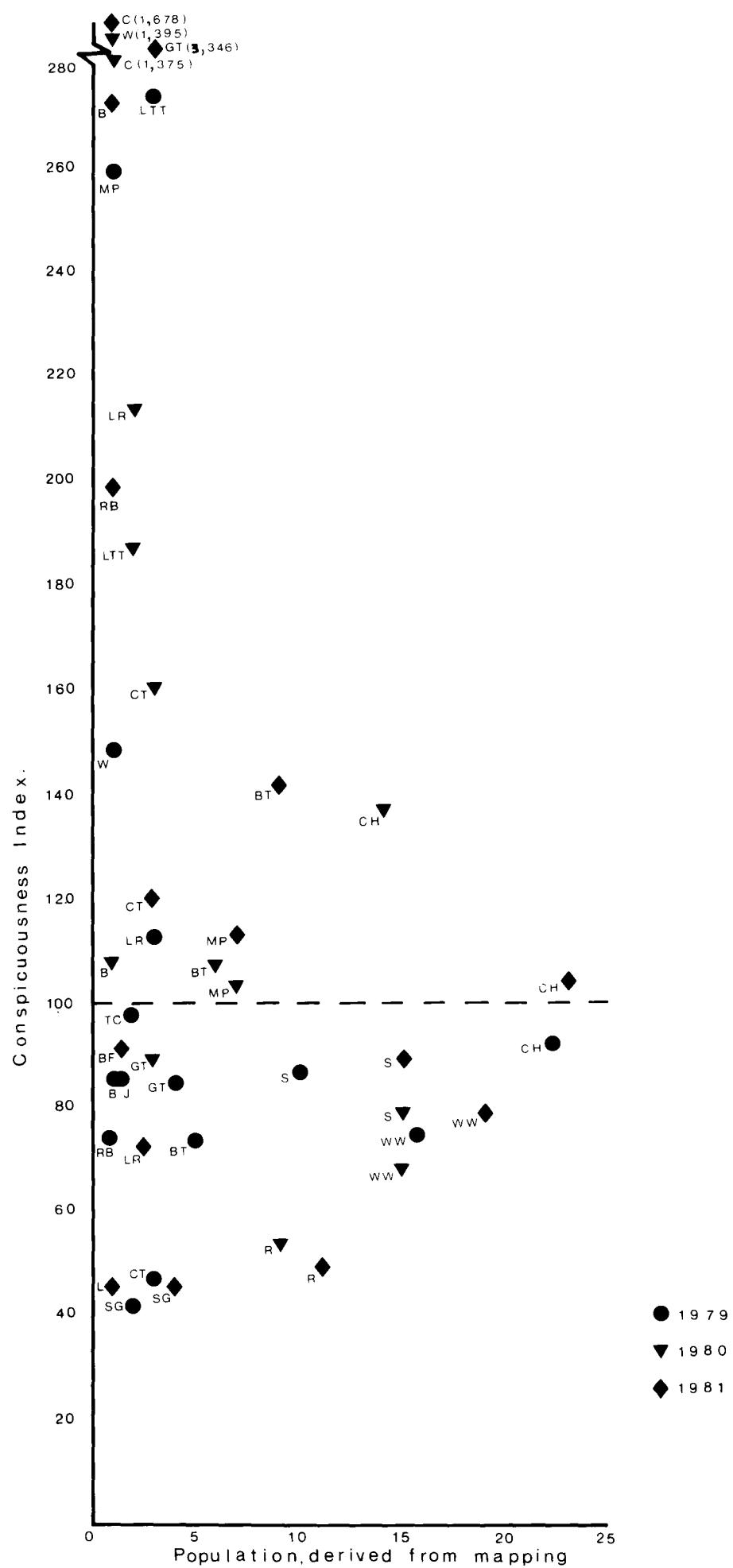
TABLE 3.12 Conspicuousness indices for species, derived from a comparison of simple line transects and mapping censuses 1979 - 1981

| Study plot | 3 | | | 5 | | |
|--------------------|----------|----------|--------|--------|--------|--------|
| Year | 1979 | 1980 | 1981 | 1979 | 1980 | 1981 |
| Skylark | | | | 86.92 | 79.06 | 89.05 |
| Meadow Pipit | | | | 258.84 | 102.69 | 113.06 |
| Pied Wagtail | | | | | | |
| Wren | 27.97* | | 11.35* | | | |
| Dunnock | | | | | | |
| Robin | 11.34* | 53.35 | 49.29 | | | |
| Wheatear | | | | 147.91 | 395.17 | |
| Blackbird | 84.62 | 107.01 | 271.56 | | | |
| Song Thrush | | 106.33** | | | | |
| Mistle Thrush | | | | | | |
| Sedge Warbler | | | | | | |
| Willow Warbler | 74.98 | 67.61 | 78.51 | | | |
| Goldcrest | | | | | | |
| Spotted Flycatcher | | | | | | |
| Long-tailed Tit | 273.66 | 186.67 | | | | |
| Coal Tit | 47.09 | 160.17 | 120.49 | | | |
| Blue Tit | 73.67 | 106.67 | 140.57 | | | |
| Great Tit | 85.11 | 88.98 | 346.48 | | | |
| Treecreeper | 98.95 | 53.50* | 22.48* | | | |
| Jay | 84.62 | | | | | |
| Jackdaw | | | | | | |
| Carriion Crow | 2052.11* | 374.52 | 677.98 | | | |
| Starling | 42.31 | | 45.18 | | | |
| Chaffinch | 92.75 | 137.19 | 104.15 | | | |
| Siskin | | | | | | |
| Linnet | 56.64* | | 44.95 | | | |
| Redpoll | 113.29 | 213.33 | 72.43 | | | |
| Crossbill | | | | | | |
| Bullfinch | | | 90.80 | | | |
| Yellowhammer | 56.64* | | | | | |
| Reed Bunting | | | | 73.95 | | 197.65 |

Notes: * Relative abundance value of <1.00 from one of the methods.

** Relative abundance value of <1.00 from each of the methods.

Fig. 3.1 : Relationship between population size and conspicuousness index



Moss (1976, p 122) presented the results of his analysis of conspicuousness index values for the six commonest species on a commercial coniferous study plot. The species common to his plot and the birch/willow scrub plot of the present study, and for which there were adequate sample sizes (in at least one year in the present study) were as follows:- Robin, Coal Tit, Treecreeper, Chaffinch. Table 3.13 compares the index values from the two studies.

TABLE 3.13 Conspicuousness index values in a commercial coniferous study plot (Moss, 1976) and a birch/willow scrub plot (this study)

| Conspicuousness index values | | |
|------------------------------|-------------|-------------------------|
| | Moss (1976) | This study ¹ |
| Robin | 181 | 49- 53 |
| Coal Tit | 110 | 47-160 |
| Treecreeper | 60 | 99 |
| Chaffinch | 139 | 93-137 |

1: excludes index values indicated by * and ** in Table 3.12.

Clearly there are differences, due either to methodology, habitat or the years studied; but the values for chaffinch are quite similar.

From the lack of consistency between the results obtained from mapping censuses and line transect sampling surveys carried out in the present study; the discrepancies in the results within a species but between years and habitats; and the lack of a relationship between population size and conspicuousness index, it would appear that simple line transect sampling is of little value for estimating the relative abundance of species and consequently is not a suitable method for the acquisition of any quantitative population data on breeding songbirds. Indeed it is not too successful at producing a species-list of territory holders. As a result, all further data (unless otherwise stated) used in this

thesis will be that derived from the more dependable mapping fieldwork.

3.5 THE BREEDING PASSERINE COMMUNITIES

Fuller (1982) presents a review of the recent literature pertaining to the structure and composition of bird communities on a practical level, while from a theoretical viewpoint there are useful reviews by Watson (1973), Cody (1974), Willson (1974), Cody and Diamond (1975), Bevanger (1977) and Krebs (1978).

An earlier discussion of the community concept pertinent to the present study, but rarely mentioned in the literature, is by Brock (1921). He suggested that "a bird-association ... includes that group of species found associated together during the nesting season on ground of a certain geological or botanical type; and the wider divisions in which botanists class their plant formations, are in practice found to mark off corresponding bird-associations." Brock listed eight major groups of associations into which the Scottish avifauna might be divided, and of these the two of interest to the present study are "maritime associations" and "woodland associations", especially their respective sub-divisions of "sand-dune associations" and coniferous and deciduous woodland associations.

Brock (1921) recognised also the close relationship between vegetation succession in e.g. young plantations, and the accompanying ornithological succession. This was recently re-examined by the present author (Dougall, 1982) who produced a tentative definition of avifaunal succession as "a series of breeding bird communities, the component stages of which alter concomitantly with the successional phases through which the breeding season habitat passes" i.e. avifaunal succession does not exist per se but is dependent on vegetation succession and follows the same stages from nudation to final stabilisation; this will be discussed in more detail later. Some doubts have been expressed on the validity and applicability of this definition (Taylor, 1982).

In describing the five communities of the present study, use is made of

species lists, species turnover (Järvinen, 1978), population density and diversity indices (Table 3.4), and relative abundance (Tables 3.14 and 3.15; Figures 3.2 and 3.3). In drawing comparisons between the communities, use is made of two indices discussed in the literature: Renkonen's "dominance affinity" and Sørensen's "quotient of similarity" (Kontkanen, 1957; Gromadzki, 1970; Fuller, 1982). Folse (1979) describes the uses of multivariate techniques to compare "sample census data" (sic) from strip transects.

The following section deals with the breeding passerine communities per se and leads into a fuller discussion of their relationships with various habitat variables.

In Tables 3.14 and 3.15 the dominance of each species in the community is expressed in terms of relative abundance, as derived from the results of mapping fieldwork. The "number of species" excludes those indicated by a "✓" in the tables. In Figure 3.2 only species with a relative abundance of at least 2% ($R.A. \geq 2.00\%$) are indicated by code-name (see Table 3.15 for key to these), those with less than 2% ($R.A. < 2.00\%$) being lumped together and not named; and where several species have equal R.A. values, they appear in Voous' sequence (Hudson, 1978), reading from bottom to top of the bars in Figures 3.2 and 3.3.

The dune grassland community was composed of only five species during the three years studied (Tables 3.14A, Figure 3.2) and was dominated by two of them - Skylark and Meadow Pipit, the dominance of the latter becoming greater as its population recovered from the effects of the 1978/79 winter weather. In each of the three years at least 75% of the study plot's population was due to these two species.

Three species - Robin, Willow Warbler and Chaffinch - made up at least 50% of the population of the birch/willow scrub in any one year, and as the Wren population recovered from the effects of the 1978/79 winter, this species with Blue Tit and the three already mentioned, accounted for 75% of the population in 1981.

TABLE 3.14 The breeding communities of each study plot, 1979-1981

A The dune grassland (5)

| | 1979 | 1980 | 1981 |
|--------------------|--------|--------|--------|
| Skylark | 74.07 | 65.22 | 63.83 |
| Meadow Pipit | 7.41 | 30.43 | 29.79 |
| Pied Wagtail | | | |
| Wren | | | |
| Dunnock | | | |
| Robin | | | |
| Wheatear | 7.41 | 4.35 | |
| Blackbird | | | |
| Song Thrush | | | |
| Mistle Thrush | | | |
| Sedge Warbler | | | |
| Willow Warbler | | | |
| Goldcrest | | | |
| Spotted Flycatcher | | | |
| Long-tailed Tit | | | |
| Coal Tit | | | |
| Blue Tit | | | |
| Great Tit | | | |
| Treecreeper | | | |
| Jay | | | |
| Jackdaw | | | |
| Carriion Crow | 3.70 | | 2.13 |
| Starling | | | |
| Chaffinch | | | |
| Siskin | | | |
| Linnet | | | |
| Redpoll | | | |
| Crossbill | | | |
| Bullfinch | | | |
| Yellowhammer | | | |
| Reed Bunting | 7.41 | ✓ | 4.26 |
| Density | 60.35 | 102.81 | 105.05 |
| Diversity Index | 0.9229 | 0.7771 | 0.8636 |
| No. of species | 5 | 3 | 4 |

TABLE 3.14 Continued

B The birch/willow scrub (3)

| | 1979 | 1980 | 1981 |
|--------------------|--------|--------|--------|
| Skylark | | | |
| Meadow Pipit | | ✓ | 0.54 |
| Pied Wagtail | | | |
| Wren | 1.43 | 4.72 | 8.72 |
| Dunnock | | | |
| Robin | 7.14 | 14.17 | 11.99 |
| Wheatear | | | |
| Blackbird | 1.43 | 1.57 | 1.09 |
| Song Thrush | | 0.79 | 1.09 |
| Mistle Thrush | | | 0.54 |
| Sedge Warbler | | | |
| Willow Warbler | 22.14 | 23.62 | 20.71 |
| Goldcrest | | | |
| Spotted Flycatcher | | | |
| Long-tailed Tit | 4.29 | 3.15 | |
| Coal Tit | 4.29 | 4.72 | 3.27 |
| Blue Tit | 7.14 | 9.45 | 9.81 |
| Great Tit | 5.71 | 4.72 | 3.27 |
| Treecreeper | 2.86 | 1.57 | 2.18 |
| Jay | 1.43 | | 1.09 |
| Jackdaw | | | ✓ |
| Carrion Crow | 0.71 | 1.57 | 1.09 |
| Starling | 2.86 | 1.57 | 4.36 |
| Chaffinch | 31.43 | 22.05 | 25.07 |
| Siskin | | | 0.27 |
| Linnet | 1.43 | | 1.09 |
| Redpoll | 4.29 | 3.15 | 2.72 |
| Crossbill | | 3.15 | |
| Bullfinch | | | 1.63 |
| Yellowhammer | 1.43 | | |
| Reed Bunting | | ✓ | |
| Density | 366.80 | 332.74 | 480.77 |
| Diversity Index | 2.1851 | 2.3330 | 2.2960 |
| No. of species | 16 | 15 | 19 |

TABLE 3.14 Continued

C The birch/alder woodland (4)

| | 1979 | 1980 | 1981 |
|--------------------|--------|--------|--------|
| Skylark | | | |
| Meadow Pipit | | | |
| Pied Wagtail | | | |
| Wren | 3.72 | 5.80 | 10.88 |
| Dunnock | | 0.97 | |
| Robin | 1.86 | 4.83 | 7.26 |
| Wheatear | | | |
| Blackbird | 0.93 | 1.93 | 0.91 |
| Song Thrush | 0.93 | 0.48 | |
| Mistle Thrush | | | 0.45 |
| Sedge Warbler | 0.93 | 0.97 | 0.91 |
| Willow Warbler | 9.77 | 9.66 | 9.98 |
| Goldcrest | | | |
| Spotted Flycatcher | 0.93 | 0.97 | |
| Long-tailed Tit | 2.79 | 1.93 | |
| Coal Tit | 1.40 | 4.83 | 3.63 |
| Blue Tit | 5.58 | 6.76 | 5.44 |
| Great Tit | 2.79 | 3.86 | 4.54 |
| Treecreeper | 0.93 | 3.86 | 1.81 |
| Jay | | | |
| Jackdaw | | | ✓ |
| Carrion Crow | 0.47 | 0.97 | 0.91 |
| Starling | 43.72 | 35.75 | 31.75 |
| Chaffinch | 19.53 | 14.49 | 18.14 |
| Siskin | | ✓ | 0.23 |
| Linnet | | | |
| Redpoll | 2.79 | 1.93 | 1.81 |
| Crossbill | | | |
| Bullfinch | | | 0.45 |
| Yellowhammer | 0.93 | | 0.91 |
| Reed Bunting | | ✓ | |
| Density | 928.80 | 894.24 | 952.56 |
| Diversity Index | 1.9109 | 2.1988 | 2.1335 |
| No. of species | 17 | 17 | 17 |

TABLE 3.14 Continued

D The semi-natural coniferous woodland (1)

| | 1979 | 1980 | 1981 |
|--------------------|--------|--------|--------|
| Skylark | | | |
| Meadow Pipit | | | 0.81 |
| Pied Wagtail | | | |
| Wren | | ✓ | 2.42 |
| Dunnock | | 2.09 | 0.81 |
| Robin | 14.57 | 12.57 | 17.74 |
| Wheatear | | | |
| Blackbird | 5.30 | 1.05 | 2.42 |
| Song Thrush | 2.65 | 2.09 | 2.42 |
| Mistle Thrush | | | |
| Sedge Warbler | | | |
| Willow Warbler | 14.57 | 6.28 | 6.45 |
| Goldcrest | ✓ | 5.24 | 11.29 |
| Spotted Flycatcher | | | |
| Long-tailed Tit | 1.32 | 3.14 | 1.61 |
| Coal Tit | 9.27 | 17.80 | 11.29 |
| Blue Tit | | 2.09 | 2.02 |
| Great Tit | 2.65 | 1.05 | 2.42 |
| Treecreeper | 2.65 | 2.09 | 2.42 |
| Jay | ✓ | 1.05 | 0.81 |
| Jackdaw | | | |
| Carriion Crow | 0.66 | 1.05 | 1.21 |
| Starling | | | |
| Chaffinch | 43.71 | 34.55 | 27.42 |
| Siskin | | 2.62 | 2.42 |
| Linnet | | | |
| Redpoll | 2.65 | 2.09 | 2.42 |
| Crossbill | | 2.09 | |
| Bullfinch | | 1.05 | 1.61 |
| Yellowhammer | | | |
| Reed Bunting | | | |
| Density | 382.79 | 484.19 | 613.47 |
| Diversity Index | 1.7745 | 2.1919 | 2.3016 |
| No. of species | 11 | 18 | 19 |

TABLE 3.14 Continued

E The commercial coniferous woodland (2)

| | 1979 | 1980 | 1981 |
|--------------------|--------|--------|--------|
| Skylark | | | |
| Meadow Pipit | | | |
| Pied Wagtail | | | |
| Wren | 2.79 | 5.96 | 7.67 |
| Dunnock | 1.86 | 2.55 | 2.00 |
| Robin | 9.30 | 14.47 | 20.67 |
| Wheatear | | | |
| Blackbird | 9.30 | 2.55 | 3.33 |
| Song Thrush | 0.93 | 2.55 | 3.33 |
| Mistle Thrush | | | |
| Sedge Warbler | | | |
| Willow Warbler | 13.95 | 10.21 | 7.33 |
| Goldcrest | 6.51 | 11.91 | 9.33 |
| Spotted Flycatcher | | | |
| Long-tailed Tit | 1.86 | 3.40 | 0.67 |
| Coal Tit | 15.81 | 14.47 | 17.33 |
| Blue Tit | 0.93 | 1.70 | 0.67 |
| Great Tit | | 0.85 | 1.33 |
| Treecreeper | 1.86 | 1.70 | 2.00 |
| Jay | 0.47 | 0.43 | ✓ |
| Jackdaw | | | |
| Carrion Crow | | | |
| Starling | | | |
| Chaffinch | 28.84 | 22.98 | 21.33 |
| Siskin | | 1.28 | 0.67 |
| Linnet | | | |
| Redpoll | 5.58 | 2.13 | 1.33 |
| Crossbill | | ✓ | 0.33 |
| Bullfinch | | 0.85 | 0.67 |
| Yellowhammer | | | |
| Reed Bunting | | | |
| Density | 522.45 | 571.05 | 729.00 |
| Diversity Index | 2.1401 | 2.3285 | 2.2200 |
| No. of species | 14 | 17 | 17 |

FIG3,2 THE BREEDING PASSERINE COMMUNITIES.

5

1980

W

1979

C

RB

W

MP

S

S

1981

RB

MP

S

3

1979

6 others

SG

TC

LR

LTT

CT

LTT

GT

BT

H

WW

CH

1980

5 others

CrB

LR

LTT

GT

CT

SG

WH

BT

H

WW

CH

1981

9 others

TC

LR

GT

CT

SG

WH

BT

H

WW

CH

4

1980

8 others

TC

GT

LTT

WR

BT

R

WW

BT

WW

CH

SG

1981

10 others

GT

BT

R

WW

WR

WW

CH

SG

3

1980

5 others

CrB

LR

LTT

GT

CT

SG

WH

BT

H

WW

CH

1981

9 others

TC

LR

GT

CT

SG

WH

BT

H

WW

CH

WW

CH

SG

FIG32: cont'd.

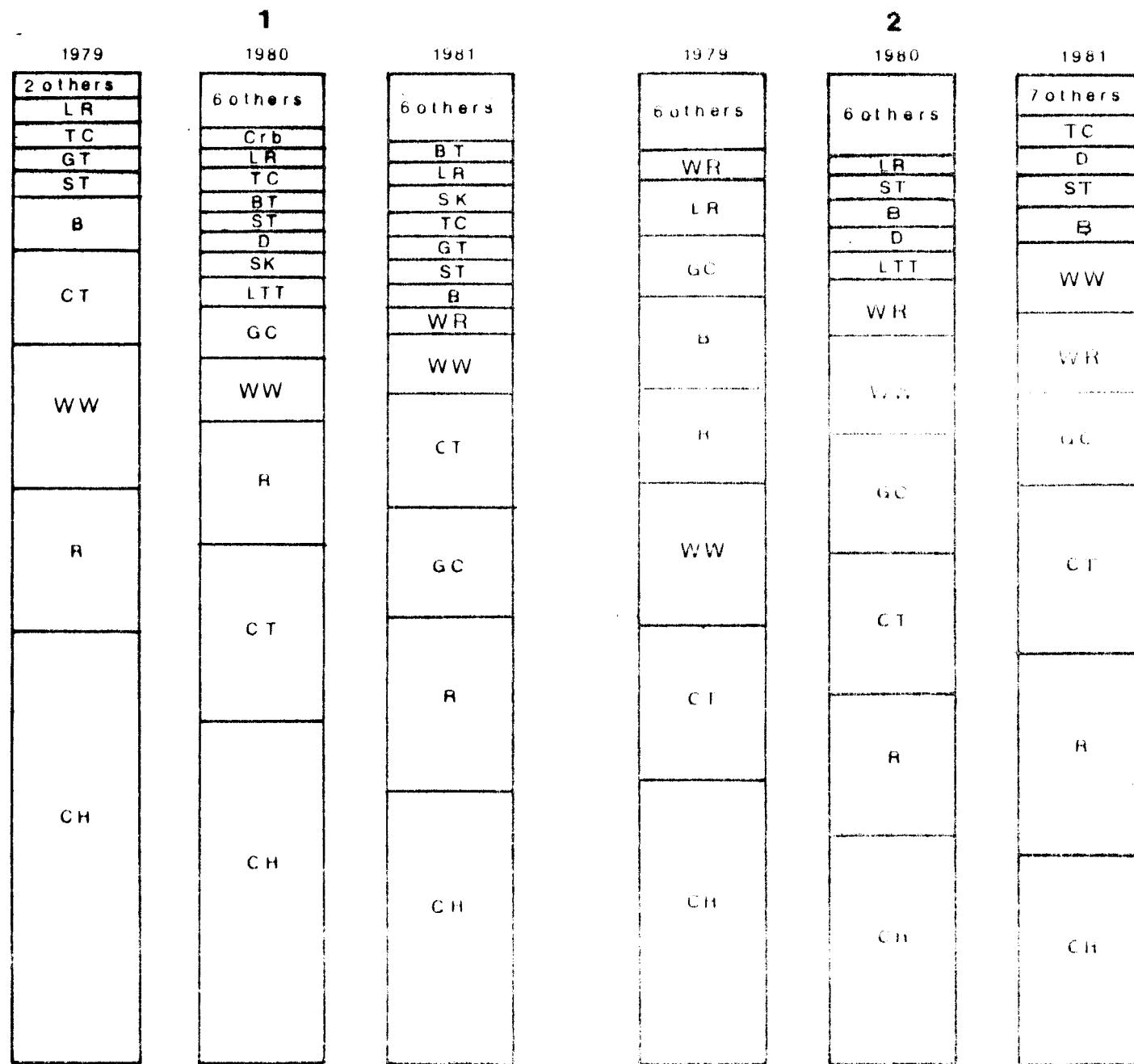
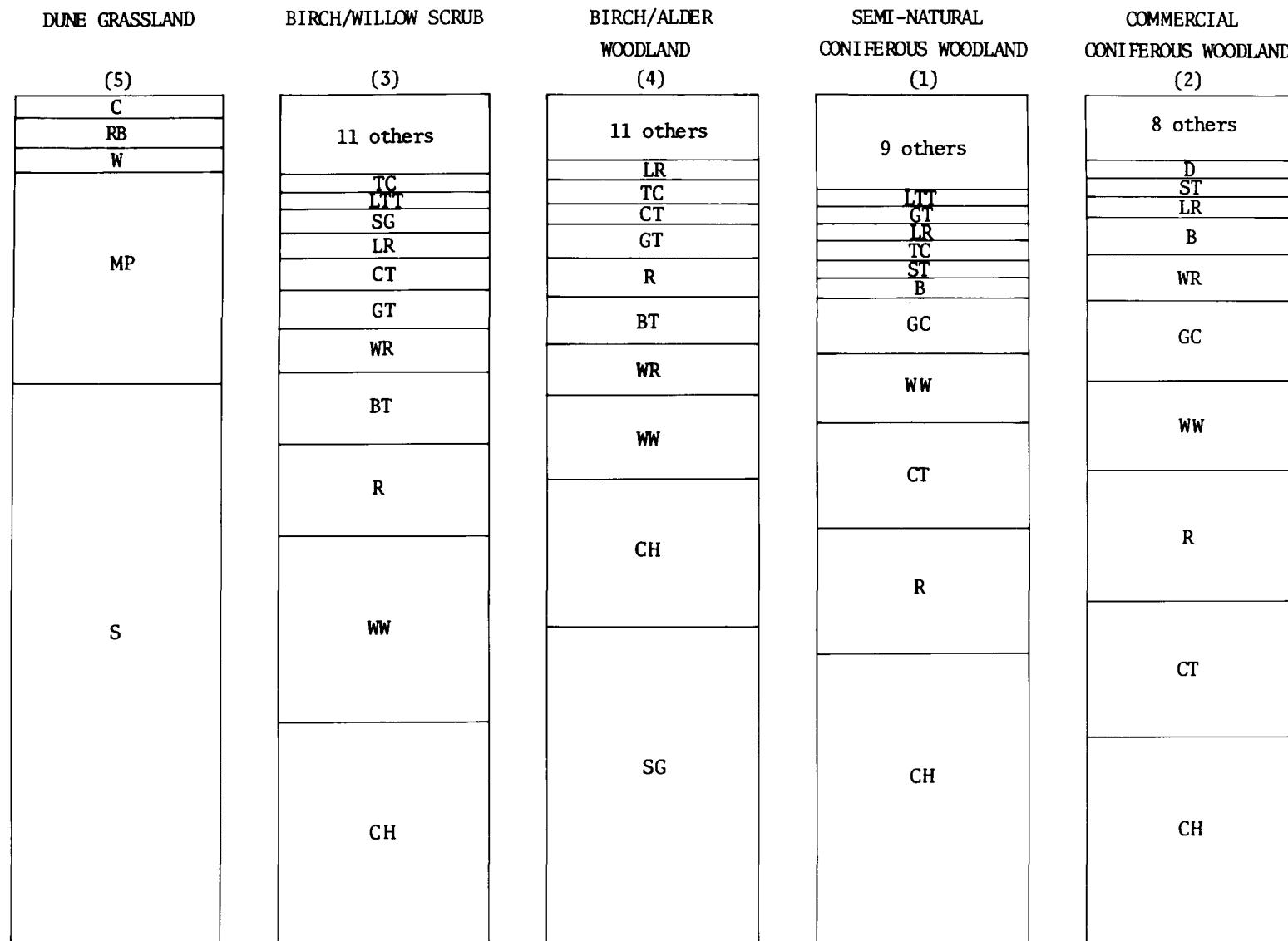


TABLE 3.15 The composite breeding community of each study plot,
1979-1981

| Code Name | | 5 | 3 | 4 | 1 | 2 |
|----------------|--------------------|-------|-------|-------|-------|-------|
| S | Skylark | 66.67 | | | | |
| MP | Meadow Pipit | 25.00 | 0.22 | | 0.34 | |
| PW | Pied Wagtail | | ✓ | | | |
| WR | Wren | | 5.33 | 6.85 | 1.02 | 5.73 |
| D | Dunnock | | | 0.31 | 1.02 | 2.13 |
| R | Robin | | 11.10 | 4.67 | 15.25 | 15.47 |
| W | Wheatear | 3.33 | | | | |
| B | Blackbird | | 1.33 | 1.25 | 2.71 | 4.80 |
| ST | Song Thrush | | 0.67 | 0.47 | 2.37 | 2.40 |
| MT | Mistle Thrush | | 0.22 | 0.16 | | |
| SW | Sedge Warbler | | | 0.93 | | |
| WW | Willow Warbler | | 21.98 | 9.81 | 8.47 | 10.13 |
| GC | Goldcrest | | | | 6.44 | 9.33 |
| SF | Spotted Flycatcher | | | 0.62 | | |
| LT | Long-tailed Tit | | 2.22 | 1.56 | 2.03 | 1.87 |
| CT | Coal Tit | | 3.99 | 3.27 | 12.88 | 16.00 |
| BT | Blue Tit | | 8.88 | 5.91 | 1.53 | 1.07 |
| GT | Great Tit | | 4.44 | 3.74 | 2.03 | 0.80 |
| TC | Treecreeper | | 2.22 | 2.18 | 2.37 | 1.87 |
| J | Jay | | 0.89 | | 0.68 | 0.27 |
| JD | Jackdaw | | ✓ | ✓ | | |
| C | Carriion Crow | 1.67 | 1.11 | 0.78 | 1.02 | |
| SG | Starling | | 3.11 | 37.04 | | |
| CH | Chaffinch | | 26.19 | 17.43 | 33.90 | 24.00 |
| SK | Siskin | | 0.11 | 0.08 | 1.86 | 0.67 |
| L | Linnet | | 0.89 | | | |
| LR | Redpoll | | 3.33 | 2.18 | 2.37 | 2.80 |
| CRB | Crossbill | | 0.89 | | 0.68 | 0.13 |
| BF | Bullfinch | | 0.67 | 0.16 | 1.02 | 0.53 |
| Y | Yellowhammer | | 0.44 | 0.62 | | |
| RB | Reed Bunting | 3.33 | ✓ | ✓ | | |
| No. of species | | 5 | 22 | 21 | 20 | 18 |

FIGURE 3.3 : THE COMPOSITE BREEDING PASSERINE COMMUNITY OF EACH STUDY PLOT, 1979-1981



(All named species have a relative abundance value over 3 years of at least 2%)

The same five species - Wren, Robin, Willow Warbler, Blue Tit and Chaffinch - all held dominant positions in the community of the more mature birch/alder woodland, but all were sub-dominant to the Starling population which accounted for 36% - 44% of the total community population over the three years. As with the birch/willow scrub community, the Wren's position became increasingly more dominant as its population increased, while the Starling's became less so as the colony declined slightly. In each of the three years at least 50% of the community population was made up by two species - Starling and Chaffinch.

In the semi-natural coniferous woodland the most abundant species was always Chaffinch followed by either Robin or Coal Tit and then Goldcrest (once its population began to recover from the effects of the 1978/79 winter) or Willow Warbler, with Wren beginning to assume some dominance (2.42%) in 1981. It was always these six species which accounted for at least 75% of the population in any one year.

In the commercial coniferous woodland the same six species were usually dominant although in 1979 the Blackbird was ranked fifth (as it was also in the semi-natural coniferous woodland) because of the scarcity of both Wren and Goldcrest. Chaffinch was always the most abundant species followed by Robin or Coal Tit, then Goldcrest or Willow Warbler, with Wren gaining in dominance after 1979. Three species - from Robin, Willow Warbler, Coal Tit and Chaffinch - always accounted for at least 50% of the population in any one year. In each year the proportion of Chaffinch was always higher in the semi-natural than in the commercial coniferous woodland, but for the other five species no clear pattern emerged for the two coniferous plots other than the increasing proportion occupied by Wren.

It would appear that for the four woodland plots studied in Fife three bird species were common to them as dominants:- Robin, Willow Warbler and Chaffinch. In the two deciduous plots, Wren, Blue Tit and Great Tit were common to both, with Starling forming a main element in the birch/alder woodland. In the two coniferous plots Goldcrest and Coal Tit were common to both as dominants.

Fuller (1982) found eight species as almost ubiquitous and occurring at high densities in a sample of 240 woods throughout Britain - Wren, Robin, Blackbird, Song Thrush, Willow Warbler, Blue Tit, Great Tit and Chaffinch; with the addition of three other species in suitable habitat - Woodpigeon, Dunnock and Starling. Of these eleven "core species" (ten passerines since Woodpigeon is a non-passserine) three - Dunnock, Blackbird and Song Thrush - were not dominant in the two deciduous woodland plots but were so in the coniferous plots in the Fife study areas over the three years as a whole (Table 3.15, Figure 3.3). On the other hand, Goldcrest and Coal Tit, though not occurring as any of Fuller's core species were amongst the dominants in the two present coniferous plots, with Coal Tit in addition appearing as a dominant in the deciduous plots.

Over the three years as a whole, at least 75% of the composite population of each study area was made up of the following species, from most to least abundant:-

| | | |
|--------------------------------------|---|--|
| Dune grassland (plot 5) | : | Skylark, Meadow Pipit. |
| Birch/willow scrub (3) | : | Chaffinch, Willow Warbler, Robin, Blue Tit, Wren, Great Tit. |
| Birch/alder woodland (4) | : | Starling, Chaffinch, Willow Warbler, Wren, Blue Tit. |
| Semi-natural coniferous woodland (1) | : | Chaffinch, Robin, Coal Tit, Willow Warbler, Goldcrest. |
| Commercial coniferous forest (2) | : | Chaffinch, Coal Tit, Robin, Willow Warbler, Goldcrest. |

The distribution of the bird groups represented in the woodland plots at relative abundances of at least 2% is shown in Table 3.16.

TABLE 3.16 The number of species* in each group in each woodland study plot
1979-81

| Study plot : | Birch/ Willow Scrub | Birch/ Alder Woodland | Coniferous woodland | |
|--------------|---------------------------|-----------------------------|---------------------|-----------------|
| | 3 | 4 | Semi-natural 1 | Commercial 2 |
| Wren | 1 | 1 | 0 | 1 |
| Accentor | 0 | 0 | 0 | 1 |
| Chat | 1 | 1 | 1 | 1 |
| Thrush | 0 | 0 | 2 | 2 |
| Warbler | 1 | 1 | 2 | 2 |
| Tit | 4 | 3 | 3 | 1 |
| Treecreeper | 1 | 1 | 1 | 0 |
| Starling | 1 | 1 | 0 | 0 |
| Finch | 2 | 2 | 2 | 2 |

* With R.A. $\geq 2\%$.

Thus, one chat (Robin) and two finches (Chaffinch and Redpoll) are common to all plots; thrushes and warblers are features of the coniferous plots; while tits and starlings are mostly represented in the deciduous plots possibly because, as hole-nesters, they can find more sites among the more mature trees of the deciduous plots some of which trees are dead or dying, unlike in the coniferous plots where the trees are younger and not holed or decaying. Indeed the hole-nesting tits in the coniferous plots probably nested in holes and crevices among tree roots or in holes in the ground made by voles and rabbits.

Fuller (1982) showed that most groups of breeding woodland birds are poorer in species content in Wales and Scotland than in England, and that in Scotland there is a striking zonation of species richness from about 45 in the south-east to between 15 and 25 in the north-west (Fuller, 1982 - his Figure 6.3) with Fife woodlands coming into the range 35 - 45. The

present study has revealed a maximum of 19 territory-holding passerine species in any one study plot in one year (plots 1 and also 3, in 1981) with a maximum of 22 occurring over a three-year period in one study plot (plot 3) (Tables 3.14 and 3.15). For all territory-holding species, including non-passerines, the equivalent figures are a maximum of 30 in any one year (plot 1, 1981) and a maximum of 35 over a three-year period (plot 3). If the adjacent plots of 3 and 4 and the ditch which separates them are taken as one "super-plot", the relevant figures are 37 species in any one year (1981) and 42 species over the three-year period (Table 3.17; Dougall, 1980; 1981).

TABLE 3.17 The numbers of territory-holding species* in the Fife woodland study plots 1979-1981

| Study plot Year | 3 Birch/ Willow | 4 Birch/ Alder | 3+4 Scrub + | 1 Semi-natural Coniferous | 2 Commercial Coniferous |
|--------------------|-----------------------|----------------------|----------------|---------------------------------|-------------------------------|
| | Scrub | Woodland | Woodland | | |
| 1979 | 26 | 25 | 31 | 17 | 20 |
| 1980 | 26 | 27 | 30 | 28 | 23 |
| 1981 | 28 | 27 | 37 | 30 | 22 |
| Mean | 26.67 | 26.33 | 32.67 | 25.00 | 21.67 |
| 3-year total | 35 | 33 | 42 | 32 | 26 |

* Source: Tables in Dougall (1980, 1981), omitting from consideration any species indicated by "✓", "?" or with a population value of < 0.5.

Thus, the Fife woodlands studied in 1979-81 do not generally fall within the range of 35 - 45 breeding species for any one year, but over a three-year period the two deciduous plots do. The commercial coniferous plot usually contained fewest breeding species.

Obvious problems, both spatial and temporal, arise in comparing a detailed

study of a few sites, such as the present one, with a more general study of many sites such as Fuller's (1982).

Fuller's useful summary table (his Table 22, p 272) detailing the mean numbers of breeding species per wood in five regions covering mainland Britain (Scotland, Northern England, Midlands and East Anglia, Southern England and Wales) reveals that the mean woodland area from the sample of 40 sites in Scotland was 300 ha - 15 times the size of the woodland areas of the present study. Most of Fuller's data were gathered over the five-year period 1973-77 rather than the three years of the present study and his years were devoid of any influence of a "hard winter". In addition, Fuller's survey involved many different observers and there was a bias to surveying ornithologically "good" sites (Fuller, 1982, p 15), while the Fife study reported here involved only one observer with no prior knowledge of the quality of the sites, which were chosen from a map and which had to be readily accessible. For these reasons, any detailed comparison between the results of the present study and those presented in Fuller's Table 22 would be largely meaningless and so none is made here, except to draw attention to the mean numbers of all species in the Fife woodlands (21.67 - 32.67, from Table 3.17) and to Fuller's mean number for Scottish woodlands of 27.45).

Detailed comparisons between the results for the plots in the present study are valid and are made below, using the indices of Renkonen and Sørensen. Renkonen's "dominance affinity" (Kontkanen, 1957; Gromadzki, 1970) measures the similarity of two communities in terms of their relative abundance values; Renkonen D.A. = the sum of the lowest dominance of every species common to both samples of two (Table 3.18).

Sørensen's "quotient of similarity" (Kontkanen, 1957; Gromadzki, 1970; Fuller, 1982) measures the similarity of two communities in terms of their species composition:

$$\text{Sørensen Q.S.} = \frac{2c}{a+b} \times \frac{100}{1}$$
, a = number of species in community A, b = number of species in community B, c = number of species common to both communities A and B (Table 3.19).

TABLE 3.18 Renkonen's "dominance affinity" values for the five study plots, 1979-1981

| Years | Study plots compared | | | | | | | | | |
|---------|----------------------|-------------|-------------|----------|---------------|---------------|---------------|---------------|---------------|---------------|
| | 5 v 3 | 5 v 4 | 5 v 1 | 5 v 2 | 3 v 4 | 3 v 1 | 3 v 2 | 4 v 1 | 4 v 2 | 1 v 2 |
| 1979 | 0.71 (1) | 0.47 (1) | 0.66 (1) | 0 (0) | 54.06 (14) | 64.50 (10) | 66.49 (11) | 42.44 (11) | 43.72 (11) | 73.42 (9) |
| 1980 | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 59.06 (14) | 60.54 (13) | 67.63 (12) | 42.99 (13) | 51.10 (13) | 78.81 (16) |
| 1981 | 1.63 (2) | 0.91 (1) | 2.02 (2) | 0 (0) | 67.01 (15) | 64.74 (16) | 60.04 (13) | 48.46 (13) | 50.76 (12) | 81.55 (16) |
| 1979-81 | 1.33 (2) | 0.78 (1) | 1.36 (2) | 0 (0) | 62.53 (18) | 66.11 (17) | 66.00 (16) | 47.39 (16) | 50.66 (15) | 83.74 (18) |

(n) = number of species common to both study plots.

TABLE 3.19 Sørensen's "quotient of similarity" values for the five study plots, 1979-1981

| Years | Study plots compared | | | | | | | | | |
|---------|----------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| | 5 v 3 | 5 v 4 | 5 v 1 | 5 v 2 | 3 v 4 | 3 v 1 | 3 v 2 | 4 v 1 | 4 v 2 | 1 v 2 |
| 1979 | 9.52 | 9.09 | 12.50 | 0 | 84.85 | 74.07 | 73.33 | 78.57 | 70.97 | 72.00 |
| 1980 | 0 | 0 | 0 | 0 | 87.50 | 78.79 | 75.00 | 74.29 | 76.47 | 91.43 |
| 1981 | 17.39 | 9.52 | 17.39 | 0 | 83.33 | 84.21 | 72.22 | 72.22 | 70.59 | 88.89 |
| 1979-81 | 7.41 | 9.09 | 16.00 | 0 | 83.72 | 80.95 | 80.00 | 78.05 | 76.92 | 94.74 |

It is obvious from the values in Tables 3.18 and 3.19 that there is no similarity at all between the communities of the dune grassland and commercial coniferous plots, and that in 1980 there was no similarity between the community of the dune grassland and any of the other four plots. The pattern for all the compared plots and years becomes clearer if the index values are ranked (Table 3.20).

From this ranking it is apparent that there are major differences between the open dune grassland and all woodland communities, especially the mature birch/alder woodland and the commercial coniferous woodland. Of the four woodland study plots, the communities of the two coniferous ones were the most similar (from both indices), while in terms of similarity of abundance the next most similar plots were the deciduous scrub and each of the two coniferous plots. In terms of species composition however, after the two coniferous plots the two deciduous plots were most similar, followed by the deciduous scrub and the semi-natural coniferous woodland.

Finally as a further aid to a comparison of the plots, an Analysis of Variance pooling three-year population data for both coniferous plots and for both deciduous plots, and comparing those species with enough data common to each set revealed differences between the two vegetation sets for only a few species (Table 3.21). Using data from this table and also Table 3.3 demonstrates that Robin and Song Thrush were more prevalent in coniferous plots and strongly suggests that Coal Tit was more prevalent in coniferous plots, with Willow Warbler and Blue Tit more prevalent in deciduous plots. For the other species in Table 3.21 there is little evidence for any prevalence in vegetation types.

TABLE 3.20 Rankings of paired comparisons, from the Renkonen and Sörensen indices

| (a) Renkonen D.A. | 5 v 3 | 5 v 4 | 5 v 1 | 5 v 2 | 3 v 4 | 3 v 1 | 3 v 2 | 4 v 1 | 4 v 2 | 1 v 2 |
|-------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1979 | 7 | 9 | 8 | 10 | 4 | 3 | 2 | 6 | 5 | 1 |
| 1980 | 8.25 | 8.25 | 8.25 | 8.25 | 4 | 3 | 2 | 6 | 5 | 1 |
| 1981 | 8 | 9 | 7 | 10 | 2 | 3 | 4 | 6 | 5 | 1 |
| 1979-81 | 8 | 9 | 7 | 10 | 4 | 2 | 3 | 6 | 5 | 1 |
| Total | 31.25 | 35.25 | 30.25 | 38.25 | 14 | 11 | 11 | 24 | 20 | 4 |

| (b) Sörensen Q.S. | 5 v 3 | 5 v 4 | 5 v 1 | 5 v 2 | 3 v 4 | 3 v 1 | 3 v 2 | 4 v 1 | 4 v 2 | 1 v 2 |
|-------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1979 | 8 | 9 | 7 | 10 | 1 | 3 | 4 | 2 | 6 | 5 |
| 1980 | 8.25 | 8.25 | 8.25 | 8.25 | 2 | 3 | 5 | 6 | 4 | 1 |
| 1981 | 7.5 | 9 | 7.5 | 10 | 3 | 2 | 4.5 | 4.5 | 6 | 1 |
| 1979-81 | 9 | 8 | 7 | 10 | 2 | 3 | 4 | 5 | 6 | 1 |
| Total | 32.75 | 34.25 | 29.75 | 38.25 | 8 | 11 | 17.5 | 17.5 | 22 | 8 |

TABLE 3.21 Results of Anovar

| Species | F-ratio | Significance level ^{1,2} |
|-----------------|---------|-----------------------------------|
| Wren | 0.72 | - |
| Robin | 21.54 | ** |
| Blackbird | 2.37 | - |
| Song Thrush | 36.29 | ** |
| Willow Warbler | 13.77 | * |
| Long-tailed Tit | 0.33 | - |
| Coal Tit | 10.27 | * |
| Blue Tit | 14.93 | * |
| Great Tit | 4.28 | - |
| Treecreeper | 0.67 | - |
| Carrion Crow | 0.75 | - |
| Chaffinch | 0.65 | - |
| Redpoll | 0.44 | - |

Notes: 1: ** $p < 0.05$, * $0.10 > p > 0.05$, - not significant.

2: A significant difference means that a coniferous and a deciduous area differ, on average, by more than coniferous areas vary amongst themselves (S.C. Richardson, in litt.).

So far, attention has been focussed on the relationships between the communities themselves - describing them and comparing them one with the other. But description is not enough - explanations should be sought for the similarities and differences found, and this is attempted in the next section. The three most important factors which influence breeding songbird populations in woodland are thought to be vegetation structure and complexity, tree species, and soil fertility (von Haartman, 1971; Blondel et al, 1973; Moss, 1976). Since the soil fertility of the study plots in question here is uniform over them (Table 2.1), then it is necessary to concentrate on the relationships between the population parameters of the breeding bird communities and the vegetation parameters of the habitats they occupy; and this is attempted in the following section.

3.6 THE RELATIONSHIPS BETWEEN THE BREEDING BIRD COMMUNITIES AND THEIR HABITATS

Before proceeding to discuss the results from the present study, it is necessary to try and consider how bird species choose the areas in which they live. The idea of "habitat selection" has been under consideration for some time and much ornithological research is still dedicated towards its understanding. Useful general reviews of the problem have been given in Lack (1933), Dunlavy (1935), Lack and Venables (1939), Svärdson (1949), Hildén (1965), Partridge (1978) and Anderson, Shugart and Smith (1979).

More particularly, Lack (1933) and Venables (1937) described how Meadow Pipits on Surrey heathland were absent as breeders from rabbit-grazed heaths, since they preferred thick ground vegetation in which to nest. Skylarks, however, were common on both vegetated and bare heaths and this latter habitat was also preferred by Wheatears.

Southern and Venables (1939) showed how, in Lappland, phenological events such as snowmelt and the production of willow "fluff" affected the selection of breeding sites, since birds would not nest on snow-covered areas and for some species - such as Redpoll - willow fluff was necessary as a nest-lining to insulate the eggs from the cold.

At the species level, Svärdson (1949) investigated habitat selection by Wood Warblers, as did Edington and Edington (1972) who in addition looked at it in relation to hole-nesting species such Green Woodpecker, Redstart, various tit species, Pied Flycatcher and Starling. Pulliainen (1977) carried this further by investigating habitat selection in relation to the provision of artificial holes in the form of nestboxes. Lachlan and Bray (1976) looked at habitat selection in spring by cock Pheasants, while Cody and Walter (1976) and Cody (1978) investigated it for Sylviid Warblers in the Mediterranean, and in England and Sweden respectively. An interesting development related to habitat selection is the association, during the breeding season, between several species and "protector" species. Slagsvold (1980) showed how the nests of other species located within the breeding

colonies of Fieldfares were safer from predation than if they had been located outside the colonies, since Fieldfares have an efficient communal defence system which keeps predators away. Indeed some of the indirectly-protected species changed their distributions annually within an individual area in phase with changes made by the protecting Fieldfares. Allied to this are associations noted between nesting ducks and gulls (Newton and Campbell, 1975) and between nesting terns and gulls (Bourne et al, 1978) where the less conspicuous ducks and terns suffered less predation from ground predators than did the more conspicuous nesting gulls.

As to the mechanisms behind habitat selection, Svärdson (1949) saw them as involving purely optical external stimuli, the principle being that a number of different external stimuli are added to an internal motivation to settle, which is probably hormonal in nature. A varying amount of stimulation may be present according to the number of external stimuli present in the environment and they may be combined freely. When the sum of the stimuli has reached a certain threshold value, the habitat selection reaction is released. Moreover, if external stimuli are absent or almost absent, the internal motivation may increase and in exceptional cases reach the threshold of the response.

If interspecific competition is dominant, a species will retreat to the "adaptive peak" - the most optimal habitat - where its general adaptation is superior. It follows that those individuals having the most perfect set of reaction elements leading them to the optimal habitat with a minimum of internal motivation, are the most probable survivors. Thus, strong inter-specific competition tends to give a still more selective releasing mechanism, corresponding to the habitat where survival is highest.

If, on the other hand, intraspecific competition is the dominant form of population pressure, quite a number of different habitats will be occupied owing to the crowding effect, whereby "unsuccessful" birds will move into sub-optimal habitats for the species, where reproductive and survival rates may be lower than in the preferred habitats.

Hildén (1965) expressed Svärdson's (1949) stimuli in terms of ultimate and proximate factors. In habitat selection, the ultimate factors are food, shelter from enemies and adverse weather, requirements imposed by the structural and functional characteristics of the species. The proximate factors are certain characteristic stimuli of the species-specific habitat but their nature is virtually unknown - speculation would suggest such stimuli as (a) landscape, (b) terrain, (c) nest, song, look-out, feeding and drinking sites, (d) other animals. In certain species (e) food also directly influences the choice of territory; in addition (f) internal motivation contributes to the release of the selection response, in some way determining the sensitivity of the bird to external stimuli. These are all positive characteristics of habitat, but there are others which have a negative effect.

Hildén assumes that habitat selection is two-staged:

- (1) settling down and exploration - this is released by features of the landscape and general characteristics of the terrain.
- (2) acceptability - whether the place is approved or rejected as a breeding territory depends on how closely certain of its details conform to the other sign stimuli constituting the proximate factors in the bird's habitat selection mechanism.

The flexibility in the selection of the breeding station is also partly due to the migratory urge: in a place which barely exceeds the threshold of habitat selection, the still-powerful migratory urge gains the upper hand after some time and the bird begins to wander again. In a place which clearly exceeds the threshold, the territorial urge permanently suppresses migratory behaviour.

James (1971) looked at 15 variables of the structure of vegetation in his study areas, variables which might form some of Hildén's (1965) proximate factors: % ground cover, number of tree species, % canopy cover, height at which canopy most widespread, number of trees/shrubs <3" diameter at

breast height (D.B.H.), 3-6" DBH, 6-9" DBH, 9-12" DBH, 12-15" DBH, >15" DBH, canopy height x shrubs, canopy height x 3-9" DBH, canopy height x >9" DBH (no. of trees 3-9" DBH)², (no. of trees >9" DBH)². James found all the vegetation variables highly interrelated, and every one had a significant ability to separate the species of birds (using principal components analysis and discriminant function analysis). By far the most powerful were the two which would probably be the most conspicuous visually - % canopy cover and canopy height; these were followed by the number of tree species.

Edington and Edington (1972) suggested that habitat selection involved two phases: (1) dividing up the habitat available.

- (2) the establishment of mutually-exclusive feeding areas on both inter- and intra-specific bases.

The Edingtons also drew attention to temporal patterns in the breeding season, where the resources of the habitat could be divided between different species, since each has a slightly different breeding season. They concluded that, in most habitats, two forms of segregation were at work:

- (1) selective segregation, where there was separation of species due to their selection of different habitat types and
- (2) interactive (competitive) segregation, where separation of the species was due to the exclusion of one by the other from a habitat which could be occupied by either.

Within a habitat, such segregation could be carried out on three planes - horizontally, vertically or non-dimensionally involving food specialization.

Partridge (1978) looked at the adaptive significance of habitat selection. To show this it was necessary to demonstrate that animals chose to live in the sorts of places where they have maximum chance of survival or of reproductive success. An adaptive trait must also in one sense be inherited. As with any other phenotypic character, habitat preference could be transmitted in a number of different ways e.g. young Blue Tits could

inherit a preference for oak trees; on the other hand they might inherit a tendency to prefer the sorts of trees to which they are exposed in early life, perhaps because they are taken there by their parents - or they could acquire a preference for trees where they find most food, or are least subject to predatory attack.

Habitat selection may remain flexible after initial settling. Migrant birds often select different habitats in their winter and summer ranges and there are instances of individual animals selecting different habitats in different years. To what extent such differences are controlled by choice and by competitive exclusion is unknown.

It appears that the experience of breeding is associated with an increase in preference for the habitat in which breeding occurred. It may be that successful breeding per se is the important cue. This may be why many young birds from species occupying a wide range of habitats tend to nest in similar habitats to their parents. The fact that they themselves were successfully raised may indicate that the area was suitable, although other areas might have been even more suitable.

One other preference for sub-optimal habitat could result from early experience, during which a young animal might learn the location of its resources and resting sites, how to catch prey and other useful skills. If it starts life in a sub-optimal habitat the animal may acquire these skills and therefore increase its fitness in the sub-optimal habitat. As a result, this habitat may eventually cease to be sub-optimal for that particular animal, because the animal is now fitter than it would have been had it moved to an optimal habitat before learning of its skills had started.

Anderson et al (1979) draw together many findings from studies of habitat selection and describe how they show that the presence of bird species in habitats is correlated with features of the vegetation structure. Bird species composition does not show sharp zones of demarcation, but varies on a continuum with vegetation structure and physical features of the

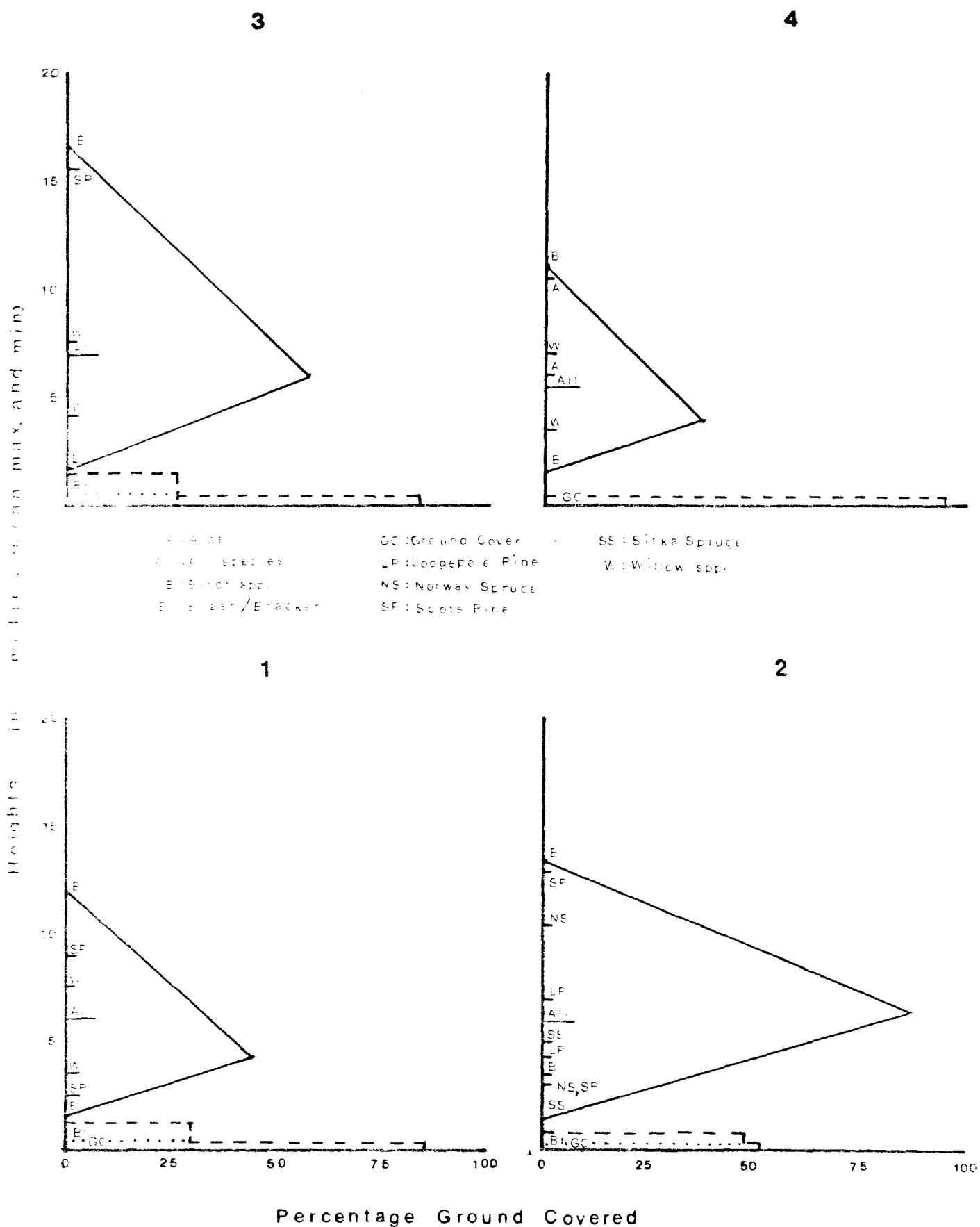
habitat. Habitat use at any point along the continuum therefore is variable and related to the habitat features which allow the species to compete and establish itself in the community, or not to compete if other species can make better use of the habitat. The coexistence of bird species depends on habitat-use patterns which evolve in each species in the community. These patterns include spatial and temporal changes in behaviour which allow different forms of habitat exploitation.

The present study does not involve itself with the behavioural factors per se, but rather how their effects manifest themselves in the resultant populations and distributions within the study plots, especially within plot 1 which exhibits signs of a vegetation succession from open mobile dunes to mature woodland.

Figure 3.4 (A and B) shows the generalised vegetation profiles and distribution of general heights of canopy for each of the four woodland plots. The profiles are arrived at by plotting graphically the points of mean maximum and mean minimum foliage heights, the mean height at which the canopy is most widespread and the mean % of ground covered by the canopy. For the field vegetation (including dead wood and brashed timber) the average height of, and % of ground covered by, the features is plotted. Clearly study plot 2 (commercial coniferous) is different in nature from the other three plots, having much more of the ground covered by the canopy and much less covered by vegetation, with an equal amount of ground cover provided by dead wood and especially brashings.

Moss (1976, 1978a) looked at the relationship between foliage height diversity (F.H.D.) and bird species diversity (B.S.D.) for 34 woodland bird censuses from 18 study plots and found a correlation of $r = 0.887$. He calculated his FHD from his vegetation profiles, as in Figure 3.4A of this study. The data in the present study were not of a similar nature and would not permit the same calculations, so the FHD indices as calculated for Tables 2.13 and 2.15 of the habitat chapter were plotted against the BSD indices for the three years, and a positive relationship found, but only when ignoring the effect of the Starling colony in plot 4.

FIG 3,4.a VEGETATION PROFILES.



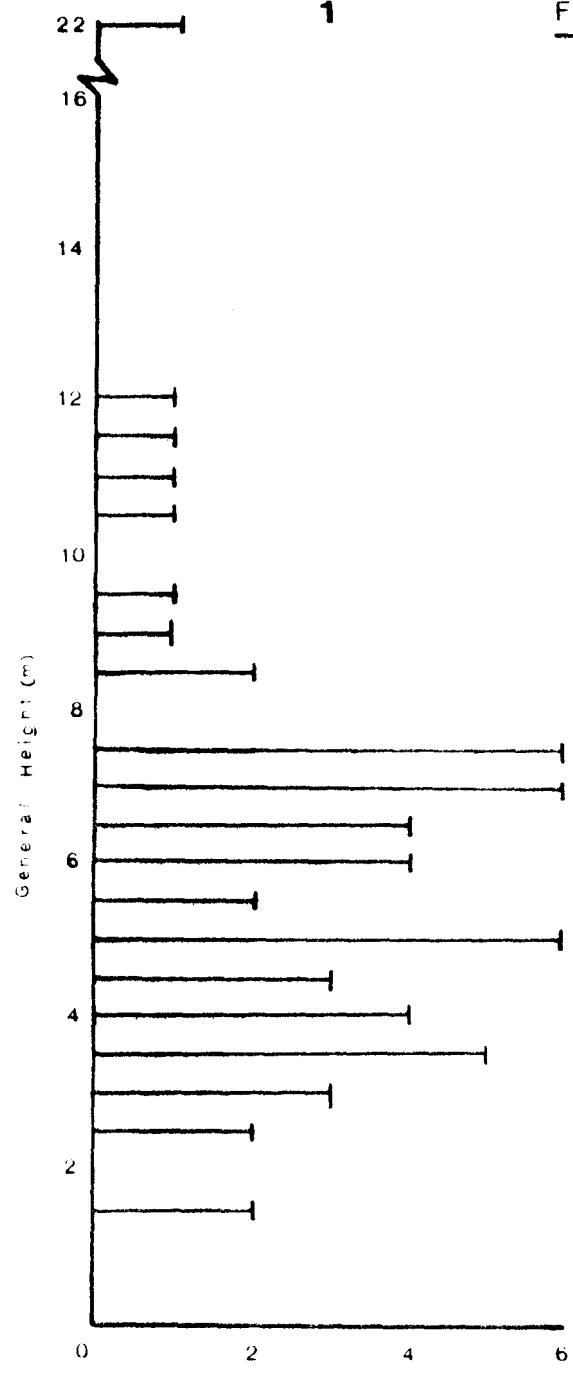


FIG 3.4.b WOODLAND PROFILES.

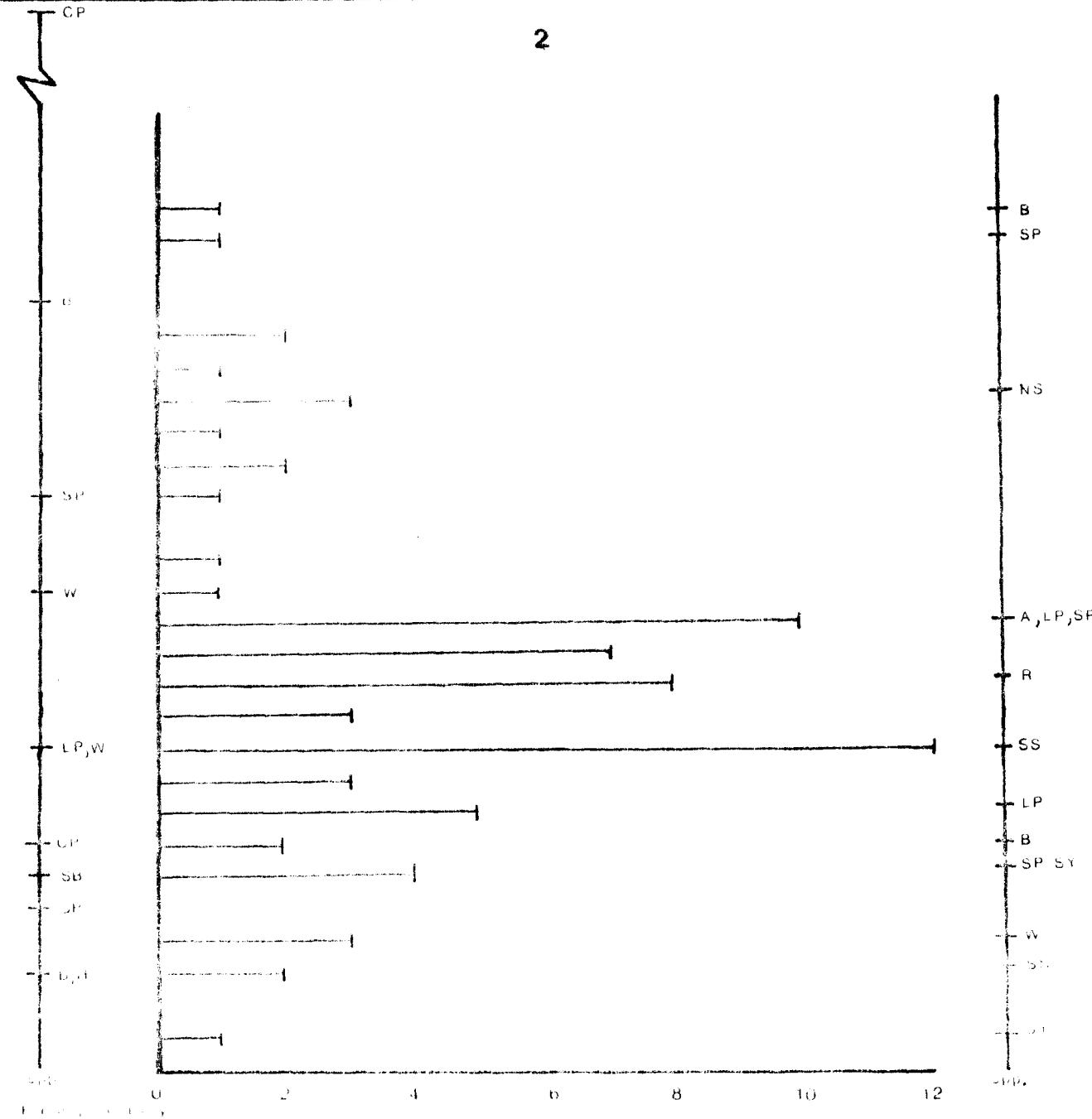
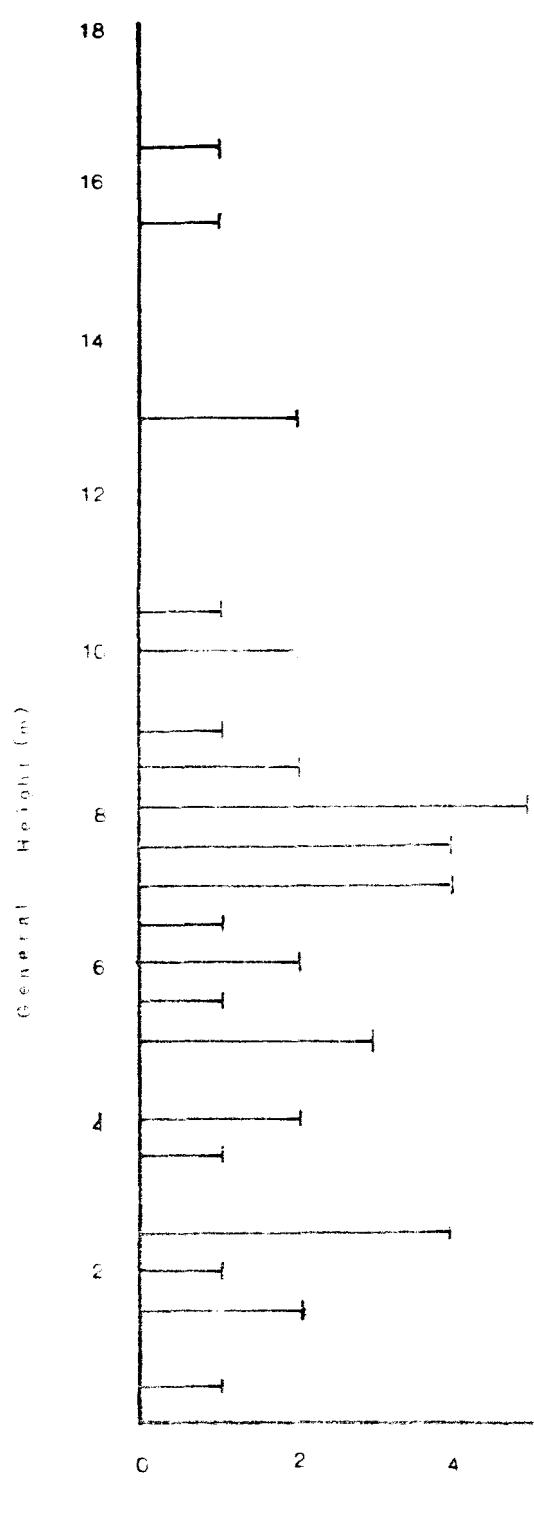
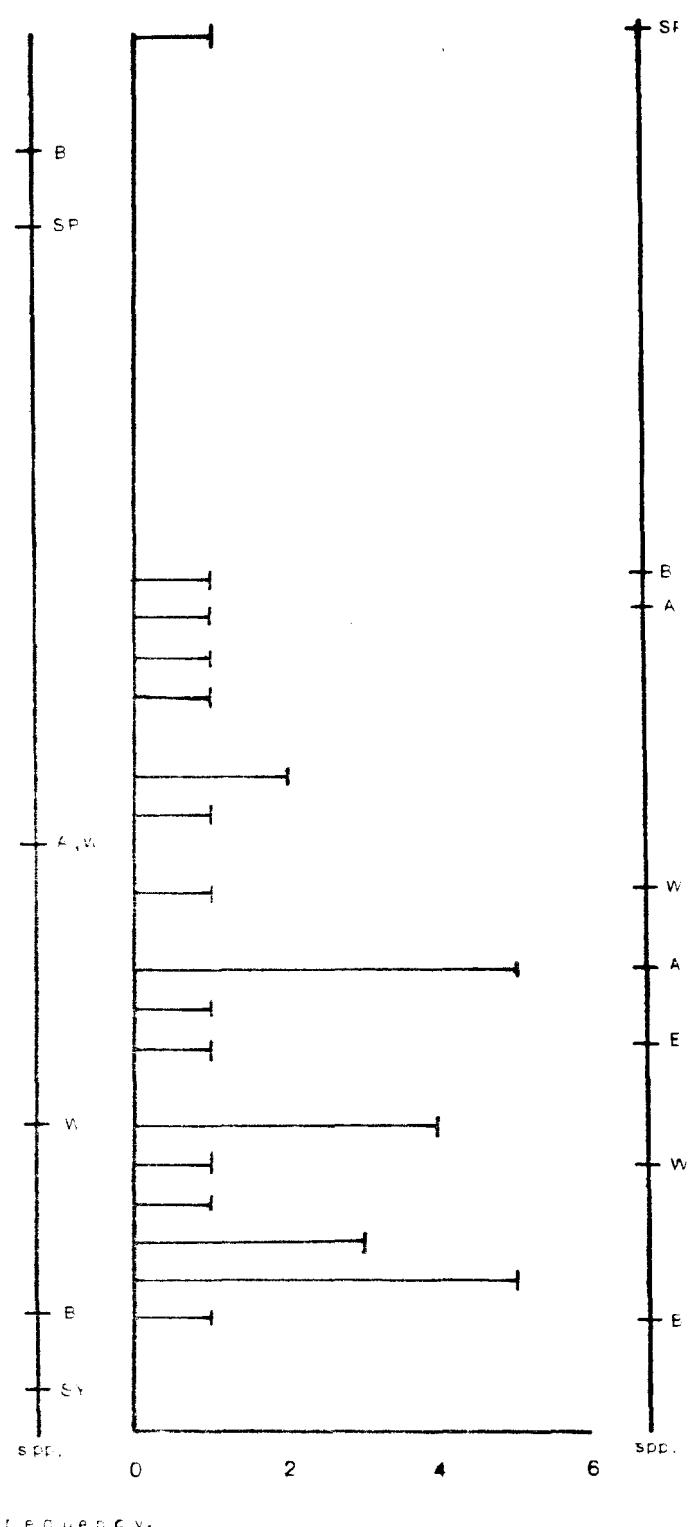


FIG 3,4b: cont'd.

3



4



Too few points precluded calculation of a correlation coefficient. This provides further evidence to the little available in the British situation that, as habitat structure becomes more complex, then the breeding bird community it supports becomes more diverse. (Figure 3.4C).

Figures 3.5 to 3.10 reveal, in more detail, the nature of the vegetation structure and related parameters which gave rise to the generalised profile of study plot 1. This study area is described in more detail here since the origin of its arboreal habitats can be dated accurately to the mid-1950s, when a reduction in grazing by rabbits (caused by a great decrease in their population due to the effects of myxomatosis) allowed tree-cover to spread eastwards (i.e. seawards) from the adjacent commercial forest. The data from three sampling points (I = range; • = mean) along each of nine northing lines reveal that light intensity at ground level decreases initially then rises again as tree density increases, then gradually decreases as the trees become younger further from source. There is a general decrease in tree height from oldest to youngest trees and commensurate with this are decreases in the height at which the canopy is most widespread and in the % of ground covered by the canopy, although both of these features have "hiccups" at the thicket stage between 50 and 150 m from the original forest edge.

Thus, going west to east from the original forest and source of the present woodland, through the recently established woodland, to that presently colonising the sand dunes, there is a gradual change from tall, sparsely-distributed trees with a moderately high canopy allowing through much light; through less tall, very densely packed trees with a lower canopy over much of the ground and allowing little light penetration; to low, well-spaced trees with low canopies covering little of the ground beneath them and allowing much light to penetrate.

To investigate how this was reflected in the populations of the bird species in the study plot, the numbers of territories along each northing line in each year for the most numerous species (≥ 5 territories over three years) were summed and plotted graphically against distance from original

FIG 3.4.c RELATIONSHIP BETWEEN FOLIAGE HEIGHT DIVERSITY
AND BIRD SPECIES DIVERSITY.

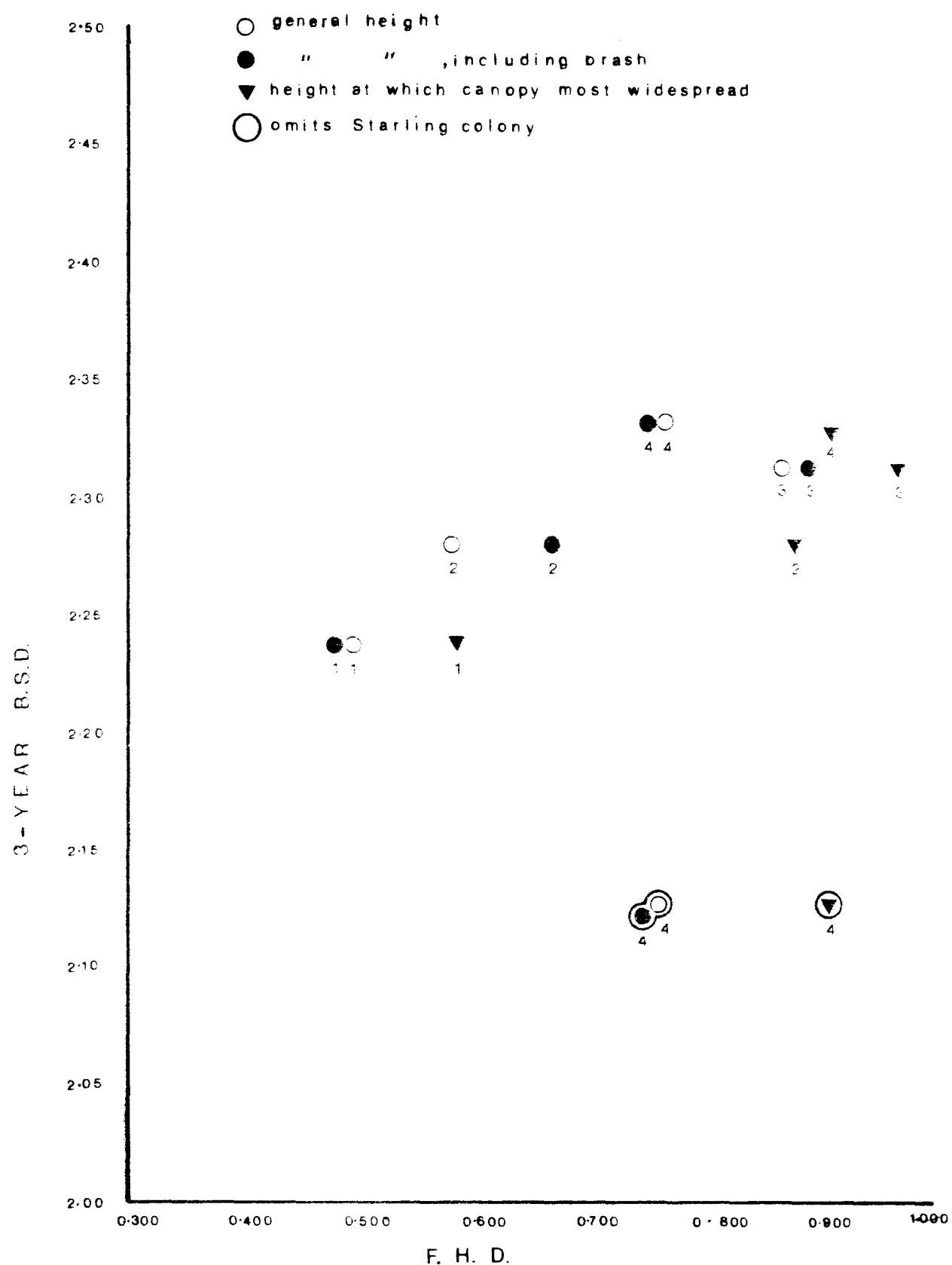


Figure 3•5: Relationship, in Plot 1, of light levels to distance from original forest edge

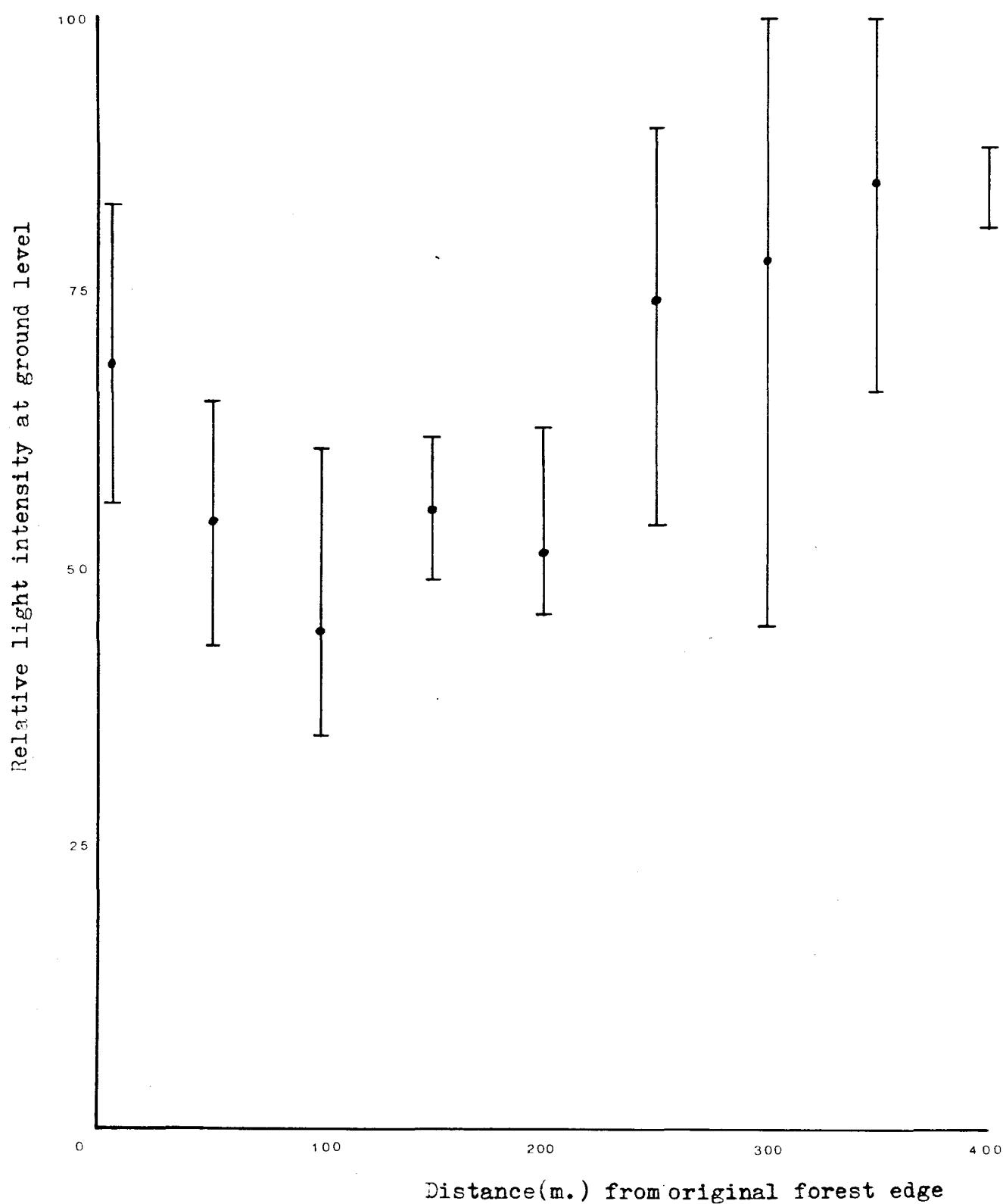
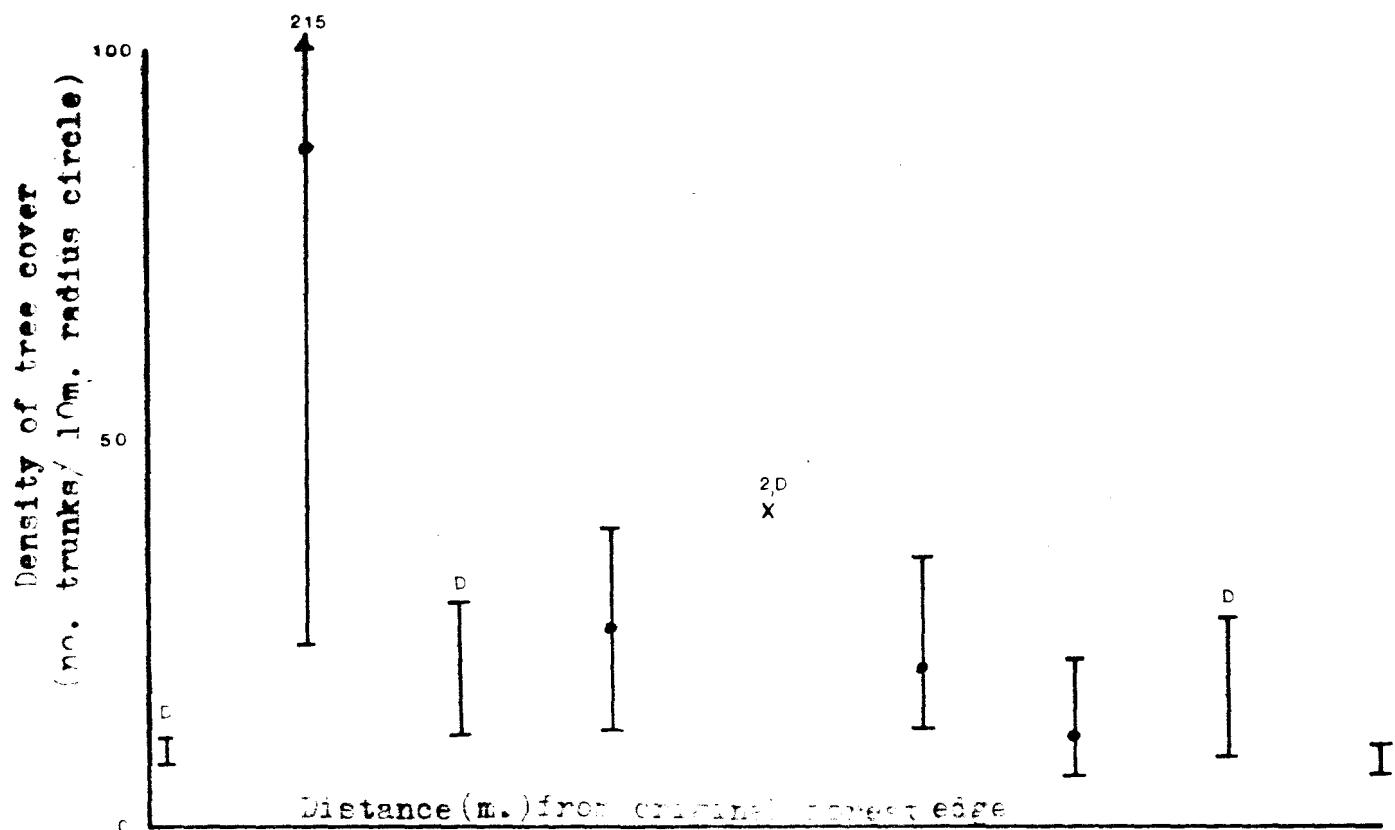
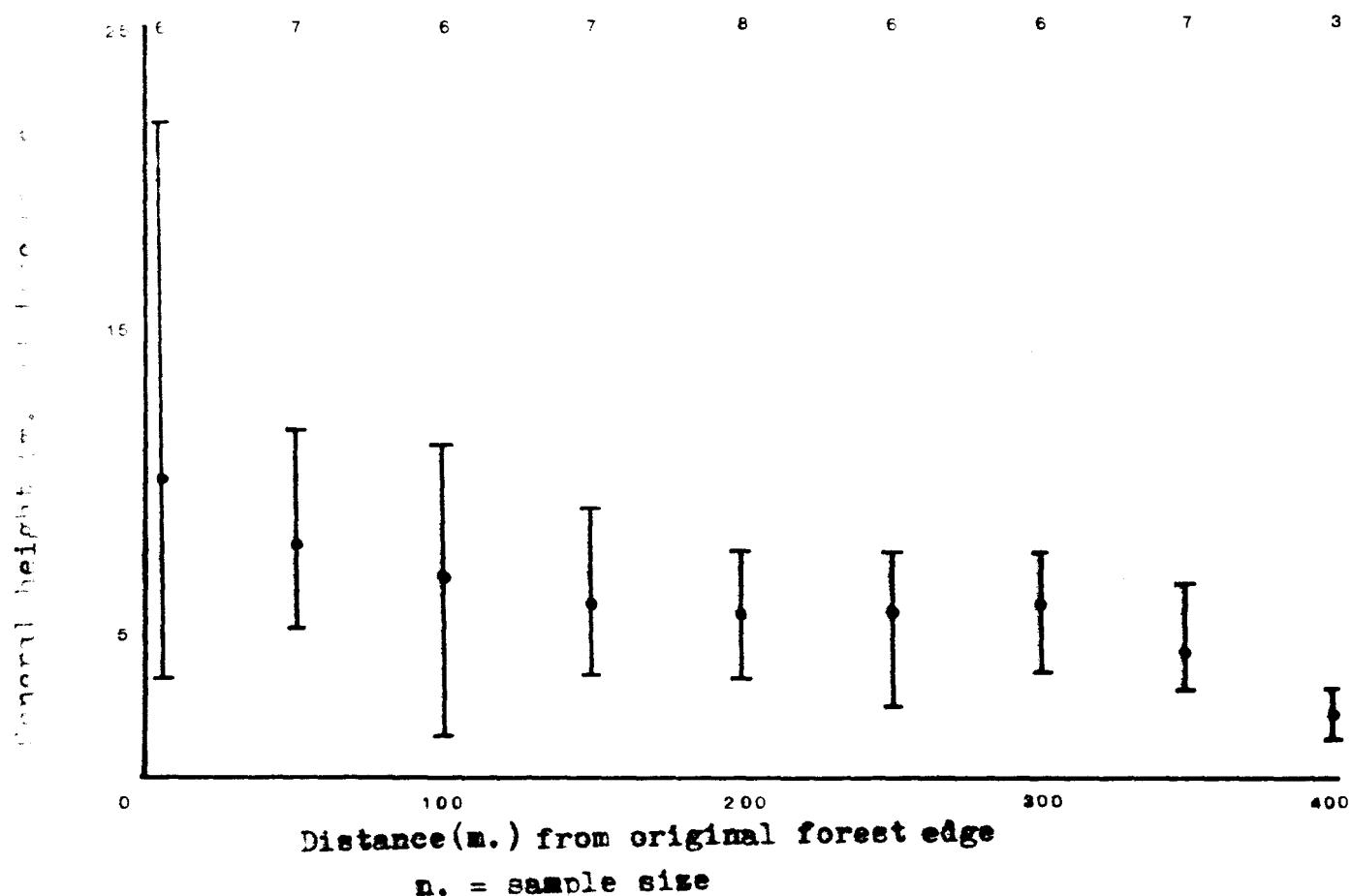


Fig 3.6: Relationship, in Plot 1, of tree density* to distance from original forest edge



* Excludes data from sampling sites where tree cover too dense to measure accurately (indicated by D on fig.)

Fig 3.7: Relationship, in Plot 1, of tree height to distance from original forest edge



n. = sample size

Fig3.8: Relationship in Plot 1, between height of canopy cover and distance from original forest edge

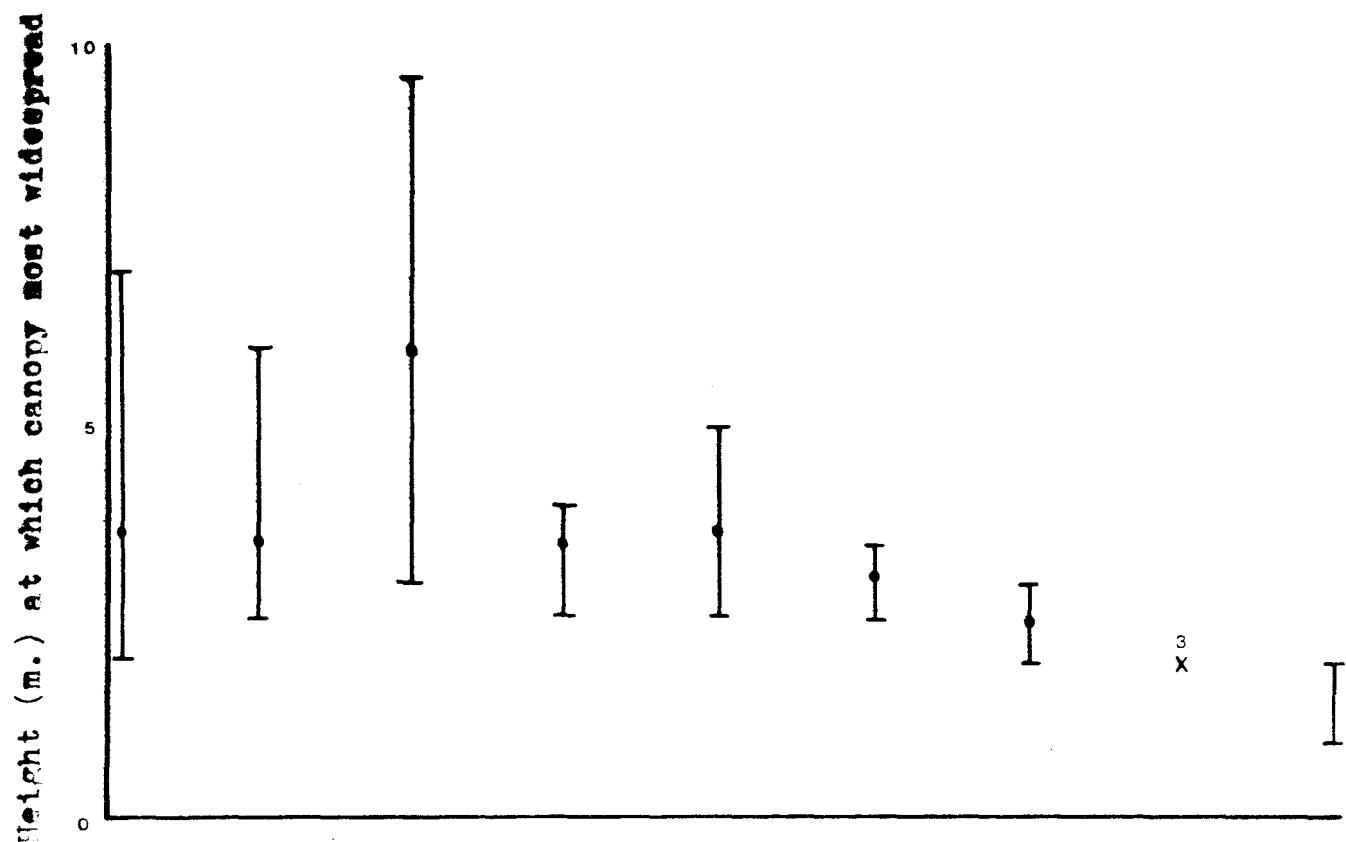


Fig3.9: Relationship, in Plot 1, between canopy cover and distance from original forest edge

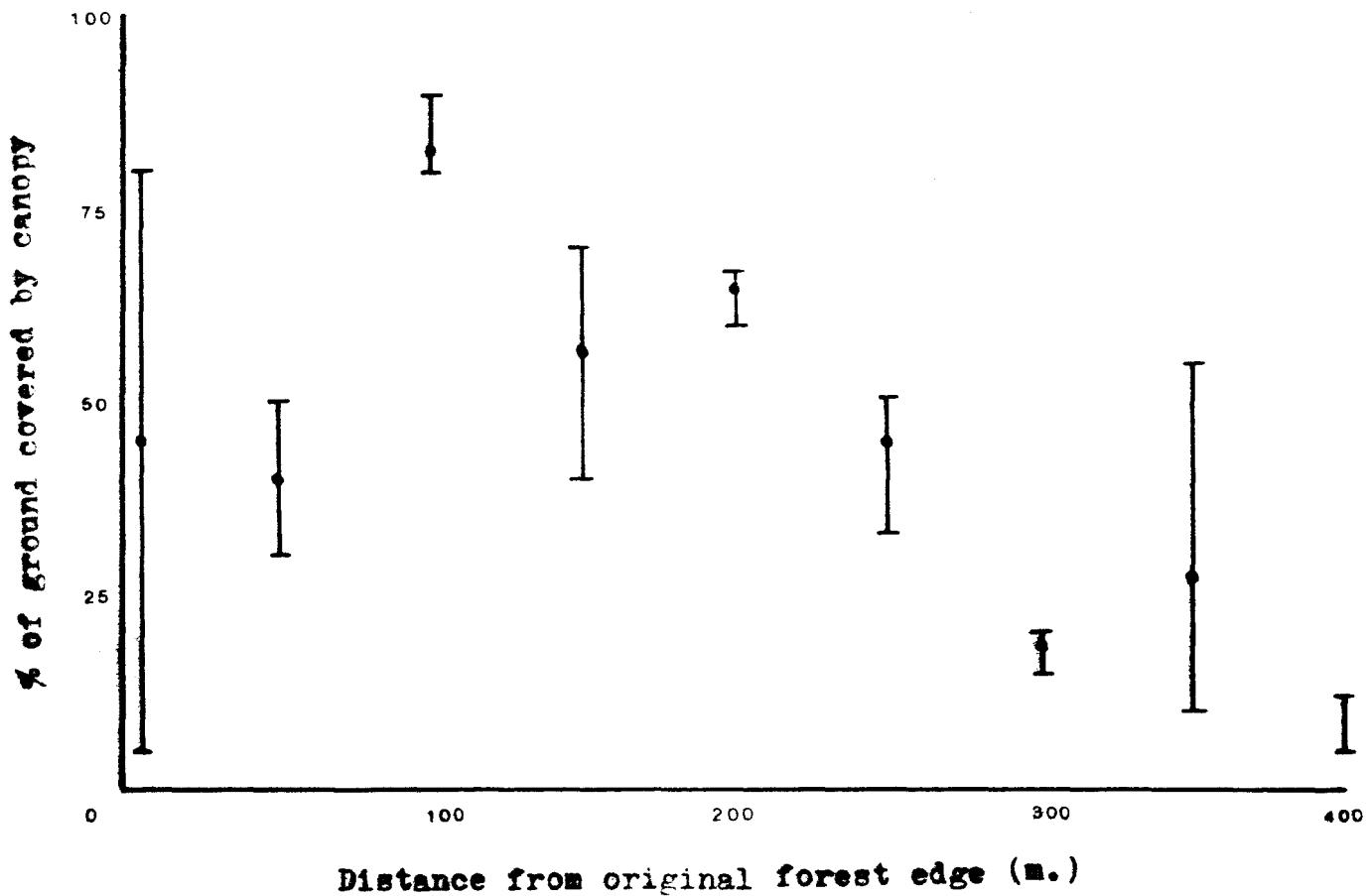


Fig3.10: Relationship between bird populations and distance from original forest edge

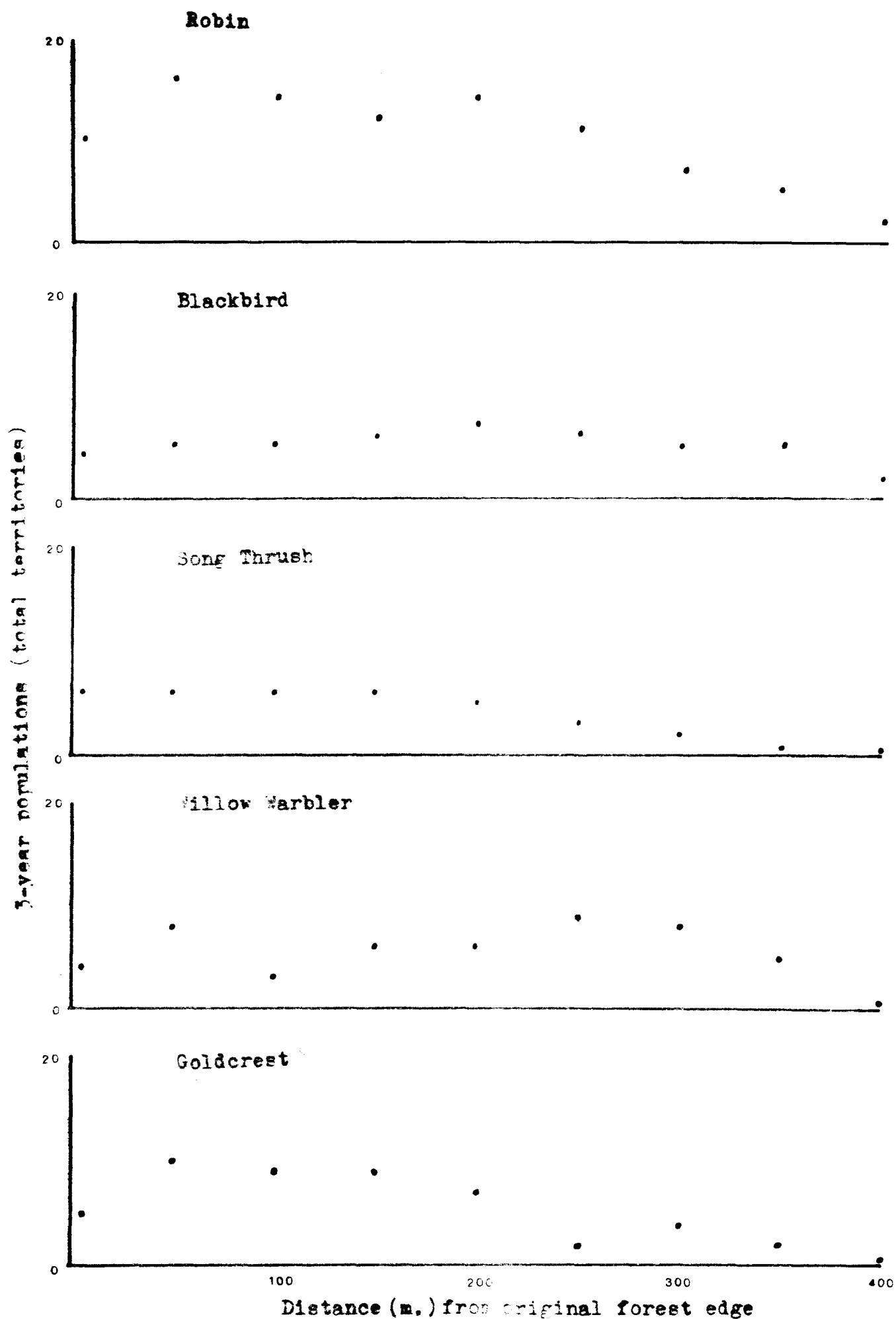


Fig 3.1c continued

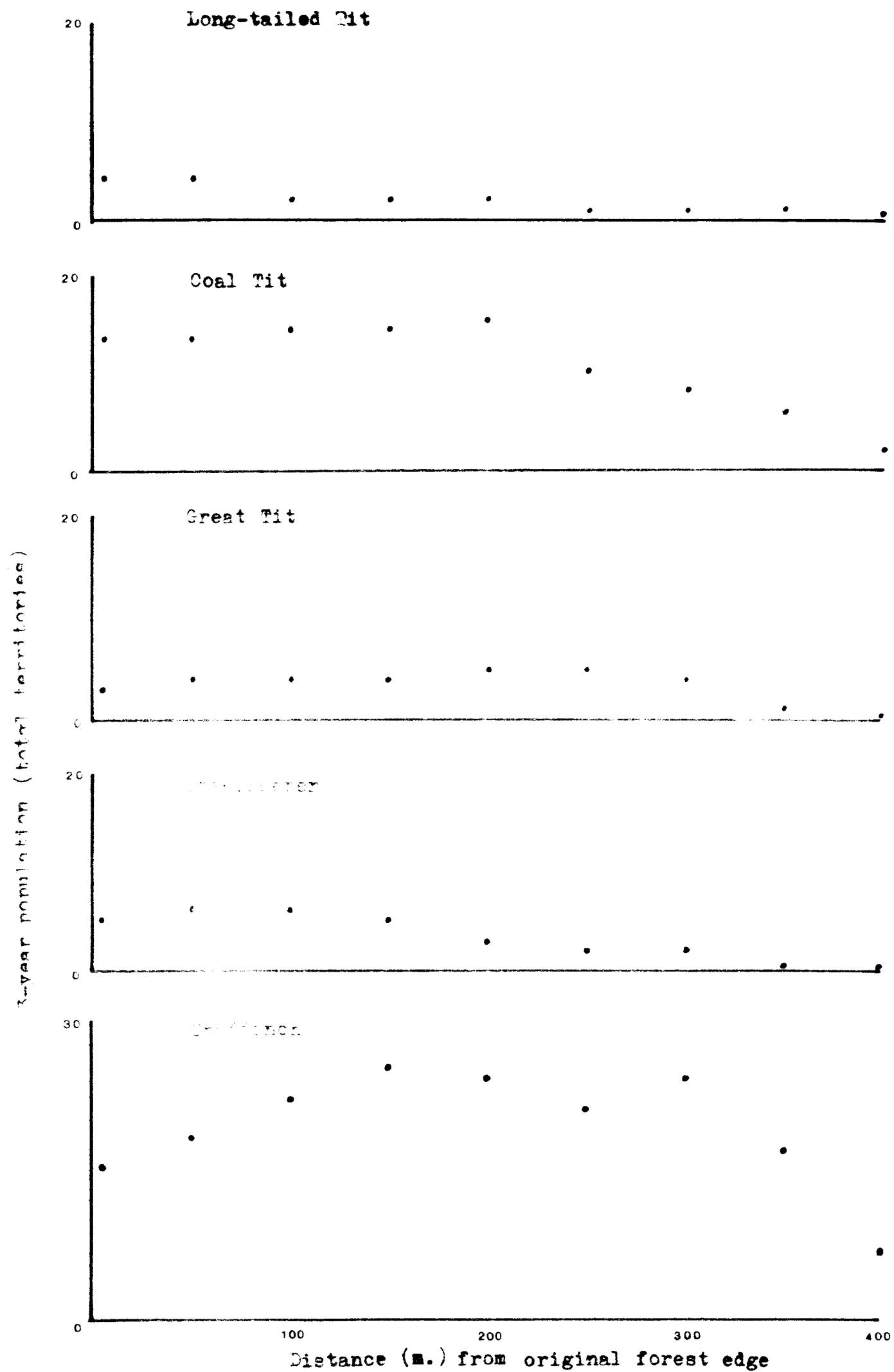
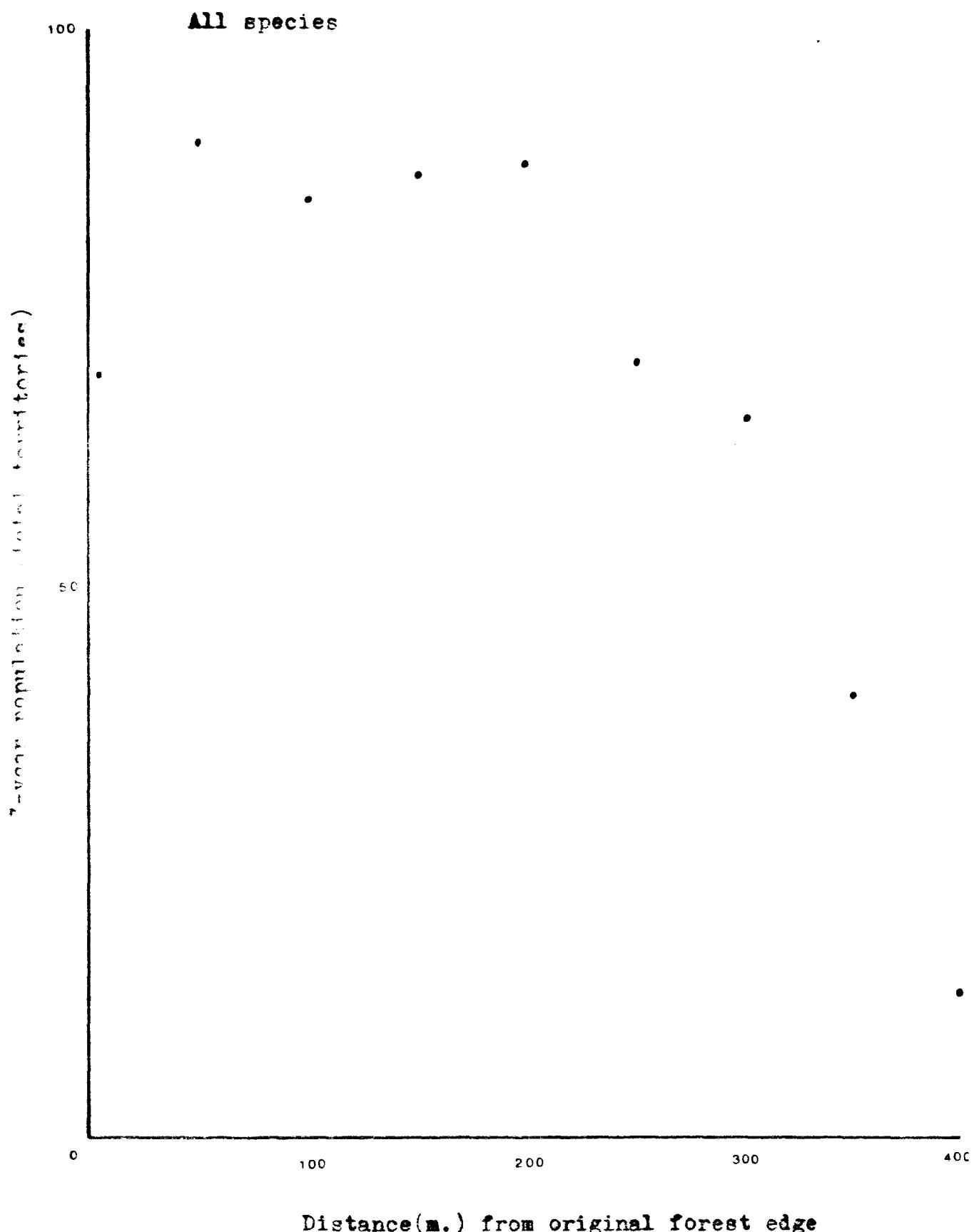


Fig 3.1c: continued



Distance(m.) from original forest edge

forest edge (Figure 3.10). Anderson (1981) revealed how studies in different forest habitats showed that many species are correlated with macro features of the community such as habitat size and distance to edge of woods.

Figure 3.10 suggests that Robin, Song Thrush, Goldcrest, Coal Tit and Treecreeper were more numerous in the taller denser woodland and that their populations decreased towards the more recent, lower and more open woodland. Blackbird, Long-tailed Tit and Great Tit populations varied little across the seral stages, although all were lowest at the younger end. Willow Warbler and Chaffinch had their lowest populations at both the oldest and youngest stages of the succession. The total populations of all species were low next to the original forest edge, high through the thicket stages and decreased abruptly towards the younger open woodland.

Examination of these relationships independent of position along the line of succession (but still using data from the northings, as described above) shows, for the whole community over the three years studied, that there are fewer territories in areas of higher light intensity (Figure 3.11); there is apparently a poor positive relationship between number of territories and general height (Figure 3.12); the number of territories increases with the increasing height at which the canopy is most widespread (Figure 3.13); and the number of territories also increases as the % of ground covered by the canopy increases (Figure 3.14).

Fig 3.11: Relationship, in Plot 1, between territories and relative light intensity

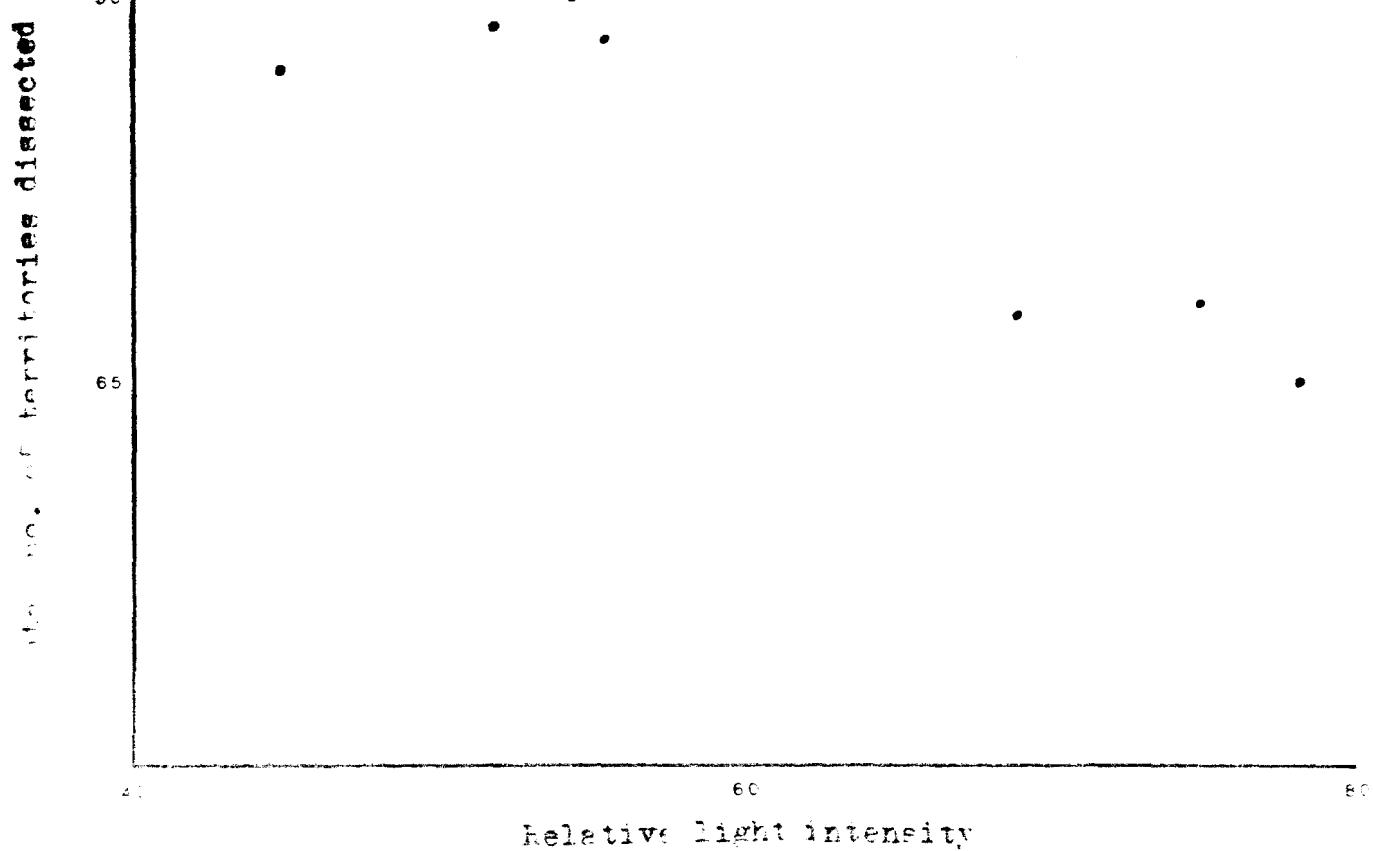


Fig 3.12: Relationship, in Plot 1, between territories and general height

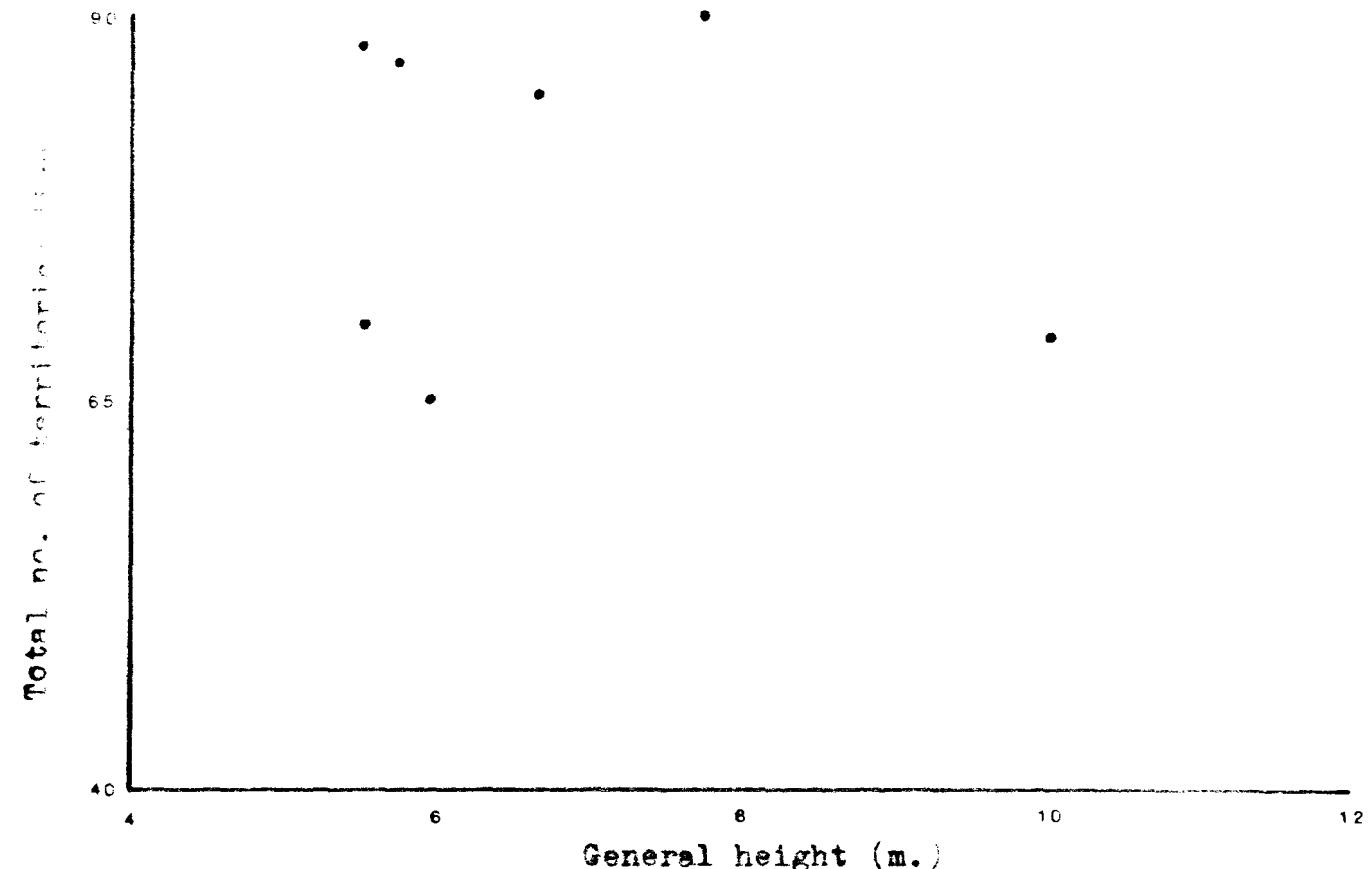


Fig 3.13: Relationship, in Plot 1, between territories and height at which canopy most widespread

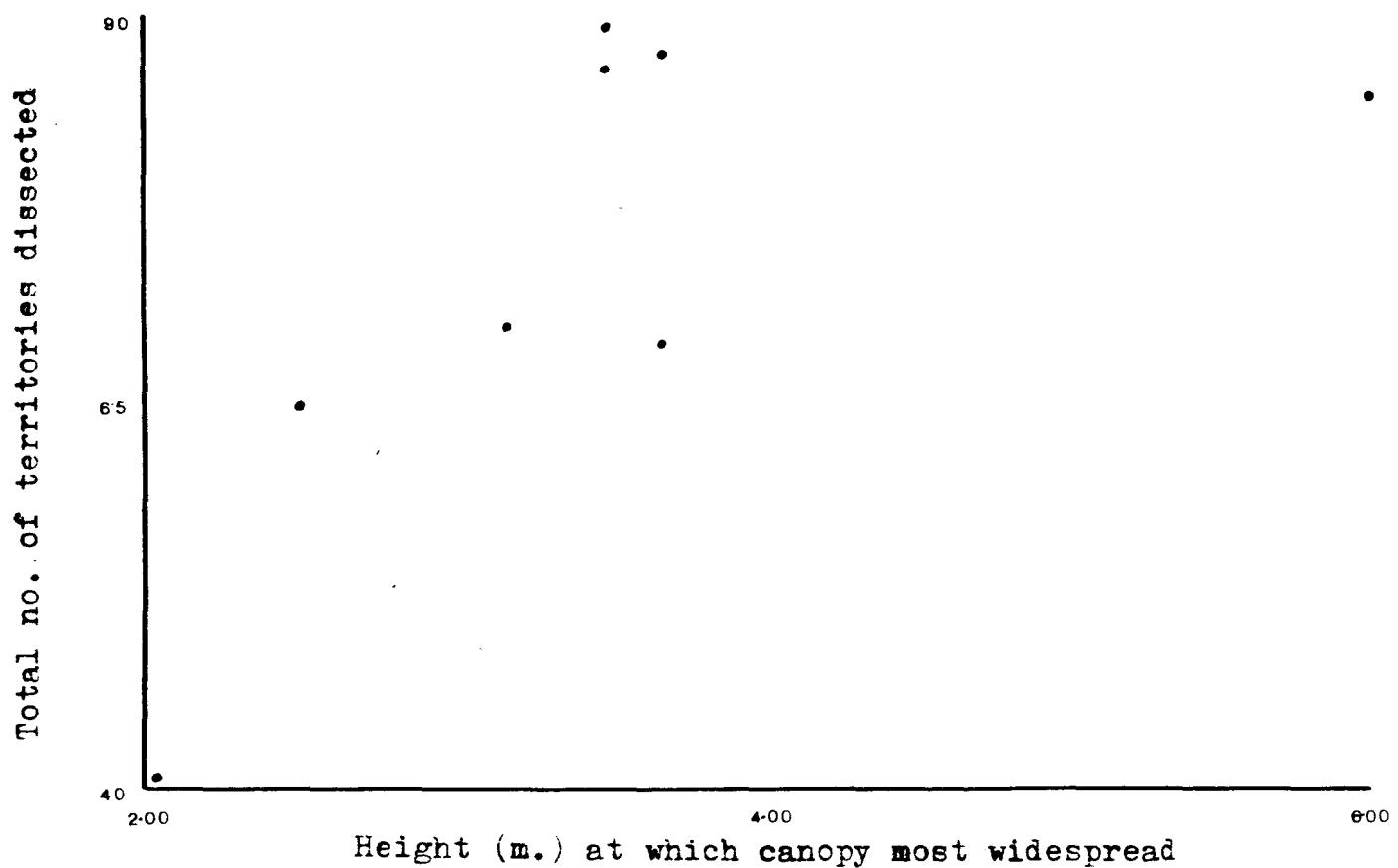
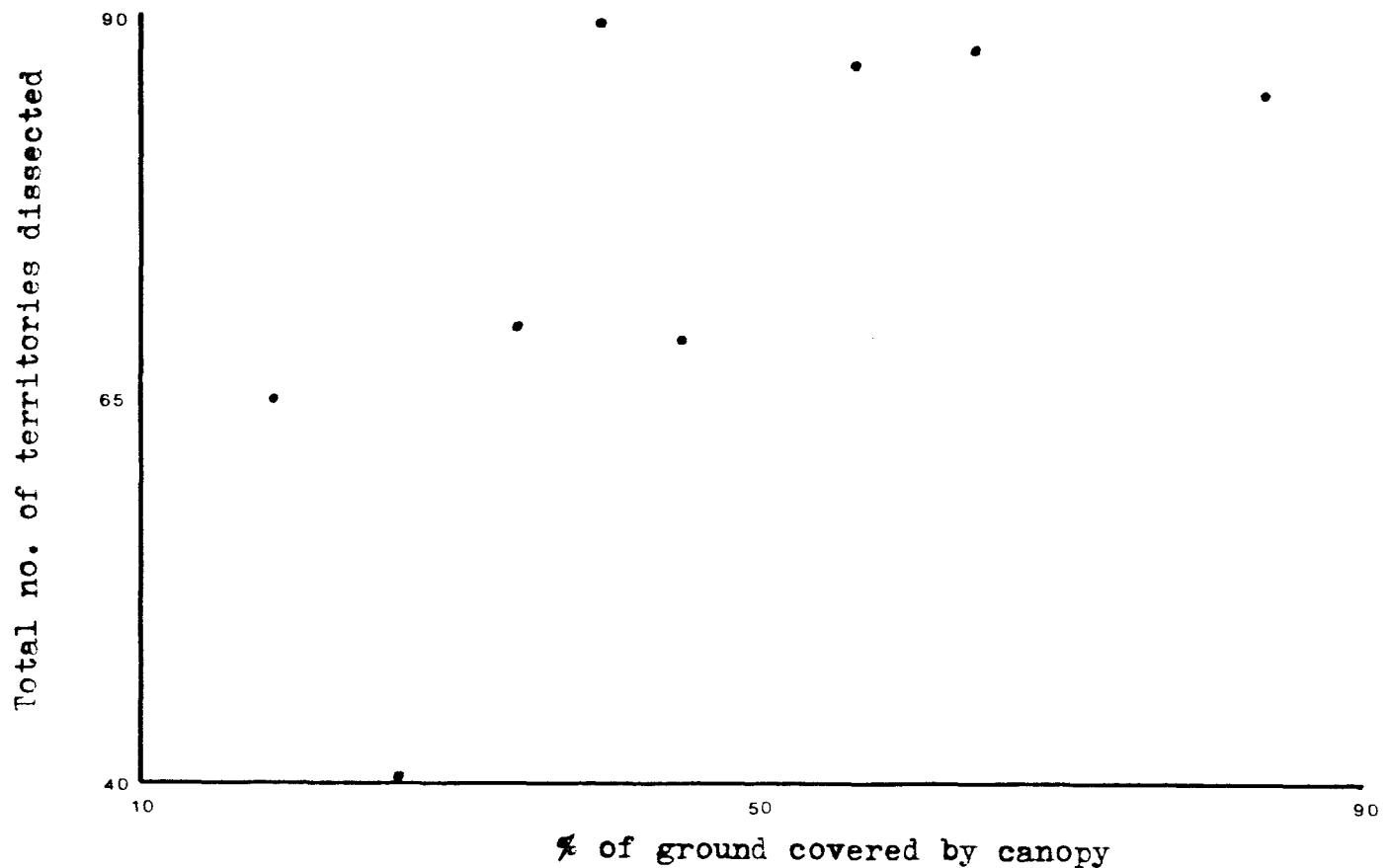


Fig 3.14: Relationship, in Plot 1, between territories and % of ground covered by canopy



At the individual species level in study area 1, Tables 3.22 - 25 suggest (sample sizes too small to be of any greater significance) that Robin, Song Thrush and Coal Tit populations are higher in areas of lower light intensity; that Song Thrush, Goldcrest and Long-tailed Tits are more numerous in taller trees; that Robin and Coal Tit populations are higher the greater the height at which the canopy is most widespread; and that Song Thrush and Coal Tit populations are greater where more of the ground is covered by the canopy.

The data for other species in study area 1 and for the other three woodland study areas are of insufficient quality to allow any firm conclusions to be reached, but there is some evidence of the following: in the commercial coniferous forest, Blackbird and Goldcrest become more numerous in dark areas than in light ones; and in the birch/willow scrub, Robin, Blue Tit and Chaffinch are less numerous among the taller trees.

Osborne (1983) has shown in hedgerow habitats that the Robin feeds on ground invertebrates and weed seeds and relies, to some extent, on dense bushes and thick canopy preventing light reaching the ground and so inhibiting plant growth in the bare areas where it feeds. In the present study such a situation occurs also in areas of conifers, such as on study plot 1.

In an attempt to gain better quality and quantity of data, the figures for the two coniferous and for the two deciduous plots were each pooled separately (Tables 3.26 - 3.29; Figures 3.15 - 3.18) for species common to plots of each type and the relationships with the same vegetation parameters investigated. However, few relationships were found at the species level, which may have been a result of the type of data used in the analysis. The basic data were the number of occupied territories dissected by north-south grid lines arranged west to east. Clearly the larger the territory, the more grid lines it will encompass and the fewer territories there will be in the study plot. This also led to problems in analysis, since the large number of tied values in rather small sample sizes precluded the use of any correlation coefficients (S.C. Richardson, pers. comm.). Of

TABLE 3.22 Relationship between average relative light intensity and number of territories over 3 years along northing lines

| R.L.I. | WR | D | R | B | ST | WW | GC | LTT | CT | BT | GT | TC | CH | Total |
|-------------------------|----|----|----|---|----|----|----|-----|----|----|----|----|----|-------|
| Study area 1 | | | | | | | | | | | | | | |
| Semi-natural coniferous | | | | | | | | | | | | | | |
| 85.33 | | 5 | 5 | 0 | 5 | 2 | 1 | 6 | | 1 | 0 | 17 | | 42 |
| 78.00 | | 7 | 5 | 2 | 8 | 4 | 1 | 8 | | 4 | 2 | 24 | | 65 |
| 74.67 | | 11 | 6 | 3 | 9 | 2 | 1 | 10 | | 5 | 2 | 21 | | 70 |
| 68.67 | | 10 | 4 | 6 | 4 | 5 | 4 | 13 | | 3 | 5 | 15 | | 69 |
| 55.33 | | 12 | 6 | 6 | 6 | 9 | 2 | 14 | | 4 | 5 | 25 | | 89 |
| 54.33 | | 16 | 5 | 6 | 8 | 10 | 4 | 13 | | 4 | 6 | 18 | | 90 |
| 51.67 | | 14 | 7 | 5 | 6 | 7 | 2 | 15 | | 5 | 3 | 24 | | 88 |
| 44.67 | | 14 | 5 | 6 | 3 | 9 | 2 | 14 | | 4 | 6 | 22 | | 85 |
| Study area 2 | | | | | | | | | | | | | | |
| Commercial coniferous | | | | | | | | | | | | | | |
| 64.00 | 2 | 1 | 8 | 4 | 3 | 5 | 3 | 1 | 15 | | 2 | 8 | | 52 |
| 62.33 | 0 | 3 | 6 | 3 | 4 | 1 | 2 | 1 | 9 | | 2 | 7 | | 38 |
| 62.33 | 2 | 1 | 12 | 4 | 4 | 4 | 8 | 2 | 16 | | 2 | 17 | | 72 |
| 58.00 | 4 | 3 | 9 | 4 | 4 | 2 | 9 | 1 | 12 | | 3 | 14 | | 65 |
| 58.00 | 2 | 1 | 10 | 6 | 3 | 5 | 4 | 2 | 14 | | 4 | 9 | | 60 |
| 58.00 | 2 | 3 | 11 | 6 | 3 | 5 | 8 | 2 | 11 | | 1 | 14 | | 66 |
| 56.67 | 9 | 4 | 10 | 7 | 5 | 13 | 10 | 4 | 9 | | 3 | 18 | | 92 |
| 56.00 | 5 | 3 | 11 | 5 | 4 | 4 | 10 | 2 | 20 | | 3 | 21 | | 88 |
| 55.67 | 2 | 1 | 11 | 9 | 2 | 9 | 5 | 3 | 13 | | 5 | 13 | | 73 |
| 43.67 | 6 | 5 | 11 | 7 | 5 | 8 | 11 | 3 | 14 | | 2 | 17 | | 89 |
| 40.33 | 9 | 3 | 10 | 9 | 5 | 18 | 12 | 4 | 11 | | 4 | 21 | | 106 |

TABLE 3.22 Continued

| R.L.I. | WR | R | WW | LTT | CT | BT | GT | TC | CH | Total |
|-------------------------|----|----|----|-----|----|----|----|----|----|-------|
| Study area 4 | | | | | | | | | | |
| Birch/alder | | | | | | | | | | |
| 100.00 | 0 | 0 | 0 | 2 | 1 | 2 | 2 | 0 | 3 | 10 |
| 76.50 | 10 | 3 | 12 | 4 | 7 | 10 | 5 | 6 | 22 | 79 |
| 68.25 | 9 | 11 | 15 | 4 | 7 | 14 | 10 | 4 | 23 | 97 |
| 63.00 | 12 | 8 | 13 | 4 | 7 | 14 | 9 | 6 | 25 | 98 |
| Study area 3 | | | | | | | | | | |
| Birch/willow | | | | | | | | | | |
| 99.75 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 6 | 11 |
| 99.00 | 2 | 1 | 3 | 4 | 6 | 3 | 6 | 0 | 8 | 33 |
| 72.50 | 1 | 4 | 18 | 2 | 4 | 4 | 6 | 0 | 18 | 57 |
| 68.75 | 6 | 10 | 8 | 3 | 5 | 10 | 10 | 5 | 20 | 77 |
| 61.75 | 7 | 12 | 13 | 5 | 5 | 12 | 8 | 5 | 19 | 86 |
| 51.50 | 1 | 11 | 11 | 2 | 1 | 8 | 7 | 3 | 13 | 57 |

TABLE 3.23 Relationship between general tree height and number of territories over 3 years along northing lines

| General Height (m) | WR | D | R | B | ST | WW | GC | LTT | CT | BT | GT | TC | CH | Total |
|--------------------------------|----|----|----|---|----|----|----|-----|----|----|----|----|-----|-------|
| Study area 1 | | | | | | | | | | | | | | |
| Semi-natural coniferous | | | | | | | | | | | | | | |
| 10.00 | | 10 | 4 | 6 | 4 | 5 | | 4 | 13 | | 3 | 5 | 15 | 69 |
| 7.71 | | 16 | 5 | 6 | 8 | 10 | | 4 | 13 | | 4 | 6 | 18 | 90 |
| 6.67 | | 14 | 5 | 6 | 3 | 9 | | 2 | 14 | | 4 | 6 | 22 | 85 |
| 5.92 | | 7 | 5 | 2 | 8 | 4 | | 1 | 8 | | 4 | 2 | 24 | 65 |
| 5.71 | | 12 | 6 | 6 | 6 | 9 | | 2 | 14 | | 4 | 5 | 25 | 89 |
| 5.50 | | 14 | 7 | 5 | 6 | 7 | | 2 | 15 | | 5 | 3 | 24 | 88 |
| 5.50 | | 11 | 6 | 3 | 9 | 2 | | 1 | 10 | | 5 | 2 | 21 | 70 |
| 4.43 | | 5 | 5 | 0 | 5 | 2 | | 1 | 6 | | 1 | 0 | 17 | 42 |
| Study area 2 | | | | | | | | | | | | | | |
| Commercial coniferous | | | | | | | | | | | | | | |
| 8.17 | 5 | 3 | 11 | 5 | 4 | 4 | 10 | 2 | 20 | | 3 | 21 | 88 | |
| 7.33 | 2 | 1 | 12 | 4 | 4 | 4 | 8 | 2 | 16 | | 2 | 17 | 72 | |
| 6.56 | 6 | 5 | 11 | 7 | 5 | 8 | 11 | 3 | 14 | | 2 | 17 | 89 | |
| 6.50 | 0 | 3 | 6 | 3 | 4 | 1 | 2 | 1 | 9 | | 2 | 7 | 38 | |
| 6.30 | 4 | 3 | 9 | 4 | 4 | 2 | 9 | 1 | 12 | | 3 | 14 | 65 | |
| 6.20 | 9 | 3 | 10 | 9 | 5 | 18 | 12 | 4 | 11 | | 4 | 21 | 106 | |
| 6.00 | 9 | 4 | 10 | 7 | 5 | 13 | 10 | 4 | 9 | | 3 | 18 | 92 | |
| 5.58 | 2 | 1 | 8 | 4 | 3 | 5 | 3 | 1 | 15 | | 2 | 8 | 52 | |
| 5.50 | 2 | 3 | 11 | 6 | 3 | 5 | 8 | 2 | 11 | | 1 | 14 | 66 | |
| 4.83 | 2 | 1 | 11 | 9 | 2 | 9 | 5 | 3 | 13 | | 5 | 13 | 73 | |
| 4.33 | 2 | 1 | 10 | 6 | 3 | 5 | 4 | 2 | 14 | | 4 | 9 | 60 | |

TABLE 3.23 Continued

| General Height | WR | R | WW | LTT | CT | BT | GT | TC | CH | Total |
|---------------------|----|----|----|-----|----|----|----|----|----|-------|
| Study area 4 | | | | | | | | | | |
| Birch/alder | | | | | | | | | | |
| 6.22 | 10 | 3 | 12 | 4 | 7 | 10 | 5 | 6 | 22 | 79 |
| 5.79 | 9 | 11 | 15 | 4 | 7 | 14 | 10 | 4 | 23 | 97 |
| 4.75 | 12 | 8 | 13 | 4 | 7 | 14 | 9 | 6 | 25 | 98 |
| 0 | 0 | 0 | 0 | 2 | 1 | 2 | 2 | 0 | 3 | 10 |
| Study area 3 | | | | | | | | | | |
| Birch/willow | | | | | | | | | | |
| 8.67 | 1 | 11 | 11 | 2 | 1 | 8 | 7 | 3 | 13 | 57 |
| 8.61 | 6 | 10 | 8 | 3 | 5 | 10 | 10 | 5 | 20 | 77 |
| 7.33 | 7 | 12 | 13 | 5 | 5 | 12 | 8 | 5 | 19 | 86 |
| 5.70 | 1 | 4 | 18 | 2 | 4 | 4 | 6 | 0 | 18 | 57 |
| 4.88 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 6 | 11 |
| 2.17 | 2 | 1 | 3 | 4 | 6 | 3 | 6 | 0 | 8 | 33 |

TABLE 3.24 Relationship between height at which canopy most widespread (m) and number of territories over 3 years along northing lines

| Height canopy most widespread | WR | D | R | B | ST | WW | GC | LTT | CT | BT | GT | TC | CH | Total |
|--|----|----|----|---|----|----|----|-----|----|----|----|----|-----|-------|
| Study area 1 | | | | | | | | | | | | | | |
| Semi-natural coniferous | | | | | | | | | | | | | | |
| 6.00 | | 14 | 5 | 6 | 3 | 9 | 2 | 14 | | | 4 | 6 | 22 | 85 |
| 3.67 | | 10 | 4 | 6 | 4 | 5 | 4 | 13 | | | 3 | 5 | 15 | 69 |
| 3.67 | | 14 | 7 | 5 | 6 | 7 | 2 | 15 | | | 5 | 3 | 24 | 88 |
| 3.50 | | 16 | 5 | 6 | 8 | 10 | 4 | 13 | | | 4 | 6 | 18 | 90 |
| 3.50 | | 12 | 6 | 6 | 6 | 9 | 2 | 14 | | | 4 | 5 | 25 | 89 |
| 3.17 | | 11 | 6 | 3 | 9 | 2 | 1 | 10 | | | 5 | 2 | 21 | 70 |
| 2.50 | | 7 | 5 | 2 | 8 | 4 | 1 | 8 | | | 4 | 2 | 24 | 65 |
| 2.00 | | 5 | 5 | 0 | 5 | 2 | 1 | 6 | | | 1 | 0 | 17 | 42 |
| Study area 2 | | | | | | | | | | | | | | |
| Commercial coniferous | | | | | | | | | | | | | | |
| 5.50 | 9 | 3 | 10 | 9 | 5 | 18 | 12 | 4 | 11 | | 4 | 21 | 106 | |
| 5.33 | 5 | 3 | 11 | 5 | 4 | 4 | 10 | 2 | 20 | | 3 | 21 | 88 | |
| 5.13 | 9 | 4 | 10 | 7 | 5 | 13 | 10 | 4 | 9 | | 3 | 18 | 92 | |
| 4.67 | 2 | 3 | 11 | 6 | 3 | 5 | 8 | 2 | 11 | | 1 | 14 | 66 | |
| 4.50 | 2 | 1 | 8 | 4 | 3 | 5 | 3 | 1 | 15 | | 2 | 8 | 52 | |
| 4.33 | 0 | 3 | 6 | 3 | 4 | 1 | 2 | 1 | 9 | | 2 | 7 | 38 | |
| 4.17 | 4 | 3 | 9 | 4 | 4 | 2 | 9 | 1 | 12 | | 3 | 14 | 65 | |
| 4.00 | 2 | 1 | 12 | 4 | 4 | 4 | 8 | 2 | 16 | | 2 | 17 | 72 | |
| 3.67 | 2 | 1 | 10 | 6 | 3 | 5 | 4 | 2 | 14 | | 4 | 9 | 60 | |
| 3.67 | 6 | 5 | 11 | 7 | 5 | 8 | 11 | 3 | 14 | | 2 | 17 | 89 | |
| 3.00 | 2 | 1 | 11 | 9 | 2 | 9 | 5 | 3 | 13 | | 5 | 13 | 73 | |

TABLE 3.24 Continued

| Height canopy most widespread | WR | R | WW | LTT | LT | BT | GT | TC | CH | Total |
|--|----|----|----|-----|----|----|----|----|----|-------|
| Study area 4 | | | | | | | | | | |
| Birch/alder | | | | | | | | | | |
| 4.33 | 12 | 8 | 13 | 4 | 7 | 14 | 9 | 6 | 25 | 98 |
| 3.60 | 9 | 11 | 15 | 4 | 7 | 14 | 10 | 4 | 23 | 97 |
| 3.36 | 10 | 3 | 12 | 4 | 7 | 10 | 5 | 6 | 22 | 79 |
| 0 | 0 | 0 | 0 | 2 | 1 | 2 | 2 | 0 | 3 | 10 |
| Study area 3 | | | | | | | | | | |
| Birch/willow | | | | | | | | | | |
| 7.56 | 6 | 10 | 8 | 3 | 5 | 10 | 10 | 5 | 20 | 77 |
| 6.70 | 1 | 11 | 11 | 2 | 1 | 8 | 7 | 3 | 13 | 57 |
| 5.67 | 7 | 12 | 13 | 5 | 5 | 12 | 8 | 5 | 19 | 86 |
| 5.33 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 6 | 11 |
| 4.30 | 1 | 4 | 18 | 2 | 4 | 4 | 6 | 0 | 18 | 57 |
| 1.50 | 2 | 1 | 3 | 4 | 6 | 3 | 6 | 0 | 8 | 33 |

TABLE 3.25 Relationship between % of ground covered by the canopy and number of territories over 3 years along northing lines

| % ground covered | WR | D | R | B | ST | WW | GC | LTT | CT | BT | GT | TC | CH | Total |
|-------------------------|----|----|----|---|----|----|----|-----|----|----|----|----|----|-------|
| Study area 1 | | | | | | | | | | | | | | |
| Semi-natural coniferous | | | | | | | | | | | | | | |
| 83.33 | | 14 | 5 | 6 | 3 | 9 | 2 | 14 | | | 4 | 6 | 22 | 85 |
| 64.67 | | 14 | 7 | 5 | 6 | 7 | 2 | 15 | | | 5 | 3 | 24 | 88 |
| 56.67 | | 12 | 6 | 6 | 6 | 9 | 2 | 14 | | | 4 | 5 | 25 | 89 |
| 45.00 | | 10 | 4 | 6 | 4 | 5 | 4 | 13 | | | 3 | 5 | 15 | 69 |
| 40.00 | | 16 | 5 | 6 | 8 | 10 | 4 | 13 | | | 4 | 6 | 18 | 90 |
| 34.33 | | 11 | 6 | 3 | 9 | 2 | 1 | 10 | | | 5 | 2 | 21 | 70 |
| 26.67 | | 5 | 5 | 0 | 5 | 2 | 1 | 6 | | | 1 | 0 | 17 | 42 |
| 18.33 | | 7 | 5 | 2 | 8 | 4 | 1 | 8 | | | 4 | 2 | 24 | 65 |
| Study area 2 | | | | | | | | | | | | | | |
| Commercial coniferous | | | | | | | | | | | | | | |
| 95.00 | 0 | 3 | 6 | 3 | 4 | 1 | 2 | 1 | 9 | | | 2 | 7 | 38 |
| 93.33 | 2 | 1 | 10 | 6 | 3 | 5 | 4 | 2 | 14 | | | 4 | 9 | 60 |
| 93.33 | 9 | 3 | 10 | 9 | 5 | 18 | 12 | 4 | 11 | | | 4 | 21 | 106 |
| 91.67 | 2 | 1 | 8 | 4 | 3 | 5 | 3 | 1 | 15 | | | 2 | 8 | 52 |
| 91.67 | 6 | 5 | 11 | 7 | 5 | 8 | 11 | 3 | 14 | | | 2 | 17 | 89 |
| 90.00 | 9 | 4 | 10 | 7 | 5 | 13 | 10 | 4 | 9 | | | 3 | 18 | 92 |
| 88.33 | 5 | 3 | 11 | 5 | 4 | 4 | 10 | 2 | 20 | | | 3 | 21 | 88 |
| 86.67 | 2 | 1 | 11 | 9 | 2 | 9 | 5 | 3 | 13 | | | 5 | 13 | 73 |
| 85.00 | 4 | 3 | 9 | 4 | 4 | 2 | 9 | 1 | 12 | | | 3 | 14 | 65 |
| 80.00 | 2 | 1 | 12 | 4 | 4 | 4 | 8 | 2 | 16 | | | 2 | 17 | 72 |
| 80.00 | 2 | 3 | 11 | 6 | 3 | 5 | 8 | 2 | 11 | | | 1 | 14 | 66 |

TABLE 3.25 Continued

| % Ground covered | WR | R | WW | LTT | CT | BT | GT | TC | CH | Total |
|---------------------|----|----|----|-----|----|----|----|----|----|-------|
| Study area 4 | | | | | | | | | | |
| Birch/alder | | | | | | | | | | |
| 37.50 | 9 | 11 | 15 | 4 | 7 | 14 | 10 | 4 | 23 | 97 |
| 35.00 | 10 | 3 | 12 | 4 | 7 | 10 | 5 | 6 | 22 | 79 |
| 30.00 | 12 | 8 | 13 | 4 | 7 | 14 | 9 | 6 | 25 | 98 |
| 0 | 0 | 0 | 0 | 2 | 1 | 2 | 2 | 0 | 3 | 10 |
| Study area 3 | | | | | | | | | | |
| Birch/willow | | | | | | | | | | |
| 85.00 | 7 | 12 | 13 | 5 | 5 | 12 | 8 | 5 | 19 | 86 |
| 80.00 | 1 | 11 | 11 | 2 | 1 | 8 | 7 | 3 | 13 | 57 |
| 76.25 | 1 | 4 | 18 | 2 | 4 | 4 | 6 | 0 | 18 | 57 |
| 62.50 | 6 | 10 | 8 | 3 | 5 | 10 | 10 | 5 | 20 | 77 |
| 6.67 | 2 | 1 | 3 | 4 | 6 | 3 | 6 | 0 | 8 | 33 |
| 5.00 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 6 | 11 |

course it should also be remembered that the delimitation of territories is still very subjective and was not based on detailed observations of individual pairs of birds. Nonetheless, the following seem possible: in coniferous plots an increase in the populations of Robin and Goldcrest associated with a decrease in light intensity, and in deciduous plots the same relationship with Robin; as regards the % of ground covered by the canopy, there was a decrease in the populations of Willow Warbler as the ground covered by canopy decreased in both coniferous and deciduous plots, with decreases also in the population of Robin in deciduous plots and Goldcrest in coniferous plots. (However, Table 3.29B reveals that the canopy cover on deciduous plots must be regarded as a special case here since there is a wide gap in the sample data between 30% and 6.67% ground covered by canopy.)

Zero values in the "territories dissected" columns of each species in Tables 3.26 - 3.29 reveal areas of the study plots which were avoided over a three-year period by the species concerned. Thus, areas of high light intensity (and so of more open tree cover) were avoided in coniferous plots by Song Thrush and Treecreeper, and in deciduous plots were avoided by Wren, Robin, Willow Warbler and Treecreeper. Some areas of low tree height in coniferous plots were avoided by Song Thrush and Treecreeper and in deciduous plots by Wren, Robin, Willow Warbler and Treecreeper, especially where there was an absence of tree cover. Likewise for both height at which the canopy is most widespread and the % of ground covered by it, the same species were absent. Clearly it would seem that Wren, Robin, Willow Warbler and Treecreeper avoid areas of low and little tree cover in the deciduous plots, whilst Song Thrush avoids similar areas in coniferous plots at least.

TABLE 3.26 Relationship between average relative light intensity and number of territories along northing lines over three years

A: In coniferous plots

| R.L.I. | R | B | ST | WW | Species | | | | | | Total |
|--------|----|---|----|----|---------|-----|----|----|----|----|-------|
| | | | | | GC | LTT | CT | TC | CH | | |
| 85.33 | 5 | 5 | 0 | 5 | 2 | 1 | 6 | 0 | 17 | 41 | |
| 78.00 | 7 | 5 | 2 | 8 | 4 | 1 | 8 | 2 | 24 | 61 | |
| 74.67 | 11 | 6 | 3 | 9 | 2 | 1 | 10 | 2 | 21 | 65 | |
| 68.67 | 10 | 4 | 6 | 4 | 5 | 4 | 13 | 5 | 15 | 66 | |
| 64.00 | 8 | 4 | 3 | 5 | 3 | 1 | 15 | 2 | 8 | 49 | |
| 62.33 | 6 | 3 | 4 | 1 | 2 | 1 | 9 | 2 | 7 | 35 | |
| 62.33 | 12 | 4 | 4 | 4 | 8 | 2 | 16 | 2 | 17 | 69 | |
| 58.00 | 9 | 4 | 4 | 2 | 9 | 1 | 12 | 3 | 14 | 58 | |
| 58.00 | 10 | 6 | 3 | 5 | 4 | 2 | 14 | 4 | 9 | 57 | |
| 58.00 | 11 | 6 | 3 | 5 | 8 | 2 | 11 | 1 | 14 | 61 | |
| 56.67 | 10 | 7 | 5 | 13 | 10 | 4 | 9 | 3 | 18 | 79 | |
| 56.00 | 11 | 5 | 4 | 4 | 10 | 2 | 20 | 3 | 21 | 80 | |
| 55.67 | 11 | 9 | 2 | 9 | 5 | 3 | 13 | 5 | 13 | 70 | |
| 55.33 | 12 | 6 | 6 | 6 | 9 | 2 | 14 | 5 | 25 | 85 | |
| 54.33 | 16 | 5 | 6 | 8 | 10 | 4 | 13 | 6 | 18 | 86 | |
| 51.67 | 14 | 7 | 5 | 6 | 7 | 2 | 15 | 3 | 24 | 83 | |
| 44.67 | 14 | 5 | 6 | 3 | 9 | 2 | 14 | 6 | 22 | 81 | |
| 43.67 | 11 | 7 | 5 | 8 | 11 | 3 | 14 | 2 | 17 | 78 | |
| 40.33 | 10 | 9 | 5 | 18 | 12 | 4 | 11 | 4 | 21 | 94 | |

B: In deciduous plots

| R.L.I. | WR | R | WW | LTT | CT | BT | GT | TC | CH | Total |
|--------|----|----|----|-----|----|----|----|----|----|-------|
| 100.00 | 0 | 0 | 0 | 2 | 1 | 2 | 2 | 0 | 3 | 10 |
| 99.75 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 6 | 11 |
| 99.00 | 2 | 1 | 3 | 4 | 6 | 3 | 6 | 0 | 8 | 33 |
| 76.50 | 10 | 3 | 12 | 4 | 7 | 10 | 5 | 6 | 22 | 79 |
| 72.50 | 1 | 4 | 18 | 2 | 4 | 4 | 6 | 0 | 18 | 57 |
| 68.75 | 6 | 10 | 8 | 3 | 5 | 10 | 10 | 5 | 20 | 77 |
| 68.25 | 9 | 11 | 15 | 4 | 7 | 14 | 10 | 4 | 23 | 97 |
| 63.00 | 12 | 8 | 13 | 4 | 7 | 14 | 9 | 6 | 25 | 98 |
| 61.75 | 7 | 12 | 13 | 5 | 5 | 12 | 8 | 5 | 19 | 86 |
| 51.50 | 1 | 11 | 11 | 2 | 1 | 8 | 7 | 3 | 13 | 57 |

TABLE 3.27 Relationship between general height and number of territories along northing lines, over three years

A: In coniferous plots

| General Height | R | B | ST | WW | GC | LTT | CT | TC | CH | Total |
|----------------|----|---|----|----|----|-----|----|----|----|-------|
| 10.00 | 10 | 4 | 6 | 4 | 5 | 4 | 13 | 5 | 15 | 66 |
| 8.17 | 11 | 5 | 4 | 4 | 10 | 2 | 20 | 3 | 21 | 80 |
| 7.71 | 16 | 5 | 6 | 8 | 10 | 4 | 13 | 6 | 18 | 86 |
| 7.33 | 12 | 4 | 4 | 4 | 8 | 2 | 16 | 2 | 17 | 69 |
| 6.67 | 14 | 5 | 6 | 3 | 9 | 2 | 14 | 6 | 22 | 81 |
| 6.56 | 11 | 7 | 5 | 8 | 11 | 3 | 14 | 2 | 17 | 88 |
| 6.50 | 6 | 3 | 4 | 1 | 2 | 1 | 9 | 2 | 7 | 35 |
| 6.30 | 9 | 4 | 4 | 2 | 9 | 1 | 12 | 3 | 14 | 58 |
| 6.20 | 10 | 9 | 5 | 18 | 12 | 4 | 11 | 4 | 21 | 94 |
| 6.00 | 10 | 7 | 5 | 13 | 10 | 4 | 9 | 3 | 18 | 79 |
| 5.92 | 7 | 5 | 2 | 8 | 4 | 1 | 8 | 2 | 24 | 61 |
| 5.71 | 12 | 6 | 6 | 6 | 9 | 2 | 14 | 5 | 25 | 85 |
| 5.58 | 8 | 4 | 3 | 5 | 3 | 1 | 15 | 2 | 8 | 49 |
| 5.50 | 11 | 6 | 3 | 5 | 8 | 2 | 11 | 1 | 14 | 61 |
| 5.50 | 14 | 7 | 5 | 6 | 7 | 2 | 15 | 3 | 24 | 83 |
| 5.50 | 11 | 6 | 3 | 9 | 2 | 1 | 10 | 2 | 21 | 65 |
| 4.83 | 11 | 9 | 2 | 9 | 5 | 3 | 13 | 5 | 13 | 70 |
| 4.43 | 5 | 5 | 0 | 5 | 2 | 1 | 6 | 0 | 17 | 41 |
| 4.33 | 10 | 6 | 3 | 5 | 4 | 2 | 14 | 4 | 9 | 57 |

B: In deciduous plots

| General Height | WR | R | WW | LTT | CT | BT | GT | TC | CH | Total |
|----------------|----|----|----|-----|----|----|----|----|----|-------|
| 8.67 | 1 | 11 | 11 | 2 | 1 | 8 | 7 | 3 | 13 | 57 |
| 8.61 | 6 | 10 | 8 | 3 | 5 | 10 | 10 | 5 | 20 | 77 |
| 7.33 | 7 | 12 | 13 | 5 | 5 | 12 | 8 | 5 | 19 | 86 |
| 6.22 | 10 | 3 | 12 | 4 | 7 | 10 | 5 | 6 | 22 | 79 |
| 5.79 | 19 | 11 | 15 | 4 | 7 | 14 | 10 | 4 | 23 | 97 |
| 5.70 | 1 | 4 | 18 | 2 | 4 | 4 | 6 | 0 | 18 | 57 |
| 4.88 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 6 | 11 |
| 4.75 | 12 | 8 | 13 | 4 | 7 | 14 | 9 | 6 | 25 | 98 |
| 2.17 | 2 | 1 | 3 | 4 | 6 | 3 | 6 | 0 | 8 | 33 |
| 0 | 0 | 0 | 0 | 2 | 1 | 2 | 2 | 0 | 3 | 10 |

TABLE 3.28 Relationship between height at which canopy is most widespread and number of territories along northing lines, over three years

A: In coniferous plots

| Height canopy most widespread | R | B | ST | WW | GC | LTT | CT | TC | CH | Total |
|--|----|---|----|----|----|-----|----|----|----|-------|
| 6.00 | 14 | 5 | 6 | 3 | 9 | 2 | 14 | 6 | 22 | 81 |
| 5.50 | 10 | 9 | 5 | 18 | 12 | 4 | 11 | 4 | 21 | 94 |
| 5.33 | 11 | 5 | 4 | 4 | 10 | 2 | 20 | 3 | 21 | 80 |
| 5.13 | 10 | 7 | 5 | 13 | 10 | 4 | 9 | 3 | 18 | 79 |
| 4.67 | 11 | 6 | 3 | 5 | 8 | 2 | 11 | 1 | 14 | 61 |
| 4.50 | 8 | 4 | 3 | 5 | 3 | 1 | 15 | 2 | 8 | 49 |
| 4.33 | 6 | 3 | 4 | 1 | 2 | 1 | 9 | 2 | 7 | 35 |
| 4.17 | 9 | 4 | 4 | 2 | 9 | 1 | 12 | 3 | 4 | 48 |
| 4.00 | 12 | 4 | 4 | 4 | 8 | 2 | 16 | 2 | 17 | 69 |
| 3.67 | 10 | 6 | 3 | 5 | 4 | 2 | 14 | 4 | 9 | 57 |
| 3.67 | 11 | 7 | 5 | 8 | 11 | 3 | 14 | 2 | 17 | 78 |
| 3.67 | 10 | 4 | 6 | 4 | 5 | 4 | 13 | 5 | 15 | 66 |
| 3.67 | 14 | 7 | 5 | 6 | 7 | 2 | 15 | 3 | 24 | 83 |
| 3.50 | 16 | 5 | 6 | 8 | 10 | 4 | 13 | 5 | 15 | 82 |
| 3.50 | 12 | 6 | 6 | 6 | 9 | 2 | 14 | 5 | 25 | 85 |
| 3.17 | 11 | 6 | 3 | 9 | 2 | 1 | 10 | 2 | 21 | 65 |
| 3.00 | 11 | 9 | 2 | 9 | 5 | 3 | 13 | 5 | 13 | 70 |
| 2.50 | 7 | 5 | 2 | 8 | 4 | 1 | 8 | 2 | 24 | 63 |
| 2.00 | 5 | 5 | 0 | 5 | 2 | 1 | 6 | 0 | 17 | 41 |

B: In deciduous plots

| Height canopy most widespread | WR | R | WW | LTT | CT | BT | GT | TC | CH | Total |
|--|----|----|----|-----|----|----|----|----|----|-------|
| 7.56 | 6 | 10 | 8 | 3 | 5 | 10 | 10 | 5 | 20 | 79 |
| 6.70 | 1 | 11 | 11 | 2 | 1 | 8 | 7 | 3 | 13 | 57 |
| 5.67 | 7 | 12 | 13 | 5 | 5 | 12 | 8 | 5 | 19 | 86 |
| 5.33 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 6 | 11 |
| 4.33 | 12 | 8 | 13 | 4 | 7 | 14 | 9 | 6 | 25 | 98 |
| 4.30 | 1 | 4 | 18 | 2 | 4 | 4 | 6 | 0 | 18 | 57 |
| 3.60 | 9 | 11 | 15 | 4 | 7 | 14 | 10 | 4 | 23 | 97 |
| 3.36 | 10 | 3 | 12 | 4 | 7 | 10 | 5 | 6 | 22 | 77 |
| 1.50 | 2 | 1 | 3 | 4 | 6 | 3 | 6 | 0 | 8 | 33 |
| 0 | 0 | 0 | 0 | 2 | 1 | 2 | 2 | 0 | 3 | 10 |

TABLE 3.29 Relationship between % of ground covered by the canopy and number of territories along northing lines, over three years

A: In coniferous plots

| % ground covered | R | B | ST | WW | GC | LTT | CT | TC | CH | Total |
|------------------------|----|---|----|----|----|-----|----|----|----|-------|
| 95.00 | 6 | 3 | 4 | 1 | 2 | 1 | 9 | 2 | 7 | 35 |
| 93.33 | 10 | 6 | 3 | 5 | 4 | 2 | 14 | 4 | 9 | 57 |
| 93.33 | 10 | 9 | 5 | 18 | 12 | 4 | 11 | 4 | 21 | 94 |
| 91.67 | 8 | 4 | 3 | 5 | 3 | 1 | 15 | 2 | 8 | 49 |
| 91.67 | 11 | 7 | 5 | 8 | 11 | 3 | 14 | 2 | 17 | 78 |
| 90.00 | 10 | 7 | 5 | 13 | 10 | 4 | 9 | 3 | 18 | 79 |
| 88.33 | 11 | 5 | 4 | 4 | 10 | 2 | 20 | 3 | 21 | 80 |
| 86.67 | 11 | 9 | 2 | 9 | 5 | 3 | 13 | 5 | 13 | 70 |
| 85.00 | 9 | 4 | 4 | 2 | 9 | 1 | 12 | 3 | 14 | 58 |
| 83.33 | 14 | 5 | 6 | 3 | 9 | 2 | 14 | 6 | 22 | 81 |
| 80.00 | 12 | 4 | 4 | 4 | 8 | 2 | 16 | 2 | 17 | 69 |
| 80.00 | 11 | 6 | 3 | 5 | 8 | 2 | 11 | 1 | 14 | 61 |
| 64.67 | 14 | 7 | 5 | 6 | 7 | 2 | 15 | 3 | 24 | 83 |
| 56.67 | 12 | 6 | 6 | 6 | 9 | 2 | 14 | 5 | 25 | 85 |
| 45.00 | 10 | 4 | 6 | 4 | 5 | 4 | 13 | 5 | 15 | 66 |
| 40.00 | 16 | 5 | 6 | 8 | 10 | 4 | 13 | 6 | 18 | 86 |
| 34.33 | 11 | 6 | 3 | 9 | 2 | 1 | 10 | 2 | 21 | 65 |
| 26.67 | 5 | 5 | 0 | 5 | 2 | 1 | 6 | 0 | 17 | 41 |
| 18.33 | 7 | 5 | 2 | 8 | 4 | 1 | 8 | 2 | 24 | 61 |

B: In deciduous plots

| % ground covered | WR | R | WW | LTT | CT | BT | GT | TC | CH | Total |
|------------------------|----|----|----|-----|----|----|----|----|----|-------|
| 85.00 | 7 | 12 | 13 | 5 | 5 | 12 | 8 | 5 | 19 | 86 |
| 80.00 | 1 | 11 | 11 | 2 | 1 | 8 | 7 | 3 | 13 | 57 |
| 76.25 | 1 | 4 | 18 | 2 | 4 | 4 | 6 | 0 | 18 | 57 |
| 62.50 | 6 | 10 | 8 | 3 | 5 | 10 | 10 | 5 | 20 | 77 |
| 37.50 | 9 | 11 | 15 | 4 | 7 | 14 | 10 | 4 | 23 | 97 |
| 35.00 | 10 | 3 | 12 | 4 | 7 | 10 | 5 | 6 | 22 | 79 |
| 30.00 | 12 | 8 | 13 | 4 | 7 | 14 | 9 | 6 | 25 | 98 |
| 6.67 | 2 | 1 | 3 | 4 | 6 | 3 | 6 | 0 | 8 | 33 |
| 5.00 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 6 | 11 |
| 0 | 0 | 0 | 0 | 2 | 1 | 2 | 2 | 0 | 3 | 10 |

Fig. 3.15 : Relationship between relative light intensity and number of territories

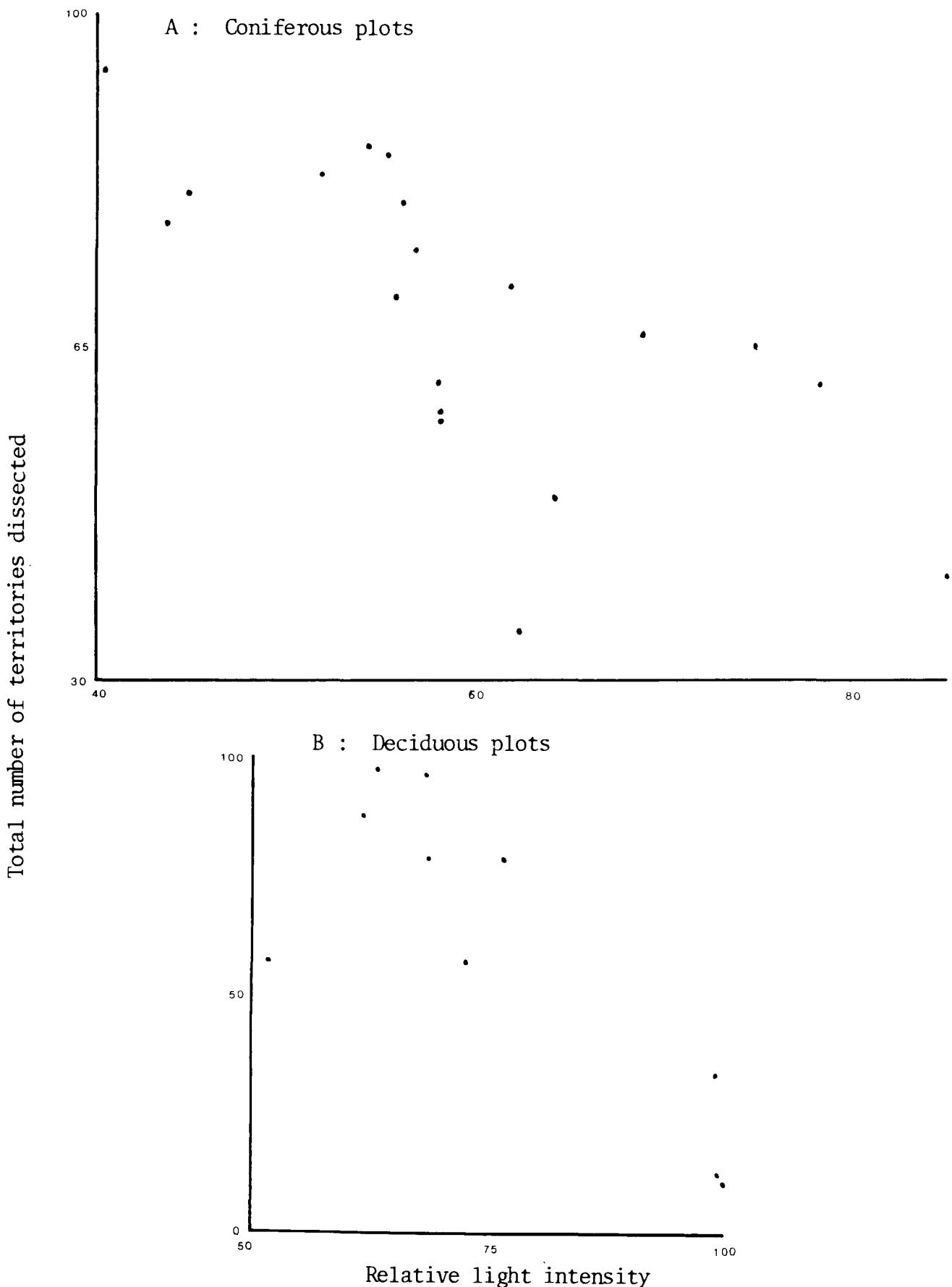


Fig. 3.16 : Relationship between general foliage height and number of territories

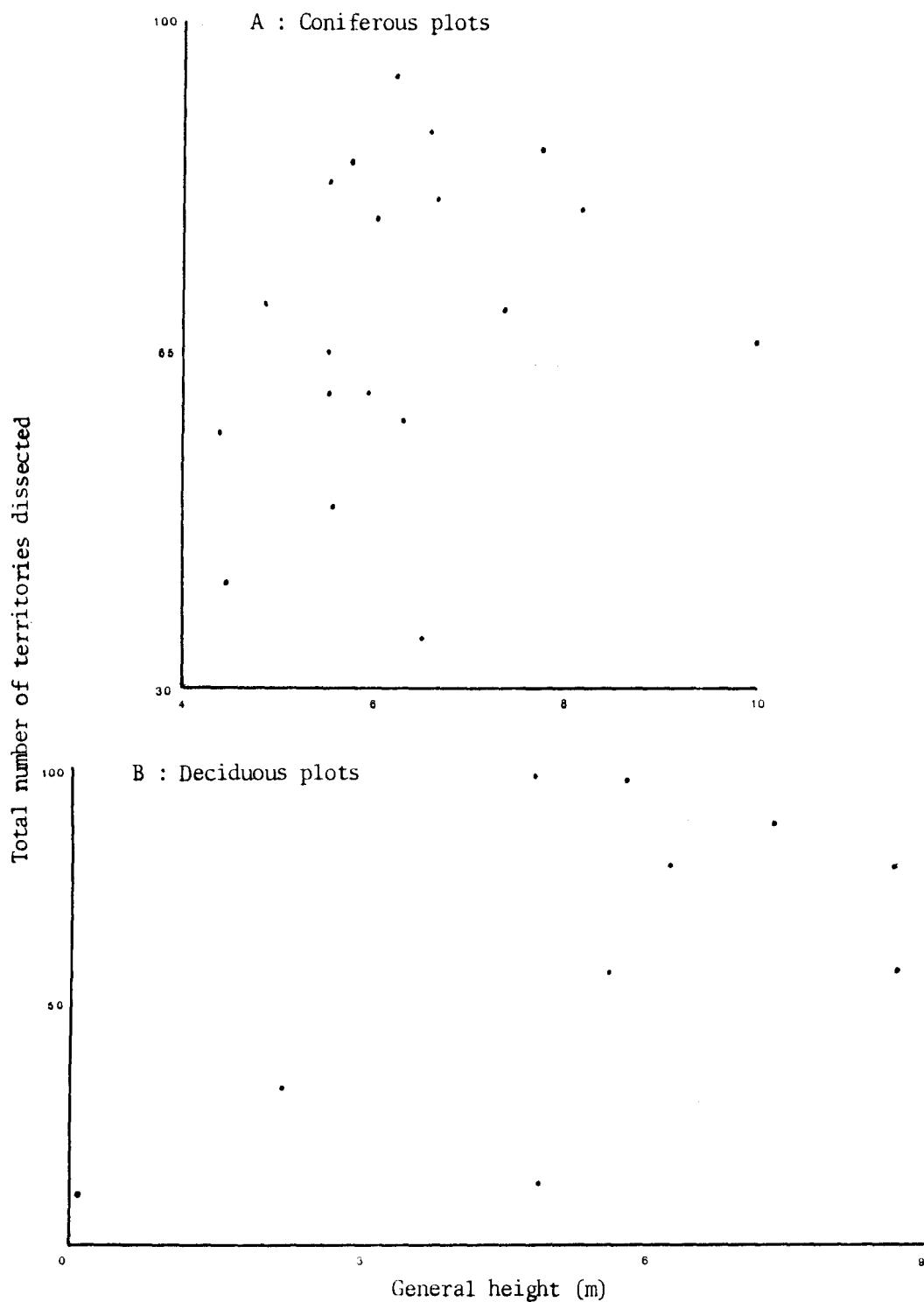


Fig 3.17: Relationship between canopy height (m.) and number of territories

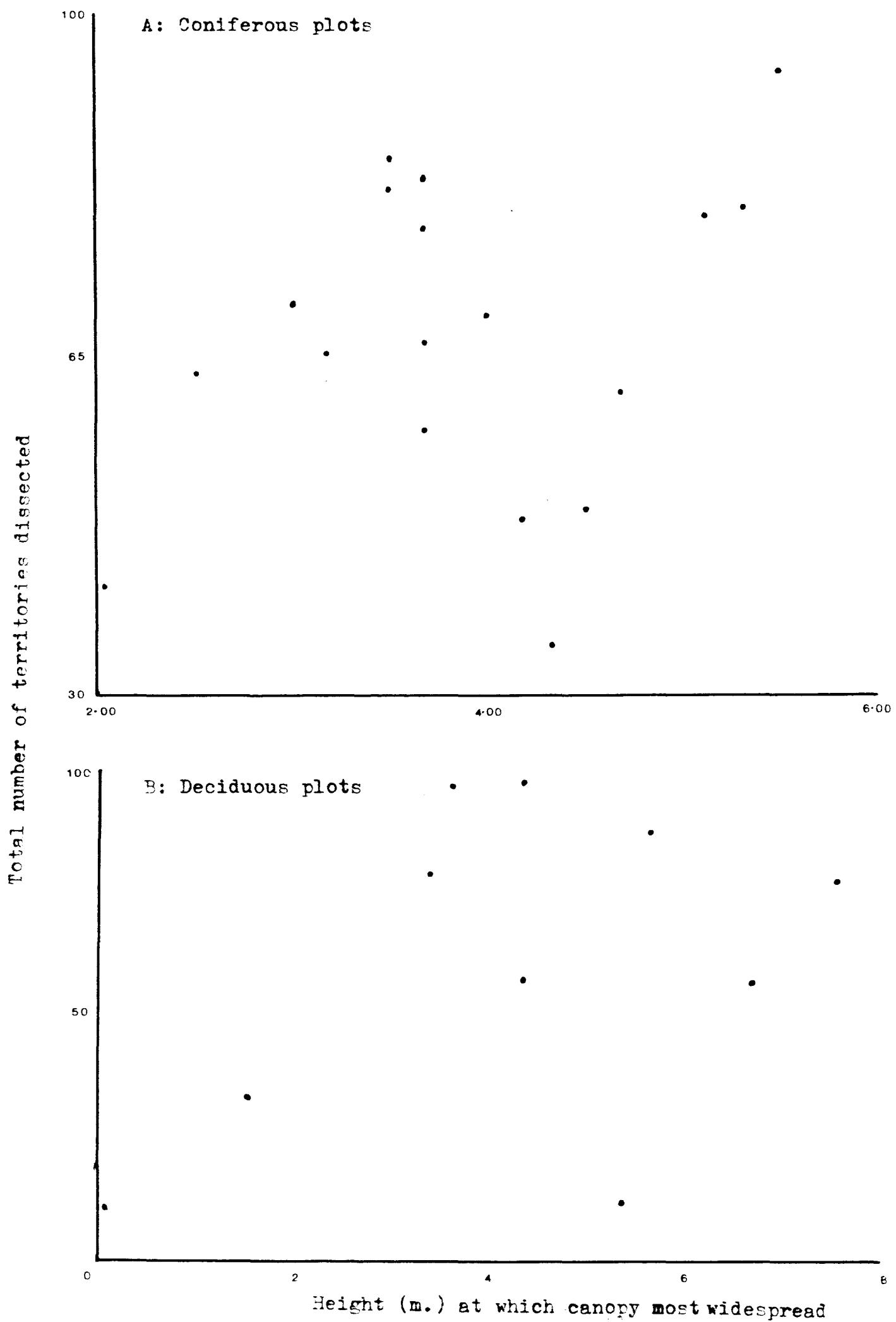
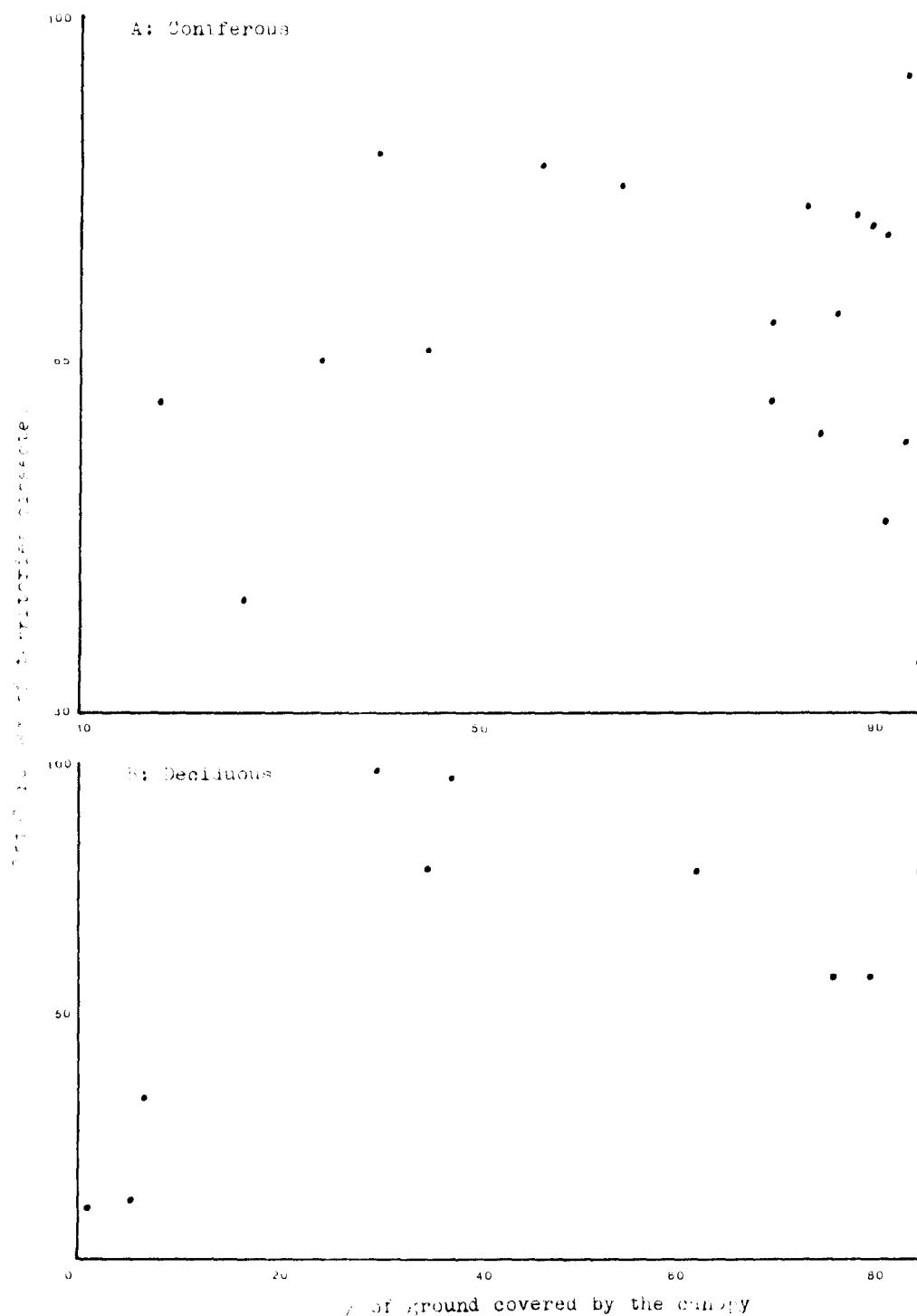


Fig. 1. Plot relating number of territories to canopy ground cover and number of territories



At a grosser level - that of the overall average figures for vegetation parameters independent of vegetation type in each study area - Tables 3.30 - 3.34 and Figure 3.19 reveal for the "density" of the three-year total population* in each study area, that there are poor relationships between tree density and bird population density, and between % of ground covered by the canopy and bird population density. The other three vegetation parameters reveal an inverse relationship to bird population density, that is the overall bird population density becomes lower as the trees become higher or as the widest part of the canopy becomes higher, or as the brash and ground cover becomes taller.

With only four data points, obviously little can be said about these relationships, especially with regard to tree density where there is a difference of over 200 density units between three of the data points and the fourth. At the individual species level, for species common to all four study plots, Robin and Coal Tit population densities showed a positive relationship with tree density while Willow Warbler and Treecreeper exhibited inverse relationships. With tree height, the four species whose populations densities probably bore a relationship to it, all had inverse relationships (Long-tailed Tit, Treecreeper, Chaffinch and Redpoll) and the same four species also had inverse relationships with brash height. Of the four species, Long-tailed Tit, Treecreeper and Chaffinch had inverse relationships with the following: height at which the canopy is most widespread and % of ground covered by the canopy.

Table 3.35 and Figure 3.20 look at the relationships between the three-year diversity indices and vegetation parameters for each study area. Apart from tree density, all the other parameters had a positive relationship with diversity indices.

* "Three-year density" was used so that there was comparability between each of the study areas, since the data were reduced to a common factor of total number of territories per km²

TABLE 3.30 Relationship between population "density" and mean tree density

| Tree Density (Study plot) | 9.69 (4) | 14.71 (3) | 25.27 (1) | 182.52 (2) |
|------------------------------|-------------|--------------|--------------|---------------|
| Skylark | | | | |
| Meadow Pipit | | | | |
| Pied Wagtail | | | | |
| Wren | 190.08 | 62.88 | | 104.49 |
| Dunnock | | | | 38.88 |
| Robin | 129.60 | 131.00 | 228.15 | 281.88 |
| Wheatear | | | | |
| Blackbird | | | 40.56 | 87.48 |
| Song Thrush | | | 35.49 | 43.74 |
| Mistle Thrush | | | | |
| Sedge Warbler | | | | |
| Willow Warbler | 272.16 | 256.76 | 126.75 | 184.68 |
| Goldcrest | | | 96.33 | 170.10 |
| Spotted Flycatcher | | | | |
| Long-tailed Tit | 43.20 | 26.20 | 30.42 | 34.02 |
| Coal Tit | 90.72 | 47.16 | 192.66 | 291.60 |
| Blue Tit | 164.16 | 104.80 | | |
| Great Tit | 103.68 | 52.40 | 30.42 | |
| Tree creeper | 60.48 | 26.20 | 35.49 | 34.02 |
| Jay | | | | |
| Jackdaw | | | | |
| Carrion Crow | | | | |
| Starling | 1028.16 | 36.68 | | |
| Chaffinch | 483.84 | 309.16 | 507.00 | 437.40 |
| Siskin | | | | |
| Linnet | | | | |
| Redpoll | 60.48 | 39.30 | 27.89 | 51.03 |
| Crossbill | | | | |
| Bullfinch | | | | |
| Yellowhammer | | | | |
| Reed Bunting | | | | |
| Total | 2775.60 | 1180.31 | 1495.65 | 1822.50 |
| Diversity Index | 2.128 | 2.312 | 2.238 | 2.281 |

TABLE 3.31 Relationship between population "density" and general tree height

| Tree Height (Study plot) | 5.58 (4) | 6.00 (2) | 6.14 (1) | 6.79 (3) |
|-----------------------------|-------------|-------------|-------------|-------------|
| Skylark | | | | |
| Meadow Pipit | | | | |
| Pied Wagtail | | | | |
| Wren | 190.08 | 104.49 | | 62.88 |
| Dunnock | | 38.88 | | |
| Robin | 129.60 | 281.88 | 228.15 | 131.00 |
| Wheatear | | | | |
| Blackbird | | 87.48 | 40.56 | |
| Song Thrush | | 43.74 | 35.49 | |
| Mistle Thrush | | | | |
| Sedge Warbler | | | | |
| Willow Warbler | 272.16 | 184.68 | 126.75 | 256.76 |
| Goldcrest | | 170.10 | 96.33 | |
| Spotted Flycatcher | | | | |
| Long-tailed Tit | 43.20 | 34.02 | 30.42 | 26.20 |
| Coal Tit | 90.72 | 291.60 | 192.66 | 47.16 |
| Blue Tit | 164.16 | | | 104.80 |
| Great Tit | 103.68 | | 30.42 | 52.40 |
| Treecreeper | 60.48 | 34.02 | 35.49 | 26.20 |
| Jay | | | | |
| Jackdaw | | | | |
| Carrion Crow | | | | |
| Starling | 1028.16 | | | 36.68 |
| Chaffinch | 483.84 | 437.40 | 507.00 | 309.16 |
| Siskin | | | | |
| Linnet | | | | |
| Redpoll | 60.48 | 51.03 | 27.89 | 39.30 |
| Crossbill | | | | |
| Bullfinch | | | | |
| Yellowhammer | | | | |
| Reed Bunting | | | | |
| Total | 2775.60 | 1822.50 | 1495.65 | 1180.31 |
| Diversity Index | 2.128 | 2.281 | 2.238 | 2.312 |

TABLE 3.32 Relationship between population "density" and canopy "width"

| Canopy "Width" (Study plot) | 3.75 (4) | 4.19 (1) | 4.29 (2) | 5.73 (3) |
|--------------------------------|-------------|-------------|-------------|-------------|
| Skylark | | | | |
| Meadow Pipit | | | | |
| Pied Wagtail | | | | |
| Wren | 190.08 | | 104.49 | 62.88 |
| Dunnock | | | 38.88 | |
| Robin | 129.60 | 228.15 | 281.88 | 131.00 |
| Wheatear | | | | |
| Blackbird | | 40.56 | 87.48 | |
| Song Thrush | | 35.49 | 43.74 | |
| Mistle Thrush | | | | |
| Sedge Warbler | | | | |
| Willow Warbler | 272.16 | 126.75 | 184.68 | 256.76 |
| Goldcrest | | 96.33 | 170.10 | |
| Spotted Flycatcher | | | | |
| Long-tailed Tit | 43.20 | 30.42 | 34.02 | 26.20 |
| Coal Tit | 90.72 | 192.66 | 291.60 | 47.16 |
| Blue Tit | 164.16 | | | 104.80 |
| Great Tit | 103.68 | 30.42 | | 52.40 |
| Treecreeper | 60.48 | 35.49 | 34.02 | 26.20 |
| Jay | | | | |
| Jackdaw | | | | |
| Carrion Crow | | | | |
| Starling | 1028.16 | | | 36.68 |
| Chaffinch | 483.84 | 507.00 | 437.40 | 309.16 |
| Siskin | | | | |
| Linnet | | | | |
| Redpoll | 60.48 | 27.89 | 51.03 | 39.30 |
| Crossbill | | | | |
| Bullfinch | | | | |
| Yellowhammer | | | | |
| Reed Bunting | | | | |
| Total | 2775.60 | 1495.65 | 1822.50 | 1180.31 |
| Diversity Index | 2.128 | 2.238 | 2.281 | 2.312 |

TABLE 3.33 Relationship between population "density" and canopy cover

| Canopy cover (Study plot) | 34.17 (4) | 44.38 (1) | 56.82 (3) | 88.64 (2) |
|------------------------------|--------------|--------------|--------------|--------------|
| Skylark | | | | |
| Meadow Pipit | | | | |
| Pied Wagtail | | | | |
| Wren | 190.08 | | 62.88 | 104.49 |
| Dunnock | | | | 38.88 |
| Robin | 129.60 | 228.15 | 131.00 | 281.88 |
| Wheatear | | | | |
| Blackbird | | 40.56 | | 87.48 |
| Song Thrush | | 35.49 | | 43.74 |
| Mistle Thrush | | | | |
| Sedge Warbler | | | | |
| Willow Warbler | 272.16 | 126.75 | 256.76 | 184.68 |
| Goldcrest | | 96.33 | | 170.10 |
| Spotted Flycatcher | | | | |
| Long-tailed Tit | 43.20 | 30.42 | 26.20 | 34.02 |
| Coal Tit | 90.72 | 192.66 | 47.16 | 291.60 |
| Blue Tit | 164.16 | | 104.80 | |
| Great Tit | 103.68 | 30.42 | 52.40 | |
| Treecreeper | 60.48 | 35.49 | 26.20 | 34.02 |
| Jay | | | | |
| Jackdaw | | | | |
| Carrion Crow | | | | |
| Starling | 1028.16 | | 36.68 | |
| Chaffinch | 483.84 | 507.00 | 309.16 | 437.40 |
| Siskin | | | | |
| Linnet | | | | |
| Redpoll | 60.48 | 27.89 | 39.30 | 51.03 |
| Crossbill | | | | |
| Bullfinch | | | | |
| Yellowhammer | | | | |
| Reed Bunting | | | | |
| Total | 2775.60 | 1495.65 | 1180.31 | 1822.50 |
| Diversity Index | 2.128 | 2.238 | 2.312 | 2.281 |

TABLE 3.34 Relationship between population "density" and height of
"brash"

| "Brash" height (Study plot) | 0 (4) | 0.94 (2) | 1.23 (1) | 1.50 (3) |
|--------------------------------|----------|-------------|-------------|-------------|
| Skylark | | | | |
| Meadow Pipit | | | | |
| Pied Wagtail | | | | |
| Wren | 190.08 | 104.49 | | 62.88 |
| Dunnock | | 38.88 | | |
| Robin | 129.60 | 281.88 | 228.15 | 131.00 |
| Wheatear | | | | |
| Blackbird | | 87.48 | 40.56 | |
| Song Thrush | | 43.74 | 35.49 | |
| Mistle Thrush | | | | |
| Sedge Warbler | | | | |
| Willow Warbler | 272.16 | 184.68 | 126.75 | 256.76 |
| Goldcrest | | 170.10 | 96.33 | |
| Spotted Flycatcher | | | | |
| Long-tailed Tit | 43.20 | 34.02 | 30.42 | 26.20 |
| Coal Tit | 90.72 | 291.60 | 192.66 | 47.16 |
| Blue Tit | 164.16 | | | 104.80 |
| Great Tit | 103.68 | | 30.42 | 52.40 |
| Tree creeper | 60.48 | 34.02 | 35.49 | 26.20 |
| Jay | | | | |
| Jackdaw | | | | |
| Carrion Crow | | | | |
| Starling | 1028.16 | | | 36.68 |
| Chaffinch | 483.84 | 437.40 | 507.00 | 309.16 |
| Siskin | | | | |
| Linnet | | | | |
| Redpoll | 60.48 | 51.03 | 27.89 | 39.30 |
| Crossbill | | | | |
| Bullfinch | | | | |
| Yellowhammer | | | | |
| Reed Bunting | | | | |
| Total | 2775.60 | 1822.50 | 1495.65 | 1180.31 |
| Diversity Index | 2.128 | 2.281 | 2.238 | 2.312 |

Fig 3.19: Relationship between vegetation parameters and bird population density

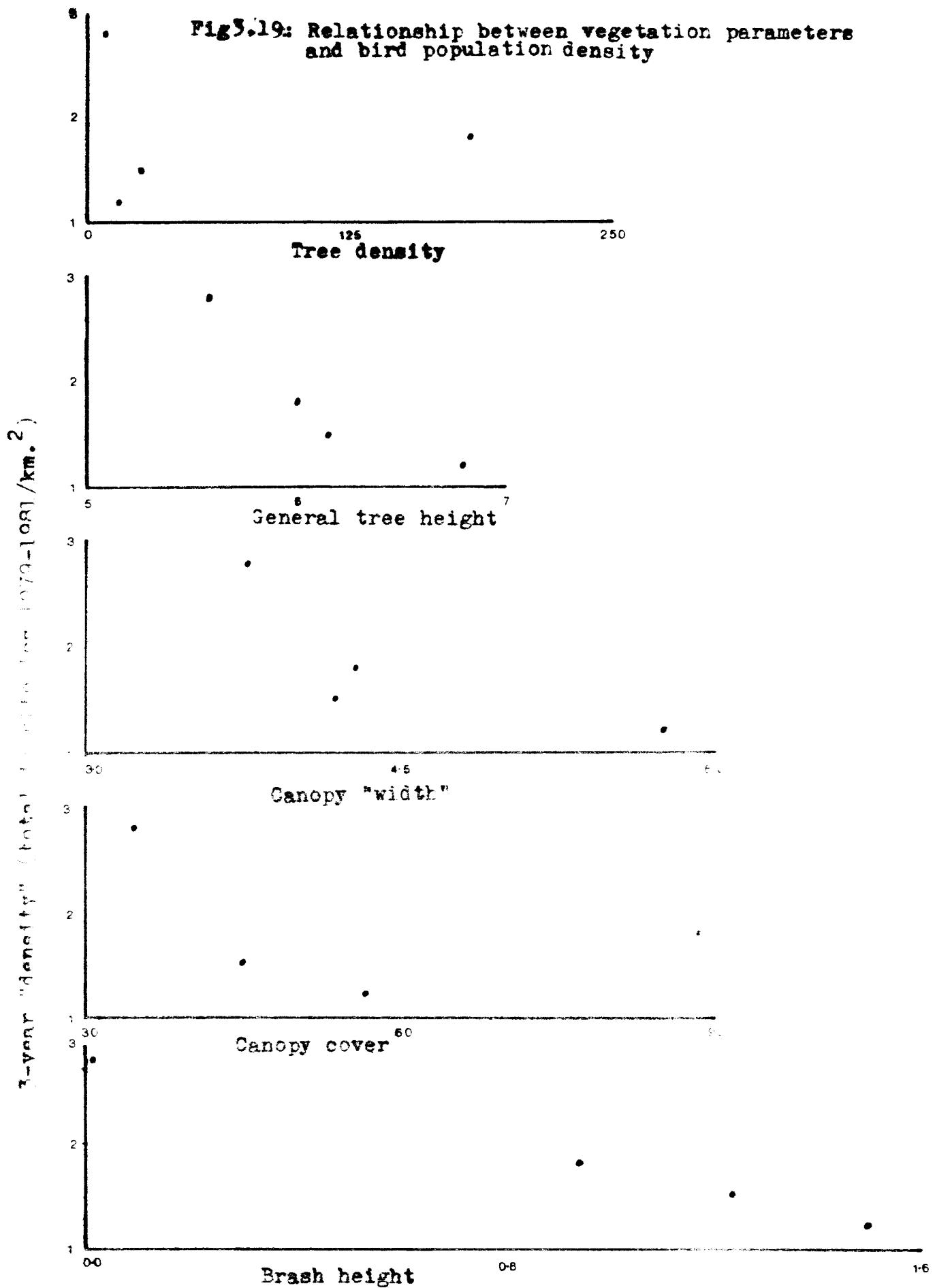
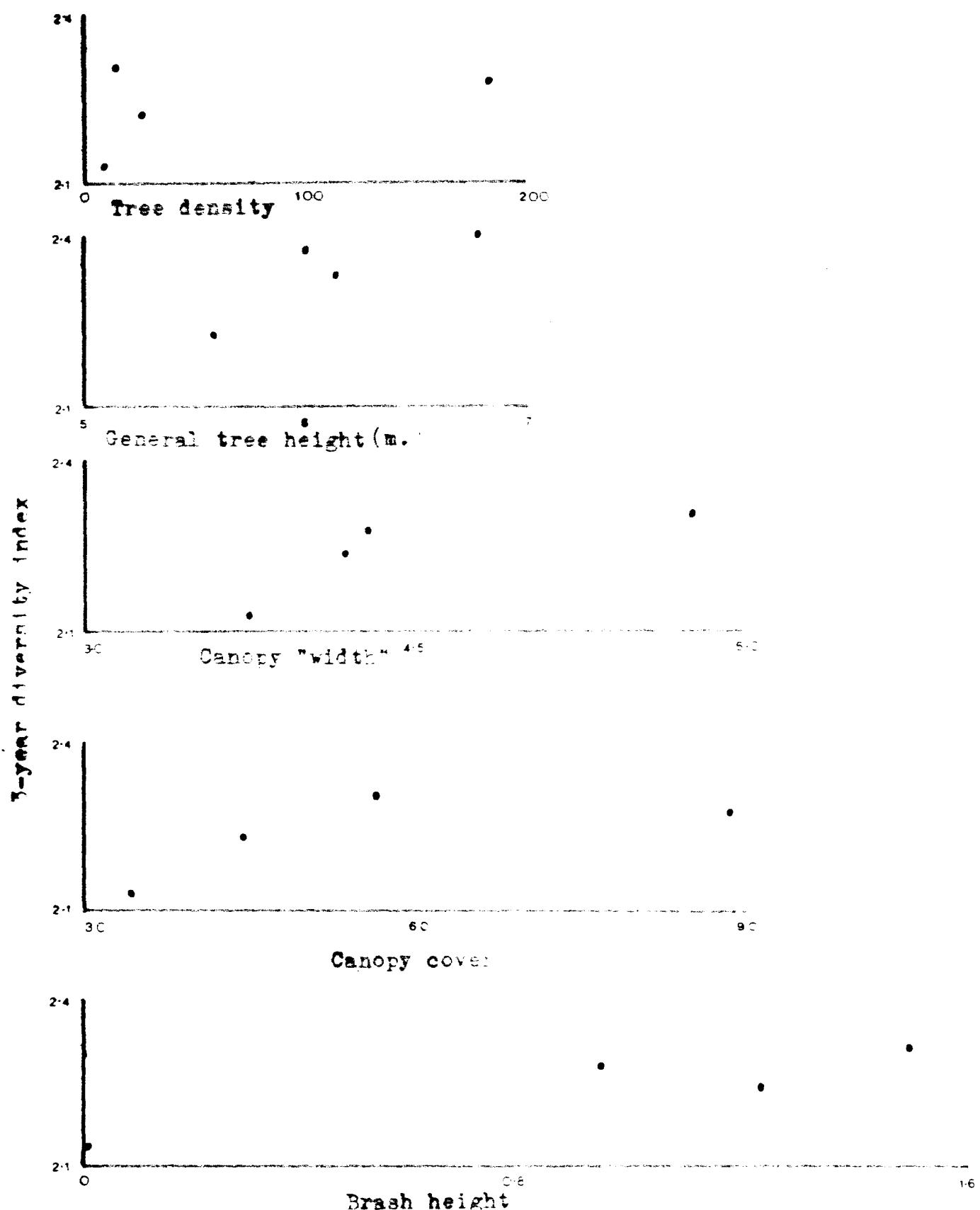


TABLE 3.35 Relationship between population diversity indices and vegetation parameters

| Population Diversity Index | 2.128 (4) | 2.238 (1) | 2.281 (2) | 2.312 (3) |
|----------------------------------|--------------|--------------|--------------|--------------|
| Tree Density | 9.69 | 25.27 | 182.52 | 14.71 |
| General Tree Height (m) | 5.58 | 6.14 | 6.00 | 6.79 |
| Canopy "width" (m) | 3.75 | 4.19 | 4.29 | 5.73 |
| Canopy cover (%) | 34.17 | 44.38 | 88.64 | 56.82 |
| "Brash" height (m) | 0 | 1.23 | 0.94 | 1.50 |

Fig 3.20: Relationship between vegetation parameters and bird population diversity



CONCLUSIONS

Only the results from fieldwork using the mapping census method have proved reliable and consistent enough to be used in the analyses presented in the present chapter.

These analyses have shown for the years 1979-81 that the poorest habitat for breeding passerine populations was the open grassland, and the richest the mature birch/alder woodland. Over the three-year study period there was an overall increase in the populations of all five study plots, greatest on the grassland and least in the mature woodland.

Of the five study plot communities the grassland plot was dominated by two species - Skylark and Meadow Pipit; whereas the four woodland communities shared a "core" of dominant species - Chaffinch, Robin, Willow Warbler and a Tit (Coal in coniferous plots and Blue in deciduous), with the addition of Starling in the mature birch/alder woodland, where there was an abundance of natural nest-holes to support a breeding colony. The relationship between the communities and the successional stages of the vegetation is described, with particular attention paid to study area 1.

In a comparison of the five communities using two indices, there was a major difference between the grassland plot and all woodland plots. Of the four woodland plots, the communities in the two coniferous ones were the most similar. At the species level, analysis of variance revealed Robin, Song Thrush and Coal Tit to be more prevalent in coniferous habitats, whilst Willow Warbler and Blue Tit were more prevalent in the deciduous habitats.

In relation to various vegetation parameters within the habitats, it was found that the breeding communities became more diverse as the vegetation structure became more complex; and the individual species' populations bore some relationship to various vegetation parameters, especially in study plot 1 with its vegetation succession from dunes through thicket to mature coniferous woodland.

CHAPTER 4DISCUSSION4.1 INTRODUCTION

Having discussed the methodology to be employed in this thesis (chapter 1), described the areas studies (chapter 2), and interpreted the results obtained in terms of the events which took place over the three breeding seasons 1979-81 (chapter 3), these events will now be examined in a wider context and their implications for various aspects of ornithology discussed.

Two main problems will be examined:-

- (1) A comparison of the results from the present study with those from other studies of comparable areas;
- (2) An investigation into how this adds to our knowledge of "avifaunal succession", while at the same time adding to the debate on afforestation.

The data used in the following sections come from a study of the relevant literature, largely in European journals, to the end of 1981 but with important additions since then published mainly in British journals ("Bird Study", "British Birds", "Ibis", "Journal of Animal Ecology", "Journal of Ecology" and "Scottish Birds") up to the I.B.C.C./E.O.A.C. conference held at Chalfont St Giles in September 1983.

4.2 CENSUS RESULTS FROM OTHER STUDIES(i) General

Much of the published literature is unfortunately rather irrelevant to the present study due either to differences in methodology or to differences in geographical location. The North-east Fife study plots are difficult to compare with others in that they represent a series of habitats little studied in the British Isles from an ornithological point of view viz. any successional series, duneland, birch woodland, alder woodland, and both

semi-natural and commercial coniferous woodland near sea-level. Much of the literature referred to in the following sections results from work elsewhere in Europe, particularly Fennoscandia, and from work in (re) afforested upland areas in the British Isles. It is to be hoped that this deficit of studies is made good in the next decade or so.

(ii) Studies in the Earlshallmuir/Tentsmuir area

Although the ornithology of North-east Fife has been well-documented this century, there has been little quantitative work done - especially on passerines - until relatively recently, post 1960.

Accounts of the habitats present in North-east Fife can be found in Sinclair (1791-99), Ovington (1951), Crawford and Wishart (1966) and in many unpublished reports deposited with the N.C.C. in Edinburgh. Ratcliffe (1977b) discussed the national importance of the Tentsmuir and Earlshallmuir areas for their physiography, botany, entomology and ornithology, and he concluded that Tentsmuir Point is a Grade 1 and Earlshallmuir a Grade 2 site of national conservation interest.

Accounts of the general ornithology of the region become more quantitative and less descriptive as they become more recent, but the early works are still important from an historical perspective. In the nineteenth and early twentieth centuries, the publications of Thomson (1877-78), Drummond-Hay (1879-82, 1885-86) and Harvie-Brown (1906) provide a backdrop to the later studies reported in Grierson (1962), Boase (1964, 1970), Dundee S.O.C. (1967a, b), Summers (1973) and culminating in Innes (1976), which acts as an immediate forerunner to the present study.

In addition to the above general studies there have been studies of particular groupings of birds or individual species - wildfowl by Berry (1930), Pounder (1974) and L.H. Campbell (1978); grouse (Berry, 1894); terns (Short, 1928); and tits (MacKenzie, 1949, 1950, 1952); but it was not until Innes' work that comparable field methods to those of the present study were employed. Consequently Innes' studies are described in some detail here.

Innes was contracted to survey the birds present on Tentsmuir Point N.N.R. in summer 1976, and as part of this survey he undertook Common Birds Census work. Unfortunately his results are not strictly comparable with those from the present study for the following reasons:-

- (1) His census visits were of a full day's duration and there were only six between 21st May and 19th July which is rather late in the season. He included non-passerine species, but did not account for the difficulties involved with them using C.B.C. methodology.
- (2) Although the whole of study plot 1 investigated in the present study was covered by Innes' census work, it was as a part of a larger area (his section B, incorporating compartments 4 and 6) and the data cannot be re-interpreted to cover only the present study plot 1.
- (3) Innes' data were analysed with reference to habitat type, of which he lists seven classes, and it was presented in terms of the percentage of the reserve's total bird population found in each habitat class. Since study plot 1 contains elements of five of Innes' habitat classes, it is clearly not possible to compare directly his results with those from the present study. However, in a systematic section, for some species Innes does give population estimates (based on singing males or pairs) for some compartments, and in such cases comparisons are drawn with the present author's work from 1979-81 (Table 4.1); the caveats in (1) and (2) above must be borne in mind. Innes' seven habitat classes were as follows, and * indicates a class found in the present study plot 1:- young Scots pines and occasional birches * ; young birches * ; alders * ; grass and lichen heath * ; heather ; coastal marram strip * ; sand and shells.

In comparing the two sets of figures in Table 4.1, it must be remembered that those from 1979-81 are from a smaller area and were also probably depressed following the "hard" winter of 1978-79; while those from 1976 followed on from a series of mild winters (Cawthorne and Marchant, 1980) and were from a larger area. Nevertheless, there is good evidence to show

that in the period between the two studies (a gap of two to four breeding seasons), the study areas became less open and more wooded in character with the decline of the Meadow Pipit population from 6 to 1 pair, and the increases in the populations of Wren, Song Thrush, Goldcrest, all tit species but especially Coal, and Bullfinch. Four species also held territory for the first time 1979-81: Treecreeper, Carrion Crow, Siskin and Crossbill, with only Carrion Crow having been recorded in 1976. No species were lost as territory-holders between the two study periods, but Willow Warbler and Yellowhammer appeared to show genuine declines whereas the apparent declines for Robin and Chaffinch may have been due to differences in the sizes of the study plots or to the effects of the hard winter which should not have affected the Willow Warbler. There were no apparent changes in the populations of Dunnock and Linnet.

TABLE 4.1 A comparison of population estimates, by Innes for 1976 and Dougall for 1979-81, for part of Tentsmuir Point N.N.R.

| | Innes ¹ | Dougall ² |
|-----------------|--------------------|----------------------|
| Skylark | a 28 ; ? | ✓ |
| Meadow Pipit | a 24 ; 6 | 0 - 1.0 |
| Pied Wagtail | b 6 ; 0 | ✓ |
| Wren | ✓ ; 0 | ✓ - 3.0 |
| Dunnock | a 4 ; 2 | 1.0 - 2.0 |
| Robin | b 59 ; 29 | 11.0 - 22.0 |
| Wheatear | ✓ ; 0 | 0 |
| Blackbird | a 12 ; √? | 1.0 - 4.0 |
| Song Thrush | a 2 ; 1 | 2.0 - 3.0 |
| Mistle Thrush | ✓ ; ? | ✓ |
| Willow Warbler | b 69 ; 34 | 6.0 - 11.0 |
| Goldcrest | a 2 ; 1 | 5.0 - 14.0 |
| Long-tailed Tit | a 3 ; 1 | 1.0 - 3.0 |
| Coal Tit | a 8+; 1+? | 7.0 - 17.0 |
| Blue Tit | a 2 ; 1 | 2.0 - 2.5 |
| Great Tit | ✓ ; 0 | 1.0 - 3.0 |
| Tree creeper | 0 ; 0 | 2.0 - 3.0 |
| Jay | a 1 ; ? | 1.0 |
| Carrion Crow | ✓ ; ? | 0.5 - 1.5 |
| Starling | ✓ ; ? | ✓ |
| Chaffinch | b 88 ; 47 | 33.0 - 34.0 |
| Siskin | 0 ; 0 | 2.5 - 3.0 |
| Linnet | a 7 ; 0 | ✓ |
| Redpoll | a 12 ; ? | 2.0 - 3.0 |
| Crossbill | 0 ; 0 | 2.0 |
| Bullfinch | ✓ ; 0 | 1.0 - 2.0 |
| Yellowhammer | a 4 ; 2 | ✓ |
| Reed Bunting | ✓ ; 0 | ✓ |

Notes:

1 : Reserve total; total for compartments 4 + 6. a = pairs; b = singing males.

2 : Range 1979-81 based on territories occupied (broadly equivalent to Innes' pairs and singing males).

✓ : Species present but not holding territory.

? : No population data.

This succession from open ground to pine/birch/alder woodland on the same study areas but between study periods is also evident from Innes' work on different study areas in one study year - 1976. His Table 3.3, based on relative abundance figures, showed that as the coastal marram grass gave way to grass/lichen heath and as this in turn gave way to tree cover, the breeding communities changed in their composition (Table 4.2, below), as was also found in the present study (Results chapter, section 3.5 with associated tables and figures) and as will be discussed later in the current chapter.

TABLE 4.2 Composition of communities in each habitat class based on the five most dominant¹ species in each (after Innes, 1976)

| | Coastal Marram | Grass + lichen Heath | Pine/birch/alder Woodland ² |
|----------------|-------------------|-------------------------|---|
| Shelduck | 11.1 | | |
| Eider | 13.0 | 59.7 | 17.4 - 17.8 (2) |
| Common Tern | 22.2 | | |
| Skylark | 33.3 | 8.3 | |
| Meadow Pipit | 14.8 | 8.3 | |
| Robin | | | 8.7 - 20.8 (3) |
| Blackbird | | | 2.1 - 5.4 (2) |
| Willow Warbler | | | 11.9 - 37.2 (3) |
| Chaffinch | | 7.3 | 23.8 - 32.6 (3) |
| Linnet | | 6.4 | |

Notes:

1 : % of total population in each habitat class, represented by each species.

2 : Range of % values, with number of habitat classes in which the species occurred (n).

(iii) Studies in other geographical areas

Before looking at particular studies from specific sites, it may be useful to get a general view from the country as a whole, as provided by Fuller (1982).

In his section on "Dunes, machair and shingle", Fuller describes briefly the vegetation succession on sand dunes and shows that the highest breeding bird densities are to be found in the fixed stable stages with their low grass/forb/moss/lichen plant communities, their grass heath communities and their scrub communities, with the possibility of added diversity provided by dune slacks throughout the succession. All of these stages can be found on plot 1 of the present study, and each of the other plots in the present study represents a stage in the same succession with the coniferous plots adding a complication, also recognised by Fuller (1982, p37).

In his Table 8, Fuller summarises the population data for breeding bird densities in sand dune habitats, and for those studies which employed the mapping method, he reports densities of 119 prs/km² on stable dune grassland on Anglesey (equivalent to study plot 5: range of 60 - 105 prs/km² of passerine species), and for sea buckthorn scrub of 1014 - 1293 prs/km² (no equivalent among Fife study plots, where birch/willow scrub densities ranged from 333 - 481 prs/km² of passerine species, and where the densities of all the types of non-scrub woodland present ranged from 383 - 953 prs/km² of passerine species).

Fuller's data on other woodland areas is rather difficult to relate to the present context of North-east Fife woodlands, but since all of the latter studied were on a stabilized sand dune complex, then they have in fact been covered by Fuller in his chapter on dunes etc.

In the following section, the results from relevant individual studies in Europe will be discussed in the order of succession found in North-east Fife viz. duneland, and birch/willow scrub, birch/alder woodland; or semi-natural coniferous woodland, commercial coniferous woodland. Later sections

will expand on two of these - commercial forestry and overall succession - and examine how the results from the present study in Fife contribute to our knowledge of these two factors.

4.2 (iii)

(a) Duneland

The work of Innes (1976), described and discussed above, is undoubtedly of most importance and relevance here, but similar work had been done earlier in North-west Wales (Jones, 1966a, b; 1973) and in Lincolnshire (Morgan, 1978).

Jones (1966a) reported on the results of a two-year study on the bird populations of successional stages on the Newborough Warren sand-dune system in North-west Anglesey, and in another paper (1966b) he elaborated on the wintering populations of birds in the same area. Jones (1966a) chose six communities to represent the transition from mobile sand-dunes to the oldest commercial plantation of Corsican Pines, planted in 1948:

- I : mobile and semi-mobile sand dunes;
- II : stable dune grassland;
- III : establishment of newly-planted pines;
- IV : early thicket stage;
- V : late thicket stage;
- VI : early pole stage.

Stages II - VI are all represented in the Fife study areas, with II being similar to plot 5, V - VI similar to plot 2, and III - IV similar to plot 1. One study plot, of about 8.9 ha, was set up in each community studied by Jones and six visits made to each between March and May 1964. All forestry plots had rides traversing them (as in Fife) giving rise to an edge effect, but since such rides are characteristic of the commercial coniferous forest, any influence of the edge effect must also be taken as a characteristic. Jones found the overall pattern of the succession showed

a decrease in breeding bird population density in the early stages of pine "colonization" by planting, with a subsequent rise to previous density levels and a continuing increase thereafter. Due to the heterogeneous nature of the self-seeded Fife study plot (plot 1) it is difficult to make a detailed comparison with Jones' results and finding on succession, but Figures 3.10 - 3.14 suggest that in Fife also, the younger stages of coniferous colonization held lower population densities than did the older stages, and with fewer bird species present.

Table 4.3 expresses Jones' data from 1964 in terms of pairs/km² and compares his figures with those from similar habitats in Fife, his quadrants being combined as follows, to correspond with Fife plots :- Anglesey V - VI = Fife 1, Anglesey III - IV = Fife 2 (Anglesey II = Fife 5).

It is also of interest that Jones' 1964 figures follow on a year after the "hard" winter of 1962/63, and are thus analogous to the present author's figures for 1980 which are a year after the "hard" winter of 1978/79. So far as the effects of the 1962/63 hard winter are concerned, it is not possible to make meaningful quantitative comparisons since Jones used a belt transect method employing longitudinal and lateral dimensions different from those used in Fife. However, Jones' general findings were that several surveys were necessary to assess a plantation's wintering population, since it is not necessarily stable and minimum population figures could occur at different times during the course of different seasons.

Jones (1973) reported on a study carried out at Morfa Dyffryn N.N.R. on Cardigan Bay - an area of wind-blown sand. He used the mapping method to census an area (11.4 ha) of unstable dunes (85% bare sand, the rest mainly marram grass) and an area (12.0 ha) of stable dune slack (less than 10% bare, the rest of low vegetation). Seven visits were made in 1967 and only 3 in 1968. No breeding pairs occurred on the mobile sand in either year, but two passerine species occurred on the dune slack: Skylark (58.31 prs/km² in 1967; 49.98 prs/km² in 1968) and Meadow Pipit (24.99 prs/km² in 1967 and 33.32 prs/km² in 1968), giving equal total community densities

for each year of 83.30 prs/km²; both species occurred at similar densities on stable dune grassland in Fife 1979-81, ranging from 44.70 - 67.05 prs/km² and from 4.47 - 31.29 prs/km² for each species respectively.

Morgan (1978) described expedition-type census work at Gibraltar Point, Lincolnshire in 1965 (Williamson, 1967) and 1974. Of relevance to the Fife study are two parallel lines of sand dunes (11.3 ha and 23.5 ha) colonized by Sea Buckthorn - a species which covered only small areas at the seaward edge of study plot 1. Extremely high breeding densities were found in this habitat at Gibraltar Point - 1477.9 prs/km² for the 11.3 ha of the older west dunes, and 1204.3 prs/km² for the 23.5 ha of the younger east dunes. For the two years 1965 and 1974, the passerine densities were, for the west dunes - 955.8 prs/km² and 1424.9 prs/km²; and for the east dunes - 873.3 prs/km² and 1141.7 prs/km². Table 4.4 compares the density ranges for Gibraltar Point 1965 - 74 with those for the four Fife woodland habitats 1979 - 81 arranged west to east (oldest to youngest) for species common to both areas.

Densities were similar for Wren, Mistle Thrush and Bullfinch, but the Gibraltar Point sea buckthorn held much higher densities than the Fife woodlands for Meadow Pipit, Dunnock, thrush species, scrub warblers (scarcer in Scotland in any case), small finches and buntings. The Fife habitats, however, were richer for leaf warblers, tits, Starling and Chaffinch, partly reflecting the older nature of the trees with their numerous holes and cavities. Clearly, though, coastal sea buckthorn scrub is a very important habitat for several species and is able to support them at high densities.

TABLE 4.3 Population densities for communities of similar habitats in Anglesey (1964) and North-east Fife (1979-81)

| | Dune Grassland | | Commercial Coniferous Forestry | | |
|-----------------|------------------------|--------------------|--------------------------------|--------------------|-------|
| | Anglesey (8.5 ha) | Fife (22.35 ha) | A | B | |
| | Anglesey (35.51 ha) | Fife (19.72 ha) | Anglesey (17.48 ha) | Fife (20.59 ha) | |
| Skylark | 70.56 | 44.70-67.05 | 8.45 | 0 | |
| Meadow Pipit | 0 | 4.47-31.29 | 0 | 5.07 (1) | |
| Wren | | | 11.28 | 15.21 (1) | 22.88 |
| Dunnock | | | 0 | 5.07- 10.14 (2) | 0 |
| Robin | | | 11.28 | 55.77-111.54 | 22.88 |
| Wheatear | 0 | 4.47 (2) | | | |
| Blackbird | | | 0 | 5.07- 20.28 | 0 |
| Song Thrush | | | 0 | 10.14- 15.21 | 0 |
| Chiffchaff | | | 2.82 | 0 | 5.72 |
| Willow Warbler | | | 28.20 | 30.42- 55.77 | 45.76 |
| Goldcrest | | | 16.92 | 25.35- 70.98 (2) | 28.60 |
| Long-tailed Tit | | | 0 | 5.07- 15.21 | 0 |
| Coal Tit | | | 2.82 | 35.49- 86.19 | 5.72 |
| Blue Tit | | | 0 | 10.14- 12.68 (2) | 0 |
| Great Tit | | | 0 | 5.07- 15.21 | 0 |
| Treecreeper | | | 0 | 10.14- 15.21 | 0 |
| Jay | | | 0 | 5.07 (2) | 0 |
| Carrion Crow | 0 | 2.24 (2) | 0 | 2.54- 7.61 | |
| Chaffinch | | | 14.10 | 167.31-172.38 | 28.60 |
| Siskin | | | 0 | 7.61- 12.68 (2) | 0 |
| Redpoll | | | 19.74 | 7.61- 10.14 | 28.60 |

/Continued over

TABLE 4.3 Continued

| | Dune Grassland | | Commercial Coniferous Forestry | | | |
|----------------|----------------------|--------------------|--------------------------------|-----------------|--------------------|----------|
| | Anglesey (8.5 ha) | Fife (22.35 ha) | Anglesey (35.51 ha) | A | Fife (19.72 ha) | B |
| Crossbill | | | 0 | 10.14 (1) | 0 | 2.43 (1) |
| Bullfinch | | | 0 | 5.07- 10.14 (2) | 0 | 4.86 (2) |
| Yellowhammer | | | 8.46 | 0 | 11.44 | |
| Reed Bunting | 11.76 | 4.47 (2) | 19.74 | 0 | 17.16 | |
| No. of species | 2 | 5 | 11 | 20 | 10 | 18 |

Notes:

A: Anglesey plots III, IV, V, VI (total of 35.51 ha)
 Fife plot 1 (19.72 ha), self-seeded.

B: Anglesey plots V, VI (17.48 ha)
 Fife plot 2 (20.5 ha).

(n) = number of years' data.

TABLE 4.4 A comparison of passerine breeding densities for areas of Sea Buckthorn at Gibraltar Point (G) in 1965 and 1974, and areas of conifers and birch-dominated woodlands on Tentsmuir/Earlshallmuir (T), 1979-81

| | G West Dunes (11.3 ha) | G East Dunes (23.5 ha) | T, West Birch/Alder Woodland (11.58 ha) | T, East Birch/Willow Scrub (19.09 ha) |
|----------------|------------------------------|------------------------------|--|--|
| Meadow Pipit | 26.55 (1) | 12.78 (2) | 0 (3) | 2.62 (1) |
| Wren | 88.50 (1) | 59.64 (1) | 34.56-103.68 | 5.24- 41.92 |
| Dunnock | 97.35-256.65 | 153.36 (2) | 8.64 (1) | 0 (3) |
| Blackbird | 44.25- 70.80 | 51.12- 55.38 | 8.64- 17.28 | 5.24 (3) |
| Song Thrush | 26.55 (2) | 21.30- 73.64 | 4.32- 8.64(2) | 2.62- 5.24 (2) |
| Mistle Thrush | 8.85- 17.70 | 4.26 (1) | 4.32 (1) | 2.62 (1) |
| Sedge Warbler | 17.70- 26.55 | 55.38- 72.42 | 8.64 (1) | 0 (3) |
| Willow Warbler | 8.85 (1) | 0 (2) | 86.40- 94.04 | 78.60- 99.56 |
| Blue Tit | 8.85- 35.40 | 0 (2) | 51.84- 60.48 | 26.20- 47.16 |
| Great Tit | 8.85 (1) | 12.78- 25.56 | 25.92- 43.20 | 15.72- 20.96 |
| Starling | 8.85 (1) | 0 (2) | 302.40-406.08 | 10.48- 20.96 |
| Chaffinch | 8.85 (1) | 4.26- 17.04 | 129.60-181.44 | 73.36-120.52 |
| Linnet | 185.85-221.25 | 132.06-230.04 | 0 (3) | 5.24 (2) |
| Redpoll | 132.75 (1) | 157.62 (1) | 17.28- 25.92 | 10.48- 15.72 |
| Bullfinch | 8.85 (1) | 4.26 (1) | 4.32 (1) | 7.86 (1) |
| Yellowhammer | 53.10- 79.65 | 8.52- 12.78 | 8.64 (2) | 5.24 (1) |
| Reed Bunting | 70.80-106.20 | 63.90-123.54 | 0 (3) | 4.47 (2) |

Note:

(n) : Number of years' data.

TABLE 4.4 Continued

| | G West Dunes | G East Dunes | T, West Commercial Coniferous (19.72 ha) | T, East Semi-natural Coniferous (20.59 ha) |
|----------------|-----------------|-----------------|---|---|
| Meadow Pipit | 26.55 (1) | 12.78 (2) | 0 (3) | 5.07 (1) |
| Wren | 88.50 (1) | 59.64 (1) | 14.58- 55.89 | 15.21 (1) |
| Dunnock | 97.35-256.65 | 153.36 (2) | 9.72- 14.58 | 5.07- 10.14 (2) |
| Blackbird | 44.25- 70.80 | 51.12- 55.38 | 14.58- 48.60 | 5.07- 20.28 |
| Song Thrush | 26.55 (2) | 21.30- 73.64 | 4.86- 24.30 | 10.14- 15.21 |
| Mistle Thrush | 8.85- 17.70 | 4.26 (1) | 0 (3) | 0 (3) |
| Sedge Warbler | 17.70- 26.55 | 55.38- 72.42 | 0 (3) | 0 (3) |
| Willow Warbler | 8.85 (1) | 0 (2) | 53.46- 72.90 | 30.42- 55.77 |
| Blue Tit | 8.85- 35.40 | 0 (2) | 4.86- 9.72 | 10.14- 12.68(2) |
| Great Tit | 8.85 (1) | 12.78- 25.56 | 4.86- 9.72 (2) | 5.07- 15.21 |
| Starling | 8.85 (1) | 0 (2) | 0 (3) | 0 (3) |
| Chaffinch | 8.85 (1) | 4.26- 17.04 | 131.22-155.52 | 167.31-172.38 |
| Linnet | 185.85-221.25 | 132.06-230.04 | 0 (3) | 0 (3) |
| Redpoll | 132.75 (3) | 157.62 (1) | 9.72- 29.16 | 7.61- 10.14 |
| Bullfinch | 8.85 (1) | 4.26 (1) | 4.86 (2) | 5.07- 10.14(2) |
| Yellowhammer | 53.10- 79.65 | 8.52- 12.78 | 0 (3) | 0 (3) |
| Reed Bunting | 70.80-106.20 | 63.90-123.54 | 0 (3) | 0 (3) |

Note:

(n) : number of years' data.

4.2 (iii)

(b) Birch/Willow Scrub

Little published work exists on bird populations in lowland birch scrub or willow scrub, most fieldwork having been done in upland areas, and then largely in Fennoscandia. As a result, few reliable comparisons can be made between other areas and Fife, especially where different years are involved.

Enemar (1962) reported on mapping work on five study plots in subalpine birch forest in Arctic Sweden, and found densities ranging from 161 - 750 territories/km², and passerine species richness ranging from 5 - 12. The species composition was very different from that on the Fife study plots, and density figures for individual species other than the two most common ones - Willow Warbler and Brambling - are not given. The former species' densities ranged from 54 - 219 territories/km², which compare with the Fife birch/willow scrub as follows:- overall densities 1979-81 ranged from 333 - 481 territories/km² involving 15 - 19 species (22 total), and densities for Willow Warbler ranged from 79 - 100 territories/km².

Eriksson et al (1971) reported on a three-year study also in Swedish Lapland, in a heath-birch forest. They found densities ranging from 276 - 285 territories /km² involving 8 - 11 species (13 total). Four species were common to their study and the present one, and the comparable density figures are as follows (Eriksson et al; Dougall): Meadow Pipit 10 territories/km² (3 years); 3 territories/km² (1 year), Willow Warbler 105 - 143 territories/km² (3 years); 79 - 100 territories/km² (3 years), Redpoll 19 territories/km² (1 year); 10 - 16 territories/km² (3 years), Reed Bunting 10 territories/km² (2 years); 4 territories/km² (2 years). The five most dominant species in the Swedish community were Willow Warbler, Bluethroat, Brambling, Redwing and Redstart; and in the Fife birch/willow one Chaffinch, Willow Warbler, Robin, Blue Tit and Wren. Only these latter two can be regarded as different since Bluethroat replaces Robin and Brambling replaces Chaffinch in more northern latitudes.

Finally in Scandinavia, Røv (1975) produced a much more detailed survey near the south-west coast of Norway between 140 - 500 m.a.s.l. in 1970 and 1971. The communities he encountered resembled the Fife ones more than did those from Sweden, and of the 24 species he found in birch forest, 14 were also found in the Fife birch/willow scrub and another one - Willow Tit - was replaced by Coal Tit in Fife. Røv encountered 10 species not recorded on the Fife plot, which in turn held 10 species not encountered by him in Norway. On Røv's three birch plots, the species richness ranged from 15 - 19 and densities from 437 - 1309 territories/km², thus generally higher than those in Fife. As with the Swedish studies reported above, the Norwegian communities were dominated by Willow Warbler and Brambling.

In a British, and indeed Scottish context, the only major published work on birch habitats is by Yapp (1974), but since he used transects, little direct comparison can be made with the present work; in fact, as was shown in the methodology chapter of this thesis Yapp's methods and results must be regarded as unreliable. The only data of his which may be of interest here is the community structure as revealed by relative abundance percentages. The five most dominant species in both 1951-52 and in 1970-71 were Willow Warbler, Chaffinch, Tree Pipit (3rd in 1951-52, 4th in 1970-71), Wren (5th in 1951-52, 3rd in 1970-71) and Robin (4th in 1951-52, 5th in 1970-71).

However, Williamson (1969) and Keymer (1980) both studied areas containing birch scrub, and both used the mapping method rather than transects. Their results are therefore discussed below.

Williamson led a two-week census expedition to north-west Scotland in 1968 and among areas visited was a 10.50 ha birch wood with an admixture of Alder, Ash and Rowan and a field layer of heather/heaths (*Calluna-Vaccinium*) or moss spp., but in general there was little secondary growth. In terms of area, the 10.50 ha is comparable to the 11.58 ha of birch/Alder woodland (Fife plot 4), but only around half of the 19.09 ha of birch/willow scrub (Fife plot 3). Twenty species occurred in the

Wester Ross plot studied by Williamson, with a total density of 1100 prs/ km^2 which is well above the values for the two Fife birch plots. The Wester Ross birchwoods were dominated by Willow Warbler (39.00% of total number of territories), Chaffinch (15.50%) and Wren (13.75%) and all other species had low relative abundance figures of 4% or less. In Fife the same species figured high in their contributions to the composition of the communities, but Robin, Blue Tit and Starling were also included among the dominant species; it is possible that the % value for Wren in the Fife study plots was still depressed after the "hard winter" of 1978/79, whereas there was no such influence on Wester Ross Wrens from the 1967/68 winter. In Fife the spread of R.A. values was much wider than in Wester Ross with 6 out of 22 and 6 out of 21 species (in plots 3 and 4 respectively) having R.A. values of over 4%. There were also differences in the population densities of species common to both regions (Table 4.5). From Table 4.5 it can be seen that most of the species common to both regions were more numerous in Wester Ross than in Fife - especially so for Wren, Willow Warbler, Spotted Flycatcher and Redpoll - and the only one more numerous in Fife was Blue Tit. However, it is difficult to take account of the effects of the 11 - 13 years gap between the two studies and to allow for the effects of the 1978/79 winter.

Keymer's study on 9.8 ha in Midlothian fortunately covered two years common to the Fife study - 1979 and 1980 - but his was at an altitude of 260 m.a.s.l. and the birch/willow scrub was only a component of a larger area of heather moorland and heather moorland admixed with open birch scrub. Consequently, open-country species such as Meadow Pipit and Reed Bunting were much more abundant than in Fife, as were several of the scrubland species, possibly due to the fact that there were fewer of them in competition (12 passerines as compared with 15 - 16 in the Fife birch/willow scrub over the same two years) (Table 4.5). Taking the mean Meadow Pipit population on Keymer's plot as 12.5 territories, then the total passerine population densities were 504.9 territories/ km^2 in 1979 (Fife plot 3 = 366.80) and 668.1 in 1980 (Fife plot 3 = 332.74); this represents an increase in Midlothian of 32.32%

TABLE 4.5 A comparison of passerine population densities (pairs/km²)
in Wester Ross, 1968 (Williamson, 1969); Midlothian, 1979-80
(Keymer, 1980); and in Fife, 1979-81 (ranges, with no. of
years, in this study)

| | Wester Ross | Midlothian | Fife | |
|--------------------|----------------|--|-----------------------------------|---------------------------------------|
| | Birch Wood | Birch/willow scrub with heather moorland (10.5 ha) | Birch/willow scrub (9.8 ha) | Birch/alder woodland (11.58 ha) |
| Meadow Pipit | 0 | 102.00-153.00 | 2.62(1) | 0 |
| Wren | 162 | 10.20(1) | 5.24- 41.92 | 34.56-103.68 |
| Dunnock | 10 | 0 | 0 | 8.64 |
| Robin | 35 | 51.00- 61.20 | 26.20- 57.64 | 17.28- 69.12 |
| Blackbird | 0 | 10.20- 30.60 | 5.24(3) | 8.64- 17.28 |
| Song Thrush | 10 | 20.40(1) | 2.62- 5.24(2) | 4.32- 8.64 |
| Mistle Thrush | 10 | 0 | 2.62(1) | 4.32(1) |
| Sedge Warbler | 0 | 10.20 | 0 | 8.64(3) |
| Willow Warbler | 425 | 244.80-255.00 | 78.60- 99.56 | 86.40- 95.04 |
| Spotted Flycatcher | 30 | 0 | 0 | 8.64(2) |
| Long-tailed Tit | 30 | 0 | 10.48- 15.72(2) | 17.28- 25.92(2) |
| Coal Tit | 20 | 0 | 15.72(3) | 12.96- 43.20 |
| Blue Tit | 20 | 10.20(1) | 26.20- 47.16 | 51.84- 60.48 |
| Great Tit | 30 | 0 | 15.72- 20.96 | 25.92- 43.20 |
| Treecreeper | 20 | 0 | 5.24- 16.48 | 8.64- 34.56 |
| Chaffinch | 170 | 30.60- 40.80 | 73.36-120.52 | 129.60-181.44 |
| Redpoll | 42 | ✓ -c.51.00 | 10.48- 15.72 | 17.28- 25.92 |
| Bullfinch | 10 | 0 | 7.86(1) | 4.32(1) |
| Reed Bunting | 0 | 30.60- 40.80 | 4.47(2) | 0 |

between the years, but a decrease of 9.29% in Fife plot 3 in the same period - clearly there were differences in the community dynamics as well as composition. A comparison of the population changes 1979-80 for species common to both study plots is given in Table 4.6. Only two species have comparable sample sizes - Robin and Willow Warbler - and there are few similarities in the changes observed in the two study areas, either in the size or direction of change.

TABLE 4.6 % annual change in population (1979-80) for passerine species common to birch/willow study plots in Midlothian (Keymer, 1980) and in Fife (this study, plot 3)

| | % annual change | | <u>Note:</u> |
|----------------|-----------------|-----------|--|
| | Midlothian | Fife | |
| Meadow Pipit | 0* | X | X : no territories held in either year. |
| Wren | * | +200.00 | |
| Robin | + 20.00 # | + 80.00 # | * : 0 in 1979, but territories held in 1980. |
| Blackbird | +200.00 | 0 | |
| Song Thrush | * | * | |
| Willow Warbler | + 4.17 # | - 3.23 # | # : at least five territories held in at least one of the two years. |
| Blue Tit | * | + 20.00 # | |
| Chaffinch | + 33.33 | - 31.82 # | |
| Redpoll | * # | - 33.33 | |
| Reed Bunting | + 33.33 | * | |

Wilson (1978) provided data for a willow scrub study plot near sea-level in Lancashire during 1969-75 (omitting 1973). He studied a 12 ha block of mature willow scrub 6-8 m high in a reedbed area, where there were also several birches, one oak and a small dense thicket of Alders. However, the study plot did not contain sufficient other species to be labelled e.g. birch/willow scrub. Over the six years studied 17 species held territory, and based on the mean total population for each year,

the "mean" breeding density was 525.67 passerine pairs/km² (the Fife birch/willow scrub held a total of 22 species - range 15 to 19 - over three years with a range of total breeding population density of 332.7 - 480.8 passerine pairs/km²). Wilson compared his results from his willow scrub block with those from a long strip of coppiced willows (7.2 ha in area) censused in 1974 and 1975. Due to coppicing the willows were of irregular height (1-8 m) and few other trees grew to natural height; in addition Bramble patches formed over six piles of brashed timber from the willows. The coppiced willow area was much richer than the willow scrub, supporting 23 passerine species at a mean total breeding population density of 1454.86 passerine pairs/km² - the highest recorded in studies of British scrub habitats.

Wilson attributed the richness of the breeding bird community to the coppicing rotation having retained a rich herb layer, not shaded out by closed-canopy willow scrub, which attracted an abundance of insects and provided an abundance of nest-sites as did the thick cover of young willows. He realised also that the "edge effect" was probably at work.

Table 4.7 compares the population densities of the ten commonest species in both of Wilson's study plots with the population densities of the same species in the Fife birch/willow scrub.

TABLE 4.7 Breeding population densities of the same passerine species in three willow habitats

| | Lancashire | | Fife |
|----------------|----------------------------|------------------------------|-------------------------------|
| | Mature Willow ¹ | Coppiced Willow ² | Birch and Willow ³ |
| Wren | 91.7 | 166.7 | 5.24- 41.94 |
| Dunnock | 8.3 | 76.4 | 0 |
| Robin | 10.8 | 55.6 | 26.20- 57.64 |
| Blackbird | 23.3 | 83.3 | 5.24 |
| Sedge Warbler | 60.8 | 166.7 | 0 |
| Willow Warbler | 119.2 | 187.5 | 78.60- 99.56 |
| Blue Tit | 45.0 | 69.4 | 26.20- 47.16 |
| Great Tit | 15.0 | 41.7 | 15.72- 20.96 |
| Chaffinch | 11.7 | 90.3 | 73.36-120.52 |
| Reed Bunting | 52.5 | 201.4 | 4.47 |

Notes

1 : From Wilson (1978), mean densities (prs/km²) 1969-75 omitting 1973.

2 : From Wilson (1978), mean densities (prs/km²) 1974 and 1975.

3 : From the present study, range of densities (prs/km²) 1979-81.

4.2 (iii)

(c) Birch/Alder Woodland

There are no published studies dealing specifically with birch/Alder woodlands - in fact the present one from Fife may be the only such study - but two dealing with Alder alone are available: Williamson (1969a) and Massey (1974).

Williamson and his party visited three small Alder-dominated areas in

Wester Ross in 1968 - 5 ha along the north side and 6½ ha along the south side of the Kinlochewe River, and 4 ha on open fields; all three were subjected to grazing by cattle and only the second had decent understorey in the form of dense patches of gorse. The plots appear to have had little in common with the Fife birch/alder woodland due to the scattered and open nature of the Wester Ross tree belts, the sub-dominance of Gorse, and the influence of the immediate environment of open fields. Half of the community dominance in the Alder/Gorse area was made up of three species out of 14: Willow Warbler (relative abundance of 23.50%), Chaffinch (14.75%) and Redpoll (10.50%), and the total population density was 543 prs/km². The two other alder areas both held 9 species at total densities of 358 prs/km² and 568 prs/km²; and these latter two areas were the only ones out of all those studied in Wester Ross to hold breeding Starlings, at a density of 11 prs/km². The birch/alder woodland in Fife (plot 4) held 21 species (range 16-17) over the three year study period with a range of total density of 894.24 - 952.56 prs/km² (552.72 - 650.16 prs/km² omitting Starling colony) and was alone important for the Starling amongst the four woodlands studied in Fife. Indeed the Starling was the dominant species in that plot (37.04% over the three years) followed by Chaffinch (17.43%) and Willow Warbler (9.81%). Redpoll was of no great importance (2.18%) unlike in the Wester Ross situation.

Massey (1974), working in south-central Wales, studied a 12.0 ha mature Alderwood in a Breconshire valley bottom at 165 m.a.s.l. The wood had a well-developed understorey of small trees (no birch mentioned), shrubs, and rich field-layer of tall herbs. The canopy cover was "mostly even and fairly well closed" with two small open areas, and the general canopy level was at 15 m. Unfortunately difficulties arise in interpreting Massey's results relative to those from the Fife birch/alder woodland since firstly he separated his species into those dependent on the wood for both nesting and feeding; and those using the wood only for nesting, while feeding outside it. Secondly the study was carried out in two separate periods - 1966-67 and 1969-72 - and the results averaged.

Table 4.8 shows Massey's data for passerines only converted from pairs/100a

TABLE 4.8 Densities (pairs or territories/km²) and community dominance of species in Alder habitats in south-central Wales and Fife

| | Normal nest situation (see Table 4.9B) | 12.0 ha Welsh woodland (mean density) | 11.58 ha Fife birch/alder woodland (density range from (n) years) | Dominance(%) Welsh plot Fife plot |
|--------------------|---|---|--|---|
| Wren | C | 125.00 | 34.56-103.68(3) | 14.41 6.85 |
| Dunnock | C | 0 | 8.64(1) | 0 0.31 |
| Robin | G | 160.00 | 17.28- 69.12(3) | 18.44 4.67 |
| Redstart | H | 42.50 | 0(3) | 4.90 0 |
| Blackbird | C | 50.00 | 8.64- 17.28(3) | 5.76 1.25 |
| Song Thrush | C | 7.50 | 4.32- 8.64(2) | 0.86 0.47 |
| Mistle Thrush | C | 7.50 | 4.32(1) | 0.86 0.16 |
| Sedge Warbler | C | 0 | 8.64(3) | 0 0.93 |
| Garden Warbler | C | 7.50 | 0(3) | 0.86 0 |
| Blackcap | C | 25.00 | 0(3) | 2.88 0 |
| Chiffchaff | G | 7.50 | 0(3) | 0.86 0 |
| Willow Warbler | G | 50.00 | 86.40- 95.04(3) | 5.76 9.81 |
| Goldcrest | C | 17.50 | 0(3) | 2.02 0 |
| Spotted Flycatcher | H | 25.00 | 8.64(2) | 2.88 0.62 |
| Pied Flycatcher | H | 42.50 | 0(3) | 4.90 0 |
| Long-tailed Tit | C | 0 | 17.28- 25.92(2) | 0 1.56 |
| Marsh Tit | H | 7.50 | 0(3) | 0.86 0 |
| Willow Tit | H | 7.50 | 0(3) | 0.86 0 |
| Coal Tit | H | 7.50 | 12.96- 43.20(3) | 0.86 3.27 |
| Blue Tit | H | 67.50 | 51.84- 60.48(3) | 7.78 5.91 |
| Great Tit | H | 35.00 | 25.92- 43.20(3) | 4.03 3.74 |
| Nuthatch | H | 17.50 | 0(3) | 2.02 0 |
| Treecreeper | H | 17.50 | 8.64- 34.56(3) | 2.02 2.18 |
| Jay | C | 7.50 | 0(3) | 0.86 0 |
| Magpie | C | 7.50 | 0(3) | 0.86 0 |
| Carrion Crow | C | 25.00 | 4.32- 8.64(3) | 2.88 0.78 |
| Starling | H | 25.00 | 302.40-406.80(3) | 2.88 37.04 |
| Chaffinch | C | 75.00 | 129.60-181.44(3) | 8.65 17.43 |
| Siskin | C | 0 | 2.16(1) | 0 0.08 |
| Redpoll | C | 0 | 17.28- 25.92(3) | 0 2.18 |
| Bullfinch | C | 0 | 4.32(1) | 0 0.16 |
| Yellowhammer | C | 0 | 8.64(2) | 0 0.62 |
| Total | | 867.50 | 894.24-952.56 | 99.96 100.02 |
| No. of species | | 25 | 16-17(total 21) | 25 21 |

into pairs/km², and compared with the data from the Fife study area 4; and a re-interpretation of his dominance data incorporating "non-dependent" species.

Since the areas of the Welsh and Fife study plots are similar in size and since the total breeding densities are of the same order of size, although composed of different species, it is instructive to compare the communities in more detail since differences may well be due to differences in habitat structure and/or altitude, which affect the availability of nest sites and food (Table 4.9).

TABLE 4.9 A comparison of the structures of the breeding passerine communities in Welsh alder woodland and Fife birch/alder woodland

| (A) Species Group | Total no. of species from study plots in both areas | Dominance (%) | | | |
|-------------------------|--|----------------------------|----|-------------------------------------|----|
| | | Welsh alder woodland | | Fife birch/ alder woodland | |
| | | % | n | % | n |
| Wren | 1 | 14.41 | 1 | 6.85 | 1 |
| Dunnock | 1 | 0 | 0 | 0.31 | 1 |
| Chats | 2 | 23.34 | 2 | 4.67 | 1 |
| Thrushes | 3 | 7.48 | 3 | 1.88 | 3 |
| "Damp" Warblers | 1 | 0 | 0 | 0.93 | 1 |
| Scrub Warblers | 2 | 3.74 | 2 | 0 | 0 |
| Leaf Warblers | 3 | 8.64 | 3 | 9.81 | 1 |
| Flycatchers | 2 | 7.78 | 2 | 0.62 | 1 |
| Tits | 6 | 14.39 | 5 | 14.48 | 4 |
| Treecreeper/Nuthatch | 2 | 4.04 | 2 | 2.18 | 1 |
| Crows | 3 | 4.60 | 3 | 0.78 | 1 |
| Starling | 1 | 2.88 | 1 | 37.04 | 1 |
| Finches | 4 | 8.65 | 1 | 19.85 | 4 |
| Buntings | 1 | 0 | 0 | 0.62 | 1 |
| | | 99.95 | 25 | 100.02 | 21 |

n = no. of species in one area out of total from both areas.

TABLE 4.9 Continued

| (B) Normal nest situation (see Table 4.8) (Harrison, 1975) | Total no.of species from study plots in both areas | | Welsh alder woodland | | Fife birch/ alder woodland |
|--|---|-------|----------------------------|--------|-------------------------------------|
| | | % | n | % | n |
| Ground (G) | 3 | 25.06 | 3 | 14.48 | 2 |
| Hole/ledge in trunk (H) | 11 | 33.99 | 11 | 52.76 | 6 |
| Canopy (C) | 18 | 40.90 | 11 | 32.78 | 13 |
| | | — | — | — | — |
| | | 99.95 | 25 | 100.02 | 21 |

Table 4.9A reveals that the two areas had similar proportions of leaf warblers and tits, even though there were differences in the numbers of species in each group. Compared to Fife, the Welsh study plot held no Dunnocks or damp habitat warblers or buntings, all of which were probably due to habitat differences since all three breed in south-central Wales (Sharrock, 1976). The Fife plot held no scrub warblers but this may have been due more to latitude than to habitat differences, since the two species are irregular breeders in north Fife and are less numerous the further north in the British Isles (Sharrock, 1976). Only in the Starling and finches did the Fife plot have higher dominance levels than the Welsh one, suggesting for the former species at least, that there was an abundance of nest-holes of the right type. This suggestion is borne out in Table 4.9B where 6 hole-nesting species comprised 53% of the Fife breeding community compared with 11 species comprising 34% of the Welsh one. This difference may have been due also to the numbers of dead and decaying mature Scots pines and birches in the Fife plot (none in the Welsh one) with their supply of holes and cracks.

Massey (1974) in a discussion of his results from the four woodland types studied by him - oak, Ash, Alder, mixed deciduous - concluded that in general the breeding bird communities and densities were affected more by woodland structure than by dominant tree species, although the latter

factor may be important for a very few species. This structure idea was later developed more fully by Moss (1976 et seq) and in the present study as will be shown in the following sections on coniferous forests and habitat succession in general.

4.2 (iii)

(d) Natural and Semi-natural Coniferous Woodland

Although conifers, both in natural situations and in planted ones, grow at around sea-level, there have been few studies at that altitude; instead attention has been focussed at upland coniferous forests, especially commercial ones, with a view to investigating their effects on the normal upland avifauna. Commercial forestry is dealt with in the next section, but here it is prudent to bear in mind the earlier caveat regarding the comparison of the results from the present study conducted near sea-level with the results from other studies at higher altitudes and also latitudes, since most studies of natural/semi-natural coniferous habitats have been carried out in Fennoscandia.

Hogstad (1967c) studied a "fairly open" Norway Spruce dominated forest and a mixed forest edge near Oslo, using strip surveys throughout the year supplemented by a mapping study of a 14 ha area of the forest in the breeding seasons of 1966 and 1967. The results from his mapping study are presented in Table 4.10 for those species common to his study area and the semi-natural coniferous plot (1) in Fife. From his strip surveys he found that although the number of species was slightly higher in the coniferous forest, density was higher along the edge of the mixed forest.

Williamson (1969a) in his expedition's study of woodland bird communities in Wester Ross, studied two coniferous plots by the mapping method - a 10.0 ha area of Old Caledonian forest and a 7.5 ha area of Scots Pine scrub inside a grazing enclosure. He found the coniferous plots to be rather impoverished, probably on account of their fragmentary nature, which contrasted with the larger and richer tracts of coniferous forest

in Speyside. Indeed the conifer plots in Wester Ross were the poorest of all the woodlands studied and were dominated by Wren, Willow Warbler, Goldcrest, Coal Tit and Chaffinch. The Old Caledonian plot had both open- and closed-canopy areas in it, and there was a high dense growth of heather on the floor. The pine scrub had mature conifers and deciduous trees along a bordering road, and these may have influenced the population estimates.

Newton and Moss (1977) in a useful review in which they took up some of the findings and ideas of Von Haartman (1971) produced results of their own work in Speyside coniferous forests. Among some of the most important factors influencing the bird populations of woodlands are found to be tree species and soil fertility, and although much attention has been paid to the former, little has been to the latter other than by Von Haartman (1971), Newton and Moss (1977) and the present study.

In Finland Von Haartman found that in any one forest type, when other factors were held constant, birds were 3-6 times more numerous in woods on the most productive rather than on the least productive soils. In those bird species examined individually, this variation was shown to result from birds taking smaller territories in the good rather than in the poor areas. This trend is understandable in terms of organic production, for all types of productivity were better on better soils, including not only wood and foliage but other crops such as flowers and fruits and earthworms (Newton and Moss, 1977). Taking such factors into account in their review, these authors concluded that in general the variety and density of birds is greater in woods (a) of birch and other broad-leaved trees than of pine, (b) on rich than on poor soils, (c) which are small rather than large, (d) which have much rather than little undergrowth and (e) which have many rather than few nest-holes. At least 70 bird species breed regularly in Scottish pinewoods but 24 depend on openings, and 13 on water, and some are unique (in a British context) to these pine-woods. The commonest birds in Scottish pine-woods are Chaffinch and Wren, followed by Goldcrest, Coal Tit and Robin in planted woods, with the addition of Willow Warbler in native woods. The

populations of three finches fluctuate according to the sizes and qualities of the pine and birch seed crops - Siskin, Redpoll and Crossbill. Census work has shown that Scottish pinewoods hold fewer birds of fewer species than do birch and other hardwoods growing nearby and that, among pinewoods, natural stands of varied structure contain more birds than do planted stands of uniform structure.

Moss (1976, 1978b) gives more specific details of the populations in the semi-natural pine plot he studied in Speyside (Table 4.10) which he identified as plot S1. This plot was at an altitude of 250 - 290 m.a.s.l., with a north-easterly aspect and occupied land of capability class 8. The ground-layer was composed of heather and Vaccinium species, with a shrub layer of Juniper - all very different from the sea-level duneland occupied by the semi-natural pine on Tentsmuir Point. Although fewer species were recorded on the Speyside plot, the community densities and diversity index values showed some similarity, as indeed did several of the individual species although Wren was much more abundant in Speyside, probably due to the dense shrub layer of Juniper; Robin and Chaffinch were more abundant on the Tentsmuir plot.

More recent studies of natural and semi-natural pine woodland have concentrated on the energetics of their breeding communities. Alatalo (1978) used the Finnish line transect method in a study of the community energetics of an area of boreal forest near Oulu in northern Finland which was composed of three main tree species: Scots Pine, Norway Spruce and Downy Birch. His population density estimates are not directly comparable with those from the present study since he used a different field technique, and he subdivided his breeding season results into different periods. However, his results in terms of energetics are interesting and were summarised as follows: The annual minimum energy consumption of the bird community was 2524×10^3 Kcal/km² of which 44% was consumed by wintering species and 73% by passerines. The daily energy consumption was $14 - 16 \times 10^3$ Kcal/km² in summer and $1 - 2 \times 10^3$ in winter. In spruce forests and woodland swamps birds required approximately 0.12% of the net primary production. Their total energy consumption was covered by invertebrates

(59%), vertebrates (2%) and vegetable matter (39%); the food being derived from the following sources: ground (55%), trees (44%), air (1%). Arboreal insectivorous passerines, ground-inhabiting passerines and gallinaceous birds were the most important ecological guilds. Among passerines, existence metabolism accounted for 73% of the annual energy consumption, extra activity for 17%, breeding activity for 1%, nestlings for 4% and moult for 4%.

Alatalo concluded that the role of birds in a forest ecosystem energy-flow is minor, and avian energy consumption makes up only 0.12 - 0.18% of the net primary production. He added that this did not preclude an important role for bird populations in the functioning or structure of ecosystems though it does suggest a subtle role. In looking at community structure it is therefore important to realise the differences between expressing the structure in terms of individuals (as has been done in the present study) and/or their masses in terms of energy consumption: in Alatalo's study, although passerines made up only 35% of the avian biomass, they consumed 73% of the energy used by all birds.

Głowacinski and Weiner (1980) also conducted an energy-flow study, but this was in stages of a cultivated pine forest, and will be discussed in the later two sections of this chapter.

The Tentsmuir semi-natural pine plot is probably richer (in terms of total density and diversity index) than those studied in Norway, N.W. Scotland and Speyside, although these other studies were of only one or two years' duration and might have exceeded the Tentsmuir values given another year's data. Wren, Robin, Willow Warbler, Goldcrest, Coal Tit and Chaffinch appear to be the regularly dominant passerine species in the natural and semi-natural pine environment, although Wren populations seem dependent on a dense shrub layer or layer of brashed timber (Hogstad, 1967c; Moss, 1976; this study).

Von Haartman (1971) found that in any one "natural" forest type (soils and vegetation field layers similar) breeding birds were more abundant

in birch than in spruce and more abundant in spruce than in pine, a finding echoed in the present study for birch and Scots Pine (no spruce stands studied), omitting the commercial forest. Among mixed forests, bird densities in spruce/pine were nearer to those in pine than in spruce, whereas densities in birch/spruce were as high or higher than those in birch and much higher than in spruce. It was not clear why pine had lowest densities but it does have less foliage per unit area than do the other tree species, and hence less habitat for insects and fewer sites for successful nesting than does spruce. Newton and Moss (1977) concurred with this finding and also found that among pinewoods, natural stands of varied structure contained more birds than did planted stands of uniform structure. The next section of this chapter will investigate this aspect further for the Fife area, concentrating now on the commercial forestry of plot 2.

TABLE 4.10 A comparison of the population densities (pairs or territories/km²) for the semi-natural coniferous woodland plot in Fife (plot 1) with those from other study plots of semi-natural and natural coniferous woodland

| Region and years | Fife 1979-1981 | Oslo 1966-67 | Wester Ross 1968 | |
|--------------------|-----------------|-----------------|--------------------|------|
| Area | 19.72 ha | 14 ha | 10 ha mature scrub | |
| Age of trees | 1-25 years | 60-80 years | 100-150 years | |
| Source | (this study) | (Hogstad 1967c) | (Williamson 1969a) | |
| Meadow Pipit | 5.07(1) | | | |
| Pied Wagtail | | | | |
| Wren | 15.21(1) | 7.14- 10.71 | 50 | 53 |
| Dunnock | 5.07- 10.14(2) | 17.85- 21.42 | 10 | 27 |
| Robin | 55.77-111.54 | 64.26- 74.97 | 10 | 40 |
| Wheatear | | | | |
| Blackbird | 5.07- 20.28 | 49.98(2) | | |
| Song Thrush | 10.14- 15.21 | 42.84- 46.41 | | |
| Mistle Thrush | | | | |
| Sedge Warbler | | | | |
| Willow Warbler | 30.42- 55.77 | 3.57(1) | 10 | 86 |
| Goldcrest | 25.35- 70.98(2) | 21.42- 42.84 | 20 | 40 |
| Spotted Flycatcher | | | | |
| Long-tailed Tit | 5.07- 15.21 | | 13 | |
| Coal Tit | 35.49- 86.19 | 3.57(2) | | |
| Blue Tit | 10.14- 12.68(2) | 7.14(1) | | |
| Great Tit | 5.07- 15.21 | 3.57- 7.14 | | |
| Treecreeper | 10.14- 15.21 | 3.57(1) | | |
| Jay | 5.07(2) | 3.57(1) | | |
| Jackdaw | | | | |
| Carrion Crow | 2.54- 7.61 | | | |
| Starling | | | | |
| Chaffinch | 167.31-172.38 | 71.40- 74.97 | 25 | 47 |
| Siskin | 7.61- 12.68(2) | 3.57- 7.14 | | 13 |
| Linnet | | | | |
| Redpoll | 7.61- 10.14 | | 20 | 40 |
| Crossbill | 10.14(1) | | | |
| Bullfinch | 5.07- 10.14(2) | 3.57- 7.14 | | |
| Yellowhammer | | | | |
| Reed Bunting | | | | |
| Passerines | | | | |
| Total density | 382.79-613.47 | 389.13-421.26* | 210 | 412* |
| No. of species | 20 | 25* | 10 | 12* |
| Diversity Index | 1.7745-2.3016 | | | |

Notes: * : includes species not on table, but recorded.

(n): no. of years' data.

TABLE 4.10 Continued

| Region and years | Fife 1979-1981 | Speyside 1973-1974 |
|--------------------|-----------------|--------------------|
| Area | 19.72 ha | 8.7 ha |
| Age of trees | 1-25 years | ? |
| Source | (this study) | (Moss 1976, 1978b) |
| Skylark | | |
| Meadow Pipit | 5.07(1) | |
| Pied Wagtail | | |
| Wren | 15.21(1) | 57- 63 |
| Dunnock | 5.07- 10.14(2) | 6(1) |
| Robin | 55.77-111.54 | 43- 49 |
| Wheatear | | |
| Blackbird | 5.07- 20.28 | |
| Song Thrush | 10.14- 15.21 | 6(1) |
| Mistle Thrush | | |
| Sedge Warbler | | |
| Willow Warbler | 30.42- 55.77 | 46- 55 |
| Goldcrest | 25.35- 70.98(2) | 57- 83 |
| Spotted Flycatcher | | |
| Long-tailed Tit | 5.07- 15.21 | |
| Coal Tit | 35.49- 86.19 | 46- 52 |
| Blue Tit | 10.14- 12.68(2) | |
| Great Tit | 5.07- 15.21 | |
| Treecreeper | 10.14- 15.21 | 11- 17 |
| Jay | 5.07(2) | |
| Jackdaw | | |
| Carrion Crow | 2.54- 7.61 | |
| Starling | | |
| Chaffinch | 167.31-172.38 | 66- 95 |
| Siskin | 7.61- 12.68(2) | 6- 46 |
| Linnet | | |
| Redpoll | 7.61- 10.14 | |
| Crossbill | 10.14(1) | 11(1) |
| Bullfinch | 5.07- 10.14(2) | 11(1) |
| Yellowhammer | | |
| Reed Bunting | | |
| Passerines | | |
| Total density | 382.79-613.47 | 385-471 |
| No. of species | 20 | 12 |
| Diversity Index | 1.7745-2.3016 | 2.109-2.210 |

4.2 (iii)

(e) Commercial Coniferous Woodland

The effects of afforestation on the flora and fauna of the British Isles have been described and debated, sometimes acrimoniously, for several decades now (for a review of the situation in Fennoscandia see Ahlen, 1975; Järvinen, Väistönen and Kuusela, 1977; Nilsson, 1979). Głowacinski and Weiner (1980) outline some findings for eastern Europe. Usually the discussion has centred around the conversion of upland moorlands and grasslands into dense stands of exotic coniferous trees, and whether or not this has "benefitted" the avifauna of the areas undergoing change (Fuller, 1982, also mentions the conversion of lowland dunes and broadleaved woods into blocks of commercial coniferous woodland). However it is difficult, if not impossible, to weigh up the pros and cons of the argument since much depends on value judgements. It has been clearly shown by many studies that coniferous plantations support a wider variety and higher densities of populations than the moorlands they replace. However the moorlands may have been important for one or more bird species which would not survive in the planted woodlands (Ratcliffe, 1977a) which themselves may support only common species widespread elsewhere; nevertheless the planted coniferous forests have been responsible for the spread of some species e.g. Hen Harrier, Siskin and Crossbill throughout much of the British Isles (Sharrock, 1976).

Fuller (1982) suggests that the conversion impact in terms of bird communities is generally less where coniferous trees are planted to replace deciduous ones in areas of broadleaved woodland, (especially if (a) the broadleaved woodland is a poor habitat for birds, for example beechwoods or (b) the coniferous plantations occupy only a small part of the overall woodland area) than where the whole ecosystem is drastically changed when moorland is replaced by coniferous woodland.

The change from moorland to coniferous woodland has received most attention and is of most relevance to the present study, especially since a massive

extension of forestry is a very real possibility now that the Forestry Commission (1977) has recommended the planting of up to another 1.8 million ha by 2025, with about 1.5 million of these in upland Scotland. For a discussion of the landscape implications of commercial afforestation see Crowe (1966) and Campbell (1978).

Interest in the "forestry versus conservation" issue has developed greatly since the 1950s and ecologists and conservationists are now in much better positions to defend their cause, with the acquisition of quantitative data such as that of the present study, which will be discussed later, below. A brief review of the recent debate is necessary, at this stage.

Condry (1960) outlined qualitatively the effects of afforestation on the populations of moorland bird species in Wales and described changes in the communities as the plantations matured. He expressed a desire for forestry and wildlife conservation to have more official links so that the two might co-operate more - a desire which is still felt twenty-five years later by both sides.

Bruns (1960) and Mutch (1967) looked at the economics of wildlife and forestry. Bruns reported on work carried out in Germany to investigate the economic importance of birds in forests, and among his findings were that although birds devoured large numbers of insect pests, it was not generally known what proportion of an insect population was removed by birds. (Bruns did not consider mammal pest species in any detail, but it has been shown that predators such as Kestrels, Long-eared and Short-eared Owls increase in numbers and breed more successfully during periods of high vole populations and may thus reduce the voles' depredations on young trees in plantations; see, for example, Goddard (1935), Picozzi and Hewson (1970), Village (1981, 1982)). Bruns went on to provide evidence that birds could remove substantial proportions of insect pest populations when these populations are low; their most important effect may thus be in preventing an insect "plague" from developing, rather than in reducing one that has already occurred.

Bruns therefore considered that efforts to increase the densities of birds, for example by providing nestboxes, should be encouraged.

Mutch (1967) outlined briefly the complexities of managing commercial forests and their wildlife, especially the larger herbivores such as deer species. He concluded that the success of multiple use between timber and wildlife depended on the intensity of management; joint products which are complementary at one level of production may be competitive at another; the more intensive the land management system the less multiple use can be tolerated. Mutch suggested that the relationship between forestry and wildlife management in Britain was deeply affected by the abnormality of the age structure of the plantations giving rise to an antagonistic relationship since smallish trees were exposed to browsing, fraying and bark-gnawing and the animals responsible had to be excluded from forestry areas. However, this was problematical and expensive since the forest area of Britain is highly fragmented and forms a patchwork with pastoral and arable land, and the small area of the individual woods requires a long perimeter fence per hectare enclosed. In addition, when deer are most hungry in cold snowy weather, they are often able to bypass fences buried to various depths in deep snow. Mutch saw the greatest economic advantage lying with the forest that was large, compact, and close to its produce market, which forest also offered the additional advantage of containing the whole territories of large herbivores and so made possible the change from the problems of tension between plantations and the wildlife that is excluded from them, to the problems of wildlife management within them.

What are these problems and what is their relevance to plantation avifauna?

Williamson (1970) urged that, so far as afforestation was concerned "we accept the inevitability of a change that is forced upon us by economic considerations" and that "we should direct our energies towards making some positive efforts, through planning and management, to alleviate the adverse effects it could have on our bird-life." More

particularly, he felt that considerable effort should be directed to studying the re-forestation of the West Highlands with native species (to offset the ravages of over-grazing) and the afforestation of other areas of the Scottish Highlands with exotic species of conifers such as Sitka Spruce and Lodgepole Pine to see how the flora and fauna were affected. Especially he favoured the conservation of the remaining native woodlands and the planting of "islands" and "edges" of native tree species among the larger plantations of exotics.

Foresters were quick to respond to Williamson's paper and added that the concept of sustained yield, which he chose to ignore, meant that future planted forests would provide diverse habitats since in a 50-year rotation, ideally 1/50 of the area would be felled and replanted each year; and this, along with rides and tracks, streams, and areas of poor timber growth would give rise to considerable edge effect, possibly up to 15 - 20% of the total area (Niles and Rice, 1971).

Reporting on the Royal Horticultural Society's "Conifer Conference" of 1971, Williamson (1971b) found that most foresters he had talked with supported the idea of multi-use of ecologically-diverse planted forests so long as this did not prejudice the final cash crop. This was in contrast to Mutch's ideas (delivered at the same conference) of a dichotomous commercial forestry practice, relying on a monoculture of Sitka Spruce planted with no amenity consideration near the market of pulp mills, but with considerations of amenity (although still mainly commercial) near the leisure markets of urban areas. Once again, Williamson argued for the diversification of commercial forests from both the viewpoints of species and structure, an argument he continued later in an important paper on the conservation of bird life in new coniferous forests (Williamson, 1972). This time he was more quantitative in his approach, suggesting that one large or two smaller and neighbouring refuges of former habitats should be retained in newly-afforested areas (0.75 ha of any former woodland in a moorland situation, and 6 ha of deciduous woodland where it, itself, was being replaced by conifers). However one problem with this approach could be expense since large

areas of any moorland would need to be retained and positively managed as such to support just a few pairs of wide-ranging species such as Red Grouse, Snipe and Curlew which would not inhabit forests beyond their earliest stages of growth.

Helliwell (1971b, 1972) reviewed the general faunistic and floristic changes accompanying the commercial afforestation of moorland and listed these as:-

- (1) a change in bird species and numbers usually involving an increase in the overall diversity of species and in the total number of breeding pairs;
- (2) a decrease or elimination of the previous vegetation cover within the planted areas, and a change in the species content of the areas left as rides or open glades, followed by an influx of a number of more shade-tolerant species;
- (3) a decrease in some species of mammals and reptiles and an increase in other species;
- (4) a reduction in invertebrate species dependent upon a moorland vegetation, and an increase in species dependent on woodland conditions.

The results of a study conducted by Helliwell in an upland area of south-west Scotland confirmed the above general findings, and he concluded that "some mixture of forested and open land would conserve the greatest variety of wildlife." The actual proportion of each which would give optimal results would vary according to factors such as tree species, crop rotation and management of non-forest land. By using a scoring system based on size, abundance and rarity (Helliwell, 1971a), it was possible to draw up a "balance sheet" of the value of moorland compared to planted land, and in his study area (Helliwell, 1971b) it transpired that an area of open hillside was worth about 53% more (from an ecological/conservation point of view) than a comparable area of plantations. From this he estimated that the optimal level of afforestation was about 30% of the study area so far as wildlife conservation was concerned.

Petty (1980, 1981) re-iterated much of Helliwell's (1971a, b) work, relating it to his own, but he emphasised the fact that most of the grass- and heather-clad hills now threatened by afforestation are themselves far from natural, even though they had developed a characteristic, if impoverished, animal community. In addition to afforestation he saw moorlands and upland grasslands threatened by improvement in the forms of drainage, followed by re-seeding with species more palatable to sheep. He conceded that economic forestry does have a dramatic effect on the environment, especially in upland areas, but drew attention to the fact that Britain has only about 8% of its land area occupied by woodland and forest, a low proportion compared with much of north and west Europe. Petty also re-emphasised some of the points raised by Niles and Rice (1971); he drew attention to (1) the possible variability within an area planted at the one time, resulting in trees of different heights and structures; (2) the idea that large areas often remain unplantable and add to the edge effect; (3) "sustained yield" concept giving rise to a crop rotation within a forest. Updating some of Williamson's ideas (1970, 1971b, 1972), Petty stated that "it is now generally accepted" that areas of broadleaved trees, especially along watercourses, should be retained and possibly expanded with indigenous species; and that a proportion of planted conifers should be allowed to reach biological maturity to add to the structural diversity of the new forests. He concluded that overall "the evidence suggests that the present level of afforestation had adversely affected few species."

Currie and Bamford (1982), in a Forestry Commission study in north Wales, confirmed the benefits to avifauna of retaining small stands of conifers beyond normal financial maturity since they increased habitat diversity and the amount of "edge" present in a larger plot. They suggested that such areas could be best retained in sites difficult to harvest or where tall, mature trees were scarce; the area should be as large as possible or in several small groups of irregular and elongated shape to maximise edge effect; and should be of irregular structure including dead, broken or wind-blown trees and branches to increase diversity of habitat. Currie and Bamford thought that the financial

cost, though significant and increasing after 5 - 10 years, would be justified for the landscape and conservation benefit and would presumably improve the "public" image of the Forestry Commission.

Despite widespread reference to, and often antagonism towards, the alien tree species used in British commercial forestry, there has in fact been comparatively little work done to estimate their ecology and conservation value. Rose (1979), in a comparative study of the native Scots Pine and introduced Corsican Pine in Suffolk, found that the breeding avifauna showed no significant difference between the two tree species and that the avifaunal diversity in areas planted with either species could be increased if a few old and over-mature trees were to be left standing after harvesting in an area. However it is felt here that Rose's findings, although encouraging, should be treated with some caution since his field methodology employed timed transects in only one month (June) in only one year (1978) - more data would have been welcomed. As regards the trees themselves, Rose found that in plantations of each species there was little difference between them until the late pole stages (trees over 60 years old) when plantations of Corsican Pine had a much more closed canopy than those of Scots Pine, due largely to a dense "thicket" of dead and live branches in the canopy of trees of the former; in addition the bark of Corsican Pine becomes increasingly creviced with age compared to the increasingly flaked nature of Scots Pine. These factors will influence the feeding and breeding conditions for birds, but no study has been carried out to investigate this further.

Currie and Bamford (1981) showed how there were large differences in the bird communities of study plots of the exotic Sitka Spruce, depending on whether the timber crop was a first planting or a restocking. Using study plots of similar age structure and growth stage, they found the bird population densities and species richness to be higher on restocked areas. (In the present Fife study, the commercial study plot (2) was partly restocked, while the self-seeded plot (1) was in effect a "first-planting"; this may account for some of the differences in the avifaunal parameters between the two, but it would be almost impossible

to isolate this factor and look at it further). Since in future much planting, especially in Wales, will be replanting of sites cleared of the first timber crop, these findings have important ramifications for the future study of the avifauna of plantations and for the forestry versus conservation debate, especially with the inclusion of the recommendations of the same authors (Currie and Bamford, 1982) for the retention of some areas of conifers beyond financial maturity. An interesting time lies ahead for ornithologists working in commercial coniferous forests!

There have been many published results describing and discussing breeding bird censuses carried out in commercial coniferous woodland, both in the British Isles and continental Europe, but few have been done near sea-level and involving the main species of the present study - Scots Pine. Differences in methodology employed in some studies also preclude comparisons with the results from the present one. However, the work of Moss (1976 et seq.) in south-west Scotland is very similar to the present study so far as methodology and tree species are concerned (but there are altitudinal differences unfortunately), and consequently Moss' findings will be dealt with in some detail later in this section, after a brief review of the work of others.

Although it is termed afforestation, the replanting of native tree species on Rhum National Nature Reserve is not of any commercial significance, but early results were reported by Batten and Pomeroy (1969) and by Williamson (1971d). The breeding bird population densities increased throughout the early establishment years and were seven times higher in eight-year-old plantations than on newly-planted moorland. However, the study plots used were small in size with a consequently large amount of edge relative to area, which may have inflated the densities.

Small plantations of single species in addition to larger areas of monoculture have occasionally been studied with results published for Japanese Larch by Williamson (1971c), and for Yew (Williamson and

Williamson, 1973; Batten, 1976; Shaw, 1977). Shaw recorded a density of 945 passerine pairs/km², but again this figure may have been inflated by the edge effect since his study plot was only 5.3 ha in size. Phillips (1973) studied one bird species - Stonechat - in large study plots of one alien tree species - Sitka Spruce. He found that the ground-cover affected the breeding densities of Stonechats, the density being twice as high in young plantations on heather as in those on grass.

Adams and Edington (1973) compared wintering and breeding songbird populations in a planted mixed-species coniferous forest and in the deciduous Forest of Dean. The authors found no appreciable difference in the total numbers of songbirds in the coniferous and deciduous study plots, but the diversity index value was apparently greater in the broadleaved plots.

Barwick (1976) presented census results for a Norway Spruce study plot in Northamptonshire and found that most bird territories were held around scattered hardwood clumps amongst the conifers, apart from the Goldcrest and Coal Tit which both preferred being in the Spruces. The five most abundant species were, in order of decreasing abundance, Wren, Goldcrest, Coal Tit, Willow Warbler and Robin.

Batten (1976) reported his findings on two study plots in Killarney investigated in 1973 - one plot of Norway Spruce (11.00 ha) and the other of Sitka Spruce (7.75 ha). The Norway Spruce plot was bounded on one side by hardwoods, on another by farmland, and elsewhere by the rest of the larger area of spruces; there was consequently a high "edge effect". A high population density from 14 species was found, of 1800 territories/km², about one third of which was due to Goldcrest (590 territories/km²) at its highest recorded density in the British Isles. The Sitka Spruce plot had a density of 1000 territories/km² formed by 8 species, again with Goldcrest being very abundant (388 territories/km²). Batten found that diversity index values of the communities were highest in a natural Yew wood, followed by planted Norway Spruce and lowest in alien Sitka Spruces, presumably due to more species being adapted to the native species. Batten also reported

having taken readings of light penetration through the canopy in the two Spruce plantations (one of the few workers to have done this) and found much higher values (mean \pm s.d. = 8.38 ± 6.34 foot-candles) in Norway than in Sitka Spruce (0.45 ± 0.40 foot-candles), due either to the heavier needles of the latter or to its planting density which was higher.

Batten (1977) presented results for mapping work carried out in 1976 in coniferous plots, largely of Sitka Spruce planted in 1970, in the uplands of West Yorkshire. The number of passerine species and territories in each of four woodland and one moorland plots (each 12 ha in area) did not differ greatly and most of the variation in the number of territories could be accounted for by altitude. Meadow Pipit and Skylark were the dominant species in each plot. All the breeding species were those of open-country habitats, which suggests that the planted areas had not reached a woodland state, or that woodland species had not yet penetrated the uplands to the new wooded areas.

Moss (1979) and Moss et al (1979) reported their findings from areas planted largely with Sitka Spruce. From a number of censuses in different forests in Dumfries and Galloway region of Scotland, Moss found that in areas of Sitka Spruce of the same age as the planted Pine in Fife, that passerine densities ranged from $231 - 252$ prs/km² of 9 species in trees up to 7 m high and aged 12 - 14 years to $302 - 443$ prs/km² of 6 - 10 species in trees from 12 - 15 m high and aged 23 - 26 years. These compare with figures from the Fife plot (2), with trees 14 - 25 years old when censused, of $522 - 729$ prs/km² of 14 - 17 (total 18) passerine species.

Of the plots studied by Moss et al, two at the same developmental stage as the Fife plot (thicket/pole stage) - A7 and C2 - have three years data (1976-78): for A7 (thicket), total density ranged from $358 - 478$ prs/km² made up of 13 - 14 species with a range in diversity index values of $1.99 - 2.19$; for C2 (polestage), the total density range was $301 - 442$ prs/km² made up of 8 - 10 species and a range of diversity index values

from 1.84 - 2.02. These density and species-richness figures are again lower than those for the Fife plot, but the diversity indices are similar, though generally lower (Fife range: 2.14 - 2.33).

Finally, Głowacinski and Weiner (1980) described the results of a study of the avifauna in five consecutive developmental stages of planted Scots Pine forest in Poland. Their work is thus of more relevance to the present study's plot 1 and is discussed in more detail below (along with more of Moss' results) and in the section on succession.

Moss (1976, 1978a, 1978b) described his work in forestry plantations in Dumfries-shire among which were censuses in each of two Scots Pine plantations; and in the Spey valley where he carried out two censuses in each of two planted Scots Pine areas. Unfortunately these plots were 40 - 50 years old - much older than the one studied in Fife (14 - 25 years old).

In Dumfries-shire, Moss' planted Pine study plots were on low ground, had no shrub layer, but did have thick ground cover of brambles. Moss discovered total passerine densities ranging from 208 - 340 prs/km² of 6 - 8 species, which were much lower than those from areas of Sitka and Norway Spruce in the same region and years (411 - 503 prs/km²). He attributed much of the difference to the lower densities of the Goldcrest in Pine, where the Wren was the dominant species, followed by Chaffinch and Coal Tit (Table 4.11).

In the Spey valley planted Pine study areas, Moss found densities of 151 - 215 passerine prs/km², which were less than half those on a plot of semi-natural Pine (385 - 471 prs/km²). For the Speyside planted Scots Pine studied in the same years as the Dumfries-shire ones, the densities ranged from 151 - 172 prs/km² of 6 - 7 species.

Głowacinski and Weiner (1980), in a Polish study of consecutive developmental stages of planted Scots Pine forest in Poland presented their results in terms both of population and bio-energetic parameters. The

forest complex studied was at an altitude of 180 - 200 m.a.s.l., and five stages were identified and their avifaunas studied:

Stage I - 0.8 ha, clear-cut, 1-yr-old, overgrown with grasses and sedges.

Stage II - 0.5 ha, 4-yrs-old plantation, trees up to 2.5 m high, lush grass and sedge growth.

Stage III - 7.7 ha, 10-yrs-old, dense thicket, trees up to 5 m high, low herbs and shrubs.

Stage IV - 5.0 ha, 35-yrs-old, dense polewood, shrub layer absent, poor herb layer.

Stage V - 8.0 ha, 80-yrs-old, forest, with secondary tree, shrub and herb layers closely resembling natural forest.

Their census results are presented in Table 4.11 and discussed more fully in the section on succession. Briefly, here, the stages corresponding to the Fife one (III, IV) had density ranges of 340 - 402 prs/km² of 9 - 11 species. These are similar to Moss' findings, but lower than those from Fife. Głowacinski and Weiner's figures may be overestimates, since their study plots were small and may have exhibited a high degree of "edge effect". Głowacinski and Weiner's plot V (80-yrs-old) which, taken with plot IV encompassed the age range of Moss' study plots (35-80 years in Poland compared with 40-50 years in Scotland) takes the density range to 402 - 570 passerine pairs/km² of 11 - 25 species, thus much richer than found by Moss.

In terms of biomass, Moss (1978b) estimated it as 5 - 9 kg/km² for adult territorial songbirds in his Scottish pine plantations (9 - 12 kg/km² in spruce, 20 - 30 kg/km² in birch/pine scrub and 70 kg/km² in mixed woodland). From Głowacinski and Weiner (1980), estimates of the biomass of passerines in their study plots are as follows:- stage I: 1 kg/km²,

stage II: 6.78 kg/km^2 , stage III: 21.86 kg/km^2 , stage IV: 16.98 kg/km^2 , stage V: 23.24 kg/km^2 , but these estimates include data for juveniles allowing for mortality, and so a direct comparison between the two sets of data cannot be made. However, from the population figures outlined briefly above and in Table 4.11, it can be assumed that the Polish Pine plantations of the same age as the Scottish ones will probably be able to support a higher biomass.

From Table 4.11 it can be seen that the commercial coniferous (Scots Pine) plot studied in Fife was richer, in terms of number of breeding species (18), than any other studied in Scotland and reported in the literature. Only the mature planted Scots Pine plot in Poland held more breeding species (25). Only one plot in Scotland held a similar number of species to the one in Fife - the 7 - 9 years old Sitka Spruce plot (A7) in Dumfries-shire, with 16 breeding species recorded over a three year period.

In terms of the total breeding density of each study plot in Table 4.11, two plots supported higher densities than the Fife one - a 30-years-old Norway Spruce plantation in Killarney with 1718 prs/km^2 , and a mixed-age Sitka Spruce plantation, also in Killarney, with 969 prs/km^2 . Three other study areas held densities within the Fife range of 522 - 729 prs/km²: - a 33-35 years old mixed spruce plot (A3) in Dumfries-shire ($454 - 549 \text{ prs/km}^2$), an 80-years-old Scots Pine plot in Poland (570 prs/km^2) and a 35-37 years old Norway Spruce plot (A2) in Dumfries-shire ($503 - 598 \text{ prs/km}^2$). Thus it would appear that the relatively young plot in Fife supported a community as rich in species and population as in many others much older, and this at a time when the Fife population was still probably at a depressed level following the hard winter of 1978/79. The four study plots of approximately the same age as the Fife one (14-25 years) - Poland III, Galloway C2 and C7, Dumfries-shire A5 - had densities at a level of at least 80 prs/km^2 below the lowest of the Fife plot.

Combining the parameters of species richness and population size in the

Shannon-Weaver diversity index, then for those studies where a diversity index value (or range) is given, three come close to the Fife range of 2.14 - 2.33:- 25-28 years old mixed Spruce in Galloway (C2) with 1.84 - 2.02; 30 years old Norway Spruce in Killarney with 2.06; and 7-9 years old Sitka Spruce in Dumfries-shire (A7) with 1.99 - 2.29.

The densities and diversity index values of the Fife commercial plot (2) are also higher than the semi-natural pine plot (1) studied in Fife and the one studied in Speyside by Moss in 1973 and 1974, where he found densities of 385 and 471 prs/km² and diversity index values of 2.11 - 2.21 (Table 4.10). Clearly then, the Tentsmuir Forest study plot is a very rich one compared with other commercial and even semi-natural coniferous ones, and this contradicts the view expressed by several authors (see earlier in this chapter for a brief review) that commercial forests are poor areas for birdlife - certainly on this occasion they can be good.

TABLE 4.11 Population densities (territories or pairs/km²) of territory-holding passerines in commercial coniferous study plots

A Scots Pine

| Study Region | This one: Fife, Scotland | Dumfries- shire, Scotland | Moss (1978b) Spey Valley, Scotland | | | |
|----------------------|-----------------------------|---------------------------------|---------------------------------------|--------------|------------|------------|
| Years | 1979-81 | 1975 | 1975 | 1973-74 | 1973-75 | 1975 |
| Plot designation | 2 | T | W | S1 | S2 | S4 |
| Area (ha) | 20.59 | 12.40 | 11.90 | 8.7 | 11.7 | 13.7 |
| Altitude (masl) | 5-10 | 75 | 60 | 250-290 | 240-290 | 335 |
| Main tree species | Scots Pine | Scots Pine | Scots Pine | Scots Pine | Scots Pine | Scots Pine |
| Date planted | 1954-65 | 1932 | c1935 | Semi-natural | 1932 | 1926 |
| Wren | 14.58- 55.89 | 75 | 92 | 57-63 | 4- 9 | 44 |
| Dunnock | 9.72- 14.58 | | 4 | 6(1) | | |
| Robin | 48.60-150.66 | 20 | 29 | 43-49 | 4- 9 | 22 |
| Blackbird | 14.58- 48.60 | | | | | |
| Song Thrush | 4.86- 24.30 | | | 6(1) | 4(1) | |
| Mistle Thrush | | | | | 4(1) | |
| Willow Warbler | 53.46- 72.90 | | 23 | 46-55 | | |
| Goldcrest | 34.02- 68.04 | 36 | 34 | 57-83 | 34-60 | 22 |
| Long-tailed Tit | 4.86- 19.44 | | | | | |
| Crested Tit | | | | 11-17 | 4(3) | 4 |
| Coal Tit | 82.62-126.36 | 34 | 57 | 46-52 | 26-43 | 35 |
| Blue Tit | 4.86- 9.72 | | | | | |
| Great Tit | 4.86- 9.72(2) | | | | | |
| Treecreeper | 9.72- 14.58 | 16 | 13 | 11-17 | 4-9(2) | |
| Jay | 2.43(2) | | | | | |
| Chaffinch | 131.22-155.52 | 30 | 88 | 66-95 | 43-74 | 26 |
| Siskin | 4.86- 7.29(2) | | | 6-46 | 13-17(2) | |
| Redpoll | 9.72- 29.16 | | | | | |
| Crossbill | 2.43(1) | | | 11(1) | | |
| Bullfinch | 4.86(2) | | | 11(1) | 4(1) | |
| Total density | 522.45-729.00 | 208 | 340 | 385-471 | 155-215 | 151 |
| Total no. of species | 18 | 6 | 8 | 13 | 11 | 6 |
| Diversity Index | 2.1401-2.3285 | | | | | |
| (n) = no. of years | | | | | | |

TABLE 4.11 Continued

A Scots Pine

| Study | This one: | Głowacinski and Weiner (1980) | | | |
|------------------------|----------------|-------------------------------|---------------|---------------|---------------|
| Region | Fife, Scotland | Cracow, Poland | | | |
| Years | 1979-81 | 1975 | 1975 | 1975 | 1975 |
| Plot designation | 2 | II | III | IV | V |
| Area (ha) | 20.59 | 0.5 | 7.7 | 5.0 | 8.0 |
| Altitude (m.a.s.l.) | 5-10 | | not given | | |
| Main tree species | Scots Pine | Scots Pine | Scots Pine | Scots Pine | Scots Pine |
| Age at census | 14-25 | 4 | 10 | 35 | 80 |
| Tree Pipit | | 10 | 7 | 50 | 81 |
| Wren | 14.58- 55.89 | | | | |
| Dunnock | 9.72- 14.58 | | | | |
| Robin | 48.60-150.66 | | 39 | 70 | 60 |
| Redstart | | | | | 3 |
| Blackbird | 14.58- 48.60 | | 33 | 6 | 8 |
| Song Thrush | 4.86- 24.30 | | 29 | 10 | 7 |
| Lesser Whitethroat | | 20 | 39 | 10 | |
| Whitethroat | | 26 | | | |
| Garden Warbler | | | 19 | | 2 |
| Blackcap | | | | 20 | 14 |
| Wood Warbler | | | | 56 | 38 |
| Chiffchaff | | | | | 10 |
| Willow Warbler | 53.46- 72.90 | 10 | 144 | 104 | 15 |
| Goldcrest | 34.02- 68.04 | | | | |
| Collared Flycatcher | | | | | 25 |
| Pied Flycatcher | | | | | 15 |
| Long-tailed Tit | 4.86- 19.44 | | | | 3 |
| Marsh Tit | | | | | 3 |
| Crested Tit | | | | | 9 |
| Coal Tit | 82.62-126.36 | | | 30 | 28 |
| Blue Tit | 4.86- 9.72 | | | | 50 |
| Great Tit | 4.86- 9.72(2) | | | | 50 |
| Nuthatch | | | | | 25 |
| Treecreeper | 9.72- 14.58 | | | | 25 |
| Short-toed Treecreeper | | | | | 15 |
| Golden Oriole | | | | | 9 |
| Red-backed Shrike | | 34 | | | |
| Jay | 2.43(2) | | 13 | 10 | 3 |
| Starling | | | | | 12 |
| Chaffinch | 131.22-155.52 | | | 36 | 60 |
| Siskin | 4.86- 7.29(2) | | | | |
| Redpoll | 9.72- 29.16 | | | | |
| Crossbill | 2.43(1) | | | | |
| Bullfinch | 4.86(2) | | | | |
| Yellowhammer | | 50 | 17 | | |
| Total density | 522.45-729.00 | 150 | 340 | 402 | 570 |
| Total no. of species | 18 | 6 | 9 | 11 | 25 |
| Diversity Index | 2.1401-2.3285 | | | | |

(n) = no. of years

TABLE 4.11 Continued

B Other coniferous species (with at least 2 years' data)

| Study | This one: | Moss (1978b) | Batten (1976) | Moss (1978b) |
|----------------------|----------------|---------------------------------|--------------------|---------------------------------|
| Region | Fife, Scotland | Dumfries- shire, Scotland | Killarney, Eire | Dumfries- shire, Scotland |
| Years | 1979-81 | 1973-74 | 1973 | 1973-75 |
| Plot designation | 2 | A4 | "Dark Wood" | A2 |
| Area (ha) | 20.59 | 5.8 | 11 | 9.2 |
| Altitude (m.a.s.l.) | 5-10 | 135-210 | 75 | 210-275 |
| Main tree species | Scots Pine | Japanese Larch | Norway Spruce | Norway Spruce |
| Date Planted | 1954-65 | 1946 | 1943 | 1938 |
| Wren | 14.58- 55.89 | 116-121 | 182 | 52- 73 |
| Dunnock | 9.72- 14.58 | | | |
| Robin | 48.60-150.66 | 30- 47 | 273 | 16- 35 |
| Blackbird | 14.58- 48.60 | | 127 | |
| Song Thrush | 4.86- 24.30 | 9(1) | 46 | |
| Mistle Thrush | | 9(1) | | |
| Willow Warbler | 53.46- 72.90 | 17(1) | | |
| Goldcrest | 34.02- 68.04 | 99-125 | 590 | 261-372 |
| Long-tailed Tit | 4.86- 19.44 | 17(1) | 27 | |
| Coal Tit | 82.62-126.36 | 47- 65 | 100 | 43- 49 |
| Blue Tit | 4.86- 9.72 | | 27 | |
| Great Tit | 4.86- 9.72(2) | | | |
| Treecreeper | 9.72- 14.58 | 9- 17 | 36 | 5- 19 |
| Jay | 2.43(2) | 9(1) | | |
| Carrion Crow | | | 9 | |
| Chaffinch | 131.22-155.52 | 73- 82 | 273 | 60-101 |
| Siskin | 4.86- 7.29(2) | | 18 | |
| Linnet | | | | 11(2) |
| Redpoll | 9.72- 29.16 | | 9 | |
| Crossbill | 2.43(1) | | | 11(1) |
| Bullfinch | 4.86(2) | | | 5(1) |
| Total density | 522.45-729.00 | 444-448 | 1718 | 503-598 |
| Total no. of species | 18 | 11 | 13 | 9 |
| Diversity Index | 2.1401-2.3285 | | 2.06 | |

(n) = no. of years

TABLE 4.11 Continued

B Other coniferous species (with at least 2 years' data)

| Study | This one: Fife, Scotland | Moss (1978b) Dumfries- shire Scotland | Moss et al (1979) Galloway, Scotland | Batten (1976) Killarney, Eire |
|----------------------|--------------------------------|---|---|--|
| Region | | | | |
| Years | 1979-81 | 1973-75 | 1976-78 | 1973 |
| Plot designation | 2 | A3 | C2 | "Muckross" Spruce |
| Area (ha) | 20.59 | 10.2 | 9.6 | 7.75 |
| Altitude (m.a.s.l.) | 5-10 | 260-300 | 140-150 | 300 |
| Main tree species | Scots Pine | Norway + Sitka Spruces | Norway + Sitka Spruces | Sitka Spruce |
| Date planted | 1954-65 | 1940 | 1951 | various |
| Tree Pipit | | | 10(1) | |
| Wren | 14.58- 55.89 | 59- 73 | 60- 83 | 52 |
| Dunnock | 9.72- 14.58 | | 10- 16(2) | |
| Robin | 48.60-150.66 | 5- 24 | 21- 42 | 129 |
| Blackbird | 14.58- 48.60 | | | 39 |
| Song Thrush | 4.86- 24.30 | 5(1) | 10(1) | |
| Mistle Thrush | | | 5(1) | |
| Chiffchaff | | | | 13 |
| Willow Warbler | 53.46- 72.90 | | 21- 42 | |
| Goldcrest | 34.02- 68.04 | 244-317 | 68-156 | 387 |
| Long-tailed Tit | 4.86- 19.44 | | | |
| Coal Tit | 82.62-126.36 | 29- 59 | 29- 39 | 78 |
| Blue Tit | 4.86- 9.72 | | | |
| Great Tit | 4.86- 9.72(2) | | | |
| Treecreeper | 9.72- 14.58 | 10(3) | | |
| Jay | 2.43(2) | | | |
| Chaffinch | 131.22-155.52 | 59- 83 | 47- 60 | 181 |
| Siskin | 4.86- 7.29(2) | 5- 29(2) | 10(2) | 90 |
| Redpoll | 9.72- 29.16 | | | |
| Crossbill | 2.43(1) | 5(2) | | |
| Bullfinch | 4.86(2) | | 5(1) | |
| Total density | 522.45-729.00 | 454-549 | 301-442 | 969 |
| Total no. of species | 18 | 9 | 12 | 8 |
| Diversity Index | 2.1401-2.3285 | | 1.84-2.02 | 1.71 |
| (n) = no. of years | | | | |

TABLE 4.11 Continued

B Other coniferous species (with at least 2 years' data)

| Study | This one | Moss (1978b) | Moss (1979) and Moss et al (1979) | Galloway Scotland | |
|----------------------|----------------|--------------------------|--------------------------------------|----------------------|---------------------------|
| Region | Fife, Scotland | Dumfries-shire, Scotland | | | |
| Years | 1979-81 | 1973-74 | 1975-76 | 1976-78 | 1977-78 |
| Plot designation | 2 | A1 | A5 | A7 | C7 |
| Area (ha) | 20.59 | 11.1 | 10.9 | 13.6 | 11.7 |
| Altitude (m.a.s.l.) | 5-10 | 210-260 | 300-365 | 140 | 230-320 |
| Main tree species | Scots Pine | Sitka Spruce | Sitka Spruce | Sitka Spruce | Sitka Spruce, Larch |
| Date planted | 1954-65 | 1927 | 1953 | 1969 | 1965 |
| Skylark | | | | 20(1) | |
| Meadow Pipit | | | | 7- 63 | 4- 9 |
| Wren | 14.58- 55.89 | 57-100 | 25- 28 | 29-103 | 64-103 |
| Dunnock | 9.72- 14.58 | | 5- 9 | | |
| Robin | 48.60-150.66 | | 25- 55 | 4- 40 | 21- 43 |
| Whinchat | | | | 7- 39 | |
| Stonechat | | | | 15(1) | |
| Wheatear | | | | | |
| Blackbird | 14.58- 48.60 | | | | |
| Song Thrush | 4.86- 24.30 | | | 4(1) | |
| Mistle Thrush | | 5- 9 | | | |
| Grasshopper Warbler | | | | 4(1) | |
| Sedge Warbler | | | | 4(2) | |
| Whitethroat | | | | | 4(1) |
| Willow Warbler | 53.46- 72.90 | | | 88-136 | 68- 79 |
| Goldcrest | 34.02- 68.04 | 136-140 | 73-172 | 15- 39 | 21- 34 |
| Long-tailed Tit | 4.86- 19.44 | | | | |
| Coal Tit | 82.62-126.36 | 20- 48 | 28- 48 | | 9- 17 |
| Blue Tit | 4.86- 9.72 | | | | |
| Great Tit | 4.86- 9.72(2) | | | | |
| Treecreeper | 9.72- 14.58 | | 9(1) | | |
| Jay | 2.43(2) | | | | |
| Chaffinch | 131.22-155.52 | 86-102 | 89-170 | 37- 83 | 9- 17 |
| Siskin | 4.86- 7.29(2) | 5- 9 | 5(1) | | |
| Linnet | | | | 15- 37 | |
| Redpoll | 9.72- 29.16 | | | 7- 22 | 9 |
| Crossbill | 2.43(1) | 9(2) | 9(1) | | |
| Bullfinch | 4.86(2) | | | | |
| Yellowhammer | | | | 4(2) | |
| Reed Bunting | | | | 4- 17 | |
| Total density | 522.45-729.00 | 351-441 | 305-411 | 358-478 | 230-290 |
| Total no. of species | 18 | 9 | 8 | 16 | 9 |
| Diversity Index | 2.1401-2.3285 | | 1.43-1.53 | 1.99-2.29 | 1.63-1.86 |
| | | | (2) | | |

(n) = no. of years

Moss (1978a, b) found in his comparisons of semi-natural and commercial Scots Pine in Speyside, that population densities and species richness were higher in the semi-natural woodland; and in his comparisons of planted Scots Pine and spruce species in Dumfries and Galloway, he found the population densities to be higher on the spruce study plots. The present study has shown that this relationship between semi-natural and commercial woodland is not quite so clear-cut and that other factors such as latitude, altitude, age of woodland and whether it is a first planting or a restocking must be carefully considered.

Taking the other four Fife study plots, the populations of the Dune grass-land (5) were richer than on a similar area on Anglesey but poorer than on an area colonized by Sea Buckthorn in Lincolnshire (Tables 4.3 and 4.4). The birch/willow scrub study plot was poorer than some, but richer than other plots in Fennoscandia. At the individual species level, densities were higher in Fife than in Midlothian, but lower than in Wester Ross, and much lower than in an area of coppiced willow in Lancashire (Table 4.7). The birch/alder woodland in Fife had higher population densities but held fewer species, especially of hole-nesters, than an alder study plot in Wales (Tables 4.8 and 4.9B). Finally, the semi-natural pine area studied on Tentsmuir is as rich as those studied in Norway and elsewhere in Scotland, including Wester Ross and Speyside (Table 4.10).

Overall, it would appear that the habitats studied on the duneland complex of Tentsmuir/Earlshallmuir are by no means poor in terms of the variety and number of passerines they support in the breeding season. Comparisons have been made with the results of other studies of similar habitats, but such comparisons are only of the broadest nature, since many variables are involved and preclude more detailed investigation of any similarities and differences.

The next section studies in more detail the habitat succession revealed by the Fife study and looks at it in the wider context of other studies of seral stage habitats.

4.3 AVIFAUNAL SUCCESSION

4.3. (i) Introduction

Having thus far investigated the breeding bird population parameters of various habitats in isolation, it is now time to look at some of these habitats in their ecological settings along successional gradients.

This section is not concerned directly with a study of vegetation succession, but rather with how seral stages along a succession contain different communities of breeding birds, with variations in their population parameters. For reviews of the theoretical and practical studies of plant and habitat succession see, for example, Clapham (1973), Krebs (1978), Odum (1950, 1969, 1977), Tivy (1971) and Watts (1971). From these, the basic stages in succession can be identified as follows:-

- (1) Nudation: initiation of the succession by a major disturbance in the environment;
- (2) Migration: movement of available species to fill the vacant ecological niches;
- (3) Ecesis: ability of the migrating species to establish themselves and reproduce successfully;
- (4) Competition: within and between species for nourishment, shelter and breeding;
- (5) Reaction: of species within themselves, to each other, and to the environment;
- (6) Final stabilization of the community.

Succession can be of two broad types:- Primary, where it is initiated on a bare or newly-created surface and Secondary, where it is initiated by a major environmental disturbance disrupting a previously-initiated succession or producing a marked modification in a stable system. Głowacinski and Järvinen (1975) described how primary and secondary successions were fundamentally different: primary succession is usually connected with time-consuming changes in e.g. soil structure, and thus has a slow start,

and in extreme conditions pioneer communities may persist for quite a long time. Secondary succession proceeds faster as it can start on e.g. a highly developed soil, and the communities change rapidly during the initial stages, but more slowly in mature stages. Birds are a relatively passive element, at least in forest succession, since the type of avian community is determined by forest type and stratification. This idea was developed further by the present author (Dougall, 1982), who introduced a working definition of avifaunal succession drawn from his own work on breeding bird communities but which also encompassed many of the ideas and findings from previous studies. Avifaunal succession is seen as "a series of breeding bird communities, the component stages of which alter concomitantly with the successional phases through which the breeding season habitat passes." As a succession progresses there are three major characteristics: a change in the species, an increase in the number of species, and an increase in the variety of forms present.

In an ornithological context, the bird communities of various seral stages in various geographical locations have been studied and some general principles have arisen, although not as much attention has yet been paid to the changes in bird communities as to plant communities along successional gradients.

Fuller (1982) presents several short reviews of various habitat successions and their associated bird communities, and of particular interest to the present study are those reviews of duneland, scrub and deciduous woodland, and coniferous woodland. On duneland, the older and more stable stages with their greater complexity of vegetation including scrub and developing woodland, support greater densities of breeding birds than do the younger unstable stages dominated by Marram Grass. Scrubland does not form a uniform environment for nesting birds since it varies in species composition, openness and height. Generally speaking, scrub becomes taller and more closed as the succession advances and as woodland develops there is a general trend for overall bird population density and species richness to increase with maturity of habitat. Individual species do not necessarily follow this trend and no species maintains a constant density from

the youngest through to the oldest stages - all show preferences for a particular growth stage. Jones (1972) found a strong positive relationship between the number of breeding bird species and the total population density for six successional stages of Sessile Oak woodland in Wales. With only three successional stages in each of deciduous and coniferous woodland development in the present study, it is not possible to draw any firm conclusions (Figure 4.1), but it is obvious that the relationship varies with the year of investigation, and emphasizes the need for more than two years' data. For the succession from dune grassland through scrub to more mature woodland in the present study, a relationship similar to Jones' obtained in 1979 and 1980 in the deciduous areas; and in 1979 only for the coniferous areas. In the remaining years, however, the scrub areas held lower population densities but more species than the more mature woodland.

Martin (1960), in a study of hydroseres and xeroseres in Canada, found that each stage of forest succession that he looked at was characterized by certain combinations of birds, their relative abundances, conspicuousness and vertical distribution.

Haapanen (1965), in a study of succession in Finnish forests, suggested that in the north European situation forest succession was initiated largely by fires or gale damage. From his work he concluded that the density of arboreal feeders increased with the development of the stand, and that the densities of such species increased most rapidly at the stage when the growth of the stand was maximal. The changes in total density of arboreal feeders did not very closely follow the development of either feeding area volume (crown volume) or feeding area surface (surface of needles). It is not clear why Haapanen did not include trunks and branches in his estimates of feeding area surface. With aerial and terrestrial feeders, Haapanen found that population density of the birds was highest on open areas, especially burned ones. With the gradual closing of the canopy and the increase in trunk density, the feeding area (and volume?) decreases in size and the population density of this group decreases. As the stands age, space in them increases, allowing

Fig 4.1: Species-richness and population density along successional gradients in N.E. Fife

A: Deciduous succession

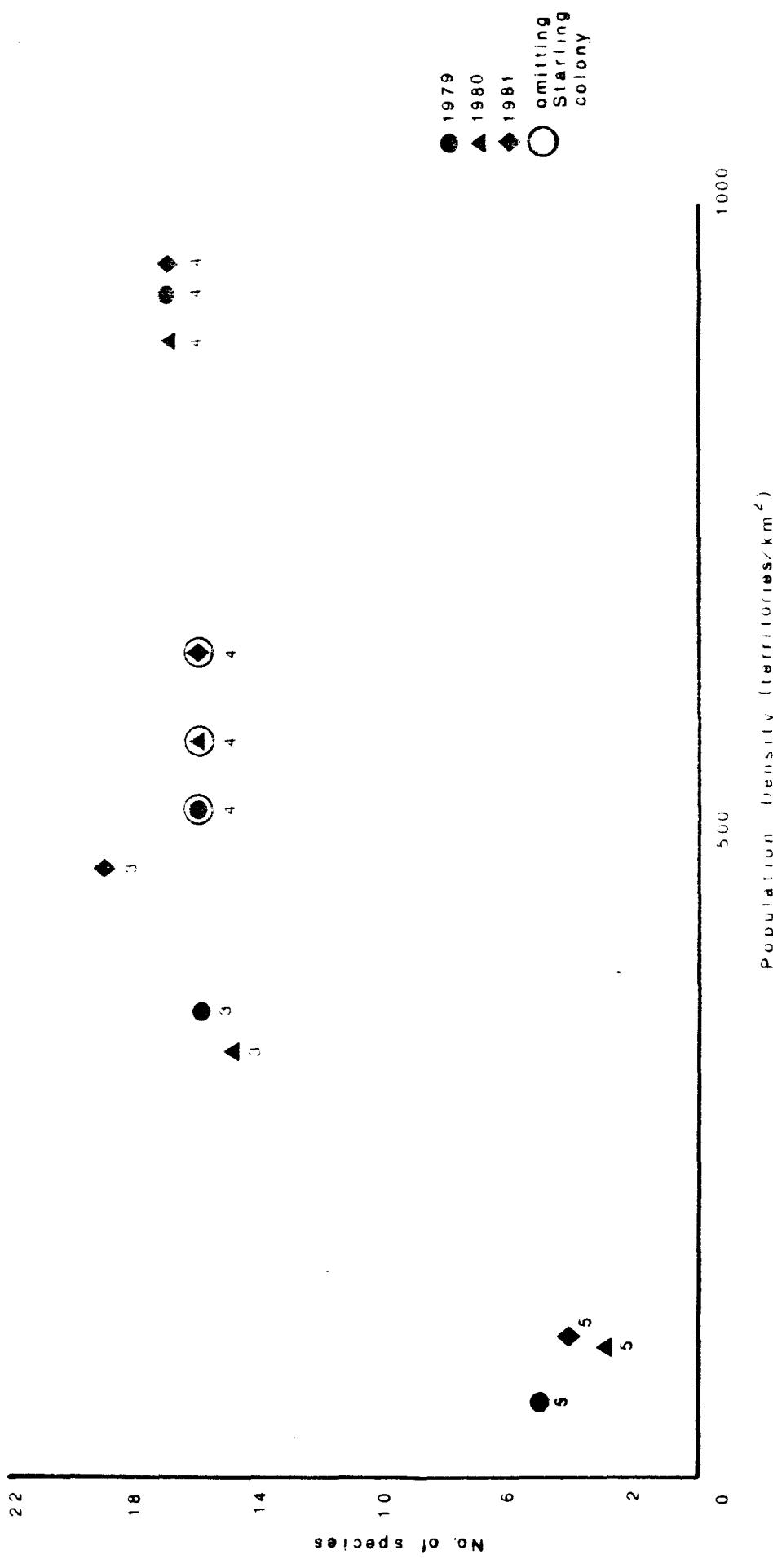
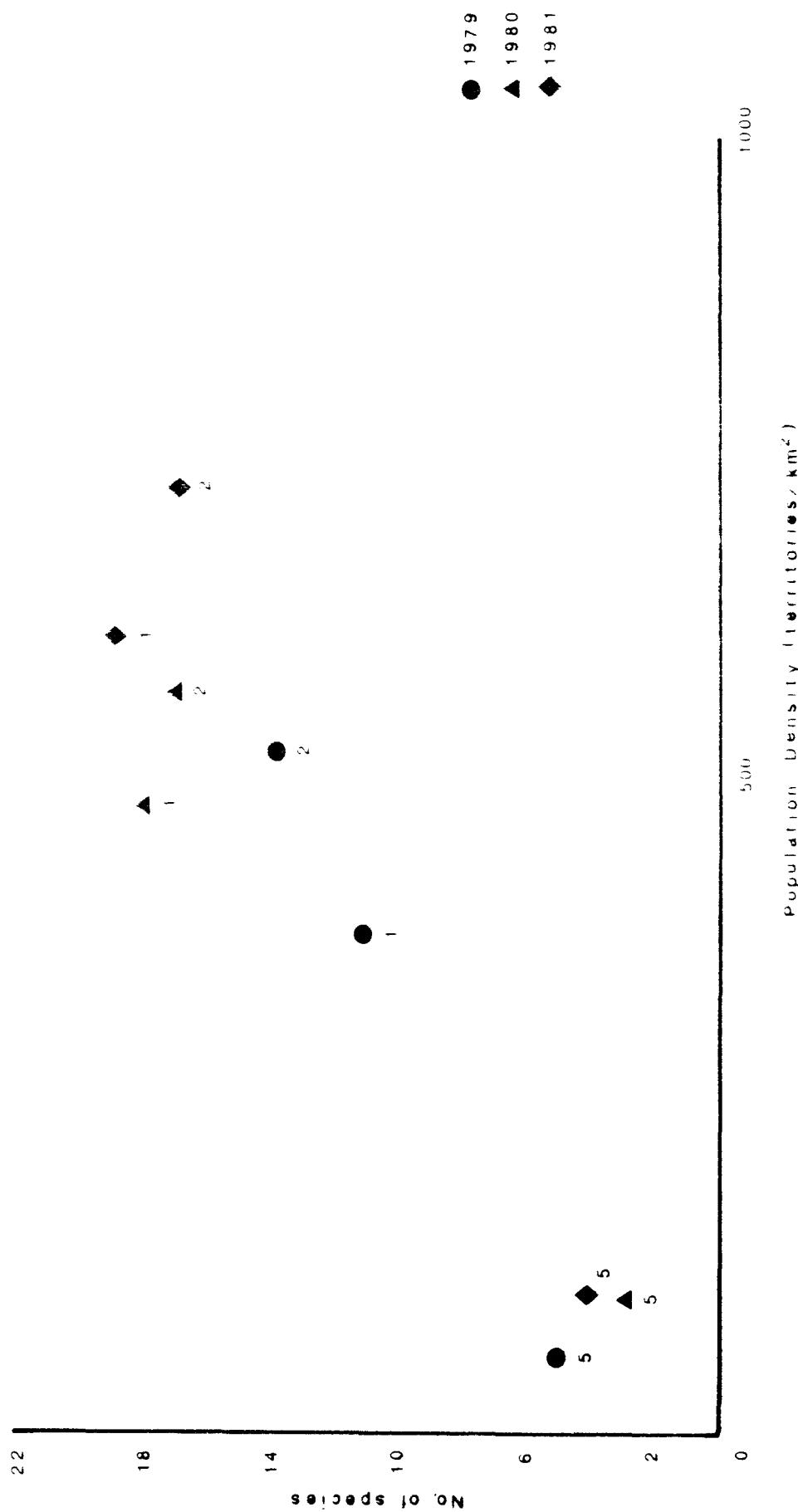


Fig 4.1: continued

B: Coniferous succession

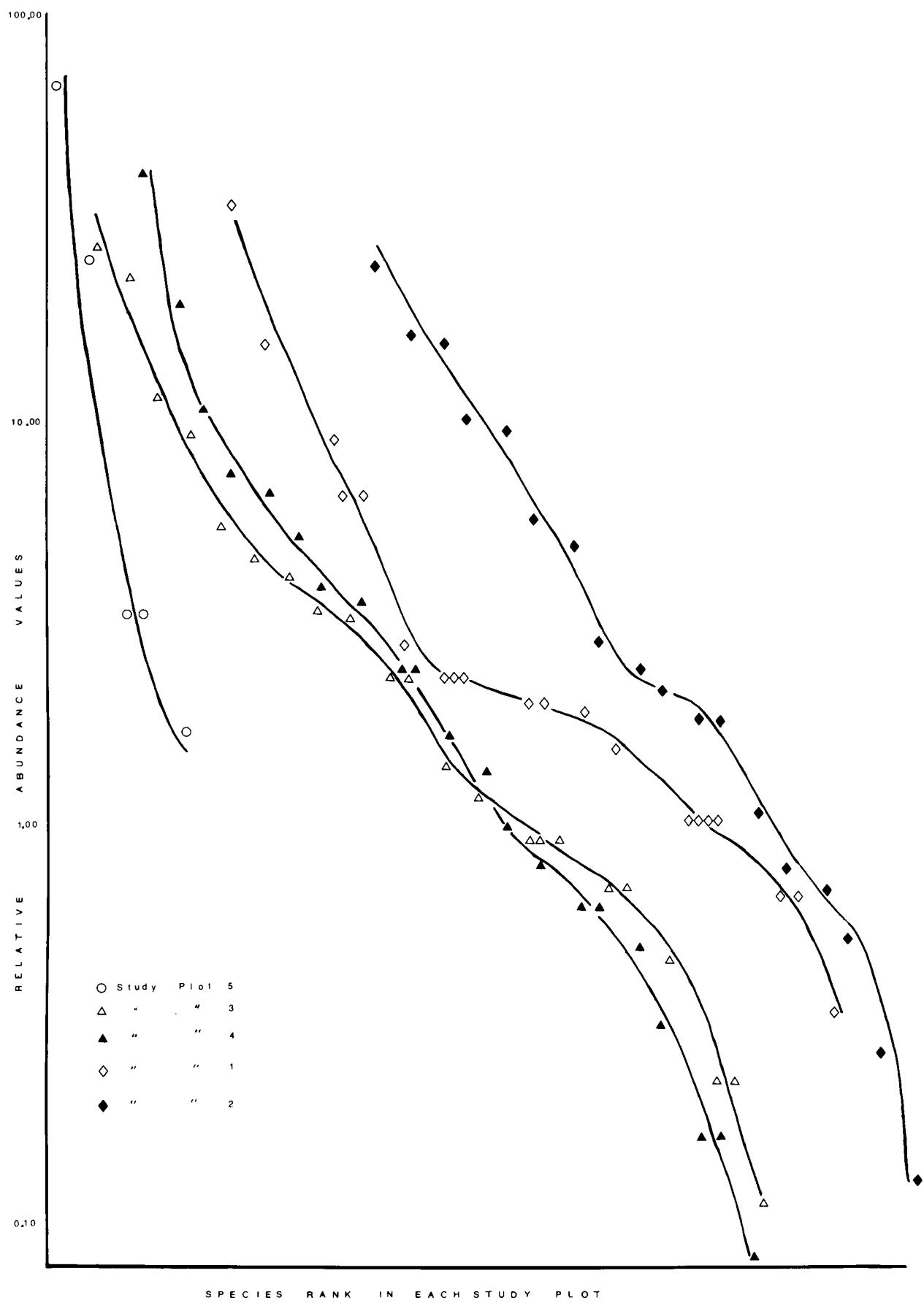


densities to increase once again.

Røv (1975) found that along an ecological gradient in deciduous forest in western Norway, the different values of diversity and dominance of the various bird communities along the succession could possibly be explained by increased diversification of the habitat, which implied increased niche space and decreased interspecific competition. One way of studying the importance of interspecific competition in a community is to plot relative abundance values on a logarithmic scale against species rank on a normal scale (Whittaker, 1965). The straighter the resulting line (that is, the relative abundance values follow a geometric sequence), the heavier the competition in that community. Figure 4.2 presents the abundance curves for the three-year relative abundance values (see Table 3.15) of the five Fife study plots. Obviously the straightest line is for plot 5 - the dune grassland - indicating heavy interspecific competition (between Skylark and Meadow Pipit) on an area with low habitat diversification. The four woodland study plots clearly have little interspecific competition, particularly in the two coniferous ones (1 and 2) whose abundance curves have pronounced kinks at the same level in each, indicating a concentration of species with R.A. values of between 1.00 and 3.00. The two deciduous study plots (3 and 4) have abundance curves which are less sigmoidal than the coniferous ones, and this possibly indicates a higher level of interspecific competition than in the coniferous plots.

Głowacinski and Weiner (1977) investigated the energetics of bird communities in a successional series through an Oak-Hornbeam forest in southern Poland. They found six stages in the forest succession from clear-cut through to 150-years-old forest. The authors suggested that birds represent one of the best gauges of forest ecosystem dynamics since they showed rapid responses to changes in habitat and showed quick occupation of any available ecological niche. In usefully comparing "avifaunal succession" with normal ideas of succession (involving a directional sequence of organisms), Głowacinski and Weiner described how the sequence in forest bird communities is represented by intense, time-

Fig. 4.2 : Curves of relative abundance and rank (fitted by eye)



dependent changes in quantitative and qualitative composition of the avifauna: species richness, diversity and population density increase in early stages, then decrease and rise again, following a bimodal curve. In addition to these structural parameters, energetics parameters also give rise to a bimodal curve, especially in terms of standing crop (maximum number of adult individuals multiplied by their body weight and caloric value of biomass), which has an "explosive increment" at the thicket stage in a succession due to a high population density comprised of several large species (Głowacinski and Weiner's figures include non-passerines). The authors concluded that the population peak at the thicket stage in their study was related to a diverse habitat structure, with a strong component of "edge effect" also present. Some features of a bird community at the thicket stage attained magnitudes equal to (diversity, energy flow) or even higher (production, standing crop) than at the mature forest stage.

Slagsvold (1977a) re-emphasized some of the findings by the various authors above, by showing how in his study of bird population changes after clearance of deciduous scrub in Southern Norway there was low population density and species diversity with few dominant pioneer species in the early seral stages, but that these species moved out, to be replaced by others as the habitat changed. Głowacinski and Weiner (1980), in a study similar to that reported by them in 1977, but this time in Scots Pine forest areas, again found a bimodal pattern in structural and bioenergetic parameters of the avifauna in redeveloping forests. This, they claimed, goes beyond the general ideas of succession put forward in Odum (1969), since the results did not confirm explicitly the prevalence of species of a higher biomass in older stages of forest succession.

Although it had been shown earlier elsewhere (Oelke, 1966; MacArthur, 1971) that, normally, breeding bird densities increase with an increasing number of vegetation layers, work by Järvinen and Väistönen (1976) showed that this was not so for the northernmost margins of Finnish forests, where other factors such as snow cover, temperature and stoniness of the

ground played a more important role. Prodon and Lebreton (1981) outlined the general methodology of studying successional stages and showed that in their study area in the eastern Pyrenees, other factors similar to those outlined by Järvinen and Väisänen (1976) (thus suggesting a latitudinal/altitudinal or arctic/alpine effect) and including details of the human history of an area, affected the progression of a succession. They believed, therefore, that the model used in most zoological studies of succession - where several sampling areas are chosen as representative of several stages of an ideal unidimensional succession in which each stage is presumed to result from the evolution of the immediately preceding one, ending in a single terminal stage - is acceptable for use only in forestry plantations or in plain forest successions subject to standardized forestry practices in a relatively uniform environment.

Milne (1974) investigated succession at a gravel pit in Huntingdonshire and found an initial rise, with a subsequent fall, in the numbers of species and sizes of populations occurring there. As the site aged and became more vegetated, the effects of terrestrial predators became less but a temporary link with a river during a flood allowed in aquatic predators such as Pike, and these had an adverse effect on the bird populations. In this case, therefore, succession did not lead ultimately to a high breeding population, but might have done so with proper management of both the habitat and the predators in it. In a study of a habitat similar to that investigated by Milne (1974) Bejček and Tyrner (1980) looked at the avian communities of four successional stages of spoil banks after surface mining of lignite in north-west Bohemia. Their results agreed closely with those of Karr (1968) in the U.S.A. who found that the succession of avian communities is influenced mostly by the vegetative cover as it changes from grassland through scrub to woodland.

In summary, along a successional vegetation gradient we can expect changes in species, an increase in the number of species, and an increase in the variety of forms. These changes are reflected by the breeding bird communities occupying each seral stage, where there is a tendency for population density and species richness to increase along the gradient,

but sometimes with interruptions due to environmental or anthropogenic factors.

4.3 (ii) Results of Present Study

In an earlier study the present author (Dougall, 1978a, unpublished; 1979, unpublished) used a modified repeated line transect method to investigate the effects of afforestation on the avifauna of moorland and uplands in southern Scotland, to the north and east of Moss' Dumfries and Galloway study areas. The methodology did not permit the derivation of reliable quantitative data on population densities and diversities, but it did produce qualitative data in terms of species richness at each stage of forest development, and in terms of changes in the variety of species between each stage in the one year studied (1977) (Table 4.12). Species unique to one stage of development are termed "habitat indicators" and are shown underlined in Table 4.12.

The species richness (including non-passerines) of each of the seven stages from moorland to clear-felled is as follows:- 4, 0, 7, 5, 12, 14 (and 18 where "edge" is included) and 1, reflecting an initial rise from the unplanted areas then a fall in the pre-thicket stage, followed by a continuous rise until clear-felling takes place. The changes in species composition mirror changes in the structure of the habitats with Red Grouse confined to heather moorland and only the Meadow Pipit of the open-country species persisting into woodland over 5 m in height at which stage scrub species move in, to be joined as the trees get taller, by woodland species and finally two species - Garden Warbler and Spotted Flycatcher - confined to the edge of the forest along a track. It would have been interesting to see if these latter two species also occupied clearings in the mature forest; and which species occupied the stage of 11 - 25 years-old forest, but in both cases no such habitat was available for study.

TABLE 4.12 Groupings of bird species in stages of forest succession, Craik Forest, 1977

| Stage | Moorland | Cultivated | Transitional | Pre-thicket | Thicket | (Pole) | Economically | Mature | Clear- |
|-----------------|----------|------------|---------------|--------------------------------|----------|-----------|--------------|-------------------|--------|
| | Habitat | Heather | Hay + Pasture | Open ground+ Young Conifers | Conifers | available | for | Conifers ; "edge" | Felled |
| Tree height (m) | - | - | ≤ 1.5 | 1.5-5.0 | 5.0-10.0 | study | ≥ 10.0 | > 10.0 | 0 |
| Tree age (yrs) | - | - | 4-5 | 5-10 | 10-11 | (11-25) | 25-28 | 28-29 | 28-29 |

| | | | | | | | | | |
|-------------------|---|--------|---------|---------------------|----------|---------|--------|---------|---------|
| <u>Red Grouse</u> | / | | | | | | | | |
| Curlew | / | absent | /-----/ | | | | | | |
| Skylark | / | absent | /-----/ | | | | | | |
| Meadow Pipit | / | absent | /-----/ | | | | | | |
| | | | | <u>Whinchat</u> | / | | | | |
| | | | | <u>Grasshopper</u> | | | | | |
| | | | | <u>Warbler</u> | / | | | | |
| | | | | <u>Reed Bunting</u> | / | | | | |
| | | | | <u>Pheasant</u> | / absent | /-----/ | | | |
| | | | | Dunnock | | /-----/ | absent | /-----/ | |
| | | | | Robin | | /-----/ | | /-----/ | |
| | | | | Willow Warbler | | /-----/ | | | |
| | | | | Wren | | /-----/ | | | /-----/ |

Note:

Species : habitat "indicator".

----- : species present and occupying territory.

() : includes family parties which may have bred elsewhere.

/absent/ : species absent from that stage.

/ : stage at which species ceases to occur.

Blackbird-----/ absent /-----/

Coal Tit-----/

Song Thrush-----/

Goldcrest-----/

Chaffinch-----/

Goldfinch-----/

Tawny Owl-----/

Woodpigeon-----/

Mistle Thrush-----/

Siskin-----/

Bullfinch-----/

(Crossbill)-----/

Garden

Warbler/

Spotted

Flycatcher/

The use of a tested and more reliable methodology, and the continuation of a study over three breeding seasons (1979-81) led to the better quality of data in the present study of successional stages from dune grassland to mature woodland in North-east Fife. As described previously in the chapter on results, the mapping method was used to estimate the sizes of the populations of territory-holding passerines in five study plots between 1979 and 1981 inclusive. Tables 3.3, 3.4 and 3.15 present the basic population data in terms of absolute numbers, densities, diversity index values, species richness and relative abundances. These parameters have been combined and are presented in Table 4.13 here, which illustrates the changes in the bird communities along both the deciduous and coniferous successional gradients in North-east Fife.

Since the habitat in each of study plots 1, 3 and 4 is not of uniform age, but itself exhibits a degree of succession it is difficult to isolate this effect from any discussion of succession overall along the two gradients - however this is not necessarily a fault of the method or the study plots chosen, but rather reflects a more realistic situation. So far as both successions are concerned, there is

- (1) an increase in population density as the habitats become older; and with both the deciduous and coniferous stages there is
- (2) a rapid increase then small drop in the species richness with
- (3) a rapid initial rise in the diversity index values, followed by their levelling off.

Changes in the species composition between the seral stages can be seen in Table 3.15, where each community (as revealed by relative abundance values) is described. From this, so far as the most dominant species are concerned, none of the species occurring on the dune grassland also occurs in any of the other communities as a dominant feature. With the deciduous plots, there is a wide overlap in mutually-occurring species, with only the dominance values changing, largely as a result of the Starling colony in the mature birch/alder woodland. With the coniferous plots, the main difference is in the occurrence of Long-tailed Tit and Great Tit as

dominants in only the semi-natural plot, and the occurrence of Wren and Dunnock as dominants solely in the commercial plot.

Looking at the density index values and differences in them in Table 4.13 of this chapter, six groups emerge in the deciduous and five in the coniferous successions. These groupings (similar groups in terms of differences in index values between study plots are given the same letter) are derived from an analysis of when a species first occurs along the successional gradient, and where a species occurs in two or more stages along the gradient, it is ranked according to its index value, indicating in which habitat it occurs at the higher population level, equalled for variation in the plot size. (Thus the deciduous succession does not have a "C" grouping, since no species in the first stage occurs there at a lower density than it does in the second stage.) The Carrion Crow can perhaps be eliminated from discussion in relation to stage 1 - the dune grassland - since its appearance in the stage 1 column in Table 4.13 is due to a single nesting attempt in an isolated tree on the grassland; nevertheless this does show that interruptions to an otherwise smooth pattern can occur, since the Crow's absence from the commercial coniferous plot was probably due to persecution by human agency.

Of the open-country species, only the Meadow Pipit occurred in woodland of the youngest stages; Skylark, Wheatear and Reed Bunting were confined solely to the dune grassland.

Three species occurred solely in the birch/willow scrub - Jay, Linnet and Crossbill - the latter species being included solely because part of a large territory in the adjacent commercial forest overlapped with the deciduous scrub. Two species - Robin and Bullfinch - occurred at higher densities in the scrub than in the more mature birch/alder woodland, while three species occurred only in this latter habitat - Sedge Warbler, Spotted Flycatcher and Dunnock. A possible reason for this is that the more open nature of the mature woodland allowed areas of rushes to develop in hollows - which attracted Sedge Warblers. The higher and more open canopy allowed the aerial-feeding Spotted Flycatcher to operate,

and the more open ground below allowed the terrestrial-feeding Dunnock to forage. The remaining species-grouping - F - represents those species occurring in both scrub and mature woodland, but with a probable preference for the latter since their Density Index values were higher there (this grouping encompasses all hole-nesting species). Thus, along the successional gradient from dune grassland through birch/willow scrub to mature birch/alder woodland there are progressive changes from species occupying the open grassland through those which occur both in that and in scrub, those which occur only in scrub, the vast majority which occur in both scrub and mature woodland but at higher densities in the latter, to those which occur solely in the more open mature woodland.

There were no representatives of this last grouping in the coniferous succession, nor any species which occurred solely in the semi-natural plot, although two - Meadow Pipit and Carrion Crow - did occur in the semi-natural plot but not in the commercial one. The probable reasons for this are the lack of persecution of the Crow on the semi-natural plot and its more open nature, particularly at the seaward edge, which allowed the Pipit to hold territory. Of the remaining 18 species which occurred in both the more open and generally younger semi-natural plot and in the older, more uniform and closed commercial plot, eight had higher Density Index values in the former and ten in the latter. It is difficult to explain this difference other than that the habitats of the study plots may be quite similar and may, in fact, represent two different forms of the same successional stage, with certainly no biological maturity of habitat being involved since the oldest trees were only 25 years old when the censuses reported here were conducted. However, the much higher Density Index values of the commercial plot would, from what is known from the literature of succession, suggest it was further along the gradient towards maturity and climax than was the semi-natural plot. There is scope for further study here.

Having described the successional stages involved with the Fife study plots, and the species-groupings along the gradients, how does this tie in with work done elsewhere, and does it contribute anything to our knowledge of avifaunal succession?

TABLE 4.13 Avifaunal succession, based on a three year density index*

| Approx. age of tree cover: [#] | Deciduous succession | | | Approx. age of tree cover: [#] | Coniferous succession | | |
|---|----------------------|---------------|---------------|---|-----------------------|---------------|---------------|
| | 0 | 1-120 | 1-230 | | 0 | 1-25 | 15-25 |
| Study plot | 5 | 3 | 4 | Study plot | 5 | 1 | 2 |
| Skylark | 178.80 | | | Skylark | 178.80 | | |
| Wheatear | A 8.94 | | | Wheatear | A 8.94 | | |
| Reed Bunting | 8.94 | | | Reed Bunting | 8.94 | | |
| Meadow Pipit | B 67.05 | 2.62 | | Meadow Pipit | B 67.05 | 5.07 | |
| Jay | | 10.48 | | Carrion Crow | C 4.47 | 15.21 | |
| Linnet | D | 10.48 | | Chaffinch | | 570.00 | 437.40 |
| Crossbill | | 10.48 | | Treecreeper | | 35.49 | 34.02 |
| Robin | E | 131.00 | 129.60 | Great Tit | | 30.42 | 14.58 |
| Bullfinch | | 7.86 | 4.32 | Siskin | | 27.89 | 12.15 |
| Starling | | 36.68 | 1028.16 | Blue Tit | E | 22.82 | 19.44 |
| Chaffinch | | 309.16 | 483.84 | Bullfinch | | 15.21 | 9.72 |
| Willow Warbler | | 259.38 | 272.16 | Jay | | 10.14 | 4.86 |
| Wren | | 62.88 | 190.08 | Crossbill | | 10.14 | 2.43 |
| Blue Tit | | 104.80 | 164.16 | Coal Tit | | 192.66 | 291.60 |
| Great Tit | | 52.40 | 103.68 | Robin | | 228.15 | 281.88 |
| Coal Tit | | 47.16 | 90.72 | Willow Warbler | | 126.75 | 184.68 |
| Redpoll | F | 39.30 | 60.48 | Goldcrest | | 96.33 | 170.10 |
| Treecreeper | | 26.20 | 60.48 | Wren | F | 15.21 | 104.49 |
| L-t Tit | | 26.20 | 43.20 | Blackbird | | 44.56 | 87.48 |
| Blackbird | | 15.72 | 34.56 | Redpoll | | 35.49 | 51.03 |
| Carrion Crow | 4.47 | 13.10 | 21.60 | Song Thrush | | 35.49 | 43.74 |
| Yellowhammer | | 5.24 | 17.28 | Dunnock | | 15.21 | 38.88 |
| Song Thrush | | 2.62 | 12.96 | L-t Tit | | 30.42 | 34.02 |
| Mistle Thrush | | 2.62 | 4.32 | | | | |
| Siskin | | 1.31 | 2.16 | | | | |
| Sedge Warbler | | | 25.92 | | | | |
| Spotted Flycatcher | G | | 17.28 | | | | |
| Dunnock | | | 8.64 | | | | |
| Range of density | 60-105 | 333-481 | 894-953 | | 60-105 | 383-613 | 522-729 |
| Range of H' | 0.77- 0.92 | 2.19- 2.30 | 1.91- 2.20 | | 0.77- 0.92 | 1.77- 2.30 | 2.14- 2.33 |
| Species richness | 5 | 22 | 21 | | 5 | 20 | 18 |

* The Density Index is simply the total population over three years of each species expressed in terms of territories per square kilometre.

Age of tree cover is in years, derived from historical documents, maps and aerial photographs.

4.3 (iii) Results and relevance of other work

Lack (1933, 1939) investigated the changes in bird communities as the East Anglian Breckland became afforested. He used a simple belt transect method, but did not allow for variations in species conspicuousness and so his results cannot be regarded as wholly reliable. He described how the short grazed turf was dominated by Stone Curlews, Skylarks and Wheatears, but as grazing pressure became relaxed, Skylarks and Meadow Pipits became dominant before they in turn were replaced by the bird communities of scrubland and then woodland.

Morley (1940), in a rather subjective study, noted how bird species re-colonized an area of burnt mixed woodland in East Sussex. He studied various habitats at different stages after the fire, and his general finding was that some species could occupy recently-burned ground and that species richness increased as the vegetation cover improved.

Martin (1960) in a mapping study of bird populations in relation to forest succession in Ontario made an important finding in that every stage of the forest succession did not necessarily have a distinct bird community; rather an intergrading or gradual change between communities was found. This, of course, has since been reported in many recent studies.

From his work in Finnish forests, Haapanen (1965, 1966) drew conclusions on the habitat preferences of several species in the northern forest context, and was able to amplify the earlier findings of Kluijver and Tinbergen (1953) and Glas (1960) on the "buffer effect", where, in Holland, territorial Chaffinches settled down earlier in the breeding season in their preferred habitat of mixed woodland than in the suboptimal pine woods. Territorial behaviour meant that the early settlers filled the optimal habitat to its capacity so that the surplus of later arrivals (possibly first-time breeders) had to move out to the suboptimal habitat where conditions were not so favourable for successful breeding. In Finland, in years even when the overall Chaffinch population was low, only the preferred pine stands came close to full capacity while the

population density in the suboptimal spruce stands was considerably lower than in other years. This was thought to be due to the snow-cover and frozen ground melting earlier in the pine stands than in the spruces.

Røv (1975) investigated three stages along an ecological gradient from temperate deciduous forest through prealpine birch forest (on both north-facing and south-facing slopes) to subalpine birch forest. He used the mapping method and studied changes in and between the following measures along the gradient:- Bird Species Diversity (B.S.D.), Foliage Height Diversity (F.H.D.) and a community Dominance Index (D.I.). His general findings were that B.S.D. varied directly with F.H.D. and inversely with D.I. B.S.D. was positively correlated with both vegetation cover and diversity of stratification, whereas D.I. was negatively correlated with the same factors. His results suggest that for a given vegetation structure along an ecological gradient, the diversity of the bird community is of about the same order of magnitude in Scandinavian deciduous forests as in corresponding habitats in North America.

Głowacinski and Järvinen (1975) used four indices to quantify the rate of secondary succession in Polish Oak-Hornbeam forests and Finnish coniferous forests. They found differences between the two forest types, which they accredited to the effects of climate and soil: the Polish Oak-Hornbeam succession made a rapid start but the rate of succession decreased monotonously with time, whereas the Finnish coniferous forests required a period of 5-25 years to reach their maximum rate of succession. This had implications for conservation of the habitats and their bird communities, and for ideas on the evolution of communities within habitats.

Slagsvold (1977a) investigated the bird population changes in an area of southern Norway after clearance of deciduous scrub either by cutting or by spraying and then replanting with spruce. He used the mapping method to quantify the bird populations and also sampled part of their food supply - invertebrates- by trapping the invertebrates on the ground and in the branches. Slagsvold found reductions in the bird populations, after clearance, of 31% in the cut areas and 29% in the sprayed ones; in addition

the populations of the Willow Warbler were especially badly-hit. The avifauna recovered and increased in the clear-cut area, but not in the sprayed one, even after five years, due probably to the effects of spraying on the populations of invertebrates. The population changes recorded for each species reflected that species' preference for certain successional stages i.e. species able to occupy and breed in pioneer habitats did not decrease so much as species which preferred older forest.

Bejček and Tyrner (1980), in their study of primary succession in an area of surface mining for lignite in Bohemia, looked at four stages of spoil banks: (a) 2-3 years after strip-mining; (b) 6 years after stripping; (c) 20 years after stripping and 6 after reforestation; (d) 20 years after reforestation. Corresponding to these stages were changes in the avifauna from a community composed of open-country species to one of woodland species. There was an increase in species richness from 3 to 6, 6, and 14, and overall increases in population density and Diversity Index values, but with fluctuations in both viz. population density as follows: 17.7 prs/km², 183.3, 160.0 and 410.0 and Diversity Index values were 1.5613, 2.4853, 2.1250, 3.5766. This suggests a "hiccup" between the stages 6 years after stripping and 6 years after reforestation. However, firm conclusions cannot be reached since the data used in the study came from separate study areas in Bohemia and also different series of years with no attempt made to look for differences within the data due to these factors.

However, three sets of published results are more reliable than the above and are much more relevant to the present study. These sets represent the work of Moss (1979) and Moss et al (1979); Głowacinski and Weiner (1980); Bednorz (1982) and Bogucki and Bednorz (1982).

Moss and his associates used the mapping method in plots composed, wherever possible, wholly of Sitka Spruce in south-west Scotland from 1976-78, to investigate the changes in the avifauna as hill grazing ground became afforested. They looked at five different stages:- (1) unplanted sheep-walk of either grass or heather; (2) establishment stage plantation;

(3) thicket stage; (4) polestage; (5) thinned plantation. Their results in terms of all-species richness, total songbird density, songbird Diversity Index, and "colonization" of the various planted stages are presented in Table 4.14, which can usefully be compared with Tables 4.12 and 4.13 detailing work by the present author. There are close similarities between the groupings of bird species in Tables 4.12 and 4.14 both of which represent upland study plots.

Moss et al found the lowest bird population densities on unplanted heather, with unplanted grass being not much higher. This contrasts with Dougall's (1978a unpublished) findings where unplanted grass held no breeding birds at all. However, there is agreement in the studies on the species composition of such habitats in S.W.Scotland, the Scottish Borders and N.E.Fife, all of which were dominated by Skylark and Meadow Pipit with Wheatear occasionally making an appearance. In general, as the Sitka plots matured, Moss et al found the densities increasing although one thicket plot (A7) held densities as high as in later stages. Diversity Index values were, as expected, low on the unplanted plots and decreased immediately after planting when a sparsely-populated community was dominated by one species - the Meadow Pipit. (This is somewhat similar to the case of the mature birch/alder woodland in Fife, where the community was dominated by a Starling colony, thus lowering the Diversity Index). Diversities were highest on the thicket plots and tended to decrease slightly at the later stages when habitat structure became simpler. In general, Moss et al concluded that total songbird densities increased steadily over the first 20 years of a plantation's development, after which they remained at a level approximately four times that of songbirds on the same ground before planting.

From the present study in N.E.Fife, the songbird population density in the 15-25 years old planted coniferous plot was 522 territories/km² in 1979, 571 in 1980 and 729 in 1981 and these were greater than those on the unplanted ground in the same years (60, 103 and 105 territories/km²) respectively by factors of 8.70, 5.54 and 6.94. In addition, the Fife study provides what may be the first comparative figures for the songbird

TABLE 4.14 Habitat distribution of species observed on census plots (after Moss et al, 1979)

o = present; * = song-bird holding territory

| Development stage | unplanted grass | | | unplanted heather | | | establishment | | | | thicket | | polestage | | | thinned | | | | |
|-------------------|-----------------|----|----|-------------------|----|----|---------------|----|----|-----|---------|----|-----------|----|----|---------|----|----|----|----|
| | C5 | A9 | A8 | E3 | E1 | C8 | E4 | E2 | C4 | A10 | A7 | C3 | C7 | C2 | A5 | A6 | C1 | A3 | C6 | A2 |
| Plot | | | | | | | | | | | | | | | | | | | | |
| Golden Plover | o | | | o | o | | | | | | | | | | | | | | | |
| Wheatear | * | | | o | | | | | | | | | | | | | | | | |
| Pied Wagtail | o | | o | | | | | | | | o | | | | | | | | | |
| Snipe | o | o | o | | o | o | | | | | o | | | | | | | | | |
| Stonechat | * | | | | | | o | | * | * | * | | | | | | | | | |
| Curlew | o | o | o | o | o | | | | | | o | | o | | | | | | | |
| Red Grouse | o | o | | o | o | | | o | o | | o | o | | | | | | | | |
| Black Grouse | o | o | o | | | o | | o | o | | o | o | | | | | | | | |
| Skylark | * | * | * | * | * | | | * | * | o | | * | * | | | | | | | |
| Reed Bunting | o | o | | | | | | o | * | | * | o | o | | | | | | | |
| Meadow Pipit | * | * | * | * | * | | * | * | * | * | * | * | * | * | * | * | | | | |
| Tree Pipit | o | | | | | | | | | | o | | * | | | | | | | |
| Mistle Thrush | o | o | o | | | | | | | | | | | * | o | | o | * | o | |
| Song Thrush | o | | o | | | | | | | | | | * | * | | * | o | * | * | * |
| Chaffinch | o | o | * | | | | o | * | | * | * | * | * | * | * | * | * | * | * | * |
| Lapwing | o | | | | | | | | | | | | * | | | | | | | |
| Partridge | o | o | | | | | | | | | | | | | | | | | | |
| Kestrel | o | o | | | | | | | | | | | | | | | | | | |
| Starling | o | | | | | | | | | | | | | | | | | | | |
| Yellowhammer | o | | | | | | | | | | * | | | | | | | | | |

/Continued

TABLE 4.14 Continued

| Development stage | unplanted grass | | | unplanted heather | | | establishment | | | | thicket | | polestage | | | thinned | | | | |
|---------------------|-----------------|----|----|-------------------|----|----|---------------|----|----|-----|---------|----|-----------|----|----|---------|----|----|----|----|
| Plot | C5 | A9 | A8 | E3 | E1 | C8 | E4 | E2 | C4 | A10 | A7 | C3 | C7 | C2 | A5 | A6 | C1 | A3 | C6 | A2 |
| Redshank | | | | | | o | | | | | | | | | | | | | | |
| Short-eared Owl | | | | o | o | o | o | | | | | | o | | | | | | | |
| Grasshopper Warbler | | | | * | | * | | | * | * | | | o | | | | | | | |
| Whinchat | | | | * | * | * | * | * | * | | | | | | | | | | | |
| Wren | | | | * | * | | | o | * | * | * | * | * | * | * | * | * | * | * | * |
| Redpoll | | | | | o | o | * | * | * | * | * | * | o | o | | | | | | |
| Willow Warbler | | | | | * | o | * | * | * | * | * | * | * | o | o | * | | | | |
| Whitethroat | | | | | | * | | | o | | * | | | | | | | | | |
| Cuckoo | | | | | | | o | o | | | | | | | | | | | | |
| Sedge Warbler | | | | | | | * | | | | | | | | | | | | | |
| Linnet | | | | | | | * | | | | | | | | | | | | | |
| Blackbird | | | | | | | | o | | | | o | o | | | | | | | |
| Chiffchaff | | | | | | | | | o | | | o | o | * | * | | | | | |
| Bullfinch | | | | | | | | | o | | | * | | * | * | | o | o | | |
| Dunnock | | | | | | | | | * | * | o | * | * | o | * | o | * | | | |
| Coal Tit | | | | | | | | | * | o | * | * | * | * | * | * | * | * | * | * |
| Goldcrest | | | | | | | | | * | * | * | * | * | * | * | * | * | * | * | * |
| Robin | | | | | | | | | * | * | * | * | * | * | * | * | * | * | * | * |
| Woodcock | | | | | | | | | o | | | | | | | o | | o | | |
| Crossbill | | | | | | | | | o | o | * | o | o | o | o | * | * | * | * | |

/Continued

TABLE 4.14 Continued

| Development stage | unplanted grass | | | unplanted heather | | | establishment | | | thicket | | | polestage | | | thinned | | | | |
|---------------------------|-----------------|---------------|--------------|-------------------|---------------|----|---------------|--------------|--------------|----------------|------|--------------|--------------|------|--------------|----------------|--------------|------|---------------|-------|
| Plot | C5 | A9 | A8 | E3 | E1 | C8 | E4 | E2 | C4 | A10 | A7 | C3 | C7 | C2 | A5 | A6 | C1 | A3 | C6 | A2 |
| Siskin | | | | | | | | | | | | | | * | o | o | * | o | * | * |
| Willow Tit | | | | | | | | | | | | | | o | | | | | | |
| Blackcap | | | | | | | | | | | | | | o | | | | | | |
| Blue Tit | | | | | | | | | | | | | | o | | | | | | |
| Great Tit | | | | | | | | | | | | | | o | | | | | | |
| Sparrowhawk | | | | | | | | | | | | | | o | | | | | | |
| Long-tailed Tit | | | | | | | | | | | | | | * | * | | | | | |
| Treecreeper | | | | | | | | | | | | | | o | * | o | * | * | | |
| Tawny Owl | | | | | | | | | | | | | | o | | o | | | | |
| Songbird* | 72- | 86- | 130- | 38 | 45 | 71 | 53 | 72- | 123- | 204 | 358 | 252 | 230 | 301 | 305 | 312 | 387 | 341 | 369 | 318 |
| Density | 86 | 93 | 130 | | | | | 100 | 167 | | -478 | | -290 | -442 | | -409 | -425 | -385 | -400 | -394 |
| Songbird Diversity Index* | 0.98 -1.10 | 0.59 -0.74 | 0.65 0.66 | 0.52 -0.69 | 0.61 -1.48 | | | 1.25 0.29 | 1.99 0.97 | -2.04 -0.99 | | 1.84 1.63 | 1.53 1.65 | | 1.74 1.84 | -1.53 -1.81 | 1.59 1.48 | | 1.50 -1.49 | -1.75 |
| Years of data | a | c | d | g | g | f | g | c | c | g | c | e | c | a | e | b | d | d | b | b |

* From Appendix 1, years involved for ranges
 (of Moss et al)

- a: 1976-78
- b: 1976-77
- c: 1977-78
- d: 1976, 78
- e: 1976
- f: 1977
- g: 1978

population densities of a semi-natural coniferous area of the same species on the same ground. The songbird population density on the self-seeded coniferous plot was 383 territories/km² in 1979, 484 in 1980 and 613 in 1981 (Results Section, Table 3.4); and these are 6.38, 4.70 and 5.84 times the densities on the unplanted ground in each respective year.

Although the semi-natural plot was not of so uniform an age as the commercial plot, the above figures suggest that the commercial plot was able to support higher songbird population densities than would have occurred naturally in coniferous woodland at approximately the same age. Since Moss et al were working in predominantly Sitka Spruce areas and the present author among Scots Pines, no conclusions can be reached regarding the differentials between unplanted and planted areas in uplands (Moss et al were working between 140 and 365 m.a.s.l., the present author between 5 and 10 m.a.s.l.) and between unplanted and planted areas near sea-level, although the differences in the differentials (factor of 4 in upland areas and 5.5 - 8.7 at sea-level) suggest that future work might provide interesting data for comparison.

Głowacinski and Weiner (1980) did, however, investigate the same vegetation species as in the present Fife study - semi-natural Scots Pine forest. As discussed earlier in this thesis, they investigated five successional stages, but each study plot was rather small and probably gave rise to edge effects. Their study plots represented the following stages:- I clear-cut; II 4 years old establishment plantation; III 10 years old dense thicket; IV 35 years old pole stage; and V 80 years old mature forest. It is arguable whether or not the clear-cut stage should come first or last along the successional gradient.

Unfortunately the authors did not present a diagram illustrating the species-groupings along the succession as was done by Moss et al (1979) and by the present author and in the more recent work reported below, but Table 4.15 illustrates the main points from Głowacinski and Weiner (1980) for passerine species only. The main differences between the species in it and in similar diagrams by Moss et al and the present author is that

one species found in the "open" habitat is able to occupy all four woodland stages, and that several species which occur by the pole stage in the British Isles do not occur until the mature stage in Poland e.g. Long-tailed Tit, Blue Tit, Great Tit and Treecreeper. Clearly the mature forest held the highest population densities and most species, with 14 of the 25 being found only in that habitat, and throughout the succession there was an increase in species-richness, Diversity Index values and population density (represented graphically in Figure 2 of Głowacinski and Weiner, 1980) which contrasts with other studies where there is usually a decrease at some stage.

One such study, in addition to those discussed previously, is by Bogucki and Bednorz (1982). They investigated the secondary succession in developing Scots Pine forests, from open clearings to mature stands, also in Poland. They found three main stages, relating to three main bird community types: open areas, coniferous "bushes" and coniferous forests, with seven phases being involved, depending on the ages of the trees. The open stage contained one phase - clearings and plantations less than 7 years old, and the structure of the bird community was very simple. The coniferous bush stage (trees 8-30 years old) was made up of two phases - bushes, followed by thickets. Overall, the Willow Warbler dominated this stage and the population density of all birds first of all increased then decreased, presumably related to the increasing density of the canopy. The third stage had four phases and was dominated overall by the Chaffinch. The structure of the bird community was more complex than previous stages, with an initially stable breeding density, which then increased into the mature and very old (100+ years) Pine forest.

The final study of which results (preliminary though they are) will be discussed here is by Bednorz (1982) and is of particular relevance to the present study since it investigated succession on a coastal duneland area which had been colonized by Scots Pine - analogous to plot 1 in N.E.Fife.

Bednorz used the mapping method on nine study plots, ranging from 14.5 - 75.0 ha (as recommended by I.B.C.C., 1969, although not followed strictly)

TABLE 4.15 Passerine species - groupings along a successional series in semi-natural Scots Pine forest in Poland (after Głowacinski and Weiner 1980)

| Successional stage: Age of plantation (years) | Clear-cut | Establishment | Thicket | Polestage | Mature |
|--|-----------|---------------|---------|-----------|--------|
| | 4 | 10 | 35 | 80 | |
| Stonechat | * | | | | |
| Tree Pipit | * | * | * | * | * |
| Red-backed Shrike | | * | | | |
| Whitethroat | * | | | | |
| Yellowhammer | * | | * | | |
| Lesser Whitethroat | * | * | * | * | |
| Willow Warbler | * | * | * | | * |
| Robin | | * | * | | * |
| Blackbird | | * | * | | * |
| Song Thrush | | * | * | | * |
| Garden Warbler | | * | | | * |
| Jay | | * | * | | * |
| Wood Warbler | | | * | | * |
| Chaffinch | | | | * | * |
| Coal Tit | | | | * | * |
| Blackcap | | | | * | * |
| Blue Tit | | | | | * |
| Great Tit | | | | | * |
| Collared Flycatcher | | | | | * |
| Nuthatch | | | | | * |
| Treecreeper | | | | | * |
| Pied Flycatcher | | | | | * |
| Short-toed Treecreeper | | | | | * |
| Starling | | | | | * |
| Chiffchaff | | | | | * |
| Crested Tit | | | | | * |
| Golden Oriole | | | | | * |
| Restart | | | | | * |
| Long-tailed Tit | | | | | * |
| Marsh Tit | | | | | * |
| Population density (prs/km ²) | 23 | 150 | 340 | 402 | 570 |
| Number of species | 2 | 6 | 9 | 11 | 25 |

in the years 1971-72, 1974 and 1977 but each study plot was censused in only one year. The study area was part of the extensive duneland along the southern coast of the Polish Baltic, and the plots studied were as follows:-

- I : sandy beach
- II : white dunes (mobile)
- III : open dark dunes (stabilizing)
- IV : dark dunes with single trees and small clumps of trees and bushes (stable)
- V : dark dunes with numerous single trees and greater clumps of young Pine forest
- VI : 11-40 years old coastal pine forest
- VII : 35-40 years old " " "
- VIII : 41-80 years old " " "
- IX : 91-130 years old " " "

(Stages III-VI inclusive correspond with those in Fife plot 1).

Bednorz distinguished three phases of development from the sandy beach, through young dunes being colonized by taller vegetation and young trees, to coastal pine forest. As in the present author's work in the Scottish Borders, as well as in N.E.Fife, Bednorz found that each phase of the succession had some species unique to it (the "indicator-species" of Dougall, 1978a). Bednorz found that the species-richness of his study plots increased steadily along the succession, but that the population density (including non-passerines) fluctuated. In the first four stages, representing low and homogeneous vegetation, the density ranged from 45-101 prs/km² but then increased rapidly as the vegetation became taller and more diverse in structure, reaching a maximum of 296 prs/km² in stage VII, decreasing to 226 prs/km² in the older forest stages (this maximum is well below the range of 383-613 passerine territories/km² found in the slightly younger plot 1 of the present study). Decreases were also found among the Diversity Index values, but which increased overall along the succession. The decreases occurred at stages II and VI, which both

represent early stages in development - the first in dune vegetation, and the second in coniferous forest - at which stages the bird communities are dominated by one or two very numerous species: Skylark on the dunes and Willow Warbler and Chaffinch in the young forest. Bednorz concluded that in studying a successional series, the transition of one community into the next one is accompanied by complete changes in the species composition, dominance and Diversity Indices.

Other studies, including the present one, do not wholly support the idea of complete changes being involved along a succession, but there does seem to be a general pattern of gradual changes. These changes include an increase in population density as habitats become older, with usually a levelling-off at mature stages; an initial rise, followed by a fall, in species-richness; which is accompanied by a rapid initial rise in Diversity Index values, which then level off or decrease. However, given that changes both in vegetation and in bird population parameters along a succession are progressive and not sudden, there are identifiable groupings of species within each definable seral stage, and these have been commented on by several of the authors in the discussion above.

Overall, Bogucki and Bednorz (1982) consider that birds are a very suitable medium for studying the changes associated with a vegetation successional series since they inhabit all the above-surface vegetation strata and are relatively easy to discover, identify and count in field studies of the type outlined in this thesis.

4.4 CONCLUSIONS

In this chapter have been two main areas of discussion of the results presented in the previous chapters: discussion of each of the study plots, and of the successional gradients on which they occur.

A review of the literature concerning the same broad habitat types as found in the present study has been given and the difficulties, both on temporal and spatial levels, of comparing results have been discussed. It was found that very little work in the given habitats near sea-level has been carried out, and so the results of the present study are important in this respect. The results also add much to our knowledge of the avifauna of commercial forestry areas since a comparison was made between the breeding bird populations of a commercially-planted area and of a self-seeded one. The recent literature revealed an increase in the numbers of studies on birds published by professional foresters and it is to be hoped that this continues and perhaps improves the sometimes poor relations between the forestry and conservation bodies.

It was found that the four woodland habitats studied on the Tentsmuir/Earlshallmuir dune complex are rich in terms of the diversities and densities of their passerine breeding populations when compared with studies carried out elsewhere in the British Isles and in continental Europe. It is in this latter geographical region that most work appears to have been conducted on "avifaunal succession", and a review of the results was presented, comparing them with the findings of the present study. One recent study on the Polish Baltic coast parallels closely the present one, and it has been concluded that birds are a very suitable medium for studying the changes associated with vegetation successional series.

CHAPTER 5 CONCLUSION

The time available for conducting the present study - three breeding seasons - although a long period in the life-span of individual songbirds, was short in terms of the life of individual communities. Thus the results presented here must be regarded as preliminary in nature, only touching on the surface of a complexity of community parameters and inter-relationships at one point in time.

A review of the literature suggested that the mapping method, in spite of several drawbacks, is the best technique presently available for estimating the populations of breeding songbirds. The present study has served to outline some of the drawbacks involved with the method, especially with regard to problematical species, but it found that mapping was not difficult to conduct by one person - even in far from ideal circumstances - and that the results obtained from its use were far more accurate and reliable than those from simple line transects, the only other method which was suited to the habitats investigated. The present author found no mechanical problems with mapping during three seasons of use, and analytical and biological problems encountered centred around subjectivity in the construction and interpretation of species maps in the laboratory and of the behavioural idiosyncrasies of species in the field. It was felt that personal experience of the study plots and the birds inhabiting them was an aid in analysing the field data, and since the same person carried out the fieldwork and analyses over the three years then errors were probably held constant. Extrinsic factors such as the "workability" of the habitats, and phenological events, also influenced efficiency of fieldwork but these factors would be common to any method employed. The simple line transect sampling procedure had little to recommend it, and so many adjustments would have been necessary to the very basic data generated by its use to bring it up to mapping data standards, that it would have ended up by being as time-consuming as using mapping censuses. Compared to mapping, transect sampling produced no evidence of breeding by the birds encountered; dominance values and relations were quite different; and it did not reveal all the species detected by mapping, whereas the converse held. Since mapping, and not transect sampling, produces

results in terms of densities which have much of ecological significance and it has so many advantages over transects, it was adopted as the field method for gathering the ornithological data in this thesis.

The habitat data for each of the five study plots was generated from field-work employing 10 m. radius vegetation sampling circles, and from laboratory work utilising maps from the 18th century to the present day, in conjunction with high-quality colour and black-and-white aerial photographs. As well as the plant species themselves, the following details were also recorded since the literature suggested they were of relevance to habitat selection by birds: presence of brashed timber; habitat interfaces and "edge", light intensity, trunk spacing, trunk diameter, general height of tree cover, height at which canopy was most widespread, percentage of ground covered by the canopy, and the height and type of the ground cover. Previous work by others suggested a good general relationship between Bird Species Diversity (B.S.D.) and Foliage Height Diversity (F.H.D.) but there were statistical problems with the way in which F.H.D. had been calculated in the past, so two surrogate measures of this (diversity indices of general height of tree cover and of general height of canopy maximum width) were used in the present thesis. The sampling procedure adopted worked well except in areas of dense scrub or plantation, and the author feels that it could be used quite widely in ornithological studies - certainly a standard method needs to be recommended to facilitate comparisons between studies, which are sometimes difficult at present due to a plethora of vegetation sampling methods.

The results of both mapping and vegetation fieldwork over the three breeding seasons 1979-81 showed that the lowest population densities occurred on the open dune grassland, whereas the highest densities were to be found in the mature birch/alder woodland; and the highest diversity indices in the commercial coniferous woodland. Over the three year period, which followed the meteorologically "hard" winter of 1978/79, there was an increase in the total breeding populations of all five study plots, the increase being highest on the dune grassland and lowest in the mature woodland. Individual species exhibited variations in their population changes between the first and final years of the study, and also between the study plots: some having increased while others

decreased. Skylark, Meadow Pipit, Wren and Robin all showed large population increases, whereas Starling showed a general decrease; other species showed no apparent trend.

Of the study plot communities - as defined by species dominance values (relative abundances) - the dune grassland plot was dominated by two passerine species - Skylark and Meadow Pipit - while the four woodland communities showed a "core" of dominants: Chaffinch, Robin, Willow Warbler and a tit (Coal Tit in coniferous habitats and Blue Tit in deciduous), with the addition of Starling in the mature birch/alder woodland where there were sufficient natural nest-holes to support a colony. Comparing the five communities by using two indices, there was a major difference between the community inhabiting the grassland and those in all the woodland plots. With the four woodland communities, those of the two coniferous plots were the most similar to each other. At the individual species level, Robin, Song Thrush and Coal Tit were more prevalent in the coniferous study plots, and Willow Warbler and Blue Tit were more prevalent in the deciduous plots.

In relation to the various habitat parameters measured in each study plot it was found that basically the breeding passerine communities became more diverse as the vegetation structure became more complex. Study Plot 1 - semi-natural coniferous woodland - was investigated in some detail since its woodland cover was primary (the commercial forestry plot was a mixture of primary and re-seeded wooded areas) and could be dated accurately. In Plot 1 from west to east, that is from the original source woodland through recently established woodland and thicket to actively colonizing trees - there is a gradual change from tall, spaced trees with a moderately high canopy allowing much light to penetrate, through less tall, more densely-packed trees with a lower canopy covering much more of the ground and allowing little light to penetrate, to low, well-spaced trees with low canopies but covering little of the ground beneath and allowing much light to penetrate. It was found that associated with these changes, the total populations of all species were low next to the original forest, were high through the established thicket stages, and decreased abruptly towards the younger open woodland. Of the individual species, Robin, Song Thrush, Goldcrest, Coal Tit, and Treecreeper were more numerous in the

taller and denser woodland stages; and Willow Warbler and Chaffinch were least numerous in the oldest and in the youngest stages. In the deciduous plots it appeared that Wren, Robin, Willow Warbler and Treecreeper avoided areas of low and sparse tree cover, while only Song Thrush avoided the same type of habitat in the coniferous plots.

The above results are important from three main points of view: they represent one of the few studies of those habitat types and successions near sea-level; they add much to our knowledge of the avifauna of commercial forestry areas; and they can be put into a European context since most of the few studies that have been conducted have taken place in Scandinavia and along the Polish Baltic coast.

Unfortunately, temporal and methodological differences preclude comparisons between several published studies and the present one, but for those which are comparable the following were found: breeding population densities of Skylark and Meadow Pipit were similar to those of duneland studied on a Cardiganshire coastal plot; the Tentsmuir semi-natural pine plot is probably richer (in terms of total population density and diversity index values) than similar study plots found at higher altitudes in Norway, north-west Scotland and Speyside; the regularly dominant passerine species in the natural and semi-natural pine environments are Wren, Robin, Willow Warbler, Goldcrest, Coal Tit and Chaffinch; and the commercial coniferous study plot in Fife was richer in terms of the number of breeding species, than any other commercial plot studied in Scotland and reported in the literature. This plot also held high breeding passerine densities, surpassed in the British Isles only by those in more mature plantations in Killarney, Eire.

Community changes along habitat successional gradients were discussed and were found to take the form of increases in both population density and species richness, as well as changes in the species composition of the communities. In the Fife study plots, a total of seven community groupings was found, with six along the deciduous succession and five along the coniferous one. The findings of the present study, in common with others, do not wholly support recent ideas from Poland that complete changes in species composition, in

dominance and in diversity indices accompany the transition of one community into the next along a succession, but rather that there is a general pattern of gradual changes.

An attempt was made to relate winter meteorological variables to various population parameters of summer communities in the study plots, but this was not entirely successful, although it would be an appropriate investigation for future studies. Strong negative relationships obtained between periods of prolonged bad winter weather and subsequent breeding populations of the smallest of the passerines - Wren, Goldcrest, Long-tailed, Coal and Blue Tits, and Treecreeper. This finding was echoed at the national scale (and reported in the literature) after analysis of the effects of the 1978/79 winter throughout the British Isles.

The above results have provided much of interest to the understanding of the five breeding communities, their relations with each other, and with the habitats they occupied. The results have also served to outline areas requiring further investigation, and had more time been available, much more fruitful fieldwork could have been conducted on particular aspects, as well as on the more general ones. In concluding the thesis, therefore, it is useful to indicate how the findings of this particular study have more general application.

It is now accepted that the mapping method, although time-consuming, is the most efficient and reliable means of estimating the numbers of territorial songbirds within a defined area. However, refinements of the methodology are necessary to take account of the "edge effect", for example, and much further work needs to be conducted on the method's reliability with individual species. At present it is really only the territorial passerines within a community which can be studied as a group using the method - to investigate a complete community requires the use of several count methods, each of which might differ in its needs in terms of labour input, reliability and efficiency, all precluding a direct comparison of population estimates within a community, let alone between communities where different habitats might introduce a further variable influencing the choice of count methods employed.

The mechanics of counting the birds, interpreting the results of such counts, and the terminology to be employed in conducting and analysing the counts have been standardised for the three main count techniques: mapping, transecting and spot-counting. It is now time that standards were introduced to the measurement, analysis and description of habitats involved in population studies such as in the present thesis. This would allow more reliable comparisons between the results of studies within one country, between countries and over time.

One further area in need of investigation is the influence of meteorological variables, especially over the winter period, on individual communities of birds, rather than at the national scale. This will be difficult to achieve since it will encompass a vast region from southern Africa to northern Europe (for studies in the western Palearctic) and will require data from the wintering zones and migration routes (neither completely known at present) of those species which winter outside Europe, as well as those which winter within the continent but away from their breeding areas. However, a useful start could, perhaps, be made with those few species (for example, Wren) which spend the whole year in the one area and which so far have been studied only in relation to high magnitude and low frequency climatological events, such as severe winters.

The results of studies and discussions of them will always be open to individual interpretation by the investigator involved, but it is important to have reduced the sources of bias (by standardisation of methodologies and analytical techniques) up to that point, so that meaningful interpretations and comparisons can be conducted. It is concluded here that the present thesis has gone some way to achieving this end, but that it is only one of several such studies needed before whole communities and their complex inter-relationships can be studied in depth. There is much still to be provided by future theses on the subject!

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APPENDIX : METEOROLOGICAL FACTORS

Birse (1971) has assessed climatic conditions in Scotland and his map classifies the North-East Fife study plots as "fairly humid northern temperate hyperoceanic". White and Smith (1982) have produced climatological maps for the British Isles overall, and Elkins (1983) provides an up-to-date review of all aspects of meteorological and climatological effects on wild birds, both as individuals and populations. Earlier in this thesis, a review of the literature pertaining to the influences of weather and climate on birds during the breeding season was given. Now, however, we are concerned with the local scale and with how various parameters of the winter weather may have affected the bird populations in the subsequent breeding seasons. An analysis of this was attempted but was unsuccessful, due to a lack of data over time, to a lack of direct observations during the winter months, and to the complexities of seasonal movements and the winter distributions of various bird species. However, suggestions for future work on this theme and an outline of the results of the present analysis are given here in the hope of encouraging others to pursue investigations.

For the Fife study plots the ornithological data were obtained by the present author while the meteorological data were provided by the nearest meteorological station, at R.A.F. Leuchars 5 km to the south (readings taken there at 10.42 m.a.s.l., 56°23'N, 02°52'W).

The main aim of the analysis was to see if there was any relationship between the winter weather and the subsequent breeding populations of the five study plots in N.E.Fife. Clearly bird species which leave the British Isles and even Europe for the winter must be excluded from such an analysis, but of the remaining species, some are "partial migrants" - that is a proportion of the population of these species leaves the British Isles for the winter and part or all of the remainder of the population moves within the British Isles (Mead, 1983). Therefore the winter weather on the breeding grounds may have little direct effect on such species, although it can affect the breeding season habitat through, for example,

frost-burn of Gorse, wind-throw of trees and flooding.

Since no winter censuses were conducted in the study plots, it is not known which species and their numbers were present during the winter months, and there is also a problem in deciding which are the winter months. However, Cawthorne and Marchant (1980), in a review of the effects of the 1978/79 winter on British bird populations, concentrated on the months November to February inclusive and this will be followed here. The species to be used in the analysis were all those known to be resident within the British Isles, and hence in the study plots, during winter and for which there is adequate data (species making up at least 2% of a breeding community over three years). Partial migrants for which there were data, such as Skylark and Meadow Pipit, were also included but with the caveat that any resulting relationships needed close scrutiny.

Three meteorological variables were chosen for investigation since they were known to affect the survival of birds in winter:-

- (1) minimum night temperatures: affect birds at roost when they cannot feed, and have to conserve heat;
- (2) average daily temperatures: influence the availability of live prey for birds, and their time-budgets for feeding;
- (3) number of days with snow falling and/or lying: affect the food-searching strategies of some species, notably ground-feeders whose food supply may be covered by snow.

The effect of each meteorological variable on the subsequent breeding population density and on the percentage population change between consecutive breeding seasons for the selected species was investigated, and an attempt was also made to measure the effects of prolongation of two of the above variables: average daily temperatures below freezing and number of snow days.

The table below summarizes on a monthly basis four meteorological variables for each winter involved in the study period 1979-81, and clearly shows

that the January and February of 1979 (the "hard" winter of 1978/79) were colder and snowier than the corresponding months in 1980 and 1981. Prolongation of meteorological variables was measured by using the number of periods of at least five days of consecutive average daily temperatures of $\leq 0^{\circ}\text{C}$, and of snow fall/cover. Five days were chosen arbitrarily, although Elkins (1983, p 62) states that Partridges can survive only 4-5 days of severe weather; and given the smaller body sizes of most passerine species, it would seem that a period of five consecutive days of extreme conditions would have an adverse effect on their survival.

Most suggested relationships (independent of strength) between the periods of bad winter weather and bird population densities in the following breeding season were negative, but apparently strong positive relationships were found (with periods of weather) as follows:- snow and Blackbird in the two coniferous plots; "minus" temperatures and Great Tit in the birch/willow scrub; and "minus" temperatures and Starling in the mature birch/alder woodland. It is difficult to account for these anomalous relationships, but perhaps in the case of the ground-feeding Blackbird the persistent snowfall and cover drove birds from more open habitats where their feeding grounds were covered, to the more sheltered coniferous woodlands and some of the surviving birds remained there to establish territories and breed.

The strong negative relationships between periods of prolonged bad winter weather and population densities in the following breeding season involved the smallest arboreal passersines: Wren, Goldcrest, Long-tailed, Coal and Blue Tits and Treecreeper; and also the smaller of the predominantly ground-feeding species such as Skylark, Meadow Pipit, Dunnock and Robin. (The data set is neither large nor reliable enough to investigate inter-plot differences). Small passerine species are known to be particularly susceptible to prolonged periods of extreme winter weather since their surface area:volume ratio is such that they lose body heat faster than larger species (Cawthorne and Marchant, 1980; Elkins, 1983).

The above discussion of the local situation has raised several points of interest which would merit further, and more detailed work, especially involving an analysis combining the meteorological parameters (and measuring wind-chill effects), rather than looking at each in isolation.

METEOROLOGICAL VARIABLES OF EACH WINTER FROM 1978-79 TO 1980-81

| MONTH | NOVEMBER | | | DECEMBER | | | JANUARY | | | FEBRUARY | | | WINTER |
|--|------------------|-----------|------|------------------|-----------|------|------------------|-------|-------------|------------------|-------|-------------|---------|
| | Total | Mean | S.D. | Total | Mean | S.D. | Total | Mean | S.D. | Total | Mean | S.D. | |
| Minimum night temperature (°C) | 147.10 | 4.90 | 4.63 | 60.40 | 1.95 | 3.49 | -75.20 | -2.43 | 3.94 | -37.10 | -1.33 | 3.36 | 1978-79 |
| | 72.30 | 2.41 | 4.33 | 48.00 | 1.55 | 3.47 | 2.60 | 0.08 | 2.40 | 58.80 | 2.03 | 2.97 | 1979-80 |
| | 114.70 | 3.82 | 3.95 | 90.70 | 2.93 | 3.38 | 33.00 | 1.06 | 3.19 | 19.10 | 0.68 | 3.23 | 1980-81 |
| Average daily temperature (°C) | 224.90 | 7.50 | 4.17 | 115.90 | 3.70 | 2.83 | 3.50 | 0.11 | 2.99 | 19.50 | 0.70 | 2.09 | 1978-79 |
| | 165.90 | 5.53 | 3.59 | 123.70 | 3.99 | 3.12 | 65.40 | 2.11 | 1.89 | 130.00 | 4.48 | 2.67 | 1979-80 |
| | 183.20 | 6.11 | 3.31 | 156.00 | 5.03 | 2.98 | 115.40 | 3.72 | 2.93 | 96.40 | 3.44 | 2.71 | 1980-81 |
| Number of days when snow fal- ling and/or lying | 2 | | | 8 | | | 23 | | | 13 | | | 1978-79 |
| | 1 | | | 4 | | | 7 | | | 7 | | | 1979-80 |
| | 3 | | | 9 | | | 14 | | | 9 | | | 1980-81 |
| Number of days of ground-frost | 11 | | | 15 | | | 29 | | | 24 | | | 1978-79 |
| | 18 | | | 22 | | | 26 | | | 14 | | | 1979-80 |
| | 14 | | | 17 | | | 26 | | | 19 | | | 1980-81 |
| Number of periods* of "poor" weather | Temperature 0 | Snow 0 | | Temperature 0 | Snow 1 | | Temperature 1 | | Snow 3.6 | Temperature 1 | | Snow 1.4 | 1978-79 |
| | 0 | 0 | | 0 | 0 | | 0 | | 0 | 0 | | 1.4 | 1979-80 |
| | 0 | 0 | | 0 | 0 | | 0 | | 1.6 | 0 | | 0 | 1980-81 |

Notes: *: one period is at least 5 days of consecutive conditions.

Total temperature = summation of positive and negative values.

Cawthorne and Marchant (1980), discussing the effects of the 1978/79 winter (using data from ringing returns during that winter, and C.B.C. returns for the breeding seasons of 1978 and 1979) also looked at the meteorological factors in isolation, but had a larger data set.

With relevance to the species in N.E.Fife discussed in some detail above, it was found by Cawthorne and Marchant (1980) from ringing data that the 1978/79 winter had an appreciable effect on Wren mortality, but that the Song Thrush mortality was little affected (although it usually is during "hard" winters) and that this latter species showed evidence of migration to the continent, from England and Wales (not enough data from Scotland and Northern England to substantiate this). From the C.B.C. results it appeared that the populations of smaller species in woodlands (as indicated by breeding season body weights) had decreased most, with significant reductions for species weighing under 10.5 g, while those weighing over 100 g showed no decreases in woodland plots. This perhaps explains the situation with the Blackbird in the Fife plots. Comparing species common to the two broad C.B.C. habitat classifications of woodland and farmland, Cawthorne and Marchant found that decreases were less in the sheltered woodlands than on the open farmland. It would have been very interesting, given the suggestion from the N.E.Fife work that survival in coniferous woodland may have been better than in deciduous for species occurring in both, had these two authors looked for differences between the two broad woodland classifications.

Cawthorne and Marchant (1980) suggest that any regional or altitudinal variations in population decreases between 1978 and 1979 could have arisen either by corresponding changes in mortality levels or by movements to alternative breeding areas by surviving birds, such as was found for the rather sedentary Wren by Williamson (1969). Although there are no data on 1978-79 population changes for the Fife study plots, there is a suggestion that in N.E.Fife the Wren population after the "hard" winter of 1978-79 was concentrated in the mature birch/alder woodland (plot 4) and the coniferous plantation (plot 2), and that survival in the birch/willow scrub (plot 3) and in the semi-natural conifers (plot 1) was very poor,

the birds either having died or moved out to more favourable areas, in terms of food and shelter. A local ringing project could have been of much value here to investigate local movements and survival rates, thus relating findings at the local scale from one worker to findings at the national scale from many workers, which feature has been oft repeated throughout this thesis, and which is a mainstay of British ornithology today (Hickling, 1983).

BIRD SPECIES LIST

Sequence and nomenclature follow that of Voous (Hudson, 1978)

| | |
|------------------|------------------------------|
| GREY HERON | <i>Ardea cinerea</i> |
| SHELDUCK | <i>Tadorna tadorna</i> |
| WIGEON | <i>Anas penelope</i> |
| MALLARD | <i>Anas platyrhynchos</i> |
| EIDER | <i>Somateria mollissima</i> |
| SPARROWHAWK | <i>Accipiter nisus</i> |
| KESTREL | <i>Falco tinnunculus</i> |
| RED GROUSE | <i>Lagopus lagopus</i> |
| BLACK GROUSE | <i>Tetrao tetrix</i> |
| GREY PARTRIDGE | <i>Perdix perdix</i> |
| PHEASANT | <i>Phasianus colchicus</i> |
| WATER RAIL | <i>Rallus aquaticus</i> |
| CORNCRAKE | <i>Crex crex</i> |
| MOORHEN | <i>Gallinula chloropus</i> |
| COOT | <i>Fulica atra</i> |
| GOLDEN PLOVER | <i>Pluvialis apricaria</i> |
| LAPWING | <i>Vanellus vanellus</i> |
| SNIPE | <i>Gallinago gallinago</i> |
| WOODCOCK | <i>Scolopax rusticola</i> |
| CURLEW | <i>Numenius arquata</i> |
| REDSHANK | <i>Tringa totanus</i> |
| GULL spp. | <i>Larus spp.</i> |
| TERN spp. | <i>Sterna spp.</i> |
| COMMON TERN | <i>Sterna hirundo</i> |
| AUK spp. | <i>Alcidae spp.</i> |
| STOCK DOVE | <i>Columba oenas</i> |
| WOODPIGEON | <i>Columba palumbus</i> |
| COLLARED DOVE | <i>Streptopelia decaocto</i> |
| TURTLE DOVE | <i>Streptopelia turtur</i> |
| CUCKOO | <i>Cuculus canorus</i> |
| LITTLE OWL | <i>Athene noctua</i> |
| TAWNY OWL | <i>Strix aluco</i> |
| LONG-EARED OWL | <i>Asio otus</i> |
| SHORT-EARED OWL | <i>Asio flammeus</i> |
| NIGHTJAR | <i>Caprimulgus europaeus</i> |
| SWIFT | <i>Apus apus</i> |
| WOODPECKER spp. | <i>Picidae spp.</i> |
| GREEN WOODPECKER | <i>Picus viridis</i> |
| SKYLARK | <i>Alauda arvensis</i> |
| SAND MARTIN | <i>Riparia riparia</i> |
| SWALLOW | <i>Hirundo rustica</i> |
| HOUSE MARTIN | <i>Delichon urbica</i> |
| TREE PIPIT | <i>Anthus trivialis</i> |
| MEADOW PIPIT | <i>Anthus pratensis</i> |
| YELLOW WAGTAIL | <i>Motacilla flava</i> |
| PIED WAGTAIL | <i>Motacilla alba</i> |

BIRD SPECIES LIST Continued

| | |
|------------------------|-----------------------------------|
| WREN | <i>Troglodytes troglodytes</i> |
| DUNNOCK | <i>Prunella modularis</i> |
| ROBIN | <i>Erithacus rubecula</i> |
| BLUETHROAT | <i>Luscinia svecica</i> |
| REDBSTART | <i>Phoenicurus phoenicurus</i> |
| WHINCHAT | <i>Saxicola rubetra</i> |
| STONECHAT | <i>Saxicola torquata</i> |
| WHEATEAR | <i>Oenanthe oenanthe</i> |
| BLACKBIRD | <i>Turdus merula</i> |
| FIELD FARE | <i>Turdus pilaris</i> |
| SONG THRUSH | <i>Turdus philomelos</i> |
| REDWING | <i>Turdus iliacus</i> |
| MISTLE THRUSH | <i>Turdus viscivorus</i> |
| GRASSHOPPER WARBLER | <i>Locustella naevia</i> |
| SEDGE WARBLER | <i>Acrocephalus schoenobaenus</i> |
| REED WARBLER | <i>Acrocephalus scirpaceus</i> |
| LESSER WHITETHROAT | <i>Sylvia curruca</i> |
| WHITETHROAT | <i>Sylvia communis</i> |
| GARDEN WARBLER | <i>Sylvia borin</i> |
| BLACK CAP | <i>Sylvia atricapilla</i> |
| WOOD WARBLER | <i>Phylloscopus sibilatrix</i> |
| CHIFFCHAFF | <i>Phylloscopus collybita</i> |
| WILLOW WARBLER | <i>Phylloscopus trochilus</i> |
| GOLDCREST | <i>Regulus regulus</i> |
| SPOTTED FLYCATCHER | <i>Muscicapa striata</i> |
| COLLARED FLYCATCHER | <i>Ficedula albicollis</i> |
| PIED FLYCATCHER | <i>Ficedula hypoleuca</i> |
| LONG-TAILED TIT | <i>Aegithalos caudatus</i> |
| MARSH TIT | <i>Parus palustis</i> |
| WILLOW TIT | <i>Parus montanus</i> |
| CRESTED TIT | <i>Parus cristatus</i> |
| COAL TIT | <i>Parus ater</i> |
| BLUE TIT | <i>Parus caeruleus</i> |
| GREAT TIT | <i>Parus major</i> |
| NUTHATCH | <i>Sitta europaea</i> |
| TREECREEPER | <i>Certhia familiaris</i> |
| SHORT-TOED TREECREEPER | <i>Certhia brachydactyla</i> |
| GOLDEN ORIOLE | <i>Oriolus oriolus</i> |
| RED-BACKED SHRIKE | <i>Lanius collurio</i> |
| JAY | <i>Garrulus glandarius</i> |
| MAGPIE | <i>Pica pica</i> |
| JACKDAW | <i>Corvus monedula</i> |
| CARRION CROW | <i>Corvus corone</i> |
| STARLING | <i>Sturnus vulgaris</i> |
| HOUSE SPARROW | <i>Passer domesticus</i> |
| TREE SPARROW | <i>Passer montanus</i> |
| CHAFFINCH | <i>Fringilla coelebs</i> |
| BRAMBLING | <i>Fringilla montifringilla</i> |
| GREENFINCH | <i>Carduelis chloris</i> |

BIRD SPECIES LIST Continued

| | |
|---------------------|---------------------------------|
| GOLDFINCH | <i>Carduelis carduelis</i> |
| SISKIN | <i>Carduelis spinus</i> |
| LINNET | <i>Carduelis cannabina</i> |
| REDPOLL | <i>Carduelis flammea</i> |
| COMMON CROSSBILL | <i>Loxia curvirostra</i> |
| BULLFINCH | <i>Pyrrhula pyrrhula</i> |
| RUFOUS-SIDED TOWHEE | <i>Pipilo erythrrophthalmus</i> |
| FIELD SPARROW | <i>Spizella pusilla</i> |
| YELLOWHAMMER | <i>Emberiza citrinella</i> |
| REED BUNTING | <i>Emberiza schoeniclus</i> |
| BOBOLINK | <i>Dolichonyx oryzivorus</i> |

MAMMAL SPECIES LIST

Species sequence follows that in Corbet and Southern (1977)

| | |
|------------|------------------------------|
| RABBIT | <i>Oryctolagus cuniculus</i> |
| BROWN HARE | <i>Lepus capensis</i> |
| VOLE spp. | <i>Microtus</i> spp. |
| RED DEER | <i>Cervus elaphus</i> |
| ROE DEER | <i>Capreolus capreolus</i> |
| CATTLE} | <i>Bovidae</i> spp. |
| SHEEP } | |

PLANT SPECIES LIST

Species sequence follows Clapham, Tutin and Warburg (1962)

| | |
|--------------------|-----------------------------|
| NORWAY SPRUCE | <i>Picea abies</i> |
| SITKA SPRUCE | <i>P. sitchensis</i> |
| LARCH HYBRID | <i>Larix spp.</i> |
| SCOTS PINE | <i>Pinus sylvestris</i> |
| CORSICAN PINE | <i>P. nigra</i> |
| LODGEPOLE PINE | <i>P. contorta</i> |
| YEW | <i>Taxus baccata</i> |
| SYCAMORE | <i>Acer pseudoplatanus</i> |
| SWEET BRIAR | <i>Rosa rubiginosa</i> |
| HAWTHORN | <i>Crataegus monogyna</i> |
| ROWAN | <i>Sorbus aucuparia</i> |
| SEA BUCKTHORN | <i>Hippophae rhamnoides</i> |
| BIRCH spp. | <i>Betula spp.</i> |
| ALDER spp. | <i>Alnus spp.</i> |
| WILLOW spp. | <i>Salix spp.</i> |
| CREEPING WILLOW | <i>Salix repens</i> |
| ELDER | <i>Sambucus nigra</i> |
| OAK spp. | <i>Quercus spp.</i> |
| HORNBEAM | <i>Carpinus betulus</i> |
| BEECH | <i>Fagus sylvaticus</i> |
| GORSE | <i>Ulex europaeus</i> |
| CLOVER spp. | <i>Trifolium spp.</i> |
| MEADOWSWEET | <i>Filipendula ulmaria</i> |
| WILLOWHERB spp. | <i>Epilobium spp.</i> |
| DOCK spp. | <i>Rumex spp.</i> |
| NETTLE | <i>Urtica dioica</i> |
| HEATHER | <i>Calluna vulgaris</i> |
| CROSS-LEAVED HEATH | <i>Erica tetralix</i> |
| CROWBERRY | <i>Empetrum nigrum</i> |
| RAGWORT | <i>Senecio jacobaea</i> |
| RUSH spp. | <i>Juncus spp.</i> |
| WOODRUSH | <i>Luzula campestris</i> |



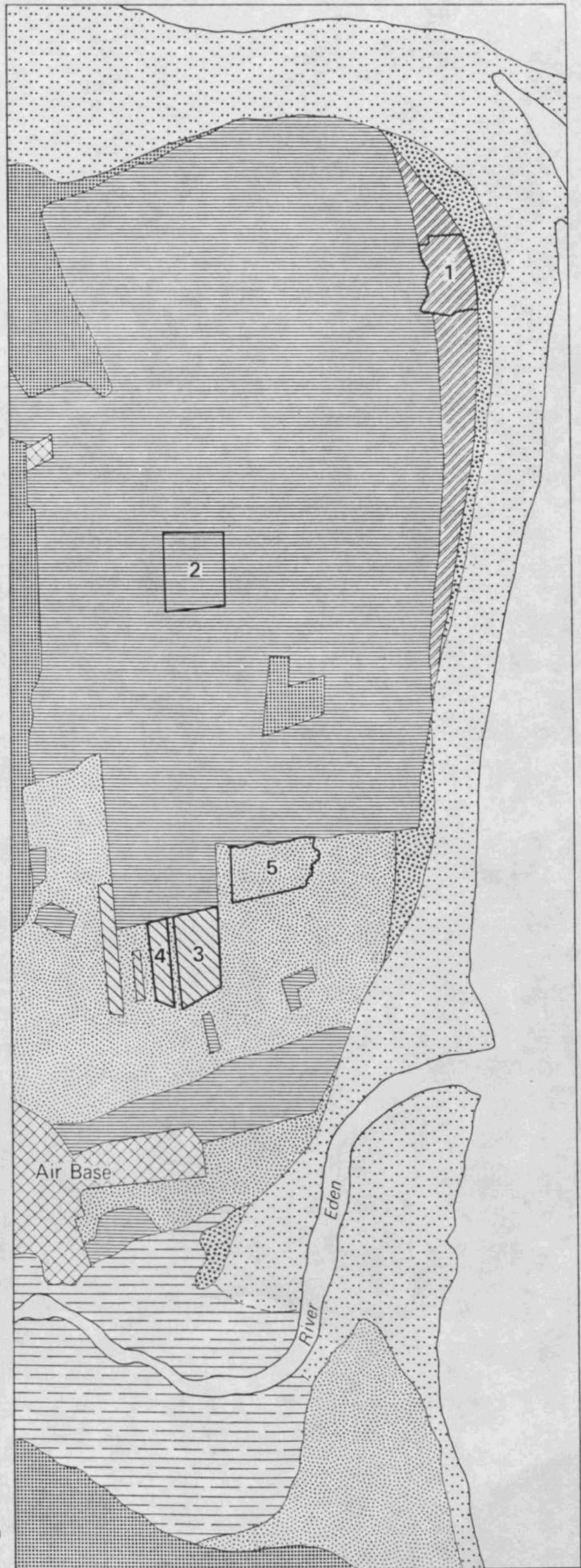
Location of study area

5 Study plots

Vegetation and land use context

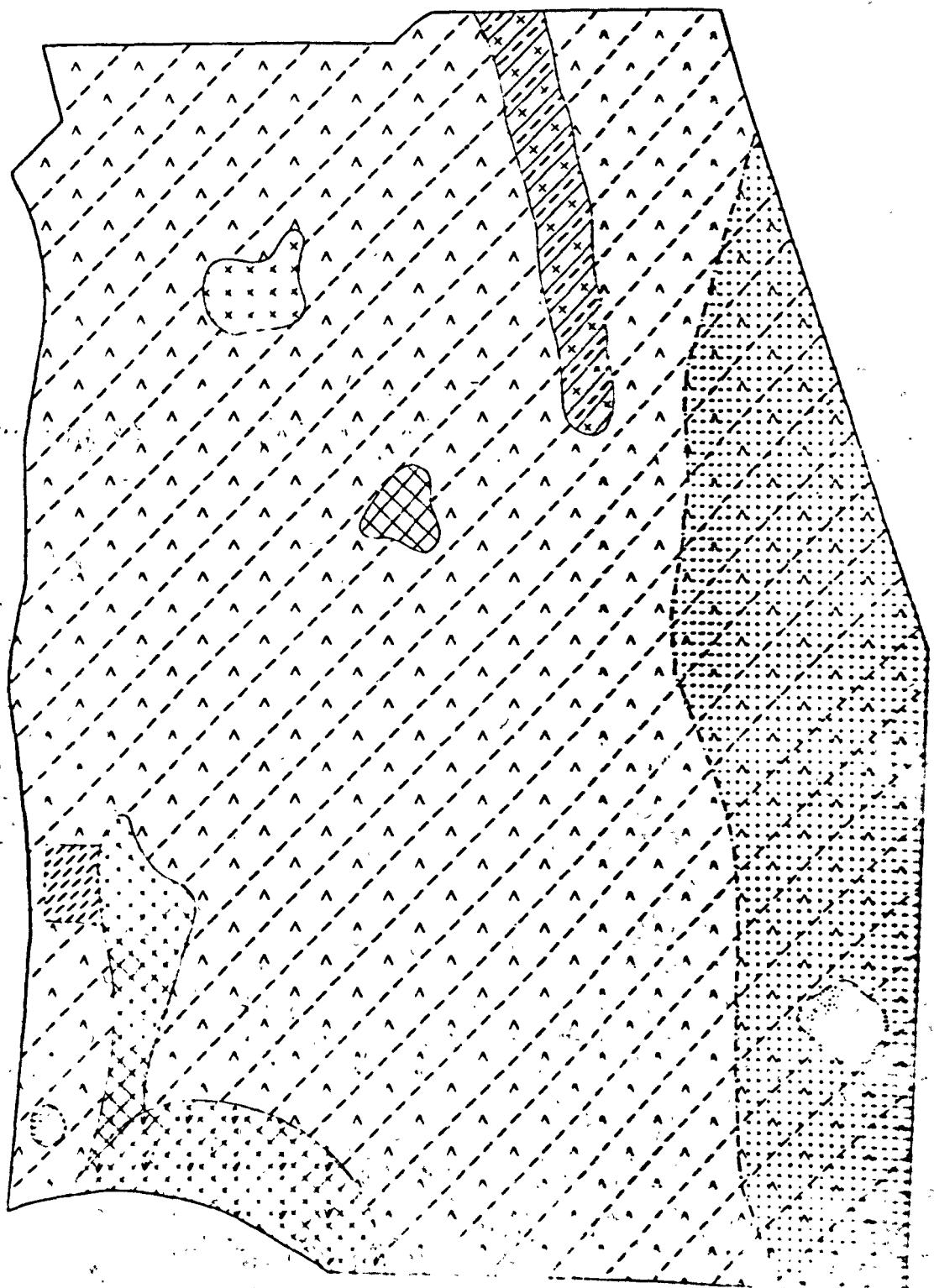
- Commercial coniferous forest
- Self regenerating coniferous woodland
- Semi-natural deciduous woodland
- Young stabilised dunes and dune margin scrub
- Old stabilised dunes
- Farmland
- Beach sands
- Estuarine mud flats
- Buildings

0 2000 m



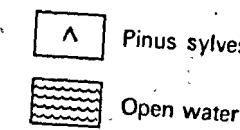
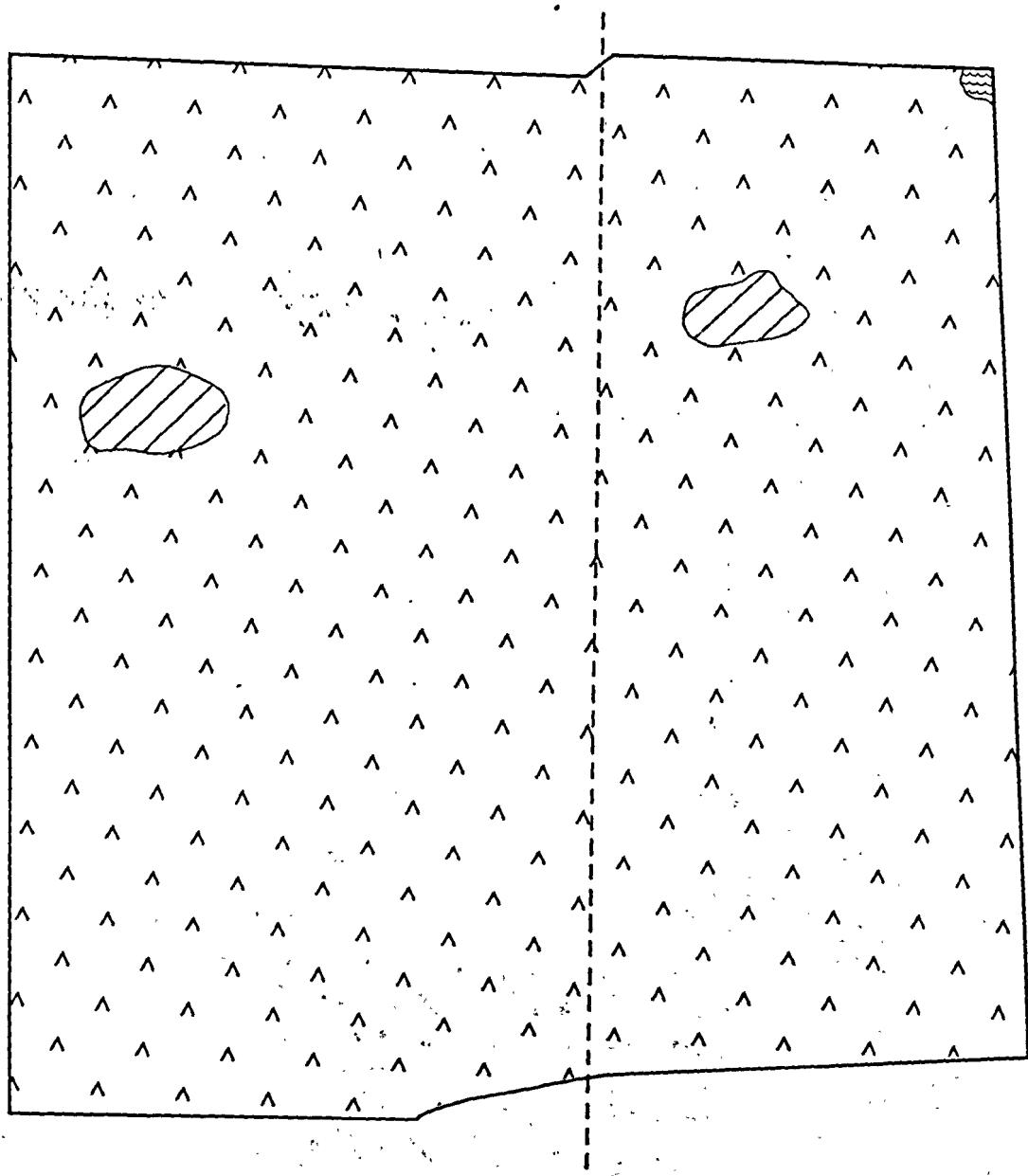
4-3.2

Plot 1



4 - 3.3

Plot 2

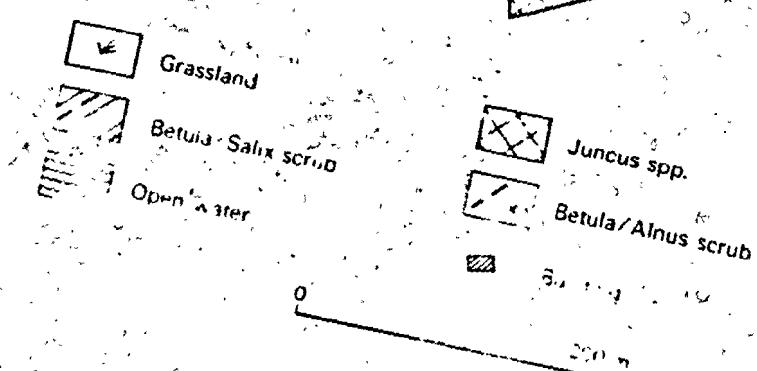
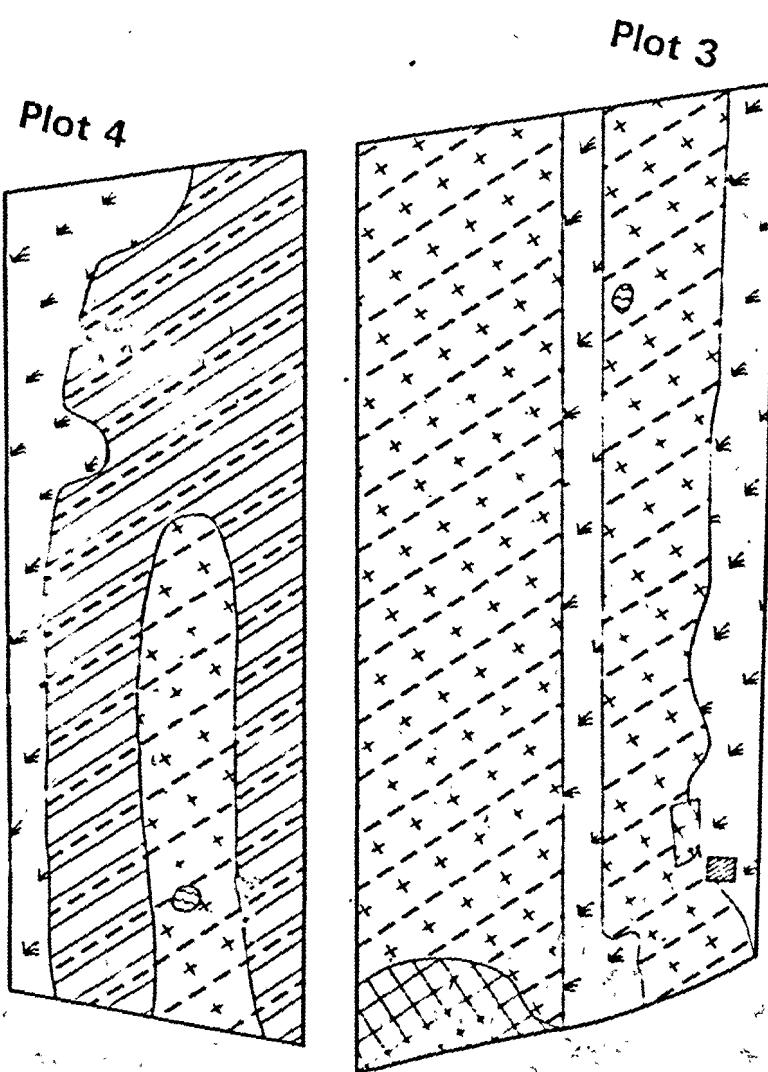


— — Track

0

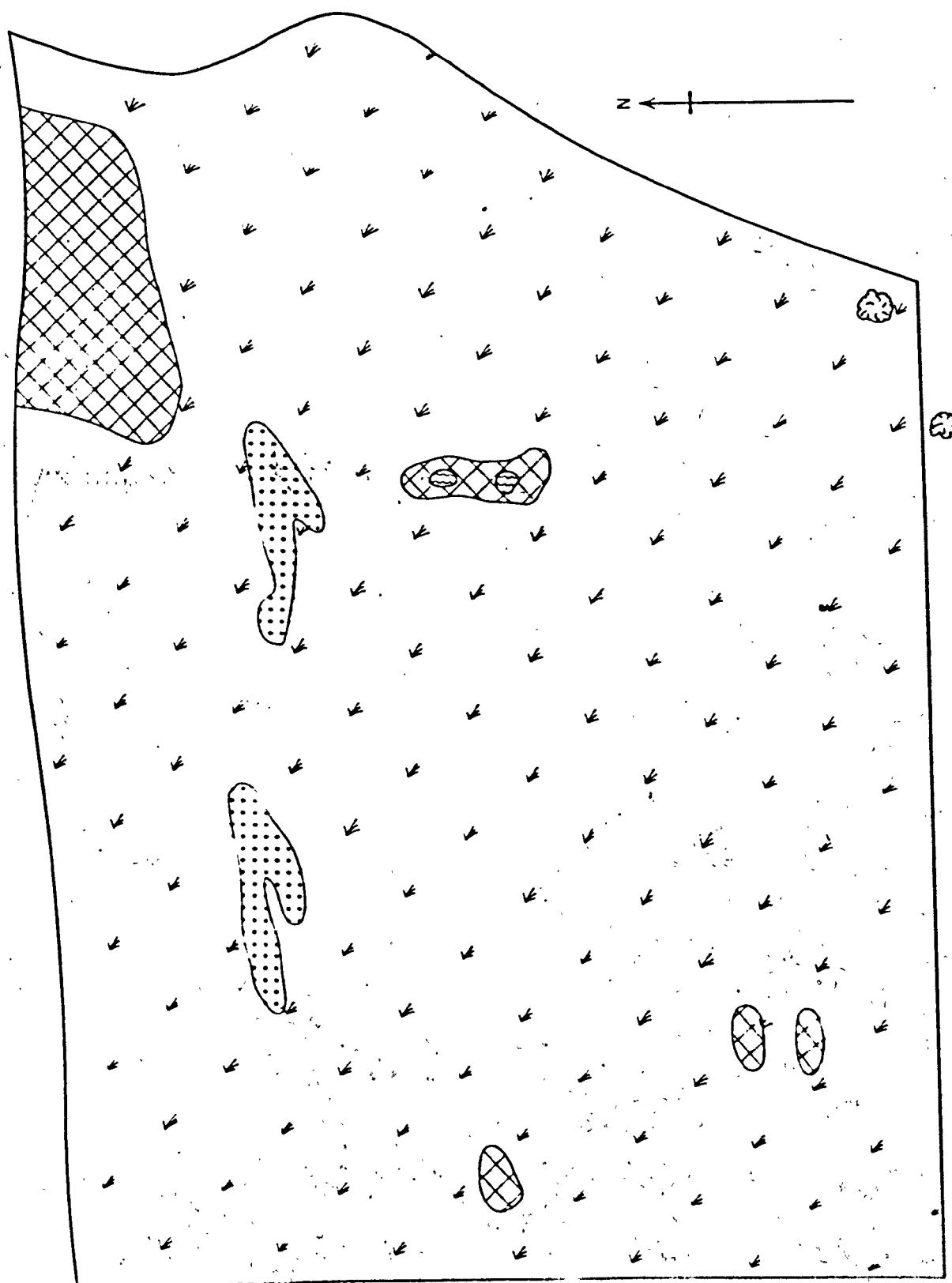
200 m

4-3-4



Plot 5

4-3.5



Juncus spp



Stabilized dune grassland



Dune blow