THE STATISTICAL ANALYSIS OF ANIMAL POPULATIONS

A THESIS SUBMITTED TO
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Abstract

This thesis is concerned with assessing the spatial variability in animal populations. Chapter 1 is a short general introduction. Chapter 2 contains a discussion of the design of a large field experiment on the effect on the local ecology of the proximity of arable crops (winter barley in this case), semi-natural habitat and mature hedgerow. The counts of the large polyphagous beetle *Pterostichus Melanarius* recovered from an array of wet pitfall traps from the above experiment is then discussed. New tests for overdispersion and spatial aggregation are given in Chapter 3. This extends the work of (Perry and Hewitt, 1991) based on the amount of effort it takes to smooth out counts data so that they are acceptably variable (variance=mean), half as variable as before, or completely smooth (variance=0). In Chapter 4 we proceed to devise indices from Chapter 3's measures so the amount of pattern in different data sets can be compared. In Chapter 5 these indices are applied to the counts of *P. melanarius* from the experiment at Long Ashton that was discussed in Chapter 2, with each month analysed separately. A generalised linear model is also fitted to the data. In Chapter 6 we look at use of a general host-parasite model by Pacala *et al.* (1991) to fit a large group of data sets. Some problems related to parameter estimation are considered. A slightly simpler model is then described and shown to be equivalent to a generalised linear model. Finally the distribution of movement distance and survival rates from ring-recovery data on blackbirds is discussed in Chapter 7

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Chapter 1

Introduction

> And Moses stretched forth his rod over the land of Egypt, and the LORD
> brought an east wind upon the land all that day, and all the night;
> and when it was morning the east wind brought the locusts.
> Exodus Chapter 10 Verse 13

The uncontrolled movement of animals birds and insects has caused problems to mankind throughout the ages. Some measure of control started around 9000 B.C. with the domestication of sheep and goats, some 2000 years before the start of arable farming (Starr, 1991). It is much more difficult to control smaller, more mobile, species such as birds and insects. Virgil, in book IV of the Georgics (37-29 BC), described suitable positions for hives of bees so as to maximise the yield of honey. He also noted that weather affects movement rates with fair weather encouraging long foraging journeys and the threat of rain restricting the range.

The assessment of spatial stratification and movement in response to heterogeneity in the environment is the subject of this thesis.

The design of a large experiment to study the effects of habitat diversity on arable crops and the local ecosystem is discussed in chapter 2. A review of the biology of a large carabid beetle *Pterostichus melanarius* is given, along with an overview of the use of pitfall trap data to assess carabid populations. The chapter then continues to analyse the changes in the mean catch of *P. melanarius* from the experiment over time and looks at the effect of habitat diversity on the catch rate, using a generalized linear model.

Chapter 3 is concerned with the development of new tests for overdispersion and spatial aggregation in counts data. A pattern is defined as overdispersed if it has more variability than would be expected if it came from the Poisson distribution. A pattern is (spatially) aggregated if the high and low counts are spatially clustered. These tests, which follow on from the work of Perry and Hewitt (1991), are based on the amount of effort required to reposition the individuals so that the sample variance has some desired property. This effort is defined as the total distance moved by all the individuals.

Chapter 4 develops these further by looking at indices of pattern based on these tests.

Chapter 5 combines the previous three chapters in order to assess the extent of heterogeneity in the field experiment. First the field is divided into blocks and the GLM from chapter 2 extended by adding the block effect. The extent of pattern is then analysed for each month using both the indices of chapter 4 and a GLM based on blocks.

Chapter 6 looks at the estimation of rates of parasitism in hosts and describes a hierarchy of models, including that from (Pacala *et al.*, 1991) that take into account possible heterogeneity in the parasitism rates. The implementation of the Pacala and Hassell model is discussed and a slightly simpler model using a GLM fitted. The chapter concludes with a look at the possible use of Generalized Linear Mixed Models (Engel and Buist, 1993) to provide a coherent framework for host-parasite models.

Chapter 7 looks at the distribution of dispersal distances and survival rates for ring recovery data using the Weibull distribution. Data for the blackbird *turdus merula* in the U.K. and the common grackle *Quiscalus quiscula* in North America are both analysed. (Manly and Chatterjee, 1992)'s use of least squares estimation and fitting by maximum likelihood techniques are both considered.

1.1 A note on notation

In order to describe complex models with many main effects and two- or even three-way interactions the following notation, used by both the Genstat and GLIM statistical packages, has been used throughout. Main effects are given by the name of the regressor and two-way interactions not including the main effects by both names separated by an "." . So sex.age indicates the sex age interaction (but not the main effects). Similarly three way interactions, excluding subsidiary two-way interactions and main effect are denoted by by two dots. For example sex.age.area. A short form for including main effects and subsidiary interactions involves replacing the "." by an asterisk. So age*sex is equivalent to age+sex+age.sex, and the three way effect sex*age*area to sex+age+area+sex.age+sex.area+age.area+sex.age.area..

As a short method of indicating the statistical significance of results in tables the following convention is used. If a result is significant at 5% then it is marked with a single asterisk, two asterisks represent a result significant at 1% and three a result significant at 0.1%.

Data which are missing are represented in both figures and tables with a question mark.

Chapter 2

Patch-crop experiment

2.1 Introduction to a large farmland ecology experiment

In this chapter we consider the motivation for and design of a large experiment on farmland ecology, run concurrently at Long Ashton Research Station (LARS) and Rothamsted Experimental Station (RES) in section 2.2. The biology of an important carabid beetle, *Pterostichus Melanarius*, is discussed in section 2.3. The monthly catches of *P. melanarius* from the experiment are described and the mean catch rates for the summer months (June to September) quantified using a generalized linear model (McCullagh and Nelder, 1989) in section 2.4. The proportion of males caught in the experiment, and how this changes with time and habitat, is discussed in section 2.5. Assessment of spatial clustering and possible trends across the data are left until chapter 5, after the development of suitable analytical techniques in Chapters 3 and 4.

2.2 A Large Field Experiment with Fragmented Habitats

With the recent changes in farming techniques and the effects of government and European Community subsidies for policies such as set-aside there has been an increasing interest in habitat fragmentation and the effect on the environment of having different habitats in close proximity.

In order to study the effect of having areas of arable land next to unfarmed areas on the local ecology it was decided to conduct an experiment at RES and LARS on environmental heterogeneity.

Designing this experiment posed a set of problems not usually considered in experimental design. Latin Square designs consider blocking up an experimental area by rows and columns to minimise the variance. Spatial considerations are not usually taken into account beyond this level, although there are designs such as nearest-neighbour designs (Freeman, 1979) where there is an attempt to balance out how often treatments occur near to one another. This doesn't really help if we wish to design an experiment where the spatial correlation is of interest in itself.

In order to have a variety of sizes of habitat patch, and to see what the effect of a nearby mature piece of hedgerow would be on plant and invertebrate populations, the design in figure 1 was selected.

This design, which is duplicated at both RES and LARS, consists of a field where most of the area was sown with winter barley which was treated in the usual way (harrowing, herbicide treatments etc.) to give a crop. Five 27m square patches and four grids of nine 9m square patches were sown with a mixture of four grasses and four broad-leaved herbaceous plants at the start of the experiment and then left to develop, apart from being mown once a year. There is a hedge running along one side of the field. This design was used because it gave an approximately constant ratio of crop to patch and could be used to study the effect of the hedgerow on the catches. The design was constrained by the need to plough the crop area, as well as sow and harvest the crop.

There is a possible problem with this design in that the grids of nine small patches are all in the corners of the experiment whereas the five large patches are nearer to the centre. It might have been better to have switched the small patches with the large patches surrounding the central patch, as in figure 2. However this alternative design would make movement between patches of the same size much more difficult than the design actually used.

In order to assess the insect populations of the patches, the hedgerow and the arable area, 152 wet pitfall traps were laid out each month in the positions marked with large dots. Because there is some confounding in this design between trap density and the patch density extra traps were placed, from 14/05/91 to 08/07/91 inclusive at RES and 14/05/91 to 9/12/91 inclusive at LARS. These extra pots are marked in figure 1 with circles. The pots were half-filled with a mixture of water and detergent and left without tops for one week. The pots were then removed from the field and the contents examined in the laboratory. For each pot the individuals were examined and the family, species and, if possible, sex and instar recorded. Sometimes it was not possible to identify individuals down to this level, in which case they were identified as far as possible. There were 313 different species categories identified.

The reported catches for the beetle *P. melanarius* in June 1990 at LARS are given in figure 3 as an example.

The first set of pitfall trap data was collected in September 1989 and trapping has

Figure 1: Patch experiment design with standard and extra sampling points

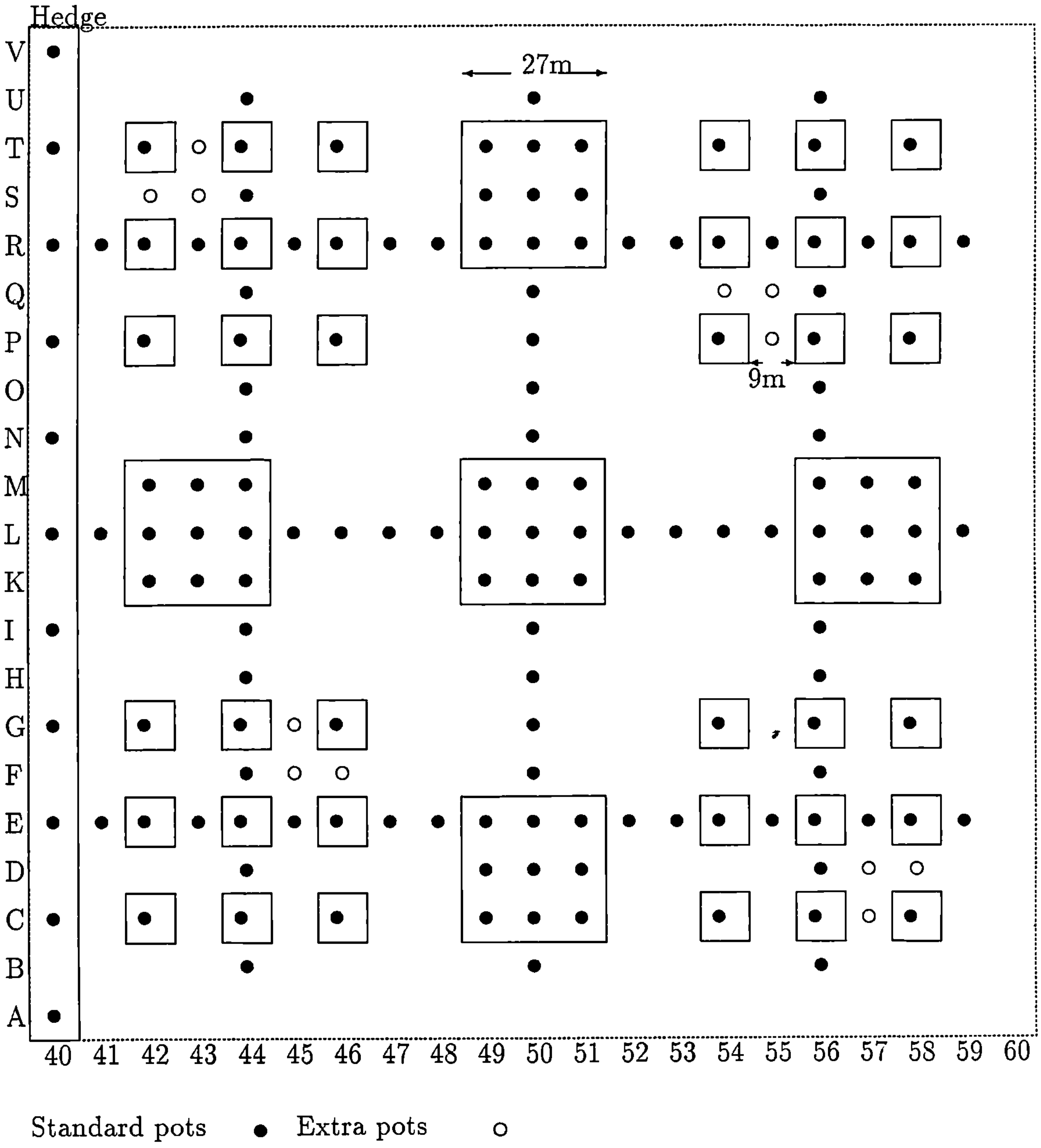


Figure 2: Alternative layout for patch crop experiment

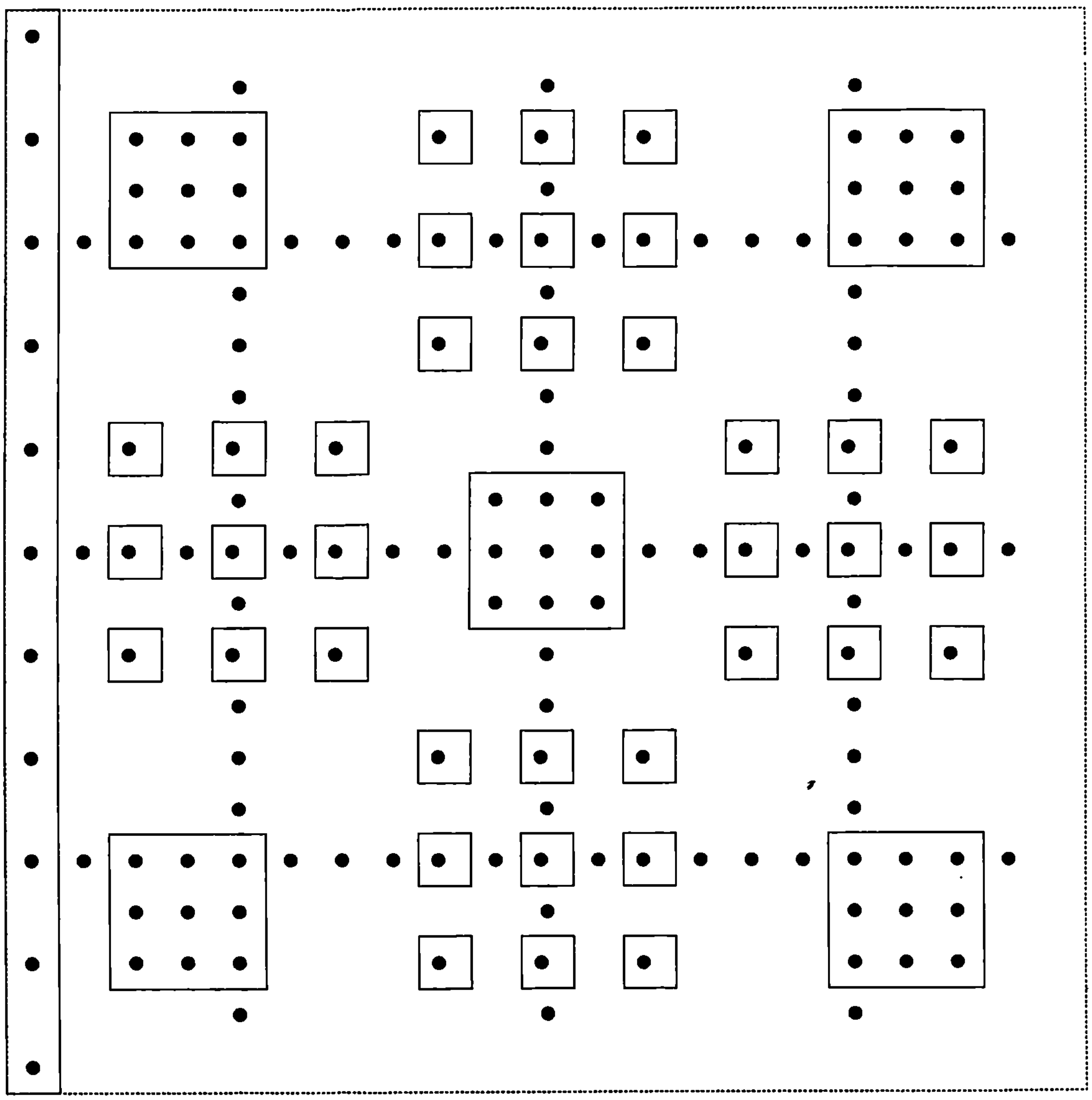
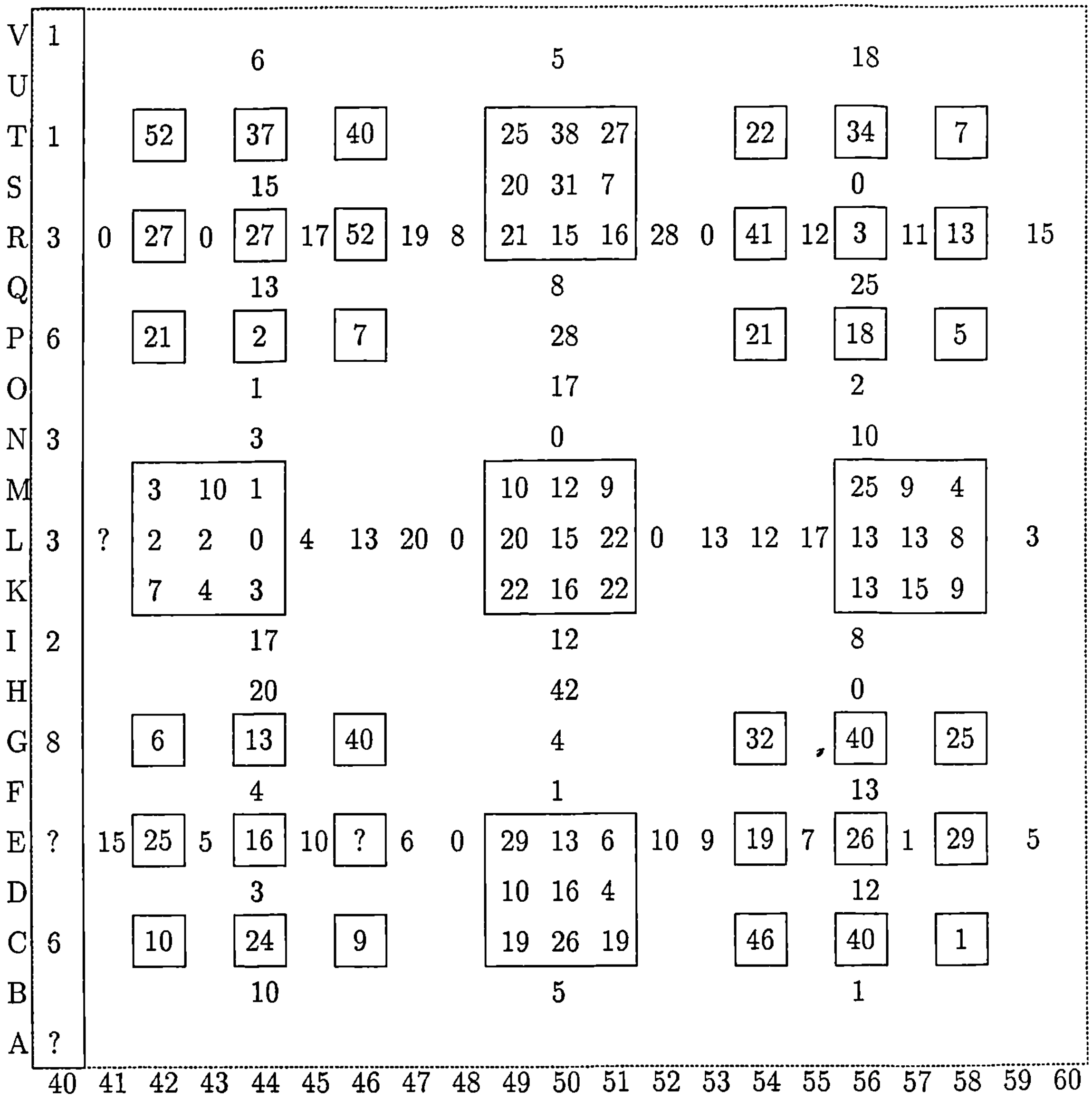


Figure 3: Patch experiment recoveries for *P. melanarius*, June 1990,LARS



	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
V	1				6						5						18				
U																					
T	1		52		37		40			25	38	27			22		34		7		
S					15					20	31	7					0				
R	3	0	27	0	27	17	52	19	8	21	15	16	28	0	41	12	3	11	13	15	
Q					13						8						25				
P	6		21		2		7				28				21		18		5		
O					1						17						2				
N	3				3						0						10				
M			3	10	1					10	12	9					25	9	4		
L	3	?	2	2	0	4	13	20	0	20	15	22	0	13	12	17	13	13	8	3	
K			7	4	3					22	16	22					13	15	9		
I	2				17						12						8				
H					20						42						0				
G	8		6		13		40				4				32		40		25		
F					4						1						13				
E	?	15	25	5	16	10	?	6	0	29	13	6	10	9	19	7	26	1	29	5	
D					3					10	16	4					12				
C	6		10		24		9			19	26	19			46		40		1		
B					10						5						1				
A	?																				

? represents missing data

continued ever since. It was occasionally impossible to set out a full set of 152 traps due either to farming activities or the weather. Sometimes the traps dried out or had sufficient leaf litter in them to allow substantial number of individuals to escape.

Full details of these events are given in tables 1 and 2.

One problem with this design is that if the presence of pitfall traps affects the population in the area surrounding it then there is a partial confounding, for pots in the crop, of the effect of the numbers of traps with the presence of patches.

A more serious problem with this design is the lack of randomisation and balance. The layouts at Rothamsted and Long Ashton were identical and systematic. This results in some serious confounding of major parameters of interest. However a randomisation of the design could well have left something that was impossible to manage from the point of view of ploughing and harvesting the crop and getting to the sampling pots without a large degree of disturbance to the experimental area. It may, with hindsight, have been better to have run a slightly smaller experiment which was properly randomised in order to avoid these problems, or at least to have had different designs at the two sites.

2.3 A review of work on *P. melanarius*

One of the most common species of beetle caught in the patch experiments at both LARS and RES was *Pterostichus melanarius*. This is a large polyphagous beetle that is very common in cereal fields across Northern Europe. It is an autumn breeding species (Wallin, 1985) that usually overwinters as a larva, although some individuals manage to overwinter as adults (Barlow, 1970).

In a study of the effect of pesticides and hunger, Chiverton (1984) described an experiment conducted in 1981 on *P. melanarius* in spring barley in the Netherlands.

Table 1: Void and unusual pitfall trap data at LARS

Date	Problem
04/10/89	)
11/10/89	) No traps put out in crop (crop not sown)
13/11/89	) LARS data not available
11/12/89	)
13/08/90	Void traps due to clever magpies
10/09/90	No traps put out in crop (crop not sown)
11/02/90	Small catches due to very cold weather
14/05/91 to 09/12/91 inclusive	12 extra traps put out in crop All appear on one standard form (e.g. C/C.57)
28/10/91	Sample late due to drilling difficulties
10/02/92	Trap G.58 is missing for carabids only
10/08/92	No traps in crop
08/09/92	No traps in crop
/12/92	Traps put out 1 week later at LARS than at RES

Table 2: Void and unusual pitfall trap data at RES

Date	Problem
25/09/89	No traps put out in crop (crop not sown)
02/10/89	No traps put out in crop (crop not sown)
16/10/89	No traps put out in crop (crop not sown)
13/08/90	No traps put out in crop (crop not sown) Traps dried out due to weather conditions. Increased numbers of unidentifiable spiders caused by drying out and predation by larger beetles.
05/10/90	8 crop traps were opened in the stubble (F.44, P.44, F.56, P.56, K.45, K.55, F.50, P.50)
10/09/90	No traps put out in crop (crop not sown)
18/02/91	Traps left open for two weeks due to weather conditions, i.e. snow on the ground, so unable to locate traps.
14/05/91 to 08/07/91 inclusive	12 extra traps put out in crop All appear on one standard form
12/08/91	Leaf debris in traps may have allowed insects to escape causing lower counts
12/08/91	No traps put out in crop (crop not sown)
09/09/91	No traps put out in crop (crop not sown)
28/10/91	Sample late due to drilling difficulties

Three large (4.3ha) plots within a field of spring barley were marked out and either left untreated or sprayed with a pesticide. Both Fenitrothion and Sumicidin were used. This experiment was repeated in a different field in 1982. In each plot five pitfall traps were half filled with a mixture of water and detergent and left out in the plots for a week at a time. At the end of each week they were brought in and the contents examined. In the treated plots the numbers caught dropped immediately after the application of pesticide but then increased to levels greater than in the untreated plots. The proportion of females caught in the treated plots was higher than in the untreated plots although the difference was only significant at the 5% level for Sumicidin in 1982 and Fenitrothion in 1981. The gut contents of the individuals recovered were examined to see if there were any systematic differences between the sexes and treatments. The proportion of males with solid food in their guts was not significantly affected by the treatment but both gravid (i.e. with fertilised eggs), and to a lesser extent non-gravid, females showed lower gut contents in those plots sprayed with pesticide than the untreated ones. This implies that the gravid females were affected by food shortages caused by spraying which affected the non-gravid females to a lesser extent and the males very little.

Wallin (1985) studied the effect of field size and neighbouring habitat on the catches of *P. melanarius* in fields containing spring barley. This crop is planted in May, harvested in August and the field ploughed again in September. Barrier pitfall traps were placed in two rows of seven in fields of 2 and 6 hectares in 1981 and then in single rows of seven in three larger fields of sizes 4, 10 and 20 hectares in 1982. These rows consisted of three traps in the middle of the field, two on the edge and two in the neighbouring habitat. They were emptied each week and the contents studied. It was found that the mean catch of *P. melanarius* increased with increasing field size

Table 3: Total monthly catches of *P. melanarius* in winter wheat (Jones,1979)

Year	May	June	July	August	September	October
1971	7	90	118	197	4	0
1972	7	9	55	73	3	8
1973	9	12	83	26	36	6
1974	5	19	74	65	?	?
1975	0	13	22	17	44	33
1976	5	36	153	157	61	12
1977	2	71	118	251	83	1

although the effect is to some extent confounded with the year of study. Temporally the count of *P. melanarius* showed an early peak in late May and then a longer period of sustained activity in July and August. The activity in May was at approximately the same level in the nearby areas as in the crop, although later on the crop catches are dominant. In order to see when the peak of activity of *P. melanarius* in arable fields occurs, the results of an experiment conduct by Jones (1979) were analysed. In that experiment, conducted over seven years, weekly samples were taken in a field of winter wheat at RES using 12 dry pitfall traps. The numbers of several species of carabid beetles caught each month were given, and are repeated for *P. melanarius* in table 3.

The total catch in July is compared to that in August in each year using the number of individuals captured in each month. The normal approximation to the binomial distribution was used, with results given in table 4.

The catch rate was higher in July than August for 1971 and 1976, which were also the years which showed the highest counts. In 1973 and 1975, when the counts were much lower there were significantly higher catch rates in July than August and a similar effect may have occurred in 1974 although the result in 1974 was not significant. This implies there may be a link between overall catch rates and periods

Table 4: Tests to see if peak catch rate occurs in July or August for *P. melanarius* in winter wheat

Year	July		August		
	Catch	No. of days	Catch	No. of days	Most abundant month (at 5%)
1971	118	31	197	24	August
1972	55	31	73	31	NS
1973	83	31	26	17	July
1974	74	31	65	31	NS
1975	22	18	17	31	July
1976	153	29	157	21	August

of peak activity, although more work would be needed to confirm this. A full analysis of this data would involve plotting the mean weekly catch against time, instead of amalgamating the catches into months, and looking at the activity peak from this graph.

The possibility of overdispersion in the counts and the effects of the weather in each week would also need to be considered and make the validity of using a simple binomial test (which implicitly assumes the data are not overdispersed) doubtful.

Chiverton (1984), in his experiment, also found a similar effect, though with a slight drop in the counts in the middle of the summer of 1981. As there were only five pitfall traps in the plot that was not treated with any insecticide it is difficult, especially if overdispersion is present in the data, to attach too much statistical significance to this. The 1982 sampling only started in mid-June, so it is impossible to tell if the population was lower then than in May. However Wallin (1985) also found this effect and attributed it to the emergence in the spring of individuals that have hibernated as adults over the winter. Such hibernation has been observed by Jorum (1980).

2.4 *P. melanarius* counts from the farmland ecology experiment

P. melanarius was more common at LARS than RES. In order to get an overall view of the patterns of catches for this species the mean monthly catch was calculated for each month for all three habitats (Hedge, Crop and patch), with the patch data further subdivided by patch size (large and small). These values were plotted against time for both sites. The plots are given in figures 4 and 5 and the numbers caught are given in tables 5 and 6.

The largest catches from the crop part of the experiment always occur in July at both sites, although for 1992 at LARS and both 1990 and 1991 at RES no pots were placed in the crop for either August or September. In each year, and at both sites, the small and large patches have very similar patterns. The peak catches again occur during July, except for 1990 at LARS, when July represented a slight lull in activity between June and August, and 1992 at RES, when only 11 individuals were caught in the patches all year. In the hedge the peaks occurs either in August (1991 and 1992 at LARS, 1990 at RES) or in July, although for RES the total catch from the hedge in 1991 was only 12 and in 1992 only two individuals were captured in the hedge.

The overall catches, certainly from the hedge and patches, show a decline from year to year at both sites. For the crop this is much more difficult to judge due to the months when there were no pots placed, although even here there does seem to be a gradual drop.

The early emergence of some individuals in March and April may be due to beetles emerging that had overwintered as adults (Wallin, 1985).

The plots for the male and female populations separately show very little difference

Figure 4: Mean catch of P. melanarius at LARS over time

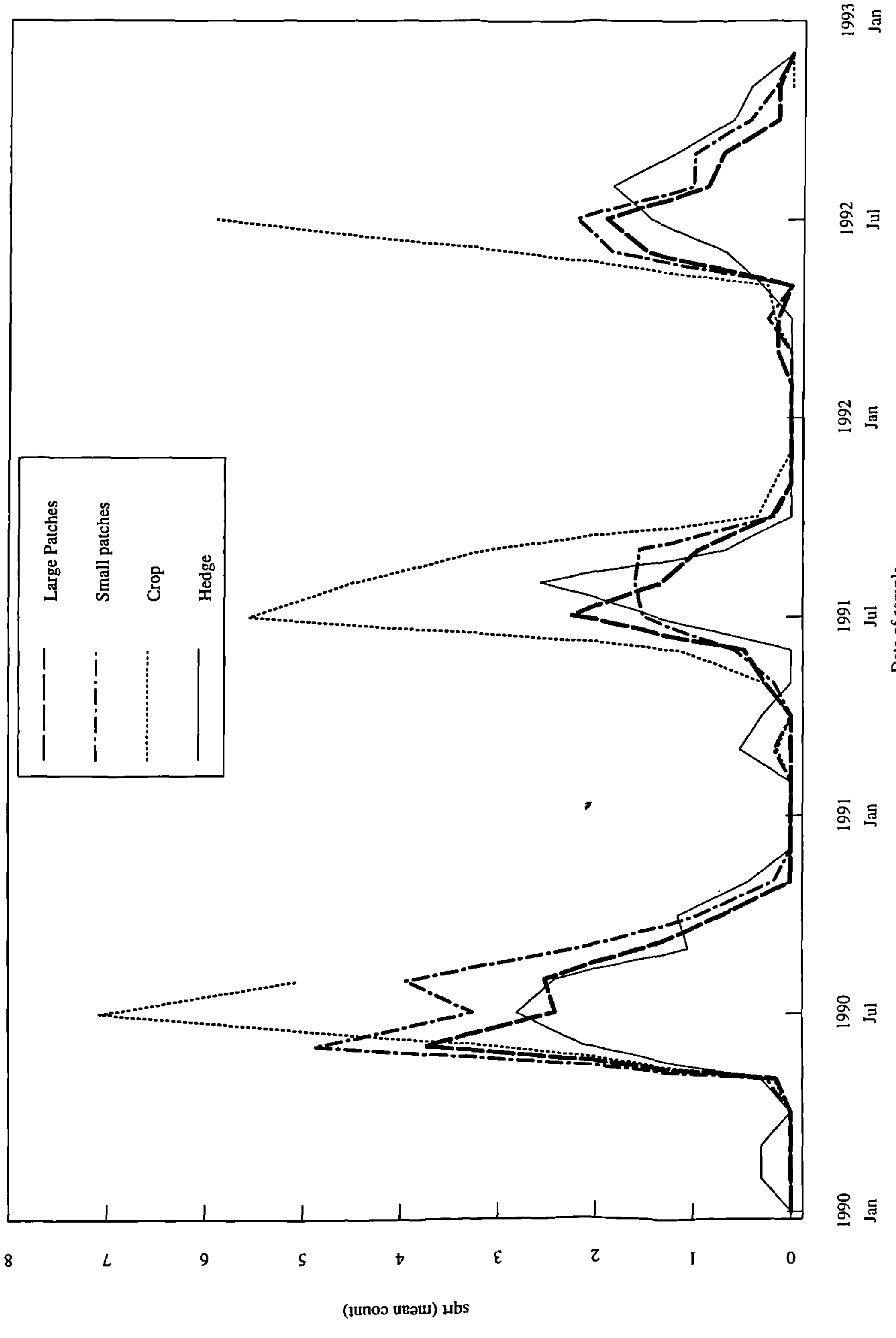


Figure 5: Mean catch of P. melanarius at RES over time

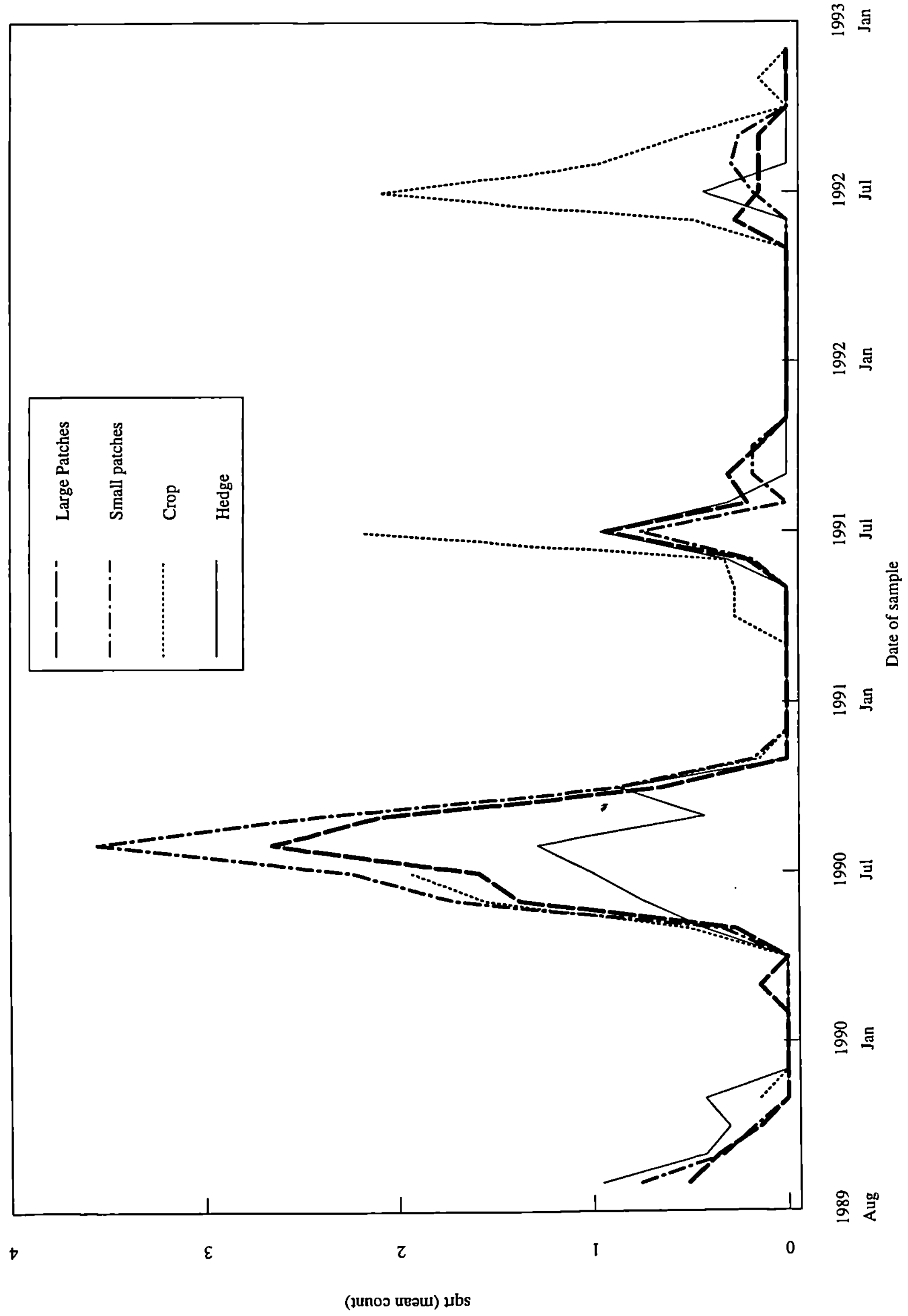


Table 5: Total catch of *P. melanarius* from Patch Experiment at RES 1989-1992
Number of pots laid out each month is given in parentheses

Month	Hedge		Crop		Small Patch		Large Patch	
1989								
September	10	(11)		(0)	20	(35)	11	(43)
October05	2	(11)		(0)	4	(36)	6	(45)
October16	1	(11)		(0)	1	(36)	1	(41)
November	2	(11)	1	(59)	0	(36)	0	(44)
1990								
March	0	(11)	0	(60)	0	(36)	1	(45)
April	0	(11)	0	(60)	0	(36)	0	(45)
May	2	(11)	15	(60)	4	(36)	3	(45)
June	6	(11)	145	(60)	106	(36)	85	(45)
July	11	(11)	224	(60)	180	(36)	113	(45)
August	18	(11)		(0)	455	(36)	317	(45)
September	2	(11)		(0)	216	(36)	195	(44)
October	8	(11)	6	(8)	28	(36)	19	(45)
November	0	(11)	1	(58)	1	(36)	0	(41)
1991								
March	0	(11)	0	(60)	0	(36)	0	(45)
April	0	(11)	4	(60)	0	(36)	0	(45)
May	0	(11)	5	(72)	0	(36)	0	(45)
June	1	(11)	7	(72)	1	(36)	2	(45)
July	10	(11)	343	(72)	20	(36)	39	(45)
August	1	(11)		(0)	0	(36)	2	(5)
September	0	(11)		(0)	1	(36)	4	(5)
October	0	(11)	1	(60)	1	(36)	1	(45)
November	0	(11)	0	(60)	0	(36)	0	(45)
1992								
March	0	(11)	0	(60)	0	(36)	0	(45)
April	0	(11)	0	(60)	0	(36)	0	(45)
May	0	(11)	0	(60)	0	(36)	0	(45)
June	0	(11)	14	(60)	0	(36)	3	(45)
July	2	(11)	262	(60)	1	(36)	1	(45)
August	0	(11)	56	(60)	3	(36)	1	(45)
September	0	(11)	16	(60)	2	(36)	1	(45)
October	0	(11)	0	(60)	0	(36)	0	(45)
November	0	(11)	1	(59)	0	(35)	0	(45)

Table 6: Total catch of *P. melanarius* from Patch Experiment at LARS 1990-1992
Number of pots laid out each month is given in parentheses

Month	Hedge		Crop		Small Patch		Large Patch	
1990								
February	1	(11)	0	(43)	0	(32)	0	(42)
March	1	(11)	0	(60)	0	(36)	0	(45)
April	0	(11)	0	(58)	0	(36)	0	(42)
May	1	(11)	2	(60)	2	(36)	1	(45)
June	45	(10)	563	(59)	830	(35)	631	(45)
July	86	(11)	2998	(60)	382	(36)	261	(45)
August	58	(10)	1114	(44)	542	(35)	271	(43)
September	12	(11)		(0)	152	(36)	99	(45)
October	12	(9)	32	(60)	32	(36)	20	(42)
November	2	(11)	0	(59)	1	(35)	0	(43)
1991								
February	0	(11)	0	(58)	0	(36)	0	(45)
March	3	(11)	1	(59)	1	(36)	0	(45)
April	1	(11)	0	(56)	0	(36)	0	(44)
May	0	(11)	6	(72)	1	(35)	3	(45)
June	0	(11)	89	(70)	12	(36)	10	(44)
July	21	(11)	2212	(72)	82	(36)	224	(45)
August	72	(11)	1477	(72)	92	(36)	82	(45)
September	5	(11)	638	(69)	84	(35)	41	(45)
October	0	(11)	7	(58)	1	(36)	2	(45)
November	0	(11)	2	(69)	0	(36)	0	(45)
1992								
February	0	(10)	0	(72)	0	(36)	0	(45)
March	0	(11)	0	(72)	0	(36)	1	(45)
April	0	(11)	2	(72)	2	(36)	1	(45)
May	1	(11)	4	(72)	0	(36)	0	(45)
June	5	(11)	584	(71)	119	(35)	99	(45)
July	23	(11)	2429	(70)	170	(35)	162	(45)
August	37	(11)		(0)	36	(35)	33	(44)
September	16	(11)		(0)	35	(35)	22	(45)
October	4	(11)		(0)	7	(36)	1	(45)
November	2	(11)	0	(65)	1	(35)	1	(45)

from those for the overall population.

2.4.1 Model Selection

This experiment raises serious problems when it comes to deciding upon a statistical model to analyse the data. The design was not randomised in any way and the two replicates, at Rothamsted Experimental Station and Long Ashton Research Station are on different types of soil. Any differences in the local ecosystems will be confounded with different weather conditions and treatments of neighbouring fields. In the event for this species the counts in 1991 and 1992 were so low at Rothamsted that it would have required a presence-absence model to analyse the results. In any event the low catches do not justify the fitting of a model with sufficiently many parameters to provide a clear description.

The experiment could be analysed as a repeated measures experiment with the sampling pots being treated as units and then analysing the effect of time and position on the catches in the units. This is sensible if there are significant differences between the environments for pots in apparently similar positions but not if the areas are approximately homogeneous. Any systematic differences between the sampling units would appear as patterns in the residuals from a fit for a model where the repeated measures effect was ignored. This is discussed further in section 5.3.1.

2.4.2 Model Fitting

It is of interest to find out if the patterns that appear to be present on a first analysis of the data are statistically significant. It would also be useful to be able to estimate the numbers of beetles that might have been caught if the pots had been laid out in the crop every month. In order to do this a Generalized Linear Model (McCullagh and Nelder, 1989) was fitted to the data. This was done using the Genstat package (Payne *et al.*, 1987). Because the totals are counts data the Poisson error model was used. The canonical log link was assumed and, due to a large degree of overdispersion in the data revealed by this analysis, the dispersion factor was estimated from the data.

Only the data from the period July to September for 1990 to 1992 inclusive from LARS were analysed. This was because the mean catch rate from LARS outside this period was low and the catch rate at RES was very low, especially in the patches for the whole of 1991 and 1992.

The effect of changes in time was accounted for by a year factor with 3 levels (1990, 1991, 1992) and a month factor with 4 levels (June, July, Aug and Sept). The effect of ground cover had a three level factor habitat with values Hedge, Crop and Patch. In order to differentiate between the small and the large patches an additional factor, patch size, was also fitted to the data. This factor had four levels, three of which were aliased with the habitat factor, so only one value needed estimating. The fourth level represents the difference between small and large patches.

Initially a model with the factors year, month and habitat was fitted. Then the effect of interactions between these factors, and the effect of patch size were considered by fitting each in turn, and including the most significant one. The significance of each effect as is it added can be measured by comparing the deviance ratio to the appropriate F-distribution. The deviances and significance are given in table 7.

If we use the deviance ratios as crude measures of the importance of each effect then the interactions and extra parameter can be divided into three groups, with month.habitat, year.habitat and patchsize all being extremely important, year.month having an intermediate effect and the last pair of interactions year.month.habitat and

Table 7: Deviance ratios for regression on mean catch of *P. melanarius* at LARS

Regressor	Degrees of freedom	Deviance Ratio	Significance
Year+month+habitat	7	242.96	0.1%
+month.habitat	6	46.03	0.1%
+year.habitat	4	36.47	0.1%
+patchsize	1	38.35	0.1%
+year.month	6	23.15	0.1%
+year.month.habitat	9	5.48	0.1%
+year.patchsize	2	5.02	1%
Overall regression	35	91.14	0.1%
Residual	1642	6.539	

year.patchsize being not as important in their effects on the predicted means but still extremely significant statistically.

The overall residual deviance ratio of 6.54 indicates that this model is nowhere near to providing a complete explanation of all the overdispersion present in the data.

A table of the regression coefficients, along with standard errors and t-statistics of deviation from 0 is given in table 8. The values are compared to a baseline of June 1990 in the crop. Some of the parameters, such as the September 1991 patch effect are not estimable because there were no pots placed in the crop at this time due to farming activities.

It was thought that the variability of the habitat parameter with month might in part be due to the change in the microclimate of the crop area that occurs when harvesting is done. Therefore the month parameter was replaced in the above model with a harvest parameter at two levels, pre-harvest (June and July) and post-harvest (August and September) and the model refitted. This resulted in a significant worsening of the model. When the effect of the monthly changes was brought back into the model by adding first the month parameter and then the interactions with year

Table 8: Parameter estimates for model for mean catch of *P. melanarius* at LARS

Regressor			Estimate	Standard error	t-statistic
Constant			2.256	0.108	20.95
1991			-2.016	0.291	-6.91
1992			-0.149	0.151	-0.98
JUL			1.656	0.117	14.10
AUG			0.976	0.132	7.39
SEP			-1.531	0.679	-2.26
Hedge			-0.752	0.396	-1.90
Patch			0.316	0.138	2.28
Time-habitat interactions					
JUL	Hedge		-1.103	0.485	-2.28
JUL	Patch		-2.493	0.168	-14.80
AUG	Hedge		-0.721	0.519	-1.39
AUG	Patch		-1.544	0.173	-8.92
SEP	Hedge		0.11	1.07	0.11
SEP	Patch		-0.247	0.656	-0.38
1991	Hedge		-4.18	4.91	-0.85
1991	Patch		-1.824	0.629	-2.90
1992	Hedge		-2.14	1.20	-1.79
1992	Patch		-1.604	0.267	-6.02
month.year interactions					
1991	JUL		1.529	0.300	5.09
1991	AUG		1.805	0.309	5.85
1991	SEP		3.515	0.614	5.72
1992	JUL		-0.216	0.166	-1.30
1992	AUG		-0.572	0.369	-1.55
1992	SEP		0.437	0.418	1.04
year.month.habitat interaction					
1991	JUL	Hedge	3.26	4.95	0.66
1991	JUL	Patch	1.928	0.648	2.97
1991	AUG	Hedge	4.51	4.93	0.91
1991	AUG	Patch	0.818	0.663	1.23
1991	SEP	Hedge	1.81	5.12	0.35
1992	JUL	Hedge	1.19	1.34	0.89
1992	JUL	Patch	1.475	0.302	4.88
1992	AUG	Hedge	2.32	1.35	1.71
1992	SEP	Hedge	2.14	1.59	1.34
Patch size					
Small			0.6440	0.0927	6.95
1991	Small		-0.695	0.226	-3.08
1992	Small		-0.265	0.216	-1.22

and habitat all these interactions proved significant. Therefore this attempted simplification of the model proved a failure.

If the model was an adequate fit to the data then the mean deviance would be approximately 1. As this is clearly not the case then either there are significant regressors which have not been taken into account or there is variability due to sampling method or random variation. There may well be a biological effect where individuals are attracted to each other and so pots which already contain individuals will catch individuals at a higher rate. Alternatively there may be strong local short-term variability in the population densities. A combination of these two effects is also likely.

The model was then used to predict the numbers of individuals that were recovered in each month for each habitat type. This was done using the Genstat PREDICT directive and the resulting values given in table 9. The values predicted are identical to the actual data for the hedge and the crop in months where samples were taken in these habitats, because of the fitting of the three way year-month-habitat interaction.

In the patches there is little difference between the predicted catches for the large and small patches for 1991, with a large difference predicted for 1990, and a smaller one for 1992. To see this more clearly the effect of the month and then patchsize was fitted using the same generalized linear model to the data for the patches only and for each year separately. The significance of adding the patchsize effect after the month effect, together with parameter estimates and confidence intervals, is given in table 10.

From this we can see that there is a very big difference in 1990, with a mean catch rate almost twice as large in the small patches as in the large ones. In 1991 there is no significant difference and in 1992 the difference, although still significant, is only

Table 9: Predicted mean catch of *P. melanarius* at LARS

	Crop		Hedge		Small Patches			Large Patches		
	Pred.	s.e.	Pred.	s.e.	Actual	Pred.	s.e.	Actual	Pred.	s.e.
1990										
JUN	9.54	(1.02)	4.50	(1.71)	23.71	24.91	(1.90)	14.02	13.08	(1.13)
JUL	49.96	(2.33)	7.81	(2.15)	10.61	10.78	(1.15)	5.80	5.66	(0.65)
AUG	25.31	(1.93)	5.80	(1.89)	15.49	14.11	(1.36)	6.30	7.41	(0.78)
SEP	2.06†	(1.41)	1.09	(0.80)	4.22	4.20	(0.69)	2.20	2.21	(0.37)
1991										
JUN	1.27	(0.34)	0.00	(0.04)	0.33	0.26	(0.14)	0.23	0.28	(0.15)
JUL	30.72	(1.67)	1.90	(1.05)	2.28	3.67	(0.68)	4.98	3.86	(0.65)
AUG	20.51	(1.36)	6.54	(1.96)	2.56	2.08	(0.47)	1.82	2.19	(0.46)
SEP	9.24	(0.93)	0.45	(0.51)	2.40	1.51	(0.38)	0.91	1.59	(0.39)
1992										
JUN	8.22	(0.87)	0.45	(0.51)	3.40	3.31	(0.64)	2.20	2.26	(0.45)
JUL	34.70	(1.80)	2.09	(1.11)	4.86	5.04	(0.83)	3.60	3.45	(0.59)
AUG	12.31†	(5.00)	3.36	(1.41)	1.03	1.05	(0.33)	0.75	0.72	(0.23)
SEP	2.75†	(2.10)	1.45	(0.92)	1.00	0.86	(0.36)	0.49	0.59	(0.20)

Crop and hedge predictions identical to catch where sample taken
Months without sample in the crop area marked with †

Table 10: Annual effect of patch size on *P.melanarius* catch at LARS

Year	Parameter estimate	(s.e.)	Significance	Difference in mean	95% c.i.
1990	0.664	(0.096)	0.1%	190%	[157%,231%]
1991	-0.051	(0.143)	NS	95%	[79%,126%]
1992	0.379	(0.150)	5%	146%	[108%,197%]

Catch in small patches is given as a percentage of that in large patches half of what it was in 1990 with about half as many again caught per pot in the small patches compared to the large ones. The statistical significance of this result relies on the catches within each large patch and each grid of nine small patches being uncorrelated. This is discussed further in section 5.6.

One of the motives behind the experiment is to discover the effect of proximity of different habitat types on the local biology.

In order to discover the effect on the crop counts of patches of semi-natural habitat a new continuous variate was defined for the crop data. This variate, *patch density*, is a weighted measure of the number of nearby plots that are covered in grass. Each edge neighbour that is grassed over contributes 1 and each corner plot gives 0.5. Thus the plot F44, which is sandwiched between two small patches, has a patch density of 2.0, plot I44 has a patch density of 1.5 and a plot away from the patches such as K47 has a value of 0. A generalized linear model, with Poisson errors and overdispersion was again fitted to the data, with both the patch and hedge data excluded. After fitting a mean activity level for every month the patch density variate was included. This was highly significant (F-statistic of 23.0 on 1 degree of freedom) and when the month-patch density interaction was added this was also a significant addition to the model (F-statistic 4.59, $P < 5\%$). Neither the two way interaction of patch density and year nor the three way month-year-patch density (implying different slopes in every month) proved significant. This implies that the effect of patch density varies with the time of year but is approximately the same each year. The parameter estimate was strongly negative, implying a decrease in catch in areas of high patch density.

Estimates of the change in catch rate for increasing patch density are given in table 11, along with significance levels. The September data are the only ones which do not give a significant result. The other parameter estimates do not appear to

Table 11: Effect of Patch density on catch rates in the crop of *P. melanarius* at LARS

Month	Years data collected	Parameter estimate	(s.e.)	Sig. level	Patch density effect	
					Estimate	95% c.i.
June	1990,1991,1992	-0.273	0.085	1%	68%	[41%,81%]
July	1990,1991,1992	-0.150	0.058	5%	74%	[59%,94%]
Aug	1990,1991	-0.369	0.098	0.1%	47%	[32%,71%]
Sept	1991	0.219	0.173	NS	155%	[77%,309%]

Predicted drop in catch for crop areas with two neighbouring patch squares compared to open field

differ significantly from one another. This could be the result of a different pattern occurring in September from the rest of the period, although this is difficult to confirm as there is only one year (1991) when pots were placed in the crop in September. The patch density parameter is closely related to the number of neighbouring pots laid out, so there is the possibility of confounding between the effect of patch density and pot density. When this possible effect was investigated it appeared that the effect of adding pot density to the above model did not significantly improve the fit, whereas adding patch density to the model with pot density did. Thus there is no evidence here of an effect of placing large numbers of sampling pots on the numbers caught.

It has already been shown that there is an effect of patch size on the catch rate of *P. melanarius*. It was decided to see if there was an effect of relative positions of pots within a large patch on the catch rate. This was done by fitting a variate patch density to the data set restricted to the large patches only. This variate was defined in the same way as patch density for the crop. However it did not have a significant effect on the goodness of fit of the model when it was applied to the data. Thus we can tentatively conclude that there does not appear to be a systematic difference between the catches in the corners, on the edges or in the middle of the large patches.

There did not appear to be any difference between the catches for pots in the blocks of small patches, on the edges or in the middle either. The difference might have to be quite large between the central pot and the others to be picked up as there are only 5 central pots for the large patches and 4 for the small ones.

2.5 The sex ratio in catches of *P. melanarius* from the patch experiment at LARS

When the catches from the pitfall traps were analysed individuals of selected species were, where possible, sexed. This leads to the possibility of analysing whether the sex ratio for these species varies between years, months or habitat, and describing these effects if they do. We will now go on to analyse and discuss the sex ratio of *P. melanarius* recovered in the pitfall traps at LARS.

In order to get a general idea of the variability in the sex ratio over time, and to see what the effect of habitat type might be, a logit transformation of the proportion of males caught in each habitat for each month at LARS was made and the results plotted against time for each habitat (figure 6). There does not appear to be any coherent trend in 1991 but in 1992 the large and small patches' seem to follow the same pattern.

In order to describe the changes in the sex ratio over time and with habitat in a more coherent fashion, and to pick out the effects that appear to be important, a Generalized Linear Model (McCullagh and Nelder, 1989) was fitted to the proportion of males recovered from each pot. This was done using the Genstat package (Payne *et al.*, 1987) and the canonical logit link function.

Significant variability in the sex ratio, apparent from the plot, is provided when

Figure 6: Logit transformation of proportion of males caught at LARS over time

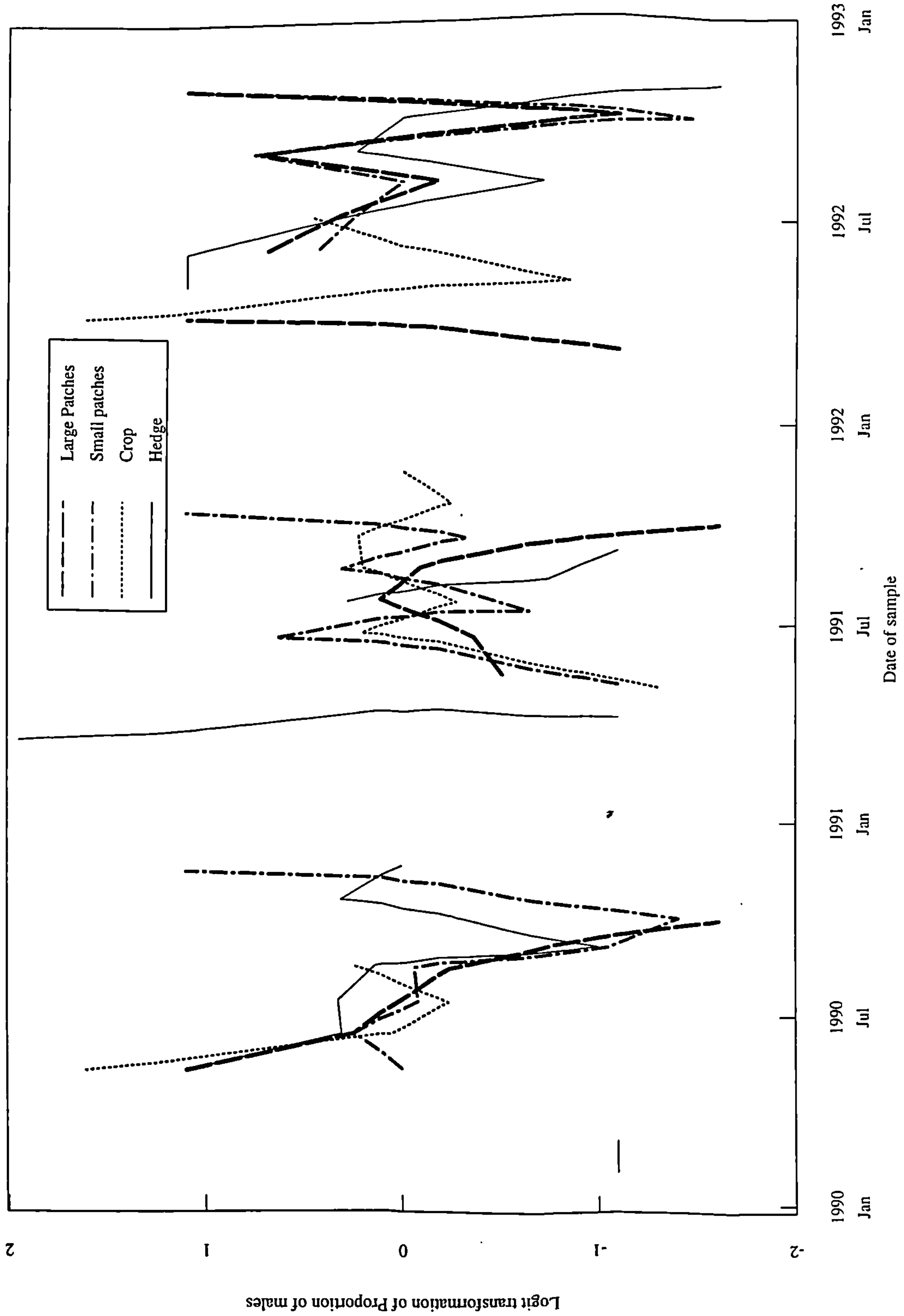


Table 12: Deviance ratios for model for sex ratio of *P. melanarius* at LARS

Regressor	Degrees of freedom	Deviance Ratio	Significance
Year	2	38.6	0.1%
Month	5	8.7	0.1%
logct	1	32.0	0.1%
year.month	10	7.2	0.1%
month.logct	5	3.7	0.1%
Overall regression	23	16.39	0.1%
Residual	1305	1.46	

a simple model consisting of just the mean proportion of males recovered was fitted to the data. It appears that the month, year and habitat are all important effects. As there were not many recoveries during the period November to May in each year, these were all grouped together as *winter* data, with the November and December data classified as being from the New Year. In order to see if there was an effect on the sex ratio in a pot of the total numbers caught in that pot, a new variable *logct* was created. The level of this variate was the log of the total number of *P. melanarius* caught in the sampling pot that month, including those individuals that had not been sexed.

The model was then fitted to the data, adding main effects and interactions (if all the relevant main effects were already present) in the order of the largest deviance ratios at each point. The order of fitting, together with the deviance ratios and significance levels for all these effects, is given in table 12, and parameter estimates related to the effect of the pot catch on the overall catch are given in table 13.

It seemed at this point to be strange that the habitat had no effect on the sex ratio of beetles caught. In order to make sure no important effects or interactions had been left out a long series of models was fitted to the data in turn and the Akaike

Table 13: Selected parameter estimates, for model for sex ratio of *P. melanarius* at LARS

Regressor		Estimate	Standard Error	t-statistic
logct		-0.0381	0.0648	-0.59
logct	Jul	0.0879	0.0729	1.21
logct	Aug	0.2803	0.0802	3.49
logct	Sep	0.244	0.113	2.16
logct	Oct	0.584	0.405	1.44
logct	Win	-0.26	1.89	-0.14

Table 14: Analysis of deviance for optimal month,year,habitat,logct fit to *P.melanarius* sex ratio at LARS

Model : Year*Month + Habitat*Month + Logct

	d.f.	deviance	deviance	deviance ratio
Regression	30	425.	14.183	9.91
Residual	1298	1858.	1.432	
Total	1328	2284.	1.720	

information criterion (AIC) (Akaike, 1969) used to determine the most parsimonious. A value of 2 for the selection criterion was used in order to get the predictions with the lowest estimated standard error (Mallows, 1973). All models up to the complexity level of three two way interactions between the effects month, habitat, year and logct were fitted. The most parsimonious of the models, both when the October and winter data were left out and included, was that the habitat effect and year effect vary with month and the effect of pot catch (logct) is constant over time and habitat. The apparent time dependence of the effect of pot count is now shown to be an effect of not fitting the habitat effect. The analysis of deviance for the model for all the months is given in table 14 and the parameter estimates in table 15.

In order to determine if the functional form of the relationship between pot catch and the sex ratio could be better described by a different transformation of the pot

Table 15: Parameter estimates for month-habitat interaction for model of *P.melanarius* sex ratio at LARS

		estimate	s.e.	t
Hedge		0.561	0.357	1.57
Patch		0.268	0.099	2.70
Jul	.Hedge	0.095	0.417	0.23
Jul	.Patch	0.011	0.131	0.09
Aug	.Hedge	-1.092	0.410	-2.66
Aug	.Patch	-0.428	0.141	-3.02
Sep	.Hedge	-1.481	0.647	-2.29
Sep	.Patch	-0.770	0.260	-2.96
Oct	.Hedge	0.071	0.850	0.08
Oct	.Patch	-1.469	0.580	-2.53
Win	.Hedge	0.15	1.10	0.14
Win	.Patch	0.411	0.933	0.44
logct	0.1338	0.0295	4.54	

catch, the log transformation was replaced by the identity and square root transformations in turn. Both of these led to a worsening of the fit implying that effect is better described by a multiplicative model than an additive one. The possibility of different sex ratios in the small and large patches was also investigated but the suspicion from figure 6 that the proportion did not differ between them was confirmed by the lack of a significant change when either the patch size alone was added, or patch size varying with month or year.

When the parameter estimates are examined it appears that there is a very close similarity between the estimates for the month-habitat interaction for the two months preceding the harvest (June and July) and for the two months after it (August and September). This was investigated by replacing interaction between the month and the habitat type with an interaction between a two level factor , Harvest, and habitat type. The harvest factor had one level for June and July, before the harvest, and another level for August and September, after the harvest. The small reduction in the overall deviance from doing this justified the fitting of this factor, but all of the other interactions were statistically significant.

Parameter estimates for this slightly simpler and now optimal model are given in table 16 and estimated proportions of males caught in pots with 1, 3 and 20 individuals are given in table 17 for 1990 and 1991 and table 18 for 1992.

The lack of any interaction between month and habitat after the harvest-habitat interaction has been taken into account and the lack of a year-habitat interaction implies the effect of ground cover on the sex ratio does not change over time.

From these tables we can also see that the predicted proportion of males rises with increasing catch, an effect which is constant over time and between habitats. In each month before harvest the proportion of males caught at any given catch rate is

Table 16: Parameter estimates for optimal model for sex ratio of *P. melanarius* at LARS

Parameter	estimate	s.e.	t
Constant	-0.420	0.123	-3.42
Hedge	0.633	0.192	3.30
Patch	0.2780	0.0644	4.32
logct	0.1352	0.0280	4.83
Jul	-0.3453	0.0742	-4.66
Aug	0.698	0.183	3.81
Harvest	-0.538	0.201	-2.68
1991	0.458	0.251	1.82
1992	0.206	0.109	1.89
Interactions			
Hedge.Harvest	-1.197	0.268	-4.47
Patch.Harvest	-0.482	0.107	-4.53
1991.Harvest	0.318	0.321	0.99
1992.Harvest	1.600	0.361	4.43
Jul.1991	-0.450	0.255	-1.76
Jul.1992	0.488	0.123	3.98
Aug.1991	-0.738	0.209	-3.53
Aug.1992	-1.715	0.423	-4.05

Table 17: *P. melanarius*, predicted proportions of males at LARS by pot count (1990 and 1991)

	Month	Habitat	Pot count 1		Pot count 3		Pot count 20	
1990	Before harvest							
	Jun	Crop	0.396	(0.029)	0.432	(0.024)	0.496	(0.018)
		Hedge	0.553	(0.049)	0.589	(0.046)	0.649	(0.044)
		Patch	0.464	(0.023)	0.501	(0.018)	0.565	(0.014)
	Jul	Crop	0.317	(0.025)	0.350	(0.020)	0.411	(0.012)
		Hedge	0.466	(0.048)	0.503	(0.047)	0.567	(0.046)
		Patch	0.380	(0.025)	0.415	(0.020)	0.479	(0.016)
	After harvest							
	Aug	Crop	0.435	(0.030)	0.471	(0.024)	0.536	(0.017)
		Hedge	0.304	(0.044)	0.336	(0.044)	0.396	(0.045)
		Patch	0.385	(0.025)	0.421	(0.021)	0.485	(0.019)
	Sep	Crop	0.277	(0.040)	0.305	(0.040)	0.365	(0.043)
		Hedge	0.179	(0.037)	0.199	(0.040)	0.246	(0.046)
		Patch	0.238	(0.031)	0.263	(0.032)	0.319	(0.037)
1991	Before harvest							
	Jun	Crop	0.509	(0.058)	0.543	(0.057)	0.609	(0.056)
		Hedge	0.661	(0.066)	0.691	(0.064)	0.745	(0.059)
		Patch	0.578	(0.057)	0.610	(0.056)	0.672	(0.055)
	Jul	Crop	0.319	(0.024)	0.349	(0.019)	0.413	(0.012)
		Hedge	0.469	(0.049)	0.502	(0.047)	0.569	(0.047)
		Patch	0.382	(0.024)	0.414	(0.020)	0.481	(0.017)
	After harvest							
	Aug	Crop	0.444	(0.026)	0.478	(0.021)	0.545	(0.014)
		Hedge	0.312	(0.043)	0.342	(0.043)	0.405	(0.046)
		Patch	0.395	(0.027)	0.427	(0.025)	0.494	(0.025)
	Sep	Crop	0.454	(0.028)	0.488	(0.024)	0.555	(0.022)
		Hedge	0.321	(0.046)	0.351	(0.047)	0.415	(0.050)
		Patch	0.404	(0.029)	0.437	(0.028)	0.504	(0.030)

Table 18: *P. melanarius*, predicted proportions of males at LARS by pot count (1992)

Year	Month	Habitat	Pot count 1		Pot count 3		Pot count 20	
1992	Before harvest							
	Jun	Crop	0.446	(0.027)	0.483	(0.023)	0.547	(0.021)
		Hedge	0.603	(0.048)	0.637	(0.046)	0.695	(0.044)
		Patch	0.516	(0.026)	0.552	(0.023)	0.615	(0.024)
	Jul	Crop	0.482	(0.028)	0.519	(0.021)	0.582	(0.012)
		Hedge	0.636	(0.045)	0.670	(0.042)	0.724	(0.038)
		Patch	0.551	(0.025)	0.587	(0.020)	0.648	(0.016)
	After harvest							
	Aug	Crop	0.457	(0.065)	0.494	(0.064)	0.558	(0.063)
		Hedge	0.324	(0.059)	0.357	(0.061)	0.418	(0.066)
		Patch	0.407	(0.060)	0.443	(0.060)	0.508	(0.062)
	Sep	Crop	0.700	(0.066)	0.730	(0.061)	0.777	(0.054)
		Hedge	0.570	(0.082)	0.606	(0.080)	0.665	(0.075)
		Patch	0.655	(0.068)	0.687	(0.065)	0.740	(0.059)

greatest in the hedge and smallest in the crop. After harvest this situation is reversed, with proportionally more males in the crop and fewer in the hedge. The predicted difference between the hedge and patch areas at any given catch rate is never more than twice the standard error for the hedge, although this value is quite large.

If we take a difference of more than two standard errors as representing a significant difference in predicted proportions, then before harvest the patch areas have a significantly greater proportion of males than the crop (although the result for June 1991 based on just 22 individuals in the patches was not significant). After the harvest the situation is reversed with significantly more males in the stubble in each August when a sample was taken, and a nearly significant result for the one year, 1991, when a sample was taken in the crop in September. There does not seem to be any general seasonal trend in the sex ratio, an impression which is reinforced by considering the size of the parameter estimates and standard errors for the year, month, year-harvest

Table 19: Actual and predicted proportions of males in *P. melanarius* catches at LARS

Month	Crop			Hedge			Patches		
	Actual	Pred.	(s.e.)	Actual	Pred.	(s.e.)	Actual	Pred.	(s.e.)
1990									
June	0.513	0.518	(0.017)	0.577	0.618	(0.045)	0.558	0.557	(0.014)
July	0.440	0.443	(0.010)	0.581	0.544	(0.046)	0.486	0.482	(0.015)
Aug	0.559	0.561	(0.016)	0.534	0.397	(0.045)	0.468	0.475	(0.018)
Sep	?	0.355	(0.043)	0.250	0.220	(0.043)	0.278	0.280	(0.033)
1991									
June	0.550	0.541	(0.058)	?	0.639	(0.068)	0.545	0.580	(0.058)
July	0.430	0.431	(0.012)	0.571	0.533	(0.047)	0.477	0.470	(0.017)
Aug	0.549	0.553	(0.014)	0.319	0.388	(0.045)	0.528	0.466	(0.024)
Sep	0.554	0.541	(0.022)	0.200	0.377	(0.048)	0.392	0.454	(0.028)
1992									
June	0.503	0.309	(0.084)	0.800	0.402	(0.105)	0.633	0.344	(0.089)
July	0.615	0.529	(0.021)	0.565	0.628	(0.047)	0.569	0.568	(0.023)
Aug	?	0.538	(0.064)	0.324	0.374	(0.063)	0.478	0.451	(0.061)
Sep	?	0.745	(0.060)	0.562	0.600	(0.081)	0.684	0.673	(0.067)

Months with no crop recoveries denoted by a ?

and year-month interactions given in table 16.

In order to obtain a simpler table, which could be used to compare predicted and actual proportions of males caught, the logct parameter was deleted from the previous model and then the model refitted. From this, predicted proportions of males and standard errors are obtained and are given, together with the proportions of males caught in each habitat in the field, in table 19.

There are large discrepancies between predicted and actual proportions of males caught in June 1992 for all the habitats and August and September 1991 in the crop areas. Apart from this the predicted and actual proportions caught seem to be modelled quite accurately. It may be that these few months are contributing considerably towards the higher than expected residual deviance for the model given in table 16.

Pots with high catches had more males, as a percentage of the catch in the pot, than pots with low counts. This effect, which appeared to be constant over time and between habitats, implies that the trapping mechanism itself is introducing biases into the study. One effect of this is that the catches for the males display a higher degree of overdispersion than they do for the females, with the model from section 2.4 having a higher residual mean deviance when applied to the males (4.98) compared to the females (3.42). When the Index of Dispersion was calculated for each occasion when the mean catch in either the small patches, the large patches or the farmed area was greater than 2.0 for both the males and the females, it was greater for the males on 11 out of 13 occasions ($P < 1\%$). A paired t-test for similarity of values also gave a significant difference ($P < 2.5\%$).

2.6 Conclusion and further work on the farmland ecology experiment

From the plots of the mean catch rate for the different habitats and the model fitted to the data of mean catch rates there appear to be changes in the pattern of catches in each year. The temporal patterns for the two sites are not similar. The catch rates at Rothamsted Experimental station in 1991 and 1992 were so low that it is difficult to make inferences about the patterns at these times.

In general the mean catch rate was highest in the crop, with the patches and hedge having about the same activity levels. For the patches at Long Ashton there was a strong relationship in the catch rates for the small and large patches. In 1990 and

1992 there were around 70% more beetles caught in the small patches than the large ones. In 1991 the difference between the two patch sizes was not significant. In the only year when the catches at Rothamsted were large enough to give a clear picture, 1990, there was also an approximately constant difference between the patch sizes with, again, the small patches having larger catches. This may be due to individuals moving a short distance from the crop areas into the field and then returning to the field. If this was the case there would be a far higher density of these temporary inhabitants in the small patches than in the large patches, as there is more boundary in the small patches. This effect may also explain why the catches decrease in the crop near to the patches when compared to crop areas which are a long way from the patches.

Inference about trends in the crop is more difficult due to the missing data for September 1990 and both August and September 1992. The mean trap rate for *P. melanarius* at LARS shows a different pattern in each year, and the relationship between the populations in the habitats also seems to change. However the difference between the catches in small and large patches is fairly stable within each year. The catches in the crop were usually lower in the pots near to the patches than in those further away.

The effects of season on catch rates are very difficult to measure in a coherent fashion because there was only one week in each month when samples were taken. If the week when the samples were taken was particularly favourable then the count will be higher than it would have been had that week's weather been unfavourable. Thus any temporal analysis on important biological questions, such as whether the annual amount of activity for members of a given species is approximately constant, is difficult to undertake with data of this type. This is the penalty for having sufficient information to be able to assess spatial pattern. Laying out the pots in every week would have resulted in an experiment that was too large for the resources available.

The sex ratio varied significantly over time and no clear overall pattern as to the overall proportions of males and females active emerged. However the effect of the harvest on the relative proportions of males and females in the crop and surrounding areas was considerable. Before harvesting more males than females were caught in traps in the patches and more females were caught in the crop but, after harvesting, the position was reversed.

An experiment that could be run to assess the effect of total catch on the proportions would be to manipulate the contents of the pots. If some pots were replaced more often than others, say emptying one group daily and leaving the rest out for the entire week, then the catches from the two sets of pots could be compared. Alternatively some pots could be baited with freshly killed (and marked) individuals and the results compared with ordinary traps. If the baited traps had a higher proportion of males than the unbaited traps then this would imply that males are more attracted to full pots than females. This might explain the difference in the overdispersion rates between the sexes overdispersion observed the end of section 2.5.

As to further work, there are a large number of species from the farmland ecology experiment whose records have not been analysed. Apart from repeating the same analytical techniques shown here it would be possible to look at pairs of species using the methods proposed by Arditi and Dacorogna (1988). Interactions between several species, which have not been considered here, are likely to require a multivariate approach.

Chapter 3

New tests for non-randomness

3.1 Introduction

This chapter deals with some new statistical tests that have been devised to assess the degree of non-randomness occurring in counts data that were collected simultaneously from points in the plane. These tests can be used to gauge the extent of the deviation from the Poisson distribution and the importance of the spatial pattern in the data. Two types of non-randomness are considered in depth in this thesis, overdispersion and spatial aggregation.

If the counts have the property that the variance of the catches is greater then the mean then they are usually described as overdispersed. If the counts have the property than there is positive correlation between neighbouring points then the pattern is described as spatially aggregated. These two properties are not mutually exclusive. Spatial aggregation can either be on a relatively small scale or on a scale with large clusters, or even to be part of an overall spatial trend. If the cluster size is so large that the experimental area consists of a cluster of high counts and a cluster of low

Figure 7: Myzus Persicae counts from a 3 × 5 grid

8	6	5	9	10
3	3	10	15	7
10	10	4	8	3

counts, then this is indistinguishable in practice from the situation of a trend. If the underlying distribution of the points is a thought to be a Poisson distribution but there is a spatial pattern such as a trend then it may be possible to estimate this trend using a model and then see if the residuals from the fit, once they have been standardised by dividing by the expected catch at each point, are consistent with coming from a Poisson distribution. If this is the case then we can describe the data as having a spatial pattern but not being overdispersed.

Underdispersion (Variance<<mean) is very rare in animal counts. Complex patterns, such as periodicity in the data, would require a more model-based approach than that taken in this chapter. Neither of these are considered further.

As an example data set we shall initially consider counts of the aphid Myzus Persicae collected by Harrington and Taylor (1990). The counts are from an equally spaced 3 × 5 grid and are given in figure 7.

The most common measure for overdispersion is the Index of Dispersion (Fisher *et al.*, 1922) which is the ratio of the sample variance to the mean which has, asymptotically, under the null hypothesis of an underlying Poisson distribution, a χ^2 distribution with degrees of freedom one less than the number of sampling points.

There are several other indices of overdispersion, e.g. Morisita's index (Morisita, 1962), Iwao's mean crowding (Iwao, 1968) and the negative binomial parameter k (Taylor *et al.*, 1979) which are simple functions of the data, usually just involving the variance and the mean, and which do not take into account the spatial context from which the data arise. These measures describe the extent of deviation from the Poisson distribution but do not attempt to look at spatial pattern.

If we consider the two artificial 4×4 grids below, grid A shows significant overdispersion (Index of Dispersion 2.133, $P = 0.65\%$) but no spatial aggregation, whereas grid B appears to have a spatial pattern but no overdispersion (Index of Dispersion 1.07, $P > 10\%$).

A

12	4	4	4
4	4	12	4
4	4	4	12
4	12	4	4

B

10	10	6	4
10	10	6	4
6	6	4	4
4	4	4	4

Thus the Index of Dispersion would describe the first pattern as over-dispersed, but not reject the hypothesis that the data come from the Poisson distribution for the second data set even though it appears to be spatially aggregated.

The tests that will be described here are suitable as alternatives to the above tests but are also able to illustrate the degree of spatial pattern among the observations.

The measures all involve rearranging the individuals that make up the samples so that the variance has some desired property. The value of each measure is the total distance moved by all the individuals so the variance reaches its required value. There are four proposed measures, the first two of which were devised by Perry and Hewitt (1991), and the latter pair by myself. Moves to Randomness (M_{rand}) is defined as the number of moves needed to reduce the sample variance to less than the mean. Moves to Crowding (M_{crowd}) is the number of moves required to maximise the variance. This occurs when all the individuals are at one sampling point. Moves to Regularity (M_{reg}) is the amount of effort required to reduce the variance to 0. This occurs when all the counts are the same. Moves to Reduction (M_{red}) is a less extreme version of M_{reg}, where moving stops after the initial variance has been halved. The statistical significance of these measures is assessed using simulation studies.

In section 3.2 we look at the initial work of (Perry and Hewitt, 1991), where M_{rand} and M_{crowd} were calculated using moves along the vertices of a lattice and then used to create an index to detect overdispersion. The methods used are discussed and some improvements to the algorithms suggested. In section 3.3 algorithms for calculating all four measures for points on a plane are given and methods for the detection of aggregation as well as overdispersion given. Section 3.4 briefly discusses calculating these measures when there is no spatial information available. Section 3.5 discusses possible extensions to the above measures to look at correlations between counts and point patterns. The chapter ends with a short conclusion in section 3.7. A full discussion of which measure should be used in practice is given in section 4.6.

3.2 Overdispersion on a lattice

In this section the problem of calculating M_{rand} and M_{crowd} within a spatial context is considered. Within this framework the cost of moving an individual from one point to another is assumed equal to the distance between the points. Finding the minimum cost in order to reach any of the above four requirements requires the distance between the points to be taken into account. The Perry and Hewitt (1991) approach, where points are considered to be on a regular two-dimensional lattice and movement is only allowed between neighbouring points, will now be considered.

As a novel alternative to the Index of Dispersion, and similar tests based on the moments of the sample, Perry and Hewitt (1991) suggested the following. Individuals should be moved from points with large counts (donors) to neighbouring points with smaller counts (receivers) until the variance is equal to the mean, which is its expected value under the null hypothesis of the Poisson distribution. The number of such moves signifies how far the data set is from randomness. The full algorithm, which applies only to a regular grid, is as follows.

1. For all pairs of points (d, r), with counts x_d and x_r respectively, that are neighbours, with $x_d < x_r$, calculate $\mathit{Diff}(d, r) = x_d - x_r$ and choose the pair with the maximum difference.
2. If more then one pair could be chosen, choose the one with the smallest receiver.
3. If there is still a choice, choose the receiver with the smallest average count among its neighbours.
4. If there is still no choice pick one at random.
5. If the variance of the new values is greater then the mean, return to (1), otherwise stop.

If we consider the data in figure 7, and compare all pairs of points then the first move is from the 15 to the 7 as shown below

$$\begin{tikzcd}
8 & 6 & 5 & 9 & 10 \\
3 & 3 & 10 & 15 \arrow[r] & 7 \\
10 & 10 & 4 & 8 & 3
\end{tikzcd}$$

After another five moves the pattern becomes

$$\begin{tikzcd}
8 & 6 & 5 & 9 & 10 \\
4 & 5 & 9 & 13 \arrow[r, Rightarrow] & 8 \arrow[d] \\
9 \arrow[u] & 9 \arrow[u] & 4 & 8 & 4
\end{tikzcd}$$

Double arrow represents 2 moves

It appears that after choosing the largest gap between points, the decision of whether to use the counts around the donor or receiver as a method of breaking ties is essentially arbitrary, as the situation is symmetric about the mean. Perry and Hewitt (1991) did not give any proof that their algorithm was optimal and indeed the algorithm is non-optimal under some circumstances. However the counterexamples are fairly extreme and involve patterns which are clearly spatially aggregated anyway, so this does not appear to be a major problem.

In order to scale the value of M_{rand}, Perry and Hewitt (1991) developed the concept of Moves to Crowding (M_{crowd}). This they defined as the amount of effort to reach the pattern at which the variance reaches its maximal value, when all the individuals are situated at a single point. In a similar fashion to M_{rand} moves are only allowed along the vertices of a regular lattice and the value is calculated by using the cheapest route. The only major problem lies in deciding which point to crowd to. Perry and Hewitt (1991) calculated M_{crowd} for every point on the grid and then chose the crowding point with lowest cost. We shall now show that there is a much simpler algorithm.

Firstly, define M^r_{crowd} as the number of moves along rows required to reach crowding and M^c_{crowd} as the number of moves along columns. Thus:

$$M_{crowd} = M^r_{crowd} + M^c_{crowd}$$

To calculate M^r_{crowd} we can collapse the grid along the columns (effectively assuming all the column moves were made first). Then all that remains to be done is to calculate M^r_{crowd} from a line of points. For the data from figure 7 the pattern is

21 19 19 32 20

Similarly M^c_{crowd} can be calculated after collapsing the grid along the columns.

M_{crowd} along a line is just the mean absolute deviation (calculated per individual and not per sampling point) multiplied by the number of individuals and the crowding point is the median. To see this label the points along the line $1, \dots n$ with counts $x_1, \dots, x_n$ then the cost of crowding to the pth position is

$$M_{crowd}(p) \;=\; \sum_{i=1}^{n} x_i |p - i|$$

The change in the cost associated with moving the crowding position from p to $p+1$ is

$$\begin{aligned} Change &= \sum_{i=1}^{n} x_i|p+1-i| - \sum_{i=1}^{n} x_i|p-i| \\ &= \sum_{i=1}^{n} x_i(|p+1-i|-|p-i|) \\ &+ \sum_{i=1}^{p} x_i(|p+1-i|-|p-i|) \sum_{i=p+1}^{n} x_i(|p+1-i|-|p-i|) \\ &= \sum_{i=1}^{p} x_i - \sum_{i=p+1}^{n} x_i \end{aligned}$$

Thus for the figure 7 data M^c_{crowd} is 73 and M^r_{crowd} is 133. The value of M_{crowd} is 206, with the crowding point being the centre of the grid.

In order to turn these two measures into an index so that the level of overdispersion could be assessed and the significance of the result considered, Perry and Hewitt (1991) defined the Index of Crowding (I_{crowd}) as $M_{rand}/(M_{rand}+M_{crowd})$. In order to assess the statistical significance of the value of this index for any given data set, Perry and Hewitt (1991) suggested using simulation studies. In their algorithm the catch at each point was replaced by a realisation of a Poisson random variable independently for all the points and then M_{rand}, M_{crowd} and I_{crowd} calculated. They found that I_{crowd} was a more powerful method of differentiating between a Poisson distributed data and that drawn using a Perry-Mead mosaic than M_{rand} on its own.

Unfortunately this method of simulating the data contains within it an unnecessary source of variability. The mean count varies between the simulations because the simulations are of independent Poisson random variables. When the simulations were performed, using the multinomial distribution, effectively conditioning on the total overall catch, the advantage of using I_{crowd} rather than M_{rand} evaporated.

The restriction of movement to the vertices of the pattern, although simplifying the calculations, artificially separates out the dimensions of the experimental area. A more serious problem is the inability to deal with patterns other than simple grids. These difficulties are considered in the next section.

3.3 Overdispersion and Aggregation without a lattice

If we try to apply the algorithm from section 3.2 to the data from the crop patch experiment looking only at the data from the crop parts of the experiment, then we have a pattern like figure 8. The example given consists of the counts of *P. melanarius* from the sown part of the field patch experiment for June 1990.

This pattern, although based on a grid, has so many holes in it that some points have no nearest neighbours 9m distant, so any algorithm must allow longer moves. Moves will now be allowed between any pair of points.

In order to develop a sensible algorithm for choosing moves it is necessary to know the cost of each possible move (which is simply the distance) and the benefit, which is measured by the possible fall in variance which would result. If we consider a move from a point with count x_i to one with catch x_j and denote the counts before moving as x_k and after as x'_k the change in variance, given there are n points with a mean of $\bar{x}$, is

$$\begin{aligned}
&\frac{1}{n-1}\sum_{k=1}^{n}(x_k-\bar{x})^2-\frac{1}{n-1}\sum_{k=1}^{n}(x'_k-\bar{x})^2\\
=&\ \frac{1}{n-1}\left[\left\{(x_i-\bar{x})^2+(x_j-\bar{x})^2\right\}-\left\{(x'_i-\bar{x})^2+(x'_j-\bar{x})^2\right\}\right]\\
=&\ \frac{1}{n-1}\left[\left\{(x_i-\bar{x})^2+(x_j-\bar{x})^2\right\}-\left\{(x_i-1-\bar{x})^2+(x_j+1-\bar{x})^2\right\}\right]
\end{aligned}$$

Figure 8: Crop data for Pterostichus at LARS, June 1990

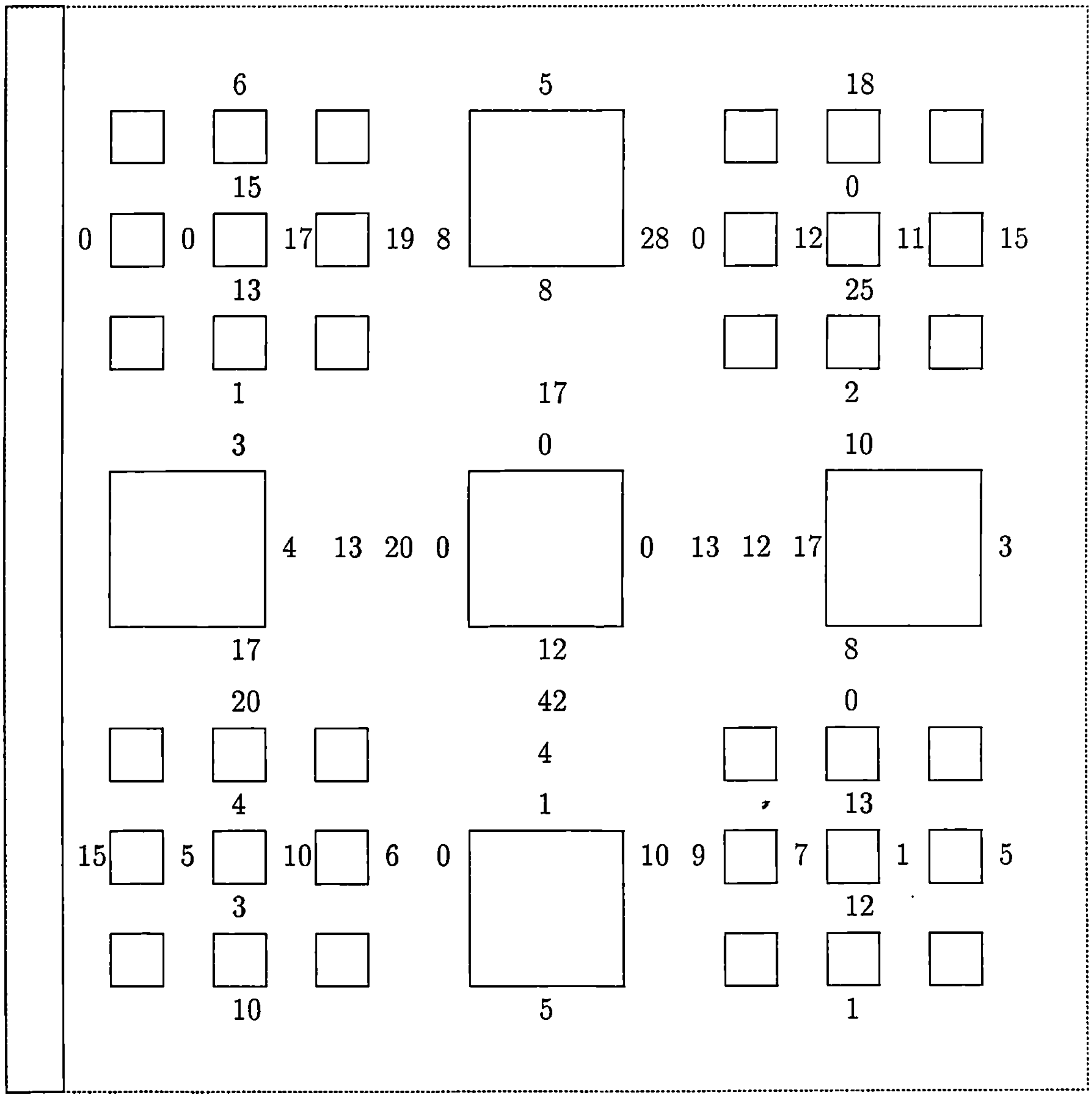
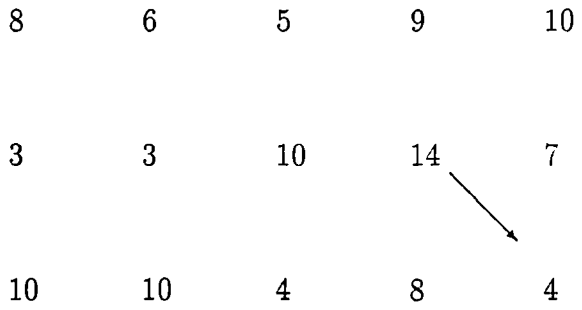


Figure 9: Harrington data, first move to randomness using new algorithm



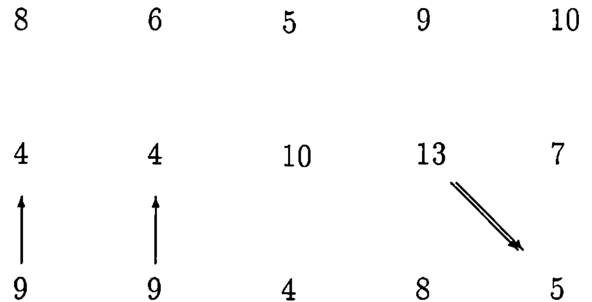
$$= \frac{2}{n-1}(x_i - x_j - 1)$$

This can be done by first noting that the reduction in variance caused by a move from i to j (with counts x_i and x_j) is proportional to $(x_i - x_j - 1)$. Therefore if the distance between them is D_{ij} then we can define the gradient of the move as $(x_i - x_j - 1)/D_{ij}$, which represents the rate of drop in variance for increase in distance. As we wish to minimise the total distance moved while reducing the variance a simple algorithm is to pick out the move with the highest gradient at each stage. If we consider the Harrington data, the first move is from the position $(4, 2)$ which has a count of 15 to the corner point $(5, 3)$ which has a count of 3. The cost of this move is 1.414. This gives the pattern in figure 9.

The next move is a repeat of the first one, but now the gradient for making a third move across that gap is 4.95, which is less than the gradient of 6.0 from one of the 10's on the bottom row to a 3 directly above. These three moves therefore leave the pattern in figure 10.

Now the variance is less than the mean, so no more moves are required and the total cost is 4.824 compared to 5 from the algorithm in section 3.2.

Figure 10: Harrington data, all M_{rand} using new algorithm



Double arrow represents 2 moves

Although it is easy to show that this algorithm has some problems with picking the right move at each stage, it has the advantage of being quick to run and easy to program. It runs into difficulties when trying to choose the last move to be made, as it can overshoot the required value of variance, making an unnecessarily long move towards the end of the algorithm. It is difficult to see any step-by-step algorithm that will not run into trouble at this point. This is therefore the algorithm that is used in all the examples, and as we are only using this value as a comparison with values also calculated by this slightly inefficient algorithm it does not appear to matter that all the solutions are non-optimal. It is however possible to devise an optimal algorithm using Operational Research techniques. Unfortunately this algorithm means throwing away the use of integer moves and utilises fractional moves instead. See Appendix A for details of this approach.

If the pattern starts off with variance < mean then M_{rand} is not applicable. Making *backwards* moves until variance > mean is not a reasonable thing to do. This is because the best first move is one that goes *up* the steepest gradient. This means the best second move, providing the donor point has not run out of individuals, is a repeat of the first one. This is likely to lead to one receiver draining all the individuals off from around itself until variance > mean, which does not give an overall measure.

For the calculation of M_{crowd} the easiest approach, once possible crowding points have been restricted to places where samples were taken, is to calculate M_{crowd} using each sampling point as the crowding point in turn and the choose the smallest.

The algorithm for reducing the variance can also be applied when a different stopping point other than variance=mean is considered. One alternative to the mean is to use the upper 95th percentile of the appropriate χ^2 distribution, as has also been suggested by Luís Afonso (personal communication). Unfortunately, as he also recognised, this lumps together all samples which are not considered aggregated using the Index of Dispersion test as having no moves, making this a poor approach.

However a more fruitful approach is to consider how many moves it takes to remove half of the variance. The same algorithm as for M_{rand} is applied but, instead of stopping when the variance reaches the mean, moves cease when the variance reaches half of its initial value. This is M_{red}. This could be particularly appropriate when testing for spatial pattern (as against overdispersion), when the variance starts off at several times greater than the mean. In some circumstances this appears to be a more powerful test. See section 4.3 for more details.

In order to calculate M_{reg} it is necessary to adjust the data so all the counts are equal to the mean. To do this the mean count is subtracted from the data set, which is then divided up into donors, which have a positive count, and receivers, which now have a negative count. An example, from the data in figure 7, is given in figure 11. Moving the excess from the donors to the receivers is a straightforward exercise in linear programming, which is best solved using the transportation algorithm described by Taha (1976), page 138.

The cost for the M_{reg} from this position is 28.0284 obtained by using the transportation algorithm.

Figure 11: Harrington data with means subtracted

0.6	-1.4	-2.4	1.6	2.6
-4.4	-4.4	2.6	7.6	-0.4
2.6	2.6	-3.4	0.6	-4.4

Table 20: Significance of non-randomness in Harrington data

	M_{rand}	M_{reg}	M_{red}
Moves	4.824	28.024	7.242
Poisson	7.67%	18.55%	8.42%
Permutation	40.81%	53.13%	28.44

The null distributions of the moves measures have not been calculated, so to test the hypothesis the counts are drawn from a Poisson distribution, multinomial simulations are done and, if the measure from the data is greater than that from 95% of the simulations then overdispersion has been detected (at the 5% level). To detect aggregation a similar procedure is undertaken but now random permutations of the observed values are made. For the data from figure 7 10,000 simulations were made for both the overdispersion and aggregation tests, with results in table 20.

From these results it appears that there is no significant deviation from the Poisson distribution either in terms of overdispersion or spatial aggregation for this data set.

3.4 Non-Spatial Tests

Perry and Hewitt (1991) also considered the situation where no spatial information was available. In this case the discrete metric (where the distance between each pair if distinct points is 1) is the only sensible choice. This makes calculating M_{crowd}, M_{rand}, M_{reg} and M_{red} much easier.

M_{crowd} can be calculated by subtracting the largest count from the total number of individuals observed. This is because the obvious place to crowd to is the point with the largest initial count. If we consider the data of figure 7 then the obvious point to move to is the one with a count of 15, and the M_{crowd} is therefore 100.

M_{rand} can be calculated by always making moves from the largest to the smallest count until the variance equals the mean. M_{red} can be calculated using the same algorithm except that it stops when the variance has been halved.

M_{reg} is the value of the total absolute deviation from the mean. This average absolute deviation from the mean, or mean deviation, has been studied by Ramasubban (1958) and its moments have been calculated for several distributions.

3.5 Extending the scope of *Moves* measures

The decision in the use of the measure M_{red} to use the stopping point at 50% was arbitrary. This value means that several moves will probably have to be made to reach the required state but that there will still be some variability left. Further work, including appropriate power tests, may well lead to a different stopping percentage being chosen.

A different sort of stopping criterion would be to stop moving when the next move that would have been made has a low gradient. This means that *local* heterogeneity would have been smoothed out but that overall trends might still remain. The number of moves made would then be a measure of local variability and the remaining variability would measure the large scale pattern in the data.

Previously we have looked at the situation where the positions where the observations arose were fixed by an experimental design. We now consider the situation where individuals are observed at random positions in an experimental area and the question of interest is whether the positions are all independent. An example would be the positions of trees in a forest.

If we simulate another data set with the same number of observations as the first one but with a uniform distribution across the area, and assign each of the original points a count of 1 and the simulated points a count of 0 then we can calculate M_{reg} as before. If a distribution of these moves measures is built up by using a large number of random simulations then we can compare it to the values obtained for moving between two grids with uniform density. The transportation algorithm could be used to calculate the moves in each case but it is computationally more efficient to use the assignment model of (Taha, 1976, page 181) to exploit the fact that each point will only donate or receive one individual.

If there areas of high and low density, due to some external factor, e.g. soil type, the total number of individuals in each of the types of area can be constrained to remain constant between the original pattern and simulations of it. If there is a continuous model fitted to the density, such as a trend, then the underlying density of the target pattern can be simulated based on this rather than on the uniform distribution.

If we have a data set consisting of two variables for each sample point, such as numbers of males and females of a species caught in a series of traps or catches on two separate occasions, then the difference between the two sets can be calculated in order to give a measure of correlation. This is done by standardising the sets so they have the same mean catch, subtracting one from the other, and then calculating M_{reg}.

The resulting value reflects the degree of difference between the patterns. In order to assess the significance of this relationship, it is necessary to simulate the two data sets in some way.

If both sets of data are simulated by independent symmetric multinomial distributions the value of M_{reg} measures the degree of difference between them. If it is felt that the values are not from the Poisson distribution but instead from some other distribution, and we are not particularly interested in which one, then it seems reasonable to take the approach that was used for detecting spatial pattern and permute the observations. If the data sets are significantly correlated, then the value for the moves for the data will be significantly higher than for the simulations of them. If one data set is spatially aggregated and we are interested in finding out if the other one is correlated with it, then permuting the positions of the counts for the second one and comparing this value to that for the original data set would measure their degree of correlation.

If the value for the number of moves between the data sets is high compared to that after a joint permutation then this implies, for observations taken at different times, that there is local movement within the data set but little movement at a larger scale.

3.6 An alternative test for Spatial Aggregation

Greig-Smith (1952) looked at assessing the scale of spatial pattern in quadrat counts by successively dividing a pattern of size 2^n by 2^m into halves, quarters, eighths etc. until each block only contained two sample points. Then he compared the sums of squares for each block with those in the next block size up. If the difference was significant then there would be evidence to conclude that there was a natural scale of aggregation at the lower block size. This method does not seem to be applicable to grids which have odd sizes. There is no natural way of amending the test to cope with this.

Although it is mathematically convenient to be able to split a square grid of side 2^n into equal sized pieces there is no biological reason to split the data like this. The area that is being studied is assumed to be physically homogeneous. If it is not, then describing this homogeneity should be done before attempting a statistical analysis. If the area does not split into neat equal-sized blocks then the analysis becomes much more difficult. An experimental layout consisting of an 7×9 array is not easily amenable to this analysis method. Another problem is that results are not invariant under a rotation. If the sampling scheme were to be rotated through 45 degrees then the splitting into four separate blocks would follow a different pattern than that for the original scheme. This is also true, to a lesser extent, for the other results in this section.

The method is not applicable if the data are known to be overdispersed. This overdispersion can either occur due to some artifact of the counting process, or be due to spatial pattern at a smaller scale than the inter-sample point distance. Also, once we have evidence for statistical pattern at one scale, the tests for patterns at greater scales become invalid.

The work was extended to transects by Kershaw (1957), and this transect work was placed in a non-parametric framework by Mead (1974). The nonparametric test relies on splitting the data down into groups of four sampling values. Each set of four values on the transect is then split into two pairs. If the first pair contain the two smallest values or the two largest values then the arrangement is given a score of 2. If the largest and third largest of the four counts are in the same half the score is 1. Finally if the largest and smallest are in the same half the score is 0. These values are summed over all sets of 4 observations and the value obtained compared to that expected from the null hypothesis of no spatial pattern. The test is repeated at several scales by considering the total of each pair as a single observation, then combining pairs into quadruples and so on until the number of observations is a multiple of four but not of eight.

This approach cannot be directly used for two-dimensional data however. At first sight it looks as though the method could be used for looking at the 7 transects running through the field ecology experiment. However 6 of the transects are through non-homogeneous habitat. For instance, if the central horizontal transect through row L is split into 4 lengths of 5 pots, each piece has a different number of crop pots in it. This means that any test would have to take this heterogeneity into account, thus making life much more complicated. With such short transects any methodology would be ad-hoc. The only transect through a homogeneous area, consisting of the hedge pots, has only 11 pots. This is insufficient to give data to enable the null hypothesis of no spatial pattern to be rejected at the 5% level if Mead's test is applied.

However it is possible to amend Mead's methodology so that it applies to data from a two-dimensional area. This is done by splitting the data down into a series of 2×2 tables. For each table, if the largest and smallest counts are on the same diagonal then this implies the strongest possible spatial pattern and this is given a score of two. If the largest and second largest are on the same diagonal then this is closest to no spatial pattern and the arrangement is given a score of -2. If the largest and third largest are on the same diagonal then there is a score of 0. The expected score if there is no spatial pattern is 0 as all three arrangements are equally likely. Ties are dealt with by taking the mean score based on both adding and subtracting a small amount to one of the two tied scores. Two pairs are dealt with in a similar fashion. If three or four counts are identical then no spatial pattern is possible. Another way of looking at this method is to see the table as a pairs of ordered pairs first in the horizontal direction and then in the vertical direction. Each pair of pairs are concordant if either the first member of each pair is larger than the second or the larger one always comes second. A pair is discordant if the orders are different.

Thus for table

5	7
1	8

the horizontal pairings (5,7) and (1,8) are concordant, whereas the vertical pairings (5,1) and (7,8) are discordant.

Under the null hypothesis of no spatial pattern concordant and discordant pairings both have probability of 0.5 independently in each direction. Scoring 1 for each concordant pair and -1 for each discordant pair, the expected score for each square is 0, with variance of $\frac{8}{3}$. Therefore the score for the above square is 0. Clearly the concordant/discordant pairs approach and the diagonal approach are equivalent.

This is illustrated using counts of Popilla Japonica given by Bliss(1941) where the data collection points formed an regular 8×8 grid. An alternative analysis of this data, along with a fuller description is given in chapter 4.

As the squares are independent under the null hypothesis of no spatial pattern

Table 21: Popilla japonica counts

9	5	9	18	13	13	11	17
17	12	16	5	11	13	10	17
9	19	14	8	13	14	15	13
14	19	14	6	9	18	21	19
28	28	21	25	23	16	18	31
30	34	25	31	22	14	18	24
29	23	30	20	16	19	20	18
24	30	30	27	21	21	17	14

the variance of the total is the sum of the variances for each square. Furthermore, this test can be applied to any grid where the number of rows and the number of columns are both even, without the need to arbitrarily split the dimensions up. If the outermost row and column are removed from the pattern, another grid of even dimensions appears. This can also be tested for spatial pattern, and the result will be independent of the test for the entire grid because the values in each new 2×2 square come from 4 different old squares. Thus, for the data in table 21, the new square in the top left hand corner is

```
12  16
19  14
```

When applied to the data in table 21, there were 16 2×2 squares and the total value of the statistic was 13. The standard deviation was 5.888, so applying a continuity correction, this gives a Z-score of 2.123, and an associated p-value for the one-sided test of 0.017. Stripping off the outermost layer to give a 6×6 table, the statistic for this table is 8, with a standard deviation of 4.83. Although this will give a p-value, again after the continuity correction, of 0.061, which is not significant, adding the two test statistics will give a combined total of 21, with a standard deviation of 7.616.

Table 22: Popilla japonica counts, amalgamated

43	48	59	55
61	42	54	68
120	102	75	91
106	97	77	69

The Z-score for the combined test is 2.692, giving a p-value of 0.0036. This implies there is a strong spatial pattern in the data.

The interpretation of this result is that the values across a diagonal are less strongly correlated than nearest neighbours. Thus this is evidence for some local pattern within the data.

In looking for spatial pattern at a larger scale, there are two methods that can be applied. Either the table can be collapsed to a 4×4 arrangement by amalgamating adjacent rows, or four separate tables can be created by eliminating every even (odd) numbered row and column. We consider these methods in turn.

Creating a 4×4 table by amalgamation yields table 22. This gives 4 2×2 tables and the additional central 2×2 table. The overall test statistic is −4, which is not significant. With a standard deviation of 3.651, the statistics would have needed to be 8 or 10 (given that there were no tied values) to give a significant result. This illustrates a severe loss of power that occurs when the grid is quite small. The accuracy of the p-value could be improved by enumerating all the possible test values, but it is clearly not a worthwhile exercise in this case.

The other method consist of dividing the area up into 4 4×4 grids, with each grid consisting of every other row and every other column of the original pattern. Thus the first grid is given in table 23.

The top-left 2×2 square gives a value of 0, as there are three identical values. The overall statistic for the square is −3. For all 4 squares combined the test statistic

Table 23: Popilla japonica counts, first quartered grid

9	9	13	11
9	14	13	15
28	21	23	18
29	30	16	20

is −5, both with and without including the central 2×2 square in each block. The standard deviation is 6.055 if the 4 central squares in each block are not considered and 7.326 if they are. This implies that there has been no spatial pattern detected at this scale.

The interpretation of these results is that the counts at a gap of 1 are closer than the counts at a gap of 1.414. There does not appear to be a spatial pattern at a large scale within the data. This is a surprising result in the light of the apparent difference between the top and bottom halves of the grid. It would have been difficult to interpret the results had there been a spatial pattern picked up by this test at a larger scale than 1.414. As it stands, it is not possible to tell if the result at the smallest spatial scale is due to a positive correlation at lag 1, a negative correlation at a distance of 1.414 or a combination of the two. There is no evidence of spatial pattern at a larger scale. We can take this procedure one step further by considering the patterns with a lag of 4 in each direction, giving 16 independent two by two grids. The test statistic in these circumstances is 6, with a standard deviation of 6.481. This is clearly not going to be significant.

If we consider the two grids in table 24, and attempt to assess the degree of spatial correlation at lag 2 compared to a distance of 2.818 (looking across the diagonals), this can be done by breaking the data down into 4 2×2 grids. The values in each of these grids will all have the same subscript. Because the smallest and largest values are always separated across the diagonal the value of the test statistic will always be at

Table 24: Four by four grids, assessing spatial pattern at lag 2

a_0	a_1	b_0	b_1		a_0	c_1	b_0	a_1
a_2	a_3	b_2	b_3		d_2	b_3	c_2	d_3
c_0	c_1	d_0	d_1		c_0	d_1	d_0	b_1
c_2	c_3	d_2	d_3		b_2	a_3	a_2	c_3

For each subscript $i = 1...4$, $a_i > b_i > c_i > d_i$ holds for both grids

its maximal value, in this case 8. However the first pattern is clearly more aggregated than the second as the top-left hand corner always has the largest of the 4 values and the bottom right the smallest of the 4 for each letter. However the relationship between the values for different letters makes no difference to the test statistic. It would seem sensible to devise a scoring system that took the similarity in the patterns between the sub-groups into account so that these two patterns could be distinguished. This would considerably increase the power, and ease the interpretation of, the test. This would require considerable further work and the resulting test statistic would be unlikely to be computable by hand.

3.7 Conclusion

These moves measures provide a method of assessing the degree of overdispersion and spatial pattern in a data set. In the detection of spatial pattern they have the advantage, over more conventional techniques, of taking into account the spatial context from which the data are taken.

In the detection of spatial pattern, these methods do not require any degree of symmetry in the positioning of the sampling points. Nor is there any assumption about the underlying pattern, in particular there is no need to assume radial symmetry. This implies advantages over the use of spatial autocorrelation, although a full comparative study has not been attempted.

These measures still need to be scaled, and their power relative to each other and more conventional approaches needs to be looked at. This is the subject of the next chapter.

Chapter 4

Indices of Aggregation

4.1 Introduction

The values of the measures in chapter 3 change with mean count, the number of sampling points, the inter-sample point distance and the layout of the sampling points. Thus the values cannot be compared between different experiments, or even counts of different species from the same experiment.

This chapter extends the work of chapter 3 in two ways. In section 4.2 we will look at the use of indices to scale measures of non-randomness from counts data so the degree of overdispersion and aggregation from different data sets can be compared. The statistical power of these tests are compared to each other and the Index of Dispersion for a variety of patterns in section 4.3. In section 4.4 the measures, and associated indices, are extended to the case where the data can, a priori, be divided into discrete sets. Possible extensions to the indices are considered in section 4.5, and the chapter is concluded with a general discussion in section 4.6.

4.2 Measuring aggregation

In order to be able to compare values of aggregation between different data sets with varying numbers of individuals captured, numbers of sampling positions and spatial layouts of the sampling positions it is useful to be able to form an index of aggregation. Green (1966), Lefkovitch (1966) and Taylor (1984) have proposed several criteria for any such index in order for it to have useful application for field biologists.

4.2.1 Requirements of an Index

1. Real and continuous values for the complete range of spatial distributions. (Green)
2. Uninfluenced by the number of sample units, size of units sampled and number of individuals. (Green)
3. Easy to calculate. (Green)
4. The index should have a central value for some appropriate distribution. (Lefkovitch)
5. Tests of significance of difference between 2 or more variables should be available. (Lefkovitch)
6. The descriptive function should be clearly separated in application and interpretation from the theoretical justification.(Taylor)

The first property is clearly one that is necessary if the index is to be widely applicable, although Green did not specify what the range of distributions was to be. It has been assumed here that the range of interest is of those distributions of counts data that show some form of overdispersion, as there is little interest in the detection of underdispersion in counts data as this rarely appears when dealing with animal counts. Indeed M_{rand} does not have any application if the variance of the data is less than the mean, although it is possible to amend it so that it does apply by reducing the value of variance after which no more moves are made. M_{reg} and M_{red} can both be applied to any distribution of counts, only giving a value of zero for data that all have identical values, in which case no serious analysis is possible anyway.

The second requirement is more difficult to satisfy as an increase in the sample size, either by increasing the number of sampling points or the average count at these points, will lead to higher precision in the estimates and more certainty about the data due to the increase in the amount of information available. Nevertheless it is clear that any index which fails to meet this criterion will have serious drawbacks. Related to this is the property that the index is not altered if the relative positions of the sampling points are changed but the underlying pattern remains the same. This would be a useful property because it would mean the results were not dependent on the layout of the sampling points and so data from different designs can be easily compared. This may be difficult to achieve.

Ease of calculation is something which is only possible for simple indices. If the index is required to take into account spatial positions then it is unlikely that an index will be simple enough to calculate by hand.

The requirement of a fixed value of the index corresponding to an appropriate null distribution begs the question of what this distribution is to be. The obvious choice if overdispersion in counts data is being investigated is the Poisson distribution. If we are interested in examining spatial pattern and the non-spatial distribution of the counts is not of interest *per se* then it seems reasonable to have a central value that corresponds to the expected catch at each point being independent of position, and uncorrelated with the catches nearby.

The existence of tests of significance to distinguish between patterns is a useful although complex concept, which has not been developed further here.

The differentiation between the descriptive function and the theoretical justification is something which is difficult to achieve for any index which is based on an intuitive idea, and not based directly on any biological model. If the index is based on a biological model then the descriptive qualities of the index which flow from the model are not applicable if the model does not accurately describe what is happening with the data. An index which does not relate to a basic model, or only describes the degree of deviation from the model, such as M_{rand} describing deviation from the Poisson distribution or M_{reg} describing deviation from evenness, can be used to test the 'goodness-of-fit' of the model, but it is doubtful whether the value of the degree of deviation from the model (measured by M_{rand} and M_{reg}) can be directly related to any biological model.

We now discuss the merits and drawbacks of 13 indices of aggregation and overdispersion, divided up into 4 general categories.

4.2.2 Indices based on Crowding

Perry and Hewitt (1991), suggest using the value of

$$I_{rand}^{crowd} = \frac{M_{rand}}{M_{rand} + M_{crowd}}$$

The analogous indices for regularity and variance reduction are

$$\begin{aligned} I_{reg}^{crowd} &= \frac{M_{reg}}{M_{reg} + M_{crowd}} \\ I_{red}^{crowd} &= \frac{M_{red}}{M_{red} + M_{crowd}} \end{aligned}$$

One of the problems with these indices is that as the grid becomes larger with increasing number of sample points the mean distance to the centre of the grid increases, so M_{crowd} will increase at a faster rate than M_{reg} and M_{rand}. The index will take a smaller value for larger grids with the same basic underlying pattern. Therefore the value of the index cannot be compared for data sets where the number of data points is different, and if a large experiment is split into smaller pieces, the individual parts should all give smaller values for the index than the data set as a whole. This makes the index worthless for comparing differing spatial layouts or even lattices of different sizes.

Also M_{crowd} is affected by the shape of the grid, being larger for long thin grids than for square ones with the same number of sampling points. The shape of the experiment also affects the value of the index.

As M_{crowd} is typically much greater than M_{reg} and M_{rand}, the typical value of the index is close to 0. Because of this, and the problems noted above, there is no value for the index that corresponds to a suitable null distribution. This means that no meaningful interpretation can be given to the absolute value for the index.

More serious difficulties arise when trying to interpret the results of the value of M_{crowd} for any given pattern. If the number of sample points is large and there is no strong trend across the data then the crowding point will be positioned near the centre of the sampling area. This means that M_{crowd} mainly depends on the mean distance to the centre of the sampling area from the sample points and the number of individuals. This means that the value is strongly affected by the shape and size of the grid, with long narrow grids having more moves than square ones with the same number of sample points. If the size of a sampling area is quadrupled by doubling both the length and the breadth, then provided the areas have about the same mean and variance and there is no large-scale spatial pattern, we might expect M_{rand} to increase by approximately a factor of 4. However M_{crowd} would increase by a factor of eight (4 times as many individuals moving on average twice as far). This would halve the value of the index even though the pattern in each of the areas was similar.

Also if we consider the patterns which lead to extreme values of M_{crowd}, then the value is zero if all the individuals are at a single point in the grid and a maximum when the population is split equally between the two most widely separated points. The second pattern is almost as badly crowded as the first, but has a high value of M_{crowd}, with the value for a pattern where all the counts are identical somewhere in the middle.

4.2.3 Indices Based on the Poisson Distribution

Instead of using M_{crowd} as a method of finding a divisor for an index, we can use the expected value for the number of moves under the hypothesis of Poisson data to calculate an index of aggregation. Because there has not been any progress on the extremely difficult problem of calculating the expected values of M_{reg}, M_{red} and M_{rand} analytically, the value is estimated using simulation studies. Using the same approach as that given at the end of section 3.2, the value of M_{rand} is calculated for a set of multinomial simulations of the data, and the mean of these values used to estimate $E(M_{rand})$. Conditioning on the total numbers observed eliminates unwanted variability, which would reduce the accuracy of the estimation. The indices are

$$\begin{aligned} I^{pois}_{rand} &= \frac{M_{rand}}{M_{rand} + E(M_{rand}|Poisson)} \\ I^{pois}_{reg} &= \frac{M_{reg}}{M_{reg} + E(M_{reg}|Poisson)} \end{aligned}$$

$$I_{red}^{pois} = \frac{M_{red}}{M_{red} + E(M_{red}|Poisson)}$$

These indices are effectively a method of scaling the number of moves given the mean count and the number and layout of the sampling points. A value of 1/2 represents the expected value for data from the Poisson distribution, and a value of more than that implies a degree of overdispersion and/or spatial pattern. A value of less than 1/2 implies that the data are less variable than might be expected for the Poisson distribution.

4.2.4 Indices Based on Permutations

If the data have such a high variance that it is no longer of interest how far they diverge from the Poisson distribution, but there is a desire to detect the extent of spatial pattern in the sample, then we can condition on the observed variability in the sample. We can also do this if the interest is solely in the spatial effects. It is possible to simulate the distribution using, say, a negative binomial distribution where the shape parameter k is estimated from the data, but it is easier, and more sensible if we are not interested in the enon-spatial) distribution of the sampling points, to use the counts observed and permute them in order to get the Monte-Carlo simulations of the data before calculating the moves. This gives a non-parametric measure of the degree of pattern.

$$\begin{aligned}
I_{reg}^{perm} &= \frac{M_{reg}}{M_{reg} + E(M_{reg}|counts)} \\
I_{rand}^{perm} &= \frac{M_{rand}}{M_{rand} + E(M_{rand}|counts)} \\
I_{red}^{perm} &= \frac{M_{red}}{M_{red} + E(M_{red}|counts)}
\end{aligned}$$

The expected value for the indices, given that there is no spatial pattern, is approximately 1/2. This is not affected by changing the numbers of individuals, sample points or the sampling layout, and the value of the index should be fairly immune to the influence of these parameters.

4.2.5 Other Indices

To assess the degree of spatial pattern there are several other candidates for the indices. One of these is based on a rough guess of what the value of M_{reg} is likely to be.

$$I_{reg}^{dist} = \frac{M_{reg}}{M_{reg} + nDev_{abs}}$$

Dev_{abs} represents the mean absolute deviation between the counts and the sample mean. Thus $nDev_{abs}$ represents the Moves to Regularity if all the points were equidistant from each other. It is an attempt to measure the mean distance travelled by each individual in the M_{reg} and so measures the scale at which the aggregation can be supposed to be occurring. If the value is not much greater than 1/2 then the mean distance travelled is low, implying that the pattern has little large scale spatial pattern. However this index is affected by the scale of the grid (increasing the separation increases the index). Because $nDev_{abs}$ is, like $E(M_{reg}')$, constant between different permutations, the index has an identical significance level to I_{reg}^{perm} for any given pattern.

The analogous index, replacing M_{reg} with M_{red}, is

$$I_{red}^{dist} = \frac{M_{red}}{M_{red} + nDev_{abs}}$$

4.2.6 Assessing the significance of an index

In order to assess the significance of a result it is necessary to find its distribution under the null hypothesis that we are using. As no results have been found for the distribution of any of the move measures, Monte-Carlo simulations have been used. Two types of simulation have been employed, multinomial simulations in order to test for overdispersion and permutations of the counts in order to test for spatial pattern.

4.3 Statistical Power

In order to assess the statistical power of these tests in the detection of deviation from the Poisson distribution and spatial pattern, it is necessary to devise null and alternative hypotheses to reflect these two requirements. The overall number of individuals is regarded as fixed. If it is desired to assess the power of the test for the detection of deviation from the Poisson distribution then the null hypothesis is always the symmetric multinomial, because this represents independent and identically distributed Poisson random variables, conditioned on the overall mean. If the detection of spatial pattern, rather than testing the Poisson hypothesis, is of interest, and the existence of overdispersion is a nuisance factor then the null hypothesis ought to have the same non-spatial distribution as the alternative. This is achieved by simulating data sets for both null and alternative hypotheses in the same way, but then permuting the values for the null hypothesis before calculating the spatial moves required for each of the conditions.

The two alternative hypotheses that have been considered so far are patchiness, represented by a Perry-Mead mosaic (Perry and Mead, 1979), and trend.

A Perry-Mead mosaic consists of a grid of squares of unit side. Each square is either *dense* with a probability p or *sparse* independently of all the other squares. Superimposed on this grid is an array of sampling circles. Each non-overlapping circle has radius r and the centres of the circles are a distance d apart. There will be spatial aggregation if the intersample point distance d is less than 1, and the cluster size will increase with decreasing d. The density for each sampling circle is the mean density of the circle on which it sits. Thus a circle entirely within a *dense* square has density *dense*, whereas one which is half in a *sparse* square and half in a dense one has density $\frac{dense+sparse}{2}$.

Trend is modelled by having the expected number of individuals observed increase in a linear fashion the further a point is away from one side of the grid with expected value *sparse* at one side and *dense* at the other.

Actual numbers of individuals observed are then simulated by an asymmetric multinomial distribution based on the relative densities at each of the sampling points and the total number of individuals observed.

For the power tests, the usual values chosen are a mean density of 10.0, a ratio between dense and sparse of 1.5 and a grid size of 8 × 5. For each hypothesis there are 5000 Monte-Carlo simulations. In order to make comparison between the patterns easier the mean density and ratio dense : sparse squares are given rather then the actual values for dense and sparse. For the mosaic pattern the probability of a dense square is 0.5, each square being independently either dense or sparse, and the distance between neighbouring sample points is 0.4. For the trend, the trend runs down the longer side of the grid. The power of the Index of Dispersion test and the mean absolute deviation are not considered for the test for spatial pattern as they do not take into account the spatial information. The power of indices based on expected values (for either of the multinomial simulations) under the Poisson hypothesis are

Table 25: Percentage Power to Detect difference Between Mosaic and Poisson.

Dense:Sparse Ratio	1.2	1.3	1.4	1.5	1.6	2.0	3.0
M_{reg}	10.6	17.8	27.4	36.5	47.7	82.0	97.3
M_{rand}	10.3	14.7	24.2	37.6	50.4	89.7	98.3
M_{crowd}	7.6	9.0	10.0	11.3	12.8	17.2	22.0
M_{red}	12.1	19.2	31.2	44.6	56.8	89.2	98.3
Dev_{abs}	7.1	11.4	19.0	31.0	41.9	86.5	97.6
Var	10.4	14.5	22.8	36.1	48.1	87.3	98.1
I^{crowd}_{rand}	10.7	16.2	26.4	39.3	52.7	89.7	98.4
I^{crowd}_{reg}	11.1	18.0	26.5	36.4	46.2	81.4	97.3
I^{crowd}_{red}	12.1	19.6	31.4	44.4	58.5	89.9	98.4
I^{dist}_{reg}	8.2	10.4	17.0	19.2	23.2	46.7	46.7
I^{dist}_{red}	8.8	12.2	15.9	15.9	26.2	52.1	52.1

not given as these should have the same value as the use of the measures which do not use expectations.

In the accompanying tables one of the parameters is varied while the others are kept constant.

When the difference between the *dense* and *sparse* areas is changed by altering the ratio, the power of the tests increase against both the Poisson hypothesis (table 25) and the overdispersed but non-spatial null hypothesis (table 26). The power results are given for both a Perry-Mead mosaic and a trend across the data.

For this range of values it appears that the indices I^{dist}_{reg} and I^{dist}_{red} perform as poorly as M_{crowd} in the detection of a mosaic when faced with the Poisson alternative. The other measures are all of similar power, with M_{red} performing best. This is particularly noticeable when the ratio is around 1.5. The indices based on crowding

Table 26: Percentage power to detect spatial element of Mosaic. Effect of varying dense:sparse ratio

Dense:Sparse Ratio	1.2	1.3	1.4	1.5	1.6	2.0	3.0
M_{reg}	9.08	13.04	16.06	21.00	24.68	39.20	47.74
M_{rand}	5.04	6.56	6.68	7.06	8.72	18.18	35.32
M_{crowd}	6.30	7.86	7.12	8.38	9.50	12.60	13.84
M_{red}	9.02	11.66	14.16	19.36	23.12	37.42	51.24
I_{rand}^{crowd}	5.24	6.42	7.10	7.74	8.86	18.46	35.40
I_{reg}^{crowd}	8.94	12.80	15.60	20.72	24.38	38.30	46.32
I_{red}^{crowd}	8.96	12.38	14.80	20.38	22.84	37.84	48.46
I_{reg}^{dist}	8.92	12.84	16.14	21.30	25.10	40.74	52.06
I_{red}^{dist}	9.24	13.42	17.74	24.32	28.74	56.06	70.20

are slightly more powerful than the the measures on which they are based.

When attempting to detect the spatial element of a spatial mosaic pattern (table 26), it appears that power of the measures is generally less than for the detection of non-randomness, except for the indices I_{reg}^{dist} and I_{red}^{dist}. These do much better than any of the other tests proposed, especially at the higher ratios. In particular the index I_{red}^{dist} is considerably more powerful than any of the other proposed measures. The indices based on crowding do not appear to have the slight advantage over their respective moves measures that they had when the null hypothesis was a Poisson distribution.

In detecting a trend, M_{reg} and the associated indices do far better than any of the other measures. It appears that the value I_{reg}^{dist} does slightly less well than I_{reg}^{crowd} and M_{reg} but is more powerful than M_{rand}. The reason for this difference may be because calculating M_{reg} involves moving individuals all the way across the grid from

Table 27: Percentage power to detect trend against Poisson.

Dense:Sparse Ratio	1.2	1.3	1.4	1.5	1.6	2.0	3.0
M_{reg}	20.32	37.50	55.64	69.92	82.94	99.22	100.00
M_{rand}	8.16	9.58	15.56	20.14	29.60	68.18	99.08
M_{crowd}	3.66	2.78	1.94	1.06	0.74	0.22	0.0
M_{red}	11.70	17.88	29.58	40.14	55.46	90.70	99.96
Dev_{abs}	5.10	7.10	11.04	14.22	19.94	56.80	95.64
Var	7.54	9.14	13.66	18.30	25.26	59.04	97.14
I_{rand}^{crowd}	8.38	10.68	17.44	22.24	32.48	68.68	99.18
I_{reg}^{crowd}	21.00	37.78	55.34	70.52	83.14	99.28	100.00
I_{red}^{crowd}	11.66	19.96	31.44	42.20	59.50	92.24	99.98
I_{reg}^{dist}	18.86	35.08	53.88	66.94	79.68	98.58	100.00
I_{red}^{dist}	10.52	16.98	24.46	33.52	45.06	80.56	99.44

the *dense* end to the *sparse* end in order to end up with the same count at every point so the value of M_{reg} is particularly high. The value of M_{red} is also likely to be affected by this factor, although to a lesser extent.

When looking for the spatial element in a trend (table 28) M_{rand} and M_{rand}^{crowd} perform poorly here compared to the other indices and M_{red} is still weaker than M_{reg}. However the index I_{reg}^{dist} does better than any of the other measures, especially at the higher densities and the power for this measure is approximately the same as for the detection of non-randomness.

In order to investigate the effect of increasing the mean density while keeping all the other parameters constant the ratio between dense and sparse was fixed as 1.5 and the mean density on the grid varied. The results are given in tables 29, 30, 31 and 32. At low densities all of these measures perform poorly.

Table 28: Percentage power to detect spatial component in trend.

Dense:Sparse Ratio	1.2	1.3	1.4	1.5	1.6	2.0	3.0
M_{reg}	17.96	34.38	48.34	59.98	73.46	95.32	100.00
M_{rand}	4.98	6.42	7.20	7.82	10.14	20.62	66.72
M_{crowd}	3.44	2.56	1.28	0.86	0.62	0.10	0.0
M_{red}	8.60	15.20	21.54	28.06	38.62	68.96	97.22
I_{rand}^{crowd}	5.52	6.70	7.54	8.56	10.60	22.16	69.02
I_{reg}^{crowd}	18.20	34.36	48.42	60.54	73.56	95.66	100.00
I_{red}^{crowd}	9.42	15.32	23.38	30.04	41.18	71.82	98.08
I_{reg}^{dist}	19.20	35.20	54.16	67.10	80.00	98.60	100.00
I_{red}^{dist}	9.14	17.30	26.46	35.42	47.20	84.02	99.66

Table 29: Percentage power, mosaic pattern against Poisson.

Mean Density	1	3	7	10	15	25	45
M_{reg}	7.98	14.04	26.68	37.92	56.34	77.30	94.38
M_{rand}	7.42	11.50	27.72	42.62	59.86	85.78	97.42
M_{crowd}	5.14	7.56	10.08	10.60	14.34	17.08	20.52
M_{red}	5.00	12.70	30.38	43.62	64.10	87.28	97.34
Dev_{abs}	3.10	9.18	19.42	30.28	51.36	80.24	96.10
Var	7.04	10.92	25.86	38.44	55.20	82.58	97.02
I_{rand}^{crowd}	7.68	12.18	28.00	42.84	60.90	85.84	97.54
I_{reg}^{crowd}	8.20	13.56	26.10	36.56	55.60	76.92	94.38
I_{red}^{crowd}	7.14	13.14	31.44	44.18	64.50	87.38	97.34
I_{reg}^{dist}	6.92	11.32	15.84	20.86	28.64	36.48	45.68
I_{red}^{dist}	4.46	9.36	14.52	22.34	29.64	44.52	56.28

Table 30: Percentage power to detect spatial element of Mosaic.

Mean Density	1	3	7	10	15	25	45
M_{reg}	7.88	10.42	16.76	21.40	28.70	33.58	44.60
M_{rand}	5.10	5.84	6.90	8.98	10.08	15.68	27.74
M_{crowd}	5.54	6.40	8.28	9.34	10.52	13.08	14.20
M_{red}	6.28	8.78	15.60	21.62	26.64	36.66	46.12
I^{crowd}_{rand}	5.68	6.26	7.38	9.04	10.12	15.84	27.64
I^{crowd}_{reg}	7.58	10.48	16.52	21.24	28.44	33.56	44.28
I^{crowd}_{red}	7.74	9.14	16.24	21.38	26.82	36.70	46.50
I^{dist}_{reg}	7.22	10.20	15.84	21.10	27.54	37.76	48.64
I^{dist}_{red}	5.66	10.04	18.20	26.36	34.90	49.74	64.66

In the detection of a mosaic the indices I^{dist}_{reg} and I^{dist}_{red} both perform poorly when compared to the other measures. The value M_{red} seems to be the most powerful measure that is available at the medium densities.

In the test for a mosaic pattern at various densities, M_{rand} performs poorly, even at the higher densities, implying that most of the moves that are made to reach randomness are not affected by the mosaic pattern with this size of square. The index I^{dist}_{red} again outperforms all the other indices and measures once the mean count exceeds 10 and the power gets above 20%. However the index I^{dist}_{reg} does not show the same power difference with M_{reg} as I^{dist}_{red} does with M_{red}.

Again M_{reg} appears to be the most powerful test for non-randomness when there is a trend across the data. All of the tests not based on M_{reg} perform poorly, with the Index of Dispersion being the poorest.

I^{dist}_{reg} is the most powerful test for the detection of a trend at all the densities shown. M_{rand} is again a very poor detector of a trend pattern when compared with the other measures. M_{red} seems to lie between the two extremes.

Table 31: Percentage power to detect trend against Poisson.

Mean Density	1	3	7	10	15	25	45
M_{reg}	11.96	27.48	53.62	71.92	88.36	98.12	100.00
M_{rand}	5.86	8.00	16.48	24.62	36.46	63.16	91.66
M_{crowd}	3.88	3.02	1.94	0.98	0.70	0.22	0.04
M_{red}	5.50	12.94	27.44	41.58	61.94	87.92	99.42
Dev_{abs}	2.28	6.44	10.72	14.46	27.80	47.62	83.92
Var	5.08	7.86	14.78	20.96	30.76	52.02	85.66
I^{crowd}_{rand}	6.14	8.80	16.98	25.50	37.68	63.82	92.14
I^{crowd}_{reg}	11.60	27.52	53.06	71.80	88.36	98.24	100.00
I^{crowd}_{red}	7.42	14.36	29.92	44.06	64.44	89.02	99.50
I^{dist}_{reg}	11.16	26.80	51.46	69.82	85.46	97.70	100.00
I^{dist}_{red}	5.50	11.82	21.38	35.92	51.56	77.28	96.74

Table 32: Percentage power to detect trend as a spatial pattern.

Mean Density	1	3	7	10	15	25	45
M_{reg}	11.14	24.34	49.54	62.14	77.54	94.62	99.40
M_{rand}	3.84	4.90	7.36	8.16	12.90	18.06	43.14
M_{crowd}	4.16	2.68	1.68	0.94	0.54	0.06	0.0
M_{red}	6.76	11.34	20.04	27.52	42.52	64.62	87.88
I^{crowd}_{rand}	4.88	6.02	8.12	8.94	13.46	18.90	44.02
I^{crowd}_{reg}	11.12	23.92	49.74	62.12	77.16	94.68	99.44
I^{crowd}_{red}	7.80	12.96	21.32	30.50	45.36	66.32	88.84
I^{dist}_{reg}	11.74	25.90	54.58	68.94	84.54	97.94	99.98
I^{dist}_{red}	6.12	11.82	24.42	36.42	55.46	80.96	97.02

These results imply that, when testing for departure from the Poisson distribution, the measures M_{rand}, M_{reg} and M_{red} provide tests that are slightly more more powerful than tests based on the variance such as the Index of Dispersion for all the measures considered here. If the interest is in the detection of spatial pattern then indices such as I_{reg}^{dist} for a trend and I_{red}^{dist} for a mosaic type pattern should be used. In order to get as full a picture as possible of the data set it is probably best to do all the tests in order to get a good description of the pattern.

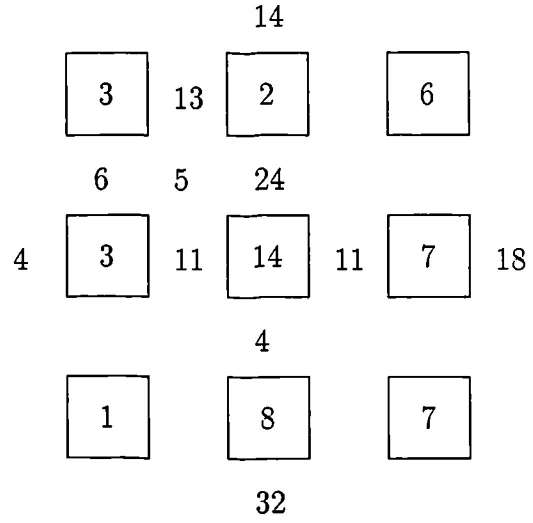
The difference in power between some of these measures, and their variation with the scale of the pattern implies that it may be possible to construct indices based on combining two or more of the measures proposed here to assess the scale of spatial pattern, but that is beyond the scope of this thesis.

Further work could be done on comparing the power of these tests with more conventional techniques for detecting pattern such as the autocorrelation function and fitting a quadratic surface.

4.4 More Complex Data

We have previously assumed that all the sampling points were equivalent. Sometimes the variability in the count between different sampling points can be partly ascribed to some external factor, such as local environment, chemical treatment or soil type. We therefore need to take such effects into account if experiments with several different treatments are to be analysed. An example data set is taken from part of the patch-crop experiment that was analysed in chapter 2. The counts are of the catch of Pterostichus Melanarius in July 1991 at LARS and consists of the top-left corner of the field. The boxes represent areas of semi-natural habitat and the rest of the area shown was sown with barley.

Catches of *P. melanarius* in July 1991 in top-left corner



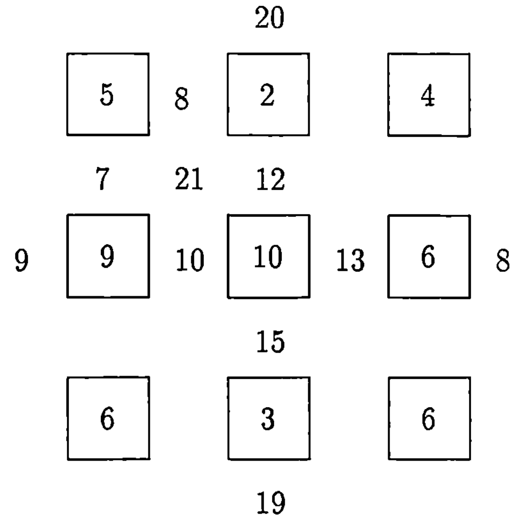
In order to be able to combine these values to estimate the overall level of deviation from the Poisson Distribution, and to see if there is significant spatial pattern, it is necessary to standardise the variance between the two treatments. This is done by dividing the catch in each group by its standard deviation, so the two sets have the same variance. This is then multiplied by the weighted mean variance for the two treatments. This is calculated as

$$W = \frac{1}{total\,df} \sum_{all\,treatments} (Num\,obs\,with\,treatment - 1) * stdev(treatment)$$

The result is that the counts are now fractional. The values of the moves can then be calculated as before. One advantage of this technique over dividing the data set into separate pieces and then analysing them separately is that that would entail a loss of power due to fewer catches being analysed in each set. Another is that the spatial relationship between pots in different areas is taken into account.

In order to assess the statistical significance of the values obtained for regularity and randomness above, the approach taken is analogous to that for the simple one set case. The degree of departure from the Poisson distribution can be assessed by simulating the Poisson distribution, conditional on the total numbers observed for each subset separately and then combining these observations to give a simulation of the original data set. For the above example a Poisson simulation is shown below

Multinomial simulation of original data

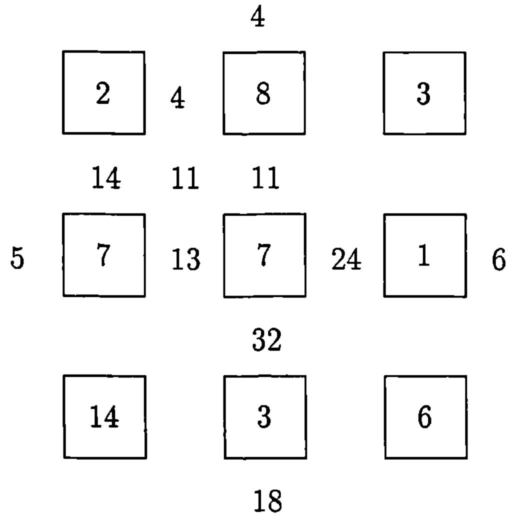


The degree of spatial pattern can be similarly assessed by randomly permuting the observations within each subset.

Table 33: Indices of pattern for a combination data set

	Total	Pots	I_{reg}	I_{rand}	I_{red}
Permutation	193	20	0.545	0.503	0.483
Multinomial	193	20	0.690^{***}	0.858^{**}	0.624^{*}
Crop					
Permutation	142	11	0.532	0.528	0.486
Multinomial	142	11	0.740^{***}	0.962^{***}	0.680^{**}
Patches					
Permutation	51	9	0.497	0.438	0.478
Multinomial	51	9	0.629^{*}	0.846^{*}	0.584

Permutation of original data



The values for I_{reg}, I_{rand}, and I_{red} for both Poisson and permutation tests, along with their statistical significance, based on 10000 Monte-Carlo simulations, are shown in table 33.

The extremely high values for the test against the Poisson alternative, both for the data as a whole and for the patch data alone, reflect the very high variance in the patch data when compared to the mean. The results for the permutation for both regularity and randomness imply that there is little or no spatial correlation in the counts data. However this is only a small number of observation points so this may not be too surprising.

Another example of an experiment on insects where the spatial layout of the recoveries was given is provided by Bliss (1941). The catches of the larvae of the Japanese beetle *Popilla japonica*, from an experiment where the layout was an 8 × 8 grid were given and are given here in table 21.

Perry and Hewitt (1991) pointed out that there appears to be a difference in the data between the upper and lower halves. They calculated the Index of Dispersion for each half separately as well as I_{rand}^{crowd} based on vertices. For the top half they found that the Index of Dispersion did not give grounds for rejection of the Poisson hypothesis (P = 0.08) but I_{rand}^{crowd} did (S=0.00849, P=0.0336). For the bottom half of the data, the Index of Dispersion again failed to reject the null hypothesis of Poisson distributed data, but I_{rand}^{crowd} did (S= 0.00725, P=0.0199). They did not look at the data at any other scale.

Greig-Smith (1952) suggested, for grids of size $2^m \times 2^n$, that the scale of spatial pattern can be assessed by splitting the experimental area in half and comparing the sums of squares within the halves to the overall sum of squares. If there is spatial pattern at a scale $2^{m-k} \times 2^{n-l}$ but not at $2^{m-k-1} \times 2^{n-l}$ then there will be a significant difference in the sums of squares. This method has the problem that it cannot easily be generalised to awkward sized grids such as 11 × 13 and that there may be a difference between the effects of splitting square grids vertically and horizontally. More seriously the method depends on the clusters in the data, of either large or small counts, not being split into separate blocks. For instance if the 8 × 8 grid considered here had had a central 4 × 4 block with a cluster of high counts and the rest of the data having similar low counts there would be no evidence of spatial

Table 34: Popilla japonica pattern evaluation(Poisson hypothesis)

Area	I_{reg}^{Poiss}	I_{rand}^{Poiss}	I_{red}^{Poiss}	Index of Dispersion
All same	0.802^{***}	0.985^{***}	0.806^{***}	175.4^{***}
Two halves	0.547	0.627	0.606	
top	0.601^{*}	0.838^{*}	0.602^{*}	43.34^{*}
Bottom	0.733^{***}	0.846^{*}	0.711^{***}	41.60
Quartered				
All together	0.608	0.780^{*}	0.668^{*}	
Top	0.682^{*}	0.851^{*}	0.675^{*}	
Bottom	0.616	0.639	0.649	
Top left	0.610^{*}	0.884^{**}	0.625^{*}	29.93^{*}
Top right	0.548	0.000	0.540	12.16
Bottom left	0.398	0.000	0.431	6.32
Bottom right	0.521	0.000	0.551	14.03

pattern until the stage of eight 4 × 2 blocks.

In order to take this division idea further and to investigate the probability of further spatial patterns in the data, the data set was divided into four blocks of 4 × 4. The new indices, based both on the Poisson hypotheses and the permutation test, were calculated. This was done for all the quarters separately, both halves separately, and for the data set as a whole. The results from these tests are given in table 34 for the test for overdispersion and table 35 for the aggregation test. Again all these were based on 10,000 simulations.

The Index of Dispersion was calculated for each set of data and is given with the indices based on the Poisson Distribution. A two sample t-test for identity of means between each of the pairs of data (top versus bottom, top-left versus top-right and bottom left versus bottom right) was also calculated and the estimated difference in mean, together with significance level, is given with the permutation tests.

Table 35: Popilla japonica pattern evaluation(Aggregation)

Area	I^{perm}_{reg}	I^{perm}_{rand}	I^{perm}_{red}	Diff in Mean
All same	0.707***	0.726***	0.710***	10.18***
Two halves				
Joint	0.541*	0.590***	0.607***	10.18***
Top	0.558	0.559*	0.554	2.06
Bottom	0.698***	0.600***	0.663***	7.69***
Four Quarters				
All together	0.511	0.548*	0.556*	
Top	0.520	0.537	0.537	
Bottom	0.512	0.563	0.548	
Top left	0.513	0.523	0.523	
Top right	0.567*	0.000	0.552	
Bottom left	0.464	0.000	0.488	
Bottom right	0.530	0.000	0.577	

In fact, when two sample t-tests were performed on the data, the only subsets that appeared to have similar means were the top-left and top right quarters.

The top half appears to be different from the bottom half, and the bottom two quarters seem to differ. The significant values at the 5% level for I^{perm}_{rand} and I^{perm}_{red} implies there may be still some small scale pattern left in the data. There still appears to be variability in the in the top-left corner of the data set. The bottom left hand corner seems to have underdispersed data when compared to the Poisson distribution.

In order to see if there was spatial pattern at a smaller scale the data were divided into eight factors and the procedure above repeated. This division was done in two ways. Pattern 1 was obtained by splitting each quarter vertically in half, and pattern 2 by splitting horizontally as shown in the diagram.

Pattern 1

1	5	2	6
3	7	4	8

Pattern 2

1	2
3	4
5	6
7	8

The moves measures and associated indices were calculated, based on just 1000 simulations, and the results are given for the permutation in table 36 and in table 37 for the multinomial alternative.

The significant result for I_{reg}^{perm} and I_{rand}^{perm} for the overall pattern for pattern 2 but not pattern 1 implies that there is a slight overall difference between the left and right hand sides of each block but that this is not a very significant occurrence, as judged by the indices. The other two results, significant at 5% for the permutations, are no more than would be expected from 48 tests. However these results are based on permuting only eight blocks per test.

For the multinomial simulations there is strong evidence of departure from the Poisson distribution in the top left hand corner with block 1 pattern 1 having a significantly high value and also the two blocks from pattern 2 that intersect it show some pattern. For the single block M_{rand} is zero for 5 out of eight blocks for both patterns.

Thus we can conclude for this data set that the two 4×4 blocks in the bottom half of the pattern have different mean values from each other and from the top half, which was more homogeneous. Once the data was divided up into these four groups, apart from some evidence of overdispersion (but not spatial aggregation) in the top

Table 36: Popilla japonica pattern evaluation(Aggregation test), 8 blocks

Area	I_{reg}^{Poiss}	I_{rand}^{Poiss}	I_{red}^{Poiss}	Index of Dispersion
Pattern 1				
All	0.506	0.525	0.530	
Block 1	0.570	0.584	0.593*	
Block 2	0.441	0.000	0.404	
Block 3	0.448	0.000	0.440	
Block 4	0.475	0.000	0.484	
Block 5	0.473	0.456	0.469	
Block 6	0.560	0.000	0.574	
Block 7	0.500	0.000	0.524	
Block 8	0.593*	0.522	0.556	
Pattern 2				
All	0.508*	0.521*	0.527	
Block 1	0.471	0.486	0.483	
Block 2	0.537	0.000	0.472	
Block 3	0.501	0.000	0.534	
Block 4	0.532	0.549	0.543	
Block 5	0.548	0.558	0.552	
Block 6	0.544	0.000	0.583	
Block 7	0.461	0.000	0.478	
Block 8	0.530	0.000	0.520	

Table 37: Popilla japonica pattern evaluation(Overdispersion test), 8 blocks

Area	I_{reg}^{Poiss}	I_{rand}^{Poiss}	I_{red}^{Poiss}	Index of Dispersion
Pattern 1				
All	0.572	0.655	0.619	
Block 1	0.664*	0.863*	0.675**	
Block 2	0.341	0.000	0.333	
Block 3	0.355	0.000	0.355	
Block 4	0.420	0.000	0.464	
Block 5	0.584	0.811	0.574	
Block 6	0.569	0.000	0.592	
Block 7	0.465	0.000	0.507	
Block 8	0.638*	0.673	0.575	
Pattern 2				
All	0.608	0.685	0.641	
Block 1	0.584	0.841*	0.589	
Block 2	0.466	0.000	0.433	
Block 3	0.440	0.000	0.471	
Block 4	0.587	0.725	0.577	
Block 5	0.631*	0.828*	0.638*	
Block 6	0.563	0.000	0.594	
Block 7	0.402	0.000	0.427	
Block 8	0.406	0.000	0.428	

left block, there was little evidence of deviation from the Poisson distribution.

4.5 Further work on indices

If it has been determined that there is spatial aggregation occurring in the data then the next task is to attempt to describe what form the aggregation appears to take. One way of describing this is to decide at what scale the aggregation occurs. A possible method of doing this is to compare M_{rand}, or M_{red} with M_{reg}, in order to find out how much extra effort is required to remove the last half of the variance. If the value of M_{red}/M_{reg} is quite high this implies it is not very difficult to remove the last half of the variance so there is no suggestion of a pattern such as a trend across the grid. If however the value is low, this implies that there is possibly pattern on the scale of the area such as a spatial trend. This idea has not been pursued any further. There may well be scope for plotting the number of moves against the percentage change in the sample variance for, not only halving the sample variance as in I_{red}, but also removing other proportions of the original variance. This plot could then be used to identify the amount of pattern occuring at various scales. This would require considerable further work, however.

If the data have been fitted with a trend or similar model where the expectation at each point is different and the degree of residual pattern remaining is to be assessed then the same approach of using the expected value from the model can be used as for the fit of a model consisting of discrete variables. Unfortunately it is no longer valid to permute the observations because each one has a different expectation. As an alternative it might be reasonable to simplify the fitted model by partitioning the data set up into a sets depending on the range of the fitted values. This would then bring the situation back to the one in section 4.4.

4.6 Conclusion

There are a wide choice of indices available to measure overdispersion. There are far fewer possibilities if the interest is in the detection and quantification of aggregation. The decision of which index or indices to use in a particular case must be directed by the sort of pattern which is suspected to exist in the data. If there is no initial reason to expect one type of pattern more than another it is best to calculate all the indices and then go on from there.

If there is an interest in whether the data come from a Poisson distribution and there is no reason to expect any sort of spatial correlation between neighbouring counts then the Index of Dispersion is the obvious choice. When there is a suspicion that there may be a spatial pattern in the data then the indices outlined in this chapter will take into account the spatial information in ways none of the other indices looked at do. In the detection of overdispersion where there is thought to be some spatial component then the best index to choose is I_{rand}^{poiss} if the pattern is on a fairly small scale, but if there is large scale structure in the data then I_{reg}^{poiss} is the best choice. If the indices for overdispersion indicate that there is overdispersion within the data then the extent to which this is due to spatial pattern needs to be addressed. Thus it is then necessary to calculate the indices of spatial pattern.

For the detection of local clusters either the index I_{rand}^{perm} or I_{red}^{perm} are appropriate. When the pattern is on a large scale, such as a trend, then I_{reg}^{perm} should be employed. A large value of I_{rand}^{perm} or I_{red}^{perm} implies that there is a strong local clustering within the data. On the other hand I_{reg}^{perm} is much more effective at highlighting larger clusters or overall trends within the data than at picking out local clusters. One intuitive problem with I_{rand}^{perm} is that, if the interest is in the spatial pattern rather than the distribution of the counts as such, there seem to be little reason for stopping the moves when the variance reaches the mean, the expected value under the Poisson hypothesis. This measure automatically has value 0 if the counts start out with variance less than the mean. Thus its use is not recommended.

The indices based on crowding are much more difficult to interpret than those based on Poisson simulations and permutations of the data. The power advantage of the original measure index proposed by Perry and Hewitt over moves to randomness was due to variability in the total catch when independent Poisson simulations were used to assess significance. When this problem was removed by using multinomial simulations the power advantage evaporated. The indices based on crowding are very dependent on the number of sampling points and their layout. Thus these indices cannot be compared for results from different experiments. For these reasons their use is not recommended.

Chapter 5

Spatial pattern in the Patch-crop experiment

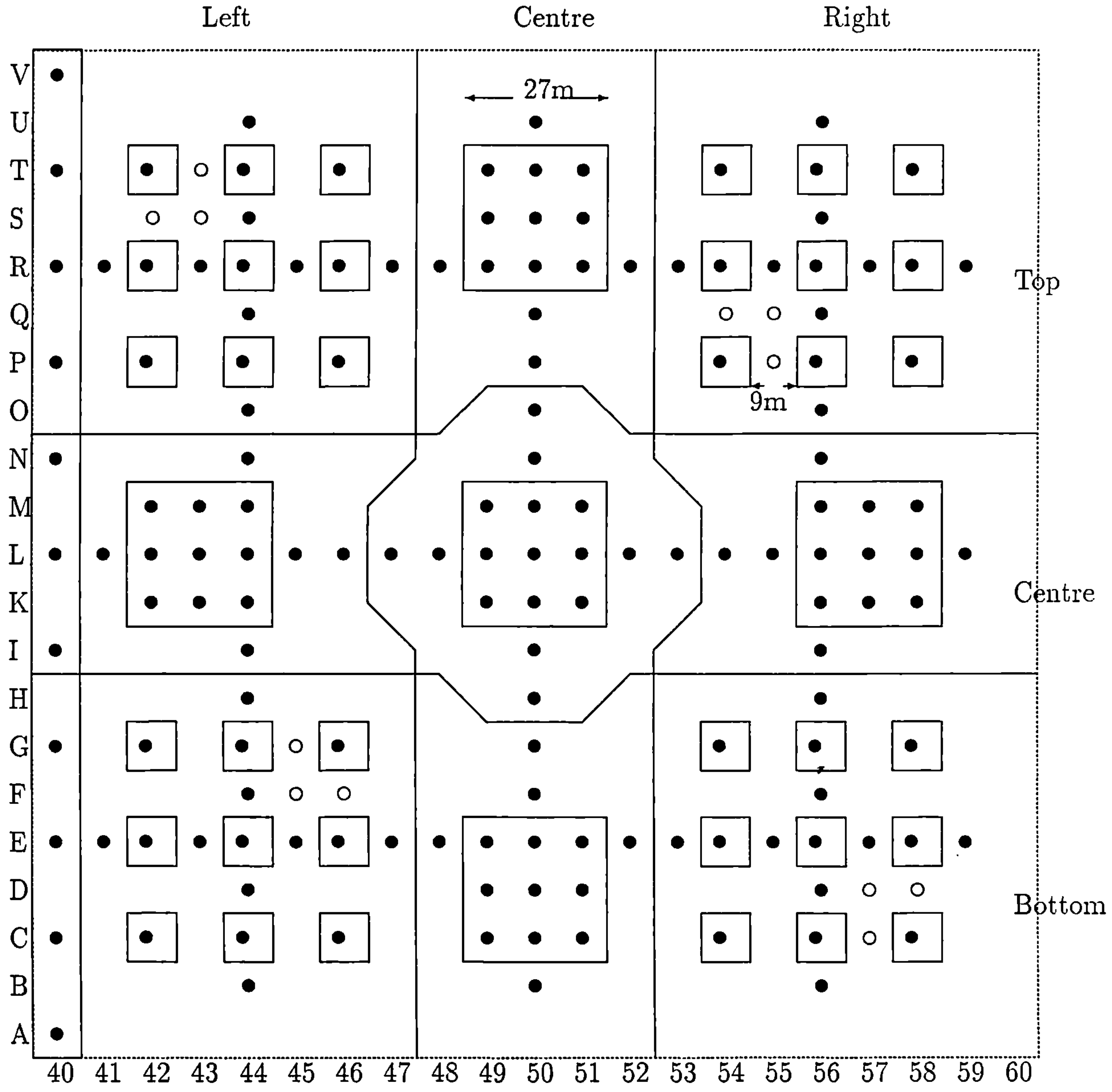
5.1 Introduction

In chapter 2 we discussed changes in the mean catch of *P. melanarius* over time, without directly taking into account the relative positions of the pots. In this chapter we will investigate extent of spatial pattern in the catches of *P. melanarius* from LARS. In order to do this the experimental area was divided up into 9 areas (see figure 12). This division was chosen because it resulted in every block having the same number of pots from patches and approximately the same number from the farmed area (of the pots in the transects) in each block.

This allows us to see of there are spatial patterns on a scale of around 50 metres (the size of the blocks) and to see if these patterns are constant over time, both within years and between them, or if they vary.

The pattern that is detected by this method is on quite a large scale. Each block

Figure 12: Patch experiment design showing blocking factor



Standard pots ● Extra pots ○

is approximately 56 metres squared and typically contains around 17 sampling points.

A preliminary study is given in section 5.2 and an extension of the model from section 2.4 incorporating the areas is given in section 5.3. As the results from this section indicate changes in the pattern over time, the data for each month are analysed for pattern in section 5.5, using both the the model from section 5.3 applied to each month separately and the techniques of chapters 3 and 4.

The hedge data are excluded from the analyses throughout this chapter because they lay on the outside of the experiment and showed a generally low mean catch.

On some of the later tables the names of the blocks have been abbreviated to just two letters for the sake of brevity. Thus the Top-Right block is shortened to TR.

5.2 A preliminary assessment of spatial pattern

In order to get an overview of the amount of spatial heterogeneity that might be present in the data, the monthly catch of *P. melanarius* from Long Ashton was calculated for each habitat and within each habitat for each block. The mean catch for each habitat and block was scaled by dividing by the overall mean catch for that habitat in that month, taking into account the differences between small and large patches. These values were then plotted against time for those months (June to October) when there were enough individuals to make this worthwhile. The plots are given in figure 13 for the crop data and figures 15 and 14 for the large and small patches.

Some of the results for October, particularly in 1991 and 1992, show extreme levels of pattern but this is because in those months there were very few recoveries so some of the blocks had no individuals recovered in them that month.

In the farmed areas there does not appear to be any consistent trend as to which

Figure 13: Variability in the mean catch rate in the crop by block for *P. melanarius* at LARS

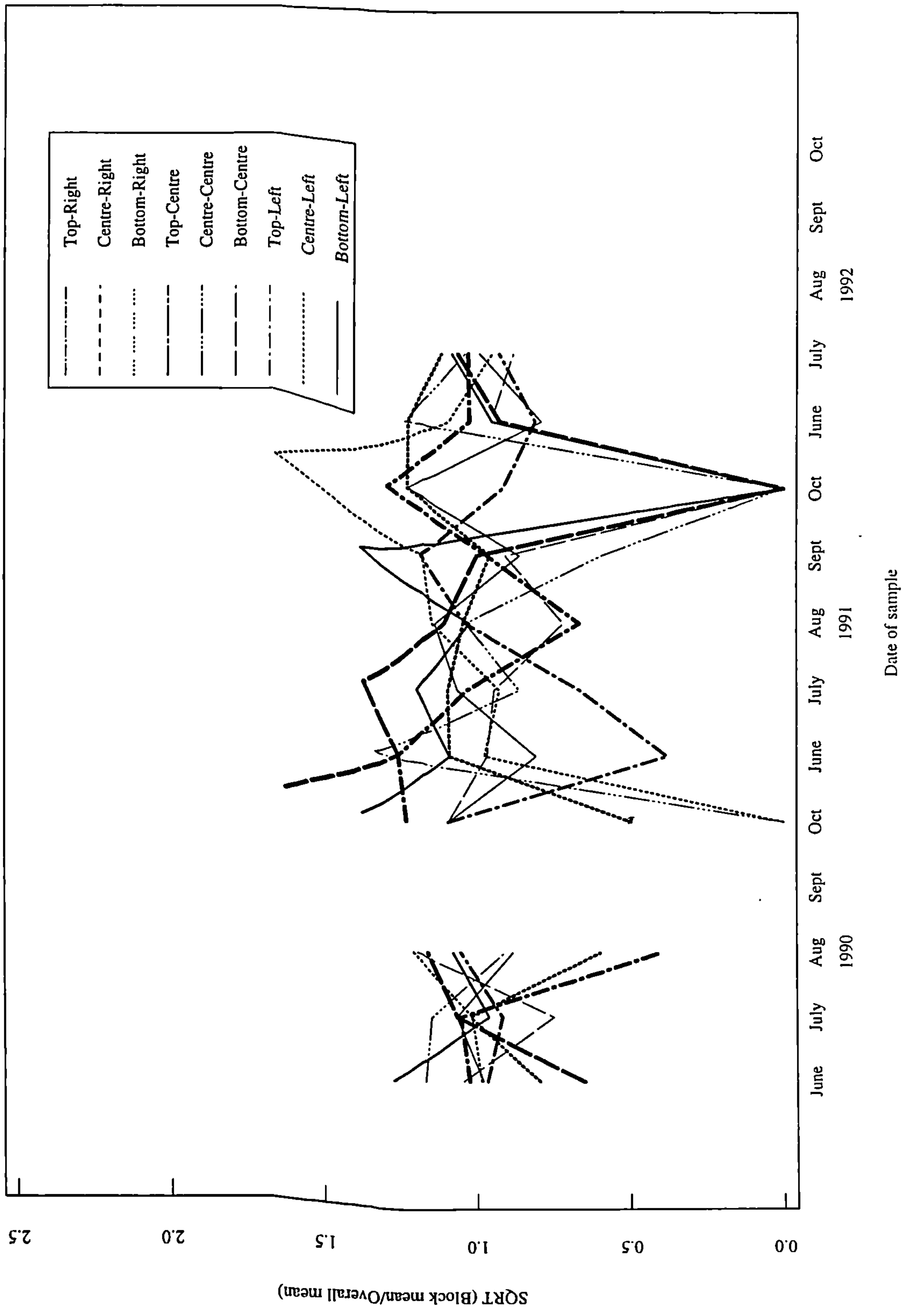


Figure 14: Variability in the mean catch rate in the small patches by block for *P. melanarius* at LARS

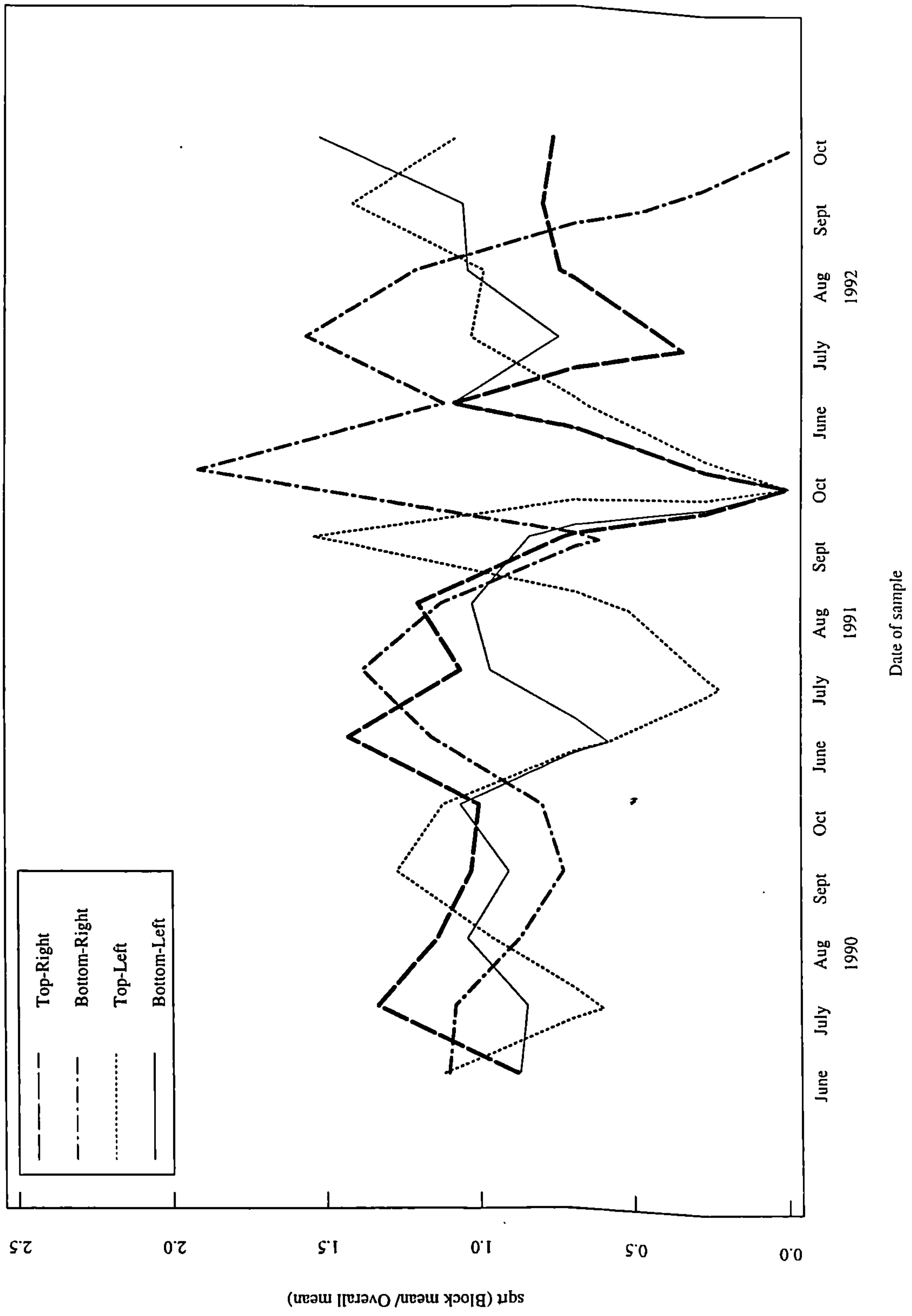
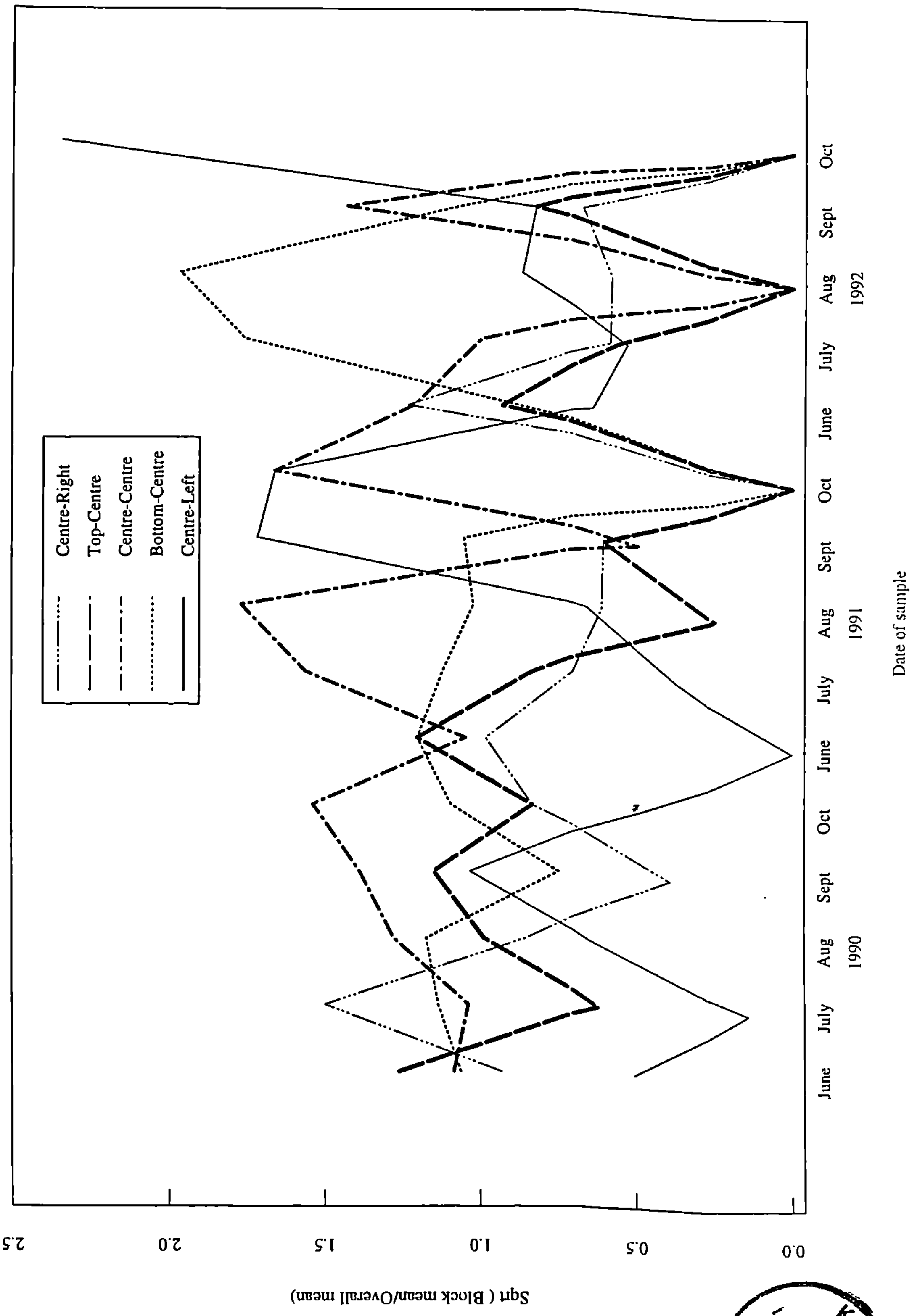


Figure 15: Variability in the mean catch rate in the large patches by block for *P. melanarius* at LARS



blocks have the highest and lowest counts in any year nor does the the same block have the most extreme value for the same month in all three years. However the Bottom-Centre block has either the largest or nearly the largest mean catch from August 1990 to August 1991 inclusive.

In the small patches there seems to be a greater consistency in the results between the blocks than was the case for the farmed area, with the Bottom-Right area having the lowest catch for August to October 1990, the Top-Left block having the lowest catch for June to August 1991 the Top-Right block having the lowest catch for July and August 1992. The block with the highest mean catch is less consistent in 1990 and 1991, although for 1992 the Bottom-Right block dominates from June to August.

For the large patches the Centre-Left patch has the lowest catch rate from June 1990 through to July 1991, with the sole exception of August 1990 when the catches were much lower than at any other time. After July 1991 the Top-Centre patch has either the lowest, or nearly the lowest catch rate until the end of the study. The highest catch rate is in the Central patch from August 1990 to June 1992, with the marginal exception of June 1991 when two individuals were recovered from eight traps as against three each from the nine traps in the Top-Centre and Bottom-Centre patches and September 1991 when the Centre-Left patch had more recoveries (24) than the other patches combined. In 1992 the Bottom-Centre patch had a higher catch rate in July and August than any other patch but in September it came second to the Centre-Centre patch

5.3 An overall spatial model

In order to determine whether the differences between areas were constant or varying in time a more extensive Generalized linear model than that obtained in section 2.4

was fitted to the data. This was done by extending the final model obtained in section 2.4 by adding a factor block which was the same as that used in figures 13, 14 and 15.

The model was chosen by fitting regressors using the generalised Akaike Information Criterion (AIC$_\alpha$) (Akaike, 1969) with $\alpha = 4$. The value of 4 was picked because, approximately, this represents the level at which a single regressor would be included using an F-ratio statistic at the 5% level (McCullagh and Nelder, 1989).

The interactions of block with year, habitat, harvest and month were considered. The block factor alone had an F-ratio of 4.12, and then the habitat-block interaction had an F-ratio of 11.15, with the next significant value being the harvest-block interaction with an F-ratio of 8.15. In habitat factor, the patches are described as Fallow. There were no other significant interactions at this level. The parameter estimates, together with standard errors and t-test values, are given in table 38 for the non-spatial parameters and table 39 for the spatial parameters. The actual and predicted counts (together with standard errors) for this model are given in table 40 (for the farmed area) and tables 41 and 42 for the small and large patches respectively.

The absence of interactions between the spatial effects of Block and the month and year components from this model implies that the major differences between the areas are the same in June and July (before the harvest) and also approximately equal in the two months after it (August and September). When the parameter estimates are examined it appears that the large patch in the Centre-Left block has a very low count when compared with the surrounding crop.

For the farmed area the Top-Left block has the lowest predicted catch rates before the harvest and the Top-Right block the highest predicted catch although the differences between the blocks are not very large. After the harvest the predicted

Table 38: Non-spatial parameter estimates for fit of block effect *P. melanarius* at LARS

	estimate	s.e.	t
Constant	2.363	0.123	19.23
1991	-1.992	0.283	-7.04
1992	-0.128	0.146	-0.88
Postharv	-0.977	0.400	-2.44
JUL	1.657	0.114	14.55
AUG	1.700	0.361	4.72
Fallow	0.645	0.171	3.78
1991 . Postharv	2.727	0.454	6.01
1992 . Postharv	0.456	0.406	1.12
1991 . Fallow	-1.839	0.608	-3.02
1992 . Fallow	-1.660	0.258	-6.44
Postharv . Fallow	-1.000	0.356	-2.81
1991 . Postharv . Fallow	0.839	0.644	1.30
1991 . JUL	1.523	0.291	5.23
1991 . AUG	-0.903	0.341	-2.65
1992 . JUL	-0.216	0.161	-1.34
1992 . AUG	-1.027	0.478	-2.15
Fallow . JUL	-2.491	0.163	-15.24
Fallow . AUG	-0.482	0.313	-1.54
1991 . Fallow . JUL	1.925	0.629	3.06
1992 . Fallow . JUL	1.478	0.293	5.04
Small	0.563	0.178	3.17
1991 Small	-0.739	0.220	-3.35
1992 Small	-0.209	0.211	-0.99

Table 39: Area parameter estimates for fit of block effect *P. melanarius* at LARS

	estimate	s.e.	t
CL	-0.191	0.121	-1.59
CR	-0.035	0.115	-0.30
BC	0.118	0.108	1.09
TC	0.064	0.110	0.59
BL	-0.1193	0.0973	-1.23
TL	-0.434	0.104	-4.17
BR	0.0286	0.0945	0.30
TR	-0.400	0.103	-3.86
Postharv CL	0.690	0.197	3.51
Postharv CR	-0.654	0.251	-2.61
Postharv BC	0.079	0.195	0.40
Postharv TC	0.150	0.197	0.76
Postharv BL	0.307	0.168	1.83
Postharv TL	0.672	0.168	3.99
Postharv BR	-0.106	0.175	-0.60
Postharv TR	0.432	0.172	2.51
Fallow CL	-1.471	0.256	-5.75
Fallow CR	-0.298	0.202	-1.48
Fallow BC	-0.213	0.182	-1.17
Fallow TC	-0.543	0.195	-2.79
Fallow BL	-0.440	0.169	-2.60
Fallow TL	-0.133	0.166	-0.80
Fallow BR	-0.178	0.160	-1.11

Table 40: Actual and predicted mean catch rates by block,*P. melanarius* in the crop at LARS

1990		June			July			August			September	
	Data	Pred.	s.e.	Data	Pred.	s.e.	Data	Pred.	s.e.	Data	Pred.	s.e.
CC	13.00	10.62	1.30	65.75	55.72	4.41	20.83	21.90	2.90	?	1.72	1.17
CL	9.25	8.77	1.23	51.40	46.02	4.77	36.80	36.05	4.68	?	2.84	1.92
CR	10.00	10.26	1.38	55.20	53.82	5.19	4.00	11.00	2.46	?	0.86	0.60
BC	4.00	11.95	1.55	56.40	62.70	5.59	34.00	26.66	4.21	?	2.10	1.43
TC	15.40	11.33	1.48	46.00	59.43	5.44	29.33	27.14	4.15	?	2.14	1.45
BL	9.13	9.43	1.14	56.63	49.45	3.81	19.63	26.43	2.99	?	2.08	1.40
TL	8.88	6.88	0.87	41.88	36.11	3.09	28.00	27.79	3.14	?	2.19	1.47
BR	6.00	10.93	1.30	52.00	57.34	4.20	9.00	20.27	2.72	?	1.60	1.07
TR	10.38	7.12	0.90	27.88	37.36	3.17	36.00	22.62	2.74	?	1.78	1.20
1991												
CC	2.25	1.44	0.39	22.63	34.83	2.96	21.88	18.50	2.38	3.25	8.33	1.23
CL	1.20	1.19	0.33	26.20	28.76	3.11	26.80	30.46	3.99	12.80	13.72	2.05
CR	2.00	1.40	0.38	32.60	33.64	3.40	9.00	9.29	2.02	8.60	4.18	0.96
BC	2.00	1.63	0.44	57.60	39.19	3.69	25.00	22.53	3.37	9.20	10.15	1.69
TC	1.50	1.54	0.42	43.80	37.15	3.58	21.40	22.93	3.38	17.60	10.32	1.70
BL	0.82	1.28	0.34	34.55	30.91	2.48	26.36	22.33	2.42	6.80	10.06	1.32
TL	0.18	0.93	0.25	13.45	22.57	2.00	21.91	23.48	2.50	12.91	10.57	1.36
BR	1.50	1.49	0.40	36.64	35.84	2.75	22.27	17.13	2.11	8.45	7.71	1.10
TR	1.18	0.97	0.26	27.18	23.35	2.05	10.45	19.11	2.20	7.56	8.61	1.19
1992												
CC	12.50	9.34	1.14	37.33	39.49	3.36	?	10.88	4.44	?	2.40	1.80
CL	9.80	7.72	1.07	31.20	32.61	3.48	?	17.91	7.31	?	3.95	2.96
CR	8.60	9.02	1.21	36.60	38.14	3.81	?	5.46	2.44	?	1.20	0.93
BC	7.00	10.51	1.35	39.00	44.43	4.12	?	13.25	5.53	?	2.92	2.20
TC	7.40	9.97	1.30	40.40	42.12	4.00	?	13.48	5.61	?	2.97	2.24
BL	5.09	8.29	0.98	34.00	35.05	2.75	?	13.13	5.30	?	2.89	2.16
TL	5.36	6.05	0.75	29.64	25.59	2.23	?	13.80	5.57	?	3.04	2.27
BR	12.30	9.61	1.12	43.09	40.63	3.04	?	10.07	4.13	?	2.22	1.66
TR	7.45	6.26	0.78	26.82	26.48	2.28	?	11.23	4.56	?	2.47	1.85

Table 41: Actual and predicted mean catch rates by small patches,*P. melanarius* at LARS

1990	June			July			August			September		
	Data	Pred.	s.e.	Data	Pred.	s.e.	Data	Pred.	s.e.	Data	Pred.	s.e.
BL	17.88	20.32	2.62	7.56	8.82	1.29	16.67	12.94	1.91	3.44	3.82	0.75
TL	29.44	20.17	2.50	3.78	8.75	1.26	14.11	18.49	2.48	6.78	5.46	1.02
BR	28.67	30.62	3.38	12.33	13.29	1.76	11.67	12.90	1.90	2.22	3.81	0.75
TR	18.22	23.85	2.83	18.78	10.35	1.44	20.00	17.20	2.42	4.44	5.08	0.97
1991												
BL	0.11	0.21	0.11	2.11	2.87	0.61	2.67	1.92	0.47	1.67	1.40	0.38
TL	0.11	0.20	0.11	0.11	2.84	0.60	0.67	2.74	0.65	5.67	2.00	0.53
BR	0.44	0.31	0.17	4.33	4.32	0.88	3.22	1.91	0.46	0.89	1.39	0.38
TR	0.67	0.24	0.13	2.56	3.36	0.70	3.67	2.55	0.61	1.25	1.86	0.50
1992												
BL	4.00	2.75	0.59	2.67	4.22	0.81	1.11	0.99	0.32	1.11	0.81	0.29
TL	1.44	2.73	0.58	5.11	4.19	0.79	1.00	1.41	0.45	2.00	1.17	0.41
BR	4.22	4.15	0.86	11.88	6.37	1.16	1.50	0.98	0.32	0.22	0.81	0.29
TR	4.00	3.23	0.68	0.56	4.96	0.92	0.56	1.31	0.42	0.63	1.08	0.38

differences between seven of the patches are quite low but the Centre-Left block has a very high predicted catch and the Centre-Right patch a very low predicted catch.

In the small patches before the harvest the Bottom-Right block has the highest predicted catch rate with all the other blocks having about the same predicted rate. After the harvest the Top-Left and Top-Right blocks have predicted catch rates that area about half as great again as those for the Bottom-Left and Bottom-Right areas.

In the large patches, the Centre-Left patch has by far the lowest predicted catch rate before harvest, with all the other patches having rates within about two standard errors of each other. After the harvest it is the Centre-Right and Centre-Left patches that have predicted catch rates that are much smaller than than the rest of the patches with the largest values being in the Centre-Centre and Top-Centre patches.

Thus there does not seem to be any association between the counts in the patches and the immediately surrounding crop. If the AIC_α is used with $\alpha = 2$, then the

Table 42: Actual and predicted mean catch rates by large patches,*P. melanarius* at LARS

1990	June			July			August			September		
	Data	Pred.	s.e.	Data	Pred.	s.e.	Data	Pred.	s.e.	Data	Pred.	s.e.
CC	16.44	35.56	5.27	6.22	15.43	2.55	10.25	16.65	3.01	4.22	4.92	1.09
CL	3.56	6.74	1.93	0.11	2.92	0.86	2.67	6.29	1.82	2.33	1.86	0.59
CR	12.11	25.50	5.76	13.00	11.07	2.62	4.56	6.21	1.79	0.33	1.83	0.58
BC	15.78	32.34	6.93	7.44	14.04	3.17	8.63	16.39	3.89	1.22	4.84	1.30
TC	22.22	22.03	4.99	2.22	9.56	2.27	6.11	11.98	2.95	2.89	3.54	0.98
1991												
CC	0.25	0.36	0.20	12.11	5.02	1.13	5.67	2.47	0.65	0.22	1.80	0.52
CL	0.00	0.06	0.04	0.67	0.95	0.31	0.78	0.93	0.32	2.67	0.68	0.25
CR	0.22	0.26	0.15	2.44	3.60	1.01	0.67	0.92	0.32	0.33	0.67	0.24
BC	0.33	0.33	0.19	6.22	4.56	1.24	1.89	2.43	0.74	1.00	1.77	0.58
TC	0.33	0.22	0.13	3.44	3.11	0.88	0.11	1.78	0.55	0.33	1.29	0.43
1992												
CC	3.22	4.82	1.10	3.56	7.39	1.53	0.00	1.27	0.43	1.00	1.05	0.39
CL	0.89	0.91	0.30	1.00	1.40	0.44	0.56	0.48	0.19	0.33	0.39	0.17
CR	3.33	3.46	0.99	1.22	5.30	1.42	0.25	0.47	0.19	0.22	0.39	0.17
BC	1.67	4.38	1.21	11.11	6.72	1.73	2.89	1.25	0.47	0.56	1.03	0.41
TC	1.89	2.98	0.85	1.11	4.58	1.23	0.00	0.91	0.35	0.33	0.75	0.30

model is extended by adding the year-block interaction, the month-block interaction and the three way interaction. Now it is no longer possible to give a simple summary of the results. In particular it is not possible to see, from this model, if the mean catches in the blocks are correlated over time. If the parameter estimates for the block effect from the generalized linear model fitted to each month in turn were to be examined for correlation then a rough estimate of the degree of correlation over time would be available. The Pearson correlation coefficients could be calculated, rather than the less powerful non-parametric versions, because of the asymptotic normality of the parameter estimates.

5.3.1 Residual correlation

The model for the mean catch rate does not explain all the variability in the catch rates for the data. One reason for this could be that there is an effect on the catches for each individual sampling pot with some pots having higher catch rates than nearby pots with apparently similar environments.

The standardised residuals from the fit for the above model were calculated and the correlation between these residuals calculated for each pair of consecutive months, with residuals in each September being compared with those in the following June. None of these correlation coefficients were significant at the 5% level implying that the excess variability in the data, when compared to the Poisson distribution, cannot be assigned to a *sample pot* factor. However when the correlations were calculated when the gap was one year then there were significant positive correlation between the catches in 1991 and 1992 in June, July and September, but not in August. This implies that there may be an effect of local environment around the sampling pots that affects the catches in the same way in each year, but this effect only started in the second year. The most obvious candidate for such an effect would be changes in the structure of the vegetation. Thus a correlated error structure, as used in a repeated measures analysis, would be appropriate but, in this case, the effect of the error would have to be variable with month and year. The data from following years would also have to be analysed in order to see if these effects are a temporary effect of the maturing of the ecosystem that eventually disappear or if they continue onwards.

5.4 Spatial analysis of a single months data

As an example data set, I chose to look at the counts of Pterostichus Melanarius from the wet pitfall traps on the patch experiment at RES for July 1990. The reason for choosing this data set was that the mean count was fairly large, and the pots were placed out in the crop as well as the patches, so a comparison of the two could be made. An initial data analysis revealed that by far the most important factor was, unsurprisingly, the habitat type. After further exploratory analysis based on factors within each habitat type, and an attempt to fit models more complex than that of just the habitat type, it was decided to use habitat type as the only factor in the analysis.

The indices from chapter 4 were calculated for this month's data. This was done considering large and small patches to have the same mean counts, and then assuming they had different mean count rates.

The results show that the hypothesis that the counts are independent Poisson random variables can be rejected by a wide margin, but that the permutations of the data do not reveal any pattern of clustering of high or low counts. This result can be considered in the light of the Index of Dispersion test for each of the variables separately, which shows that the data are overdispersed ($p \ll 0.05\%$) for all factors. The result for the permutation test, when looking at the data after the habitat type residuals after a habitat model had been fitted, showed a slight negative correlation between adjoining rows, but otherwise no pattern. This implies that the data do not show any overall clustering, or that the size of the clusters is less than the interpoint distance.

However when the two level factor grassed is used instead of the three level factor habitat, the hypothesis of aggregation is only just rejected at the 5% level, implying that a failure to take account of relevant factors may produce false results, in a similar way to that pointed out by Mardia and Marshall (1984) for correlation of residuals.

Thus there does not appear to be any spatial pattern for the data from RES for this month. We will now go on to look at the pattern of counts of *P. melanarius* from LARS.

5.5 Applying Indices of Spatial Pattern to *P. melanarius* catches from LARS

In order to assess how important the degree of spatial pattern was for each month, the values of three indices from chapter 4 based on permutations (I_{reg}^{perm}, I_{rand}^{perm} and I_{red}^{perm}) were calculated for all the recoveries of *P. melanarius* (excluding the hedge), from months where at least 50 individuals were recovered and pots were laid in all the areas. These values, along with their significance levels, are given in table 43. The values were based on 1000 simulations. This was done assuming that the crop, small patches and large patches all had different mean catch rates.

The indices based on the Poisson distribution (I_{reg}^{pois}, I_{rand}^{pois} and I_{red}^{pois}) were not calculated because the high level of overdispersion in the data as illustrated in chapter 2, made the Poisson hypothesis completely untenable. It is of little interest to look at hypotheses based on the Poisson distribution when the data are overdispersed and even neighbouring counts have cery large differences. Because of the problem with the indices based on crowding (I_{reg}^{crowd}, I_{rand}^{crowd} and I_{red}^{crowd}), as pointed out in section 4.2.2, these indices were not calculated either.

The data for each month were also fitted using a generalized linear model with Poisson errors. Again the differences between the habitats and patch sizes were taken

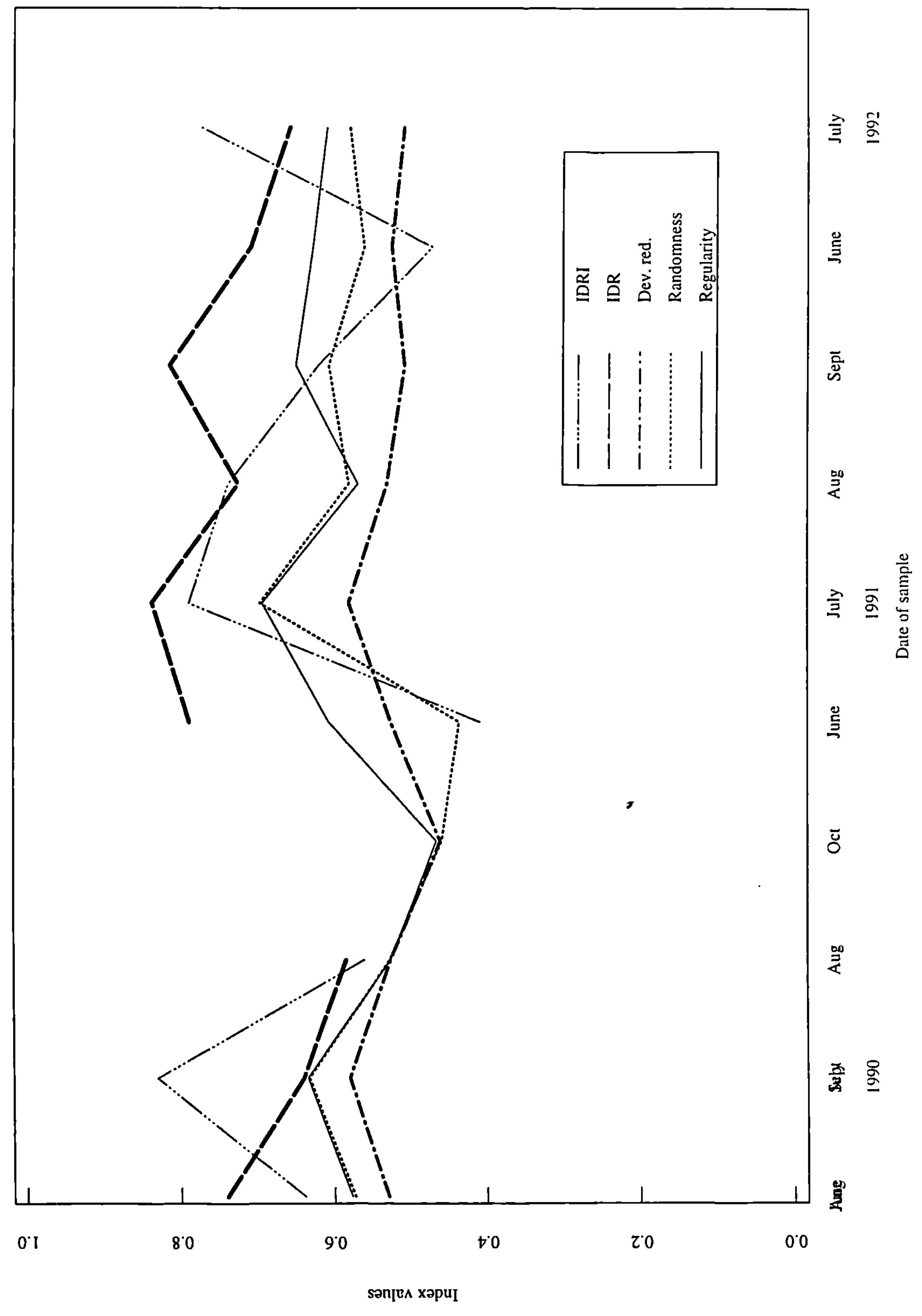
Table 43: Overall indices of pattern for *P. melanarius* at LARS

Month	Total	Pots	I^{perm}_{reg}	I^{perm}_{rand}	I^{perm}_{red}	DR	DRI
1990							
June	2034	140	0.577^{*}	0.573^{**}	0.529	2.84^{**}	1.76
July	3641	141	0.634^{***}	0.632^{***}	0.579^{***}	1.77	4.89^{***}
Aug	1927	122	0.525	0.526	0.525	1.40	1.27
Sept	No crop						
Oct	84	138	0.465	0.458	0.460		
1991							
June	111	150	0.606^{**}	0.435	0.525	3.72^{***}	0.69
July	2518	153	0.693^{***}	0.696^{***}	0.580^{***}	5.12^{***}	3.73^{***}
Aug	1651	153	0.568^{*}	0.580^{***}	0.530^{*}	2.63^{**}	2.81^{**}
Sept	763	149	0.649^{***}	0.606^{***}	0 507	4.38^{***}	1.63
1992							
June	802	151	0.627^{***}	0.560^{**}	0.524	2.43^{*}	0.89
July	2761	150	0.609^{***}	0.579^{***}	0.508	1.92	3.40^{***}

into account, this time by fitting the habitat and patch size parameters. The spatial pattern was then measured by fitting a nine level block parameter, with deviance ratio given in the column labelled DR. The deviance ratio for the Block-habitat interaction is given in column DRI (Deviance Ratio Interaction). This second value measures the difference of the effect of area between the crop and patch areas. For DR there were eight degrees of freedom but for DRI there were only seven, as one had been lost due to estimating the difference between small and large patches.

The information from table 43 is repeated in the plot of indices versus time in figure 16. In order to get the significance of the Deviance from the Generalized linear model onto a 0-1 scale two new measures, $IDR = DR/(1 + DR)$ and $IDRI = DRI/(1 + DRI)$ were created. This enables the values of all the indices to be plotted on the same graph. Although not meant as indices in the sense of chapter 4 they still,

Figure 16: Indices of pattern for all data on *P. melanarius* at LARS



to some extent, measure spatial variability.

From this table we can see the amount of spatial pattern in July is highly significant for all three years, with this month giving the highest annual values in 1990 and 1992 for all the measures apart from 1990, when the value of the deviance ratio was greatest in June. However the overall level of pattern combining DR and DRI is much greater in July than June. There appears to be little aggregation in August and October 1990, but in 1991 the aggregation (as well as the overall mean catch) stay quite high.

As the form of spatial pattern seems to vary between the habitats, as shown by the high level of the IDRI index, the data from each habitat was then analysed separately. The results for the crop are given in table 45. The same was done for the patches, this time including months without pots in the crop, with results given in table 44. For the patches the difference between small and large patches is indicated the column patch size. The spatial effect (as measured by the deviance ratio for the block parameter) is in the column labelled DRI. A selection of these indices is plotted against time in figure 17.

The relative lack of variability between the blocks for the farmed area that is apparent in figure 13 is confirmed here with, apart from for July 1991, only one result significant at 1%. July 1990 shows a reasonable amount of aggregation, but, despite the high mean catches in many months, the overall impression is of little aggregation. This could be due to higher mobility or, overall, a more uniform environment. The lack of spatial pattern in the farmed areas after harvest is very noticeable, especially when compared to the variability in the patches, even though the mean catches there were lower. This coincides with the changes in the sex-ratio (table 17) where the proportion of males in the crop increases after harvest when compared to the proportion

Table 44: Indices of pattern for *P. melanarius* at LARS in all patches

Month	Total	Pots	I_{reg}^{perm}	I_{rand}^{perm}	I_{red}^{perm}	Patch size DR	DRI
1990							
Jun	1471	81	0.610^{**}	0.665^{***}	0.633^{***}	12.62^{***}	4.50^{***}
Jul	643	81	0.694^{***}	0.737^{***}	0.652^{***}	6.45^{*}	7.28^{***}
Aug	813	78	0.493	0.518	0.544^{*}	18.82^{***}	1.28
Sep	251	81	0.636^{**}	0.623^{***}	0.601^{***}	8.89^{**}	4.02^{***}
Oct	52	78	0.494	0.500	0.517		
1991							
Jun	22	80	0.553	0.497	0.501	0.98	2.12^{*}
Jul	306	81	0.641^{***}	0.671^{***}	0.631^{***}	8.59^{**}	10.32^{***}
Aug	174	81	0.579^{*}	0.652^{***}	0.625^{***}	1.32	6.11^{***}
Sep	125	80	0.657^{***}	0.692^{***}	0.669^{***}	11.05^{***}	7.44^{***}
1992							
Jun	218	80	0.605^{**}	0.579^{**}	0.513	3.64	1.94
Jul	332	80	0.606^{**}	0.627^{***}	0.528	0.83	6.74^{***}
Aug	69	79	0.595^{*}	0.558	0.508	0.74	5.95^{***}
Sep	57	80	0.575^{*}	0.495	0.567	5.36^{*}	2.84^{**}

Table 45: Indices of pattern for *P. melanarius* at LARS in crop areas

Month	Total	Pots	I_{reg}^{perm}	I_{rand}^{perm}	I_{red}^{perm}	DR
1990						
Jun	563	59	0.478	0.453	0.443	0.89
Jul	2998	60	0.591^{*}	0.594^{*}	0.598^{**}	1.51
Aug	1114	44	0.549	0.551	0.516	1.05
Sep	32	60	0.389	0.401	0.394	
1991						
Jun	89	70	0.587^{*}	0.571	0.540	2.19^{*}
Jul	2212	72	0.648^{***}	0.672^{***}	0.646^{***}	3.28^{***}
Aug	1477	72	0.594^{*}	0.595^{*}	0.538	1.81
Sep	638	69	0.526	0.516	0.499	1.93
1992						
Jun	584	71	0.584^{*}	0.576^{*}	0.551	1.49
Jul	2429	70	0.558	0.517	0.523	0.69

in the patches. Even so, there is little evidence of spatial regularity in the data, with values for the indices based on moves being greater than 0.5 in all months with a mean catch of greater than 1, apart from June 1990 and, very marginally, September 1991.

Table 44 presents a mass of highly significant results. If we discount June 1991, when only 22 individuals were recovered from the patches, I_{reg}^{perm} and I_{rand}^{perm} gave results before the harvest that were significant at 1%, although this is also the period when the catches were highest. After the harvest the results are less consistent, with September giving a high level of aggregation (taking into account the low catch in September 1992) and August having a high Deviance Ratio for the fit of area in 1991 and 1992 but a very low value in 1990. In general 1991 (after the low catch in June) is the year with the highest level of aggregation, showing higher values of all the indices

Table 46: Difference in aggregation level between crop and patches,*P. melanarius* at LARS

Measure	Number Obs.	Mean difference	St. Dev.	S.E. mean	t-statistic	P-value
I_{reg}^{perm}	10	0.0428	0.0709	0.0224	1.91	0.089
I_{rand}^{perm}	10	0.0692	0.0944	0.0299	2.32	0.046
I_{red}^{perm}	10	0.0565	0.0835	0.0264	2.14	0.061
Total Index	30	0.0561		0.0152	3.68	>0.001
Dev. Rat.	9	3.64	2.77	0.92	3.96	0.004

after harvest than either of the other years, although the peak indices for July occur in 1990.

In order to compare the levels of aggregation in the farmed area and the patches paired t-tests were performed between the values of the three indices I_{reg}^{perm}, I_{rand}^{perm} and I_{red}^{perm} and for the Deviance ratio, with results given in table 46. The value for the mean difference for all three indices was also given in line Total Index.

These values imply that there is significantly more aggregation in the patches than in the crop, although the significance level of the difference in the deviance ratio should be treated with caution, as the F-statistic is not normally distributed and the blocking factor, although a natural one for the patches, does not follow any natural demarcation lines for the crop.

From figure 17 we can see that the Deviance ratio for the patches is considerably higher than it is for the crop in every month except June 1991. I_{rand}^{perm} is greater for the crop than the patches in June 1991, approximately equal in August 1990,July 1991 and June 1992 and considerably less in all the other months. I_{reg}^{perm} for patches starts off as greater than that for the crop in June and July 1990, and is then slightly smaller from August 1990 through to August 1991, after which the value for the patches is

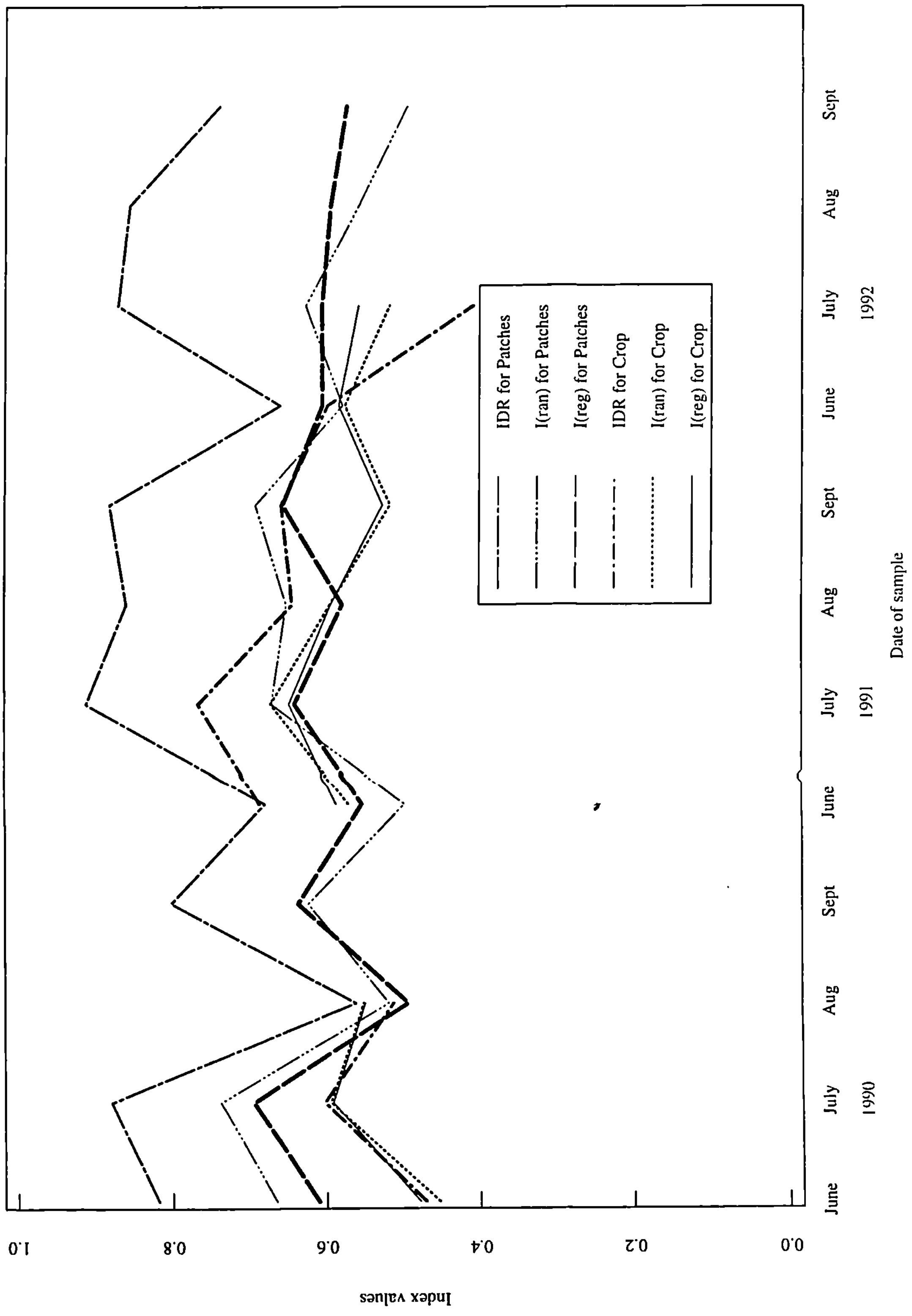


Figure 17: Indices of pattern for crop and patch data on *P. melanarius* at LARS

Table 47: Indices of pattern for *P. melanarius* at LARS in small patches

Month	Total	Pots	I_{reg}^{perm}	I_{rand}^{perm}	I_{red}^{perm}	DR
1990						
Jun	840	36	0.565	0.587	0.541	1.57
Jul	382	36	0.583	0.643^{*}	0.607^{**}	4.33^{**}
Aug	542	35	0.491	0.481	0.518	0.76
Sep	152	36	0.582	0.624^{*}	0.568^{*}	2.44
Oct	32	36	0.482	0.486	0.470	
1991						
Jun	12	36	0.555	0.500	0.515	2.58
Jul	82	36	0.665^{***}	0.699^{***}	0.640^{**}	7.02^{***}
Aug	92	36	0.545	0.536	0.561	2.25
Sep	84	35	0.649^{**}	0.686^{**}	0.669^{**}	8.29^{***}
1992						
Jun	119	35	0.562	0.569	0.516	1.54
Jul	170	35	0.556	0.578	0.502	5.64^{***}
Aug	36	35	0.473	0.540	0.553	0.66
Sep	35	35	0.639^{**}	0.470	0.632	4.26^{**}

the greater.

As there may be differences in the amount of spatial aggregation between the large and small patches the data from the patches were split by patch size, and the indices and mean deviation from the fit of the block parameter calculated for each patch size. The results of these calculations are given in tables 47 and 48 for the large and small patches respectively, with some of the indices plotted against time in figure 18. The values of the index I_{rand}^{perm} were undefined in October 1990 and June 1991 for the large patches because the M_{rand} for the data was zero.

For the small patches there were no significant results in 1990 nor in either June or August in any other year. This may be due, in part, to a decrease in the power of the tests with a decreasing number of observations being considered. The Deviance Ratio was significant in each July and September, except for September 1990, when

Table 48: Indices of pattern for *P. melanarius* at LARS in large patches

Month	Total	Pots	I_{reg}^{perm}	I_{rand}^{perm}	I_{red}^{perm}	DR
1990						
Jun	631	45	0.659^{**}	0.767^{***}	0.723^{***}	11.16^{***}
Jul	261	45	0.720^{***}	0.802^{***}	0.742^{***}	12.71^{***}
Aug	271	43	0.485	0.545	0.562	1.79
Sep	99	45	0.615^{*}	0.587	0.569	6.51^{***}
Oct	20	42	0.525	?	0.623^{**}	
1991						
Jun	10	44	0.484	?	0.499	1.73
Jul	224	45	0.622^{*}	0.739^{***}	0.756^{***}	12.14^{***}
Aug	82	45	0.587	0.742^{***}	0.767^{***}	11.49^{***}
Sep	41	45	0.649^{**}	0.726^{**}	0.707^{*}	6.58^{***}
1992						
Jun	99	45	0.597^{*}	0.602^{*}	0.620	2.53^{*}
Jul	162	45	0.613^{***}	0.677^{***}	0.553^{*}	8.04^{***}
Aug	33	44	0.646^{**}	0.777^{***}	0.707^{**}	12.10^{***}
Sep	22	45	0.491	0.500	0.493	1.54

both I_{red}^{perm} and I_{rand}^{perm} were significant at 5%. Apart from in 1992, at least two of the three indices were significant in both July and September.

For the large patches (table 48) the values of the indices and the number of significant results are far higher than for any other habitat. This could be due to each large patch being treated by the beetles as an area of habitat, whereas the small patches are too small to be treated as a different sort of habitat. Also the pots in the large patches are much closer together than either in the crop or the small patches. If we ignore the results from when there were less than 25 individuals recovered then there is significant aggregation in every month indicated by at least one index and the Deviance Ratio in every month except August 1990. The only month when only one index gave a significant result was September 1990. In July 1990 the amount of pattern reached its highest point, with $I_{reg}^{perm} = 0.72$ and $I_{rand}^{perm} = 0.802$.

Table 49: Difference in aggregation level between small and large patches,*P. melanarius* at LARS

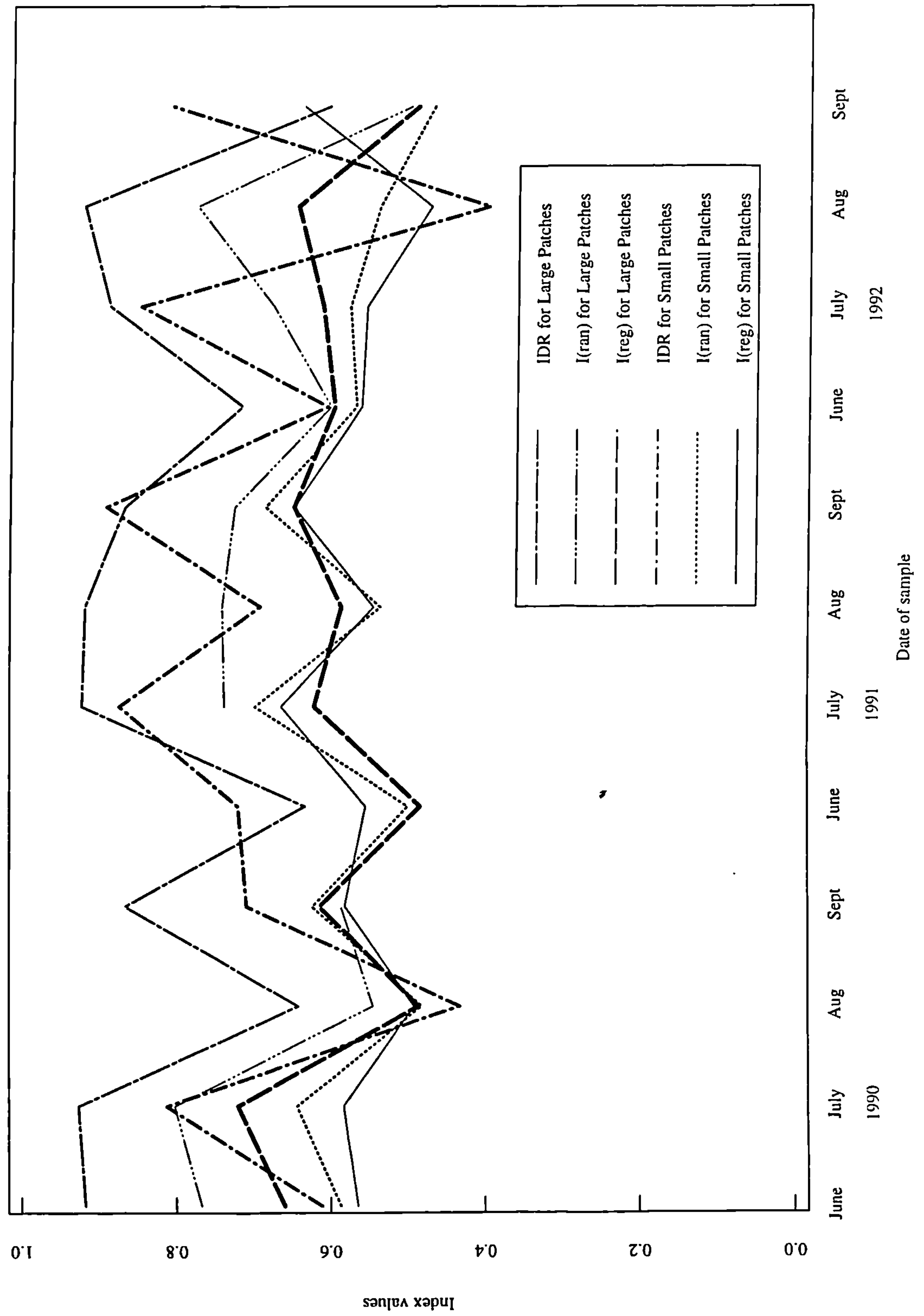
Measure	Number Obs.	Mean difference	St. Dev.	S.E. mean	t-statistic	P-value
I_{reg}^{perm}	13	0.0266	0.0848	0.0235	1.13	0.280
I_{rand}^{perm}	11	0.0955	0.0874	0.0263	3.63	0.005
I_{red}^{perm}	13	0.0792	0.0954	0.0265	2.99	0.011
Dev. Rat.	12	3.92	4.82	1.39	2.81	0.017

A formal test of whether the overall spatial aggregation is greater for large patches than small ones was performed using paired t-tests on the indices, with results in table 49.

From figure 18 we can see that I_{rand}^{perm} is always greater for the large patches than the small ones, apart from September 1990, when the result was significant at 5% for the small patches and not significant at all for the large ones. I_{reg}^{perm} for the large patches is approximately equal to the value for the small patches in August 1990 and September 1991, smaller in June and July 1991 and greater in all the other months. However fewer of the values for I_{reg}^{perm} were significant than for I_{rand}^{perm}.

The level of spatial aggregation in the small patches appears, from the values of the indices, to be slightly greater than that for the crop. There are more significant results for the small patches, even though the number of sampling points is fewer. Some of these aspects are dealt with further in the conclusion.

Figure 18: Indices of pattern for large and small patch data on *P. melanarius* at LARS



5.6 Conclusion and further work on spatial pattern

The spatial pattern in the field, as measured by the block effect in the fit of a Generalised linear model to the data, was different in each month and also varied with the habitat. The fit for AIC$_\alpha$ with $\alpha = 2$ led to a model with where a different mean catch level was fitted for each block in each month. There was no evidence of correlation between counts in patches and those in the immediately surrounding crop. The results on the indices of spatial pattern imply that the spatial pattern was important in some months and habitats while at other times the counts were relatively homogeneous, after differences between habitats were taken into account. When the data for each month were considered separately there was a statistically significant amount of pattern in every month (at the 5% level) between June and September when pots were laid in the crop except for August 1991. However, when the data are broken down into crop, small patches and large patches it immediately becomes apparent that the crop is relatively homogeneous, as are the small patches but that there are large differences between the catches in different large patches. The reasons for this may be due to the small separation between the sampling points in the large patches when compared to the separation for sampling points in the crop and the small patches. The pattern may also be due to the beetles treating each large patch as a distinct piece of habitat and considering some patches as more desirable to inhabit than others. For the small patches each patch has a single sampling point so it is impossible to tell if it is being treated as a distinct piece of habitat or if it is too small to merit the distinction. The crop areas cannot be neatly split up in this fashion. In general it appears, from the values of the indices, that the patterns consist of local clusters of high and low counts rather than significant trend or other large scale pattern.

The problem of assessing whether the small patches are being treated, as the large patches seem to be being treated, as distinct pieces of habitat, with slightly different populations, rather than as part of the general area, cannot be addressed unless there is more than one observation at a time from each of the small patches. The only way of assessing the spatial effect of the small patches is to put more than one sampling pot in each patch. If four pots were placed in each of the nine patches in one corner of the experiment then it would be possible to assess the correlation between the counts in the same patch and thus find out if there really is a "small patch effect". The extra effort entailed in doing this could be compensated for by not placing any pots out in any of the other 27 small patches. There may be a slight problem with interference between the four pots in each of the small patches, but this should be minimized by placing the pots further apart.

As it stands, because of the correlation between the catches for the large patches, there are effectively only 5, rather than 45, estimates of the activity levels in the large patches. This is insufficient to give an overall test of whether the activity levels are greater in the large patches than in the small ones.

The presence of these spatial effects imply that small scale studies, with only a few closely spaced sampling points, may not be reliable guides to overall population levels. This has important consequences for the design and analysis of field experiments intended to measure activity rates. Not only must the number of sampling pots placed be sufficient to get accurate estimates despite the overdispersion in the data, but they must be sufficiently widely spread out to make sure that the activity levels over the entire area of interest can be estimated, and the spatial variability in the amount of activity measured.

If, as is often the case in the literature, only the mean catch rate is cited and then analyses based on the assumption that the data come from a Poisson distribution are performed, such as using the binomial distribution to compare activity rates at different times, then the validity of the p-values and confidence intervals rests crucially on the assumption of no overdispersion.

A Generalized Linear Mixed model (Engel and Keen, 1993) could be fitted to the catch data. This type of model, described more fully in section 6.7, allows the correlated error structure used in Linear Mixed models to be added to to a generalized linear model. If an error term stratified by block is added to the model for the patch data then the significance of the difference between the catches in the large and small patches could be assessed. It may also be possible to assess how consistent the differences between the patches are over time. This could be done by fitting an error term for block and then examining the effect of adding block-habitat, block-month and block-year (and possibly higher order interactions) as error terms.

A very similar approach to that of Engel and Keen (1993) is given by Morton (1987) who developed a log-linear model based on quasi-likelihood with multiplicative errors and overdispersion.

The overall biological conclusions from the model are that the large patches seem to be being treated as distinct pieces of habitat, and differ between each other in terms of the mean number of *P. melanarius* caught in each of the patches. It is impossible to take this inference for the small patches because there is only one sampling point in each pot in each month. It is also difficult to compare overall mean activity levels between the large and the small patches because the catches within each large patch are known to be correlated. The crop areas seem to be far more homogeneous than the either the large patches or the small patches.

As far as the experimental design goes the lack of randomisation and the substantial differences in the insect populations at the two sites, which effectively negates the replication, make overall inferences very difficult to substantiate. This is exacerbated by the loss of crop data in the months when harvesting activities are going on.

Apart from the result that mean catch rates varying between blocks in an apparently haphazard manner over time, the most useful inference is probably that from chapter 2 about the catch rate in the crop decreasing near the patches. It is comforting to see that this is an effect which is fairly constant between the years, although it varies between the months.

Chapter 6

Hosts and parasites

6.1 Introduction

This chapter starts with a look at the biological motivation for studying host-parasitoid systems, briefly describes the literature and introduces the terminology to be used. Section 6.3 describes the model of Pacala *et al.* (1991) and its application to a large group of data sets. Some problems with their model, along with a possible solution, are given in section 6.4. A look at the effect of introducing extra variability is given in section 6.5. The important issue of stability is briefly discussed in section 6.6. Possible further work, both biological and statistical, is considered in section 6.7 and overall conclusions drawn in section 6.8.

Farmers often face serious problems from unwanted biological agents (animals, fungi, viruses etc.) either spoiling or consuming their crops before they can be harvested. This is a particular problem if plants and animals have been introduced into new areas without their natural enemies. Historically there has been a lot of interest in methods of getting rid of these agents, or at least reducing their effects to economically insignificant levels.

Direct methods, such as shooting or trapping, can only be applied to larger creatures such as mammals and birds. Pesticides have been used widely in agriculture to control invertebrate pests but there are major problems associated with their use. These poisons are often indiscriminate, killing or reducing the activity levels (Chiverton, 1984) of predator species that were eating the pests. They may also introduce long-lived poisons into the environment, affecting fish and higher life forms. Another method of control is to introduce a predator species to eat the pest. Unfortunately these may eat some of the native creatures instead, so upsetting the natural balance. A more attractive proposition is to go back to the original native area and look for species-specific parasites that were effective there in keeping the population of the pest down.

An example of the effect of introducing parasites of a pest population is given by Murdoch *et al.* (1984). They examined the effect of the introduction of first one parasite *Aphytis paramculicornis* and then a second *Coccophyoides utilis* on the populations of Olive Scales *Paralatoria oleae* in California. They found that the first parasitoid was not very effective in reducing the levels of scale found but that when the second one was introduced the population of the host dropped considerably, from a peak of around 50 scales per twig to around one or two per 50 twigs.

In the study of host-parasite interactions it is convenient, and often biologically sound, to divide the habitat into discrete patches and then look at the parasitism rates and host densities on each patch separately. These patches could be individual leaves, twigs or plants. They could also be quadrats chosen by an experimenter from an overall experimental area. The populations of hosts and parasites are also, often, divided up into separate generations, with no overlap between the generations and identical generation lengths for both host and parasite. In species in temperate regions with one or two generations per year this is a reasonable thing to do. Even in areas without much seasonal variability some host parasite systems show cyclic variability with a period of about one generation (Gordon *et al.*, 1991).

The parasites that are considered here are assumed to have the following life-cycle. The female parasite first looks for a patch of hosts. Upon finding a patch she then searches it for suitable hosts to parasitise. Having found a host she then lays one or more eggs or larvae upon the host's body. These then grow, feeding upon the body of the host, and eventually kill it. The parasites then emerge to mate and parasitise new hosts.

The usual method of experimentation is to sample several patches to find out what the host density is on each patch, and then to see how many of the hosts were parasitised. Whether a host has been parasitised can be found either from dissection or by waiting to see if any parasites emerge from it. This is usually done for all the hosts unless there are too many of them, in which case a random sample is taken. It would be nice to estimate the local female parasite density at this point as well, but unfortunately this is very difficult to do in the field (Rosenheim *et al.*, 1991).

In the study of host-parasite systems it is often of primary importance to know if the system is stable, or if outbreaks or extinction of the host population are likely to occur. May (1978) and Hassell (1982) emphasised the importance of how the reaction of the parasites to changes in host density could affect the stability of a system. There is said to be direct density dependence if the parasitism rate increases with host density among the patches, inverse density dependence if it decreases with host density, and the relationship is host density independent if it does neither. Pacala *et al.* (1991) called variability in the parasitism rate that can be ascribed to changes

Table 50: Symbols used for host parasite models

Fixed parameters and observed values	
N	The mean host density
Q	The number of discrete patches
C	Number of age categories
n_i	Host density in the ith patch
Y_i	Number of hosts tested for parasitism in the ith patch
X_i	How many Y_i are parasitised
P	The overall mean searching female parasite density
p_i	Effective searching density of searching female parasitoids in the ith patch
ϵ_i	Multiplicative error term for ith patch mean 1
b_k	Risk of parasitism in kth age category if found by parasite

in the host density as Host Density Dependent heterogeneity (HDD) and that which is independent of the host density as Host Density Independent heterogeneity (HDI).

6.2 A unifying notation for some host-parasite models

We will now develop a unifying notation for the models in the rest of this chapter. This is done in the same spirit as the notations for queueing models developed by Kendal (1953).

Each model is described by three letters and is in the form X/Y/Z. The first letter represents the way in which the searching parasite density depends on the host density for each patch, the second one represents the effect of the developmental stage of the host alters its chance of being parasitised and the third one, the variability in the risk of becoming parasitised between hosts in the same patch. There is some overlap between the second and third parts of the models.

The risk factor has been assumed to follow a beta distribution for each age group.

Table 51: Notation for Host-Parasite models

Model part	Symbol	Formula	Description
Parasite density			
I	(Same)	1	Same across all patches
E	(Error)	ϵ_i	Random variation in p_i
D	(Deterministic)	$(n_i/N)^{\mu}$	Fixed function of host density
R	(Regression)	$(n_i/N)^{\mu}\epsilon_i$	E and D multiplied together
F	(Fixed)	F_i	Estimated from parasitism rate
Host risk of being parasitised if found			
Age effects			
I	(Same)		No age effects
A	(Age)		Risk varies with age group
Distribution of risk factor (with age)			
I	(Same)	1	All fixed at 1
U	(Uniform)	b_k	Risk has uniform distribution on $[0,1]$
E	(Error)		Fixed variance ,Expectation varies
H	(Half)		Expectation fixed at 0.5 variance changes
V	(Variable)		Both expectation and variance change
General symbol			
?	Any	?	All models appropriate

It represents the probability of being parasitised if found by a searching parasite, assuming all hosts of in the patch are equally easy to find. Some models for estimating the parameters for the distributions of p_i and b_k including restrictions that could improve the interpretation of the models are given in table 51

Thus I/I/I represents a model where the probability of a host being found by a parasites, p, is independent of age category and patch, and the probability of being parasitised once found is 1. R/A/I is a model where the searching parasite density p_i (and the chance of a host being found) is related to, but not a deterministic function of, the host density in each patch, and each host has a chance b_k of avoiding parasitism each time it is found, where b_k depends on the age category but is the same for all hosts in that age category. ?/I/I gives all the models where all the hosts in any given patch run the same risk of being parasitised.

6.3 Pacala and Hassell model

Pacala *et al.* (1991) and Pacala and Hassell (1991) considered a model for a host parasite system where the amount of host density dependent and host density independent variability in the density of searching parasitoids could be set to any required value. In a system with Q patches overall, they assumed that the mean density over all patches of searching female parasitoids was P and that the mean host density was N.

In order to have a functional form for the parasitism rate that could be related to the density in each patch, they described the expected density of female searching parasitoids in the ith patch with host density n_i as

$$E(P_i) = cP\left(\frac{n_i}{N}\right)^{\mu}$$

where c is a constant.

If the value of μ is positive then there is direct density dependence, if it is negative the density dependence is inverse and if it is zero then the searching parasitoid density is independent of host density. This functional form was chosen because it would represent the change from direct to inverse density dependence better than a linear model.

The actual searching density of the parasitoids in the ith patch was assumed to be

$$p_i = cP\left(\frac{n_i}{N}\right)^{\mu}\epsilon_i$$

where ϵ_i is an error term. This is an R/I/I model.

The variable ϵ was chosen to have a Gamma density with unit mean and variance σ^2. This was chosen because Griffiths (1969) and Griffiths and Holling (1969) have observed that the number of attacks per host has an approximately negative binomial distribution. If the parasites search randomly and independently within a patch and all hosts in it are equally vulnerable to parasitism then the probability of a host in the ith patch escaping parasitism is $\exp(-ap_i)$ where a is the per capita searching efficiency of the parasites and p_i the local searching parasite density. This is the zero term of a Poisson distribution representing the number of times a randomly selected host is found by the searching parasites.

If we bring all this together then the probability of a host not being parasitised in the ith patch is

$$P(\text{avoiding parasitism}|\epsilon, n_i) = \exp\left[-acP\left(\frac{n_i}{N}\right)^{\mu}\epsilon_i\right]$$

If we substitute $b = acP/(N^{\mu})$ then

$$P(\text{avoiding parasitism}|\epsilon, n_i) = \exp\left(-bn_i^{\mu}\epsilon_i\right) \tag{1}$$

If there are Y_i individuals tested for parasitism from this patch and X_i are parasitised then X_i has a binomial distribution.

$$P(X_i|Y_i, \epsilon_i, n_i) = \begin{pmatrix} Y_i \\ X_i \end{pmatrix} \exp\left(-bn_i^{\mu}\epsilon_i\right)^{Y_i - X_i}\left[1 - \exp(bn_i^{\mu}\epsilon_i)\right]^{X_i}$$

In order to remove the conditioning with respect to the parameter ϵ this expression is multiplied by the gamma density $\gamma(\epsilon)$ and then integrated with respect to ϵ. The log-likelihood is taken over all Q patches.

$$l = \sum_{i=1}^{Q}\log\left(\int_0^{\infty} P(X_i|Y_i, \epsilon_i, n_i)\gamma(\epsilon)d\epsilon\right) \tag{2}$$

This was expanded out and integrated with respect to ϵ as follows

$$\begin{aligned}
l &= \sum_{i=1}^{Q} \log \left[\int_0^\infty \gamma(\epsilon) \begin{pmatrix} Y_i \\ X_i \end{pmatrix} \{\exp(-bn_i^\mu \epsilon)\}^{Y_i - X_i} \{1 - \exp(-bn_i^\mu \epsilon)\}^{X_i} \, d\epsilon \right] \\
&= \sum_{i=1}^{Q} \log \left[\int_0^\infty \gamma(\epsilon) \begin{pmatrix} Y_i \\ X_i \end{pmatrix} \sum_{j=0}^{X_i} \begin{pmatrix} X_i \\ j \end{pmatrix} \exp(-bn_i^\mu \epsilon (Y_i - X_i)) \{-\exp(-bn_i^\mu \epsilon)\}^j \, d\epsilon \right] \\
&= \sum_{i=1}^{Q} \log \left[\begin{pmatrix} Y_i \\ X_i \end{pmatrix} \sum_{j=0}^{X_i} \begin{pmatrix} X_i \\ j \end{pmatrix} (-1)^j \int_0^\infty \gamma(\epsilon) \exp\{-bn_i^\mu \epsilon (Y_i - X_i + j)\} \, d\epsilon \right] \\
&= \sum_{i=1}^{Q} \log \left[\begin{pmatrix} Y_i \\ X_i \end{pmatrix} \sum_{j=0}^{X_i} \begin{pmatrix} X_i \\ j \end{pmatrix} (-1)^j \left\{1 + \sigma^2 bn_i^\mu (Y_i - X_i + j)\right\}^{-1/\sigma^2} \right]
\end{aligned}$$

This can be expressed in a slightly shorter form as

$$l = \sum_{i=1}^{Q} \begin{pmatrix} X_i \\ Y_i \end{pmatrix} \sum_{j=0}^{X_i} (-1)^j \begin{pmatrix} j \\ X_i \end{pmatrix} (1 + \sigma^2 bn_i^\mu (Y_i - X_i + j))^{-\frac{1}{\sigma^2}} \qquad (3)$$

If $\sigma^2 = 0$ and $\mu \neq 0$ then we have a Pure Regression (PR) model (Chesson and Murdoch, 1986) , denoted here as D/I/I). If $\mu = 0$ and $\sigma^2 > 0$ then we have a Pure Error model (PE) (or E/I/I). If they are both zero then the area is being treated as a single large patch (an I/I/I model).

Pacala and Hassell went on to obtain maximum likelihood estimates $\hat{\sigma^2}$, $\hat{b}$ and $\hat{\mu}$ by numerically maximising the above likelihood for 32 example data sets. This proved difficult numerically for equation 3 when there were more than 20 patches, so they used equation 2 and integrated numerically in those cases.

There was still a problem with the estimation of σ^2 because occasionally the routine had numerical overflows when the estimate became too small. Therefore the constraint $\sigma^2 \geq 0.05$ was introduced. The maximum likelihood estimates for σ^2 are constrained at this value for 13 of the 32 data sets. When 95% confidence intervals for the parameter estimates were calculated, the lower estimate of σ^2 was constrained at 0.05 for a further 6 data sets. There was no obvious reason for choosing 0.05 except possible numerical convenience. An attempt to get around this problem is discussed in section 6.4.

6.4 Setting σ^2 to zero

It seems sensible in the light of the constraint on σ^2 in section 6.3 to consider the case where $\sigma^2 = 0$ separately. This represents the situation where the density of the searching parasitoids is a deterministic function of the host population density. If this is the case then the random variable ϵ can be replaced by unity in equation 1 and then we can proceed as before without the need to integrate. This is very similar to model II of Hassell (1982). The density of the searching parasite population is now

$$acP\left(\frac{n_i}{N}\right)^{\mu}$$

The log-likelihood in this case is

$$\begin{aligned} l &= \sum_{i=1}^{Q} \log P(X_i|Y_i, n_i) \\ &= \sum_{i=1}^{Q} \log \begin{pmatrix} Y_i \\ X_i \end{pmatrix} \exp(-bn_i^{\mu})^{Y_i - X_i} \{1 - \exp(-bn_i^{\mu})\}^{X_i} \\ &= \sum_{i=1}^{Q} \log \begin{pmatrix} Y_i \\ X_i \end{pmatrix} \exp(-bn_i^{\mu})^{Y_i - X_i} \sum_{j=0}^{X_i} \begin{pmatrix} X_i \\ j \end{pmatrix} (-1)^j \{\exp(-bn_i^{\mu})\}^j \end{aligned}$$

$$= \sum_{i=1}^{Q} \log \begin{pmatrix} Y_i \\ X_i \end{pmatrix} \sum_{j=0}^{X_i} \begin{pmatrix} X_i \\ j \end{pmatrix} (-1)^j [\exp\{-bn_i^{\mu}(Y_i - X_i + j)\}]$$

This can be maximised as in the previous case.

However it is possible to express this model in the framework of a generalized linear model using a complementary log-log link based on the probability of being parasitised. The probability of being parasitised, π, is $1 - \exp(-bn_i^{\mu})$. The link function gives a linear predictor of

$$\begin{aligned} g(\pi) &= \log[-\log\{1 - (1 - e^{-bn_i^{\mu}})\}] && (4) \\ &= \log(b) + \mu \log(n_i) && (5) \end{aligned}$$

All that needs to be done is to regress the proportion parasitised against the log of the host density. Thus the model can be fitted using any computer package that allows a generalized linear model to be fitted to binomial data using the complementary log-log link. Here the GLIM package (Payne, 1986) has been used to fit the models (Aitkin *et al.*, 1989). We now consider an example of a host-parasite study.

6.4.1 A Study of a Host-parasite system

Thorarinsson (1990) conducted an experiment to attempt to determine the extent of density dependence in a host-parasite system. The involved evaluation of the parasitism rate of the cottony cushion scale *Icerya purchasi* by the parasitic fly *Cryptochaetum iceryae* (Cryptochaetidae), which in conjunction with the vedalia beetle *Rodolia cardinalis* has controlled the level of the scale in California for a number of years. This data was subsequently analysed as data sets 29 to 32 by Pacala and Hassell (1991).

The experimental area was a hedge of mock orange *Pittosporum tobira* which measured approximately 5m by 20m with a height of about 160cm. In each experiment a vial containing a number of crawling *C iceryae* was fixed to a shoot and the shoot and vial were covered with a fine mesh to protect them from natural enemies. After about 6 weeks the mesh was removed and 11 to 15 days after that the shoots were removed from the site and refrigerated ready for further analysis.

On each leaf of each shoot the number of scales present was recorded. The stage of development (1st instar, 2nd instar, 3rd instar and adult) was recorded by looking at the morphology of the antennae. The insects were then dissected and the remains studied for signs of parasitism. This method only reveals parasites that are more than 3 to 4 days old as it is difficult to spot eggs and first stage larvae of the parasites.

Three separate experiments were conducted with varying host densities.

In experiment 1 a row of three blocks was set up. Each block consisted of a 3 × 3 grid of shoots, with the shoots separated by about 50-70cm. The blocks were approximately 2m apart. The first block was exposed earlier than the others for monitoring purposes and the results for this block were not given. In the other two blocks the hosts, which were placed during 4-8 April 1986, were exposed on 5 June for a period of 15 days to natural enemies. The shoots were then brought in. Unfortunately 3 of the shoots had been damaged prior to exposure and so only 15 shoots remained for analysis. The initial numbers exposed and the scale sizes were not recorded.

The second experiment consisted of an identical pair of 4 × 4 grids of shoots (data sets 2A and 2B), with four different levels of initial scale densities arranged in a latin square. The four levels of density were 11-17 individuals, 23-28, 36-65 and 72-132. The shoots were again 50 to 70 cm apart and the two blocks were separated by about

Table 52: Recoveries from Thorarinsson experiments

Experiment	Patches	Hosts recovered	Total Parasitised	Parasitism rate
1	15	423	252	59.5%
2A	16	180	94	52.2%
2B	16	212	142	67.0%
3	22	385	251	65.2%

2m. These colonies were put out during 10-12 May 1986 and exposed on 23 June. The scales were recovered 11 days after they were exposed.

In the third experiment a single block of twenty five shoots was set up in a 5 × 5 grid with each shoot separated form its neighbour by about 15-20 cm. Five of the shoots received between 117 and 156 scales each and the rest between 14 and 19 scales each. The shoots with high densities were chosen so that there was one in each row and column of the grid. The vials were placed during the 4-8 August 1987, exposed on the 13 September and recovered 13 days later.

The number of patches from which hosts were recovered, the total number of hosts recovered and mean parasitism rate for each experiment are given in table 52 .

No evidence was found of density dependence in the rates of parasitism at either the scale of the colonies or of individual leaves for any of these experiments once the effect of host size was taken into account.

The data in the paper were published in the form of a series of dot-plots of percentage parasitism against colony size. This was converted to the form of colony size and numbers parasitised using an automatic reader. This appeared to introduce some errors into the data due to the size of the dots compared to the scale. The data in these plots were not broken down by size of scale.

In order to estimate the values of the parameters b and μ when the value of σ^2 was zero, the generalized linear model detailed above was fitted to each of the four data sets. The chance that $\mu = 0$ (I/I/I) was looked at by fitting the model with $\mu = 0$ as well. The results of these fits together with the original parameter estimates and the correlation between μ and $\log acP$ for the density dependent deterministic model, are shown in table 53.

The standard errors for the estimate of the overall parasite density $\log(acP)$ are greater for the Generalized Linear Model that includes μ than for the Pacala model but, apart from for set 31, the estimate of μ is more precise. In none of these models does the estimate of μ vary significantly from 0, implying there is no overall evidence of host density dependent heterogeneity in the parasitism rate. When the parameter μ was set to zero, the scaled deviance did not significantly increase, and the standard errors of the estimate of the mean parasitism rate dropped considerably. This could be because of the high negative correlation between μ and $\log(acP)$ given in table 53. For all the replicates, the 95% confidence interval for $\log(acP)$ from the Pacala and density dependent deterministic model include the value from the simple fit. If the χ^2 approximation for the scaled deviance holds then all the models appear to fit apart from the third one.

The relationship between the parasitism rate and the host density is illustrated by the plots of the percentage parasitism against the log of the host density in figures 19, 20, 21 and 22.

The assumptions on which this model are based are dubious for this system. In particular Thorarinsson (1990) points out that the rate of parasitism in the third instar and adults is higher than the first and second instars. Therefore the data ought to be split up by age category before any analysis is attempted (as in section 6.5.3). If this age difference is taken into account, the parasitism rates in the colonies are approximately the same. This can either be explained by a lack of spatial density

Table 53: Parameter estimates, Confidence intervals and correlations for Thorrarinson's data

Parameter	Pacala estimates		Density dependence		Dens. Indep.	
	Estimate	95% c.i.	Estimate	s.e.	Estimate	s.e.
Set 1						
σ^2	0.05	[0.05 , 0.179]				
μ	0.008	[-0.215 , 0.245]	-0.050	0.098	0*	
acP	1.109	[0.920 , 1.331]				
$\log acP$	0.103	[-0.08 , 0.286]	0.125	0.367	-0.060	0.064
Deviance			44.6		44.9	
Correlation			-0.98			
Set 2A						
σ^2	0.05	[0.05 , 0.200]				
μ	0.047	[-0.231 , 0.336]	0.035	0.130	0*	
acP	0.735	[0.573 , 0.941]				
$\log acP$	-0.308	[-0.557, -0.061]	-0.404	0.387	-0.303	0.105
Deviance			16.8		16.8	
Correlation			-0.96			
Set 2B						
σ^2	0.299	[0.108 , 0.807]				
μ	0.254	[-0.752 , 0.256]	-0.253	0.126	0*	
acP	1.418	[1.007 , 2.028]				
$\log acP$	0.349	[0.007 , 0.707]	0.810	0.365	0.089	0.088
Deviance			57.8		61.7	
Correlation			-0.97			
Set 3						
σ^2	0.05	[0.05 , 0.192]				
μ	-0.014	[-0.162 , 0.140]	-0.044	0.062	0*	
acP	1.109	[0.920 , 1.342]				
$\log acP$	0.103	[-0.083 , 0.294]	0.213	0.234	0.054	0.066
Deviance			28.10		28.6	
Correlation			-0.95			

* μ fixed at 0 in density independent model

Figure 19: Percentage parasitism plot for set 1

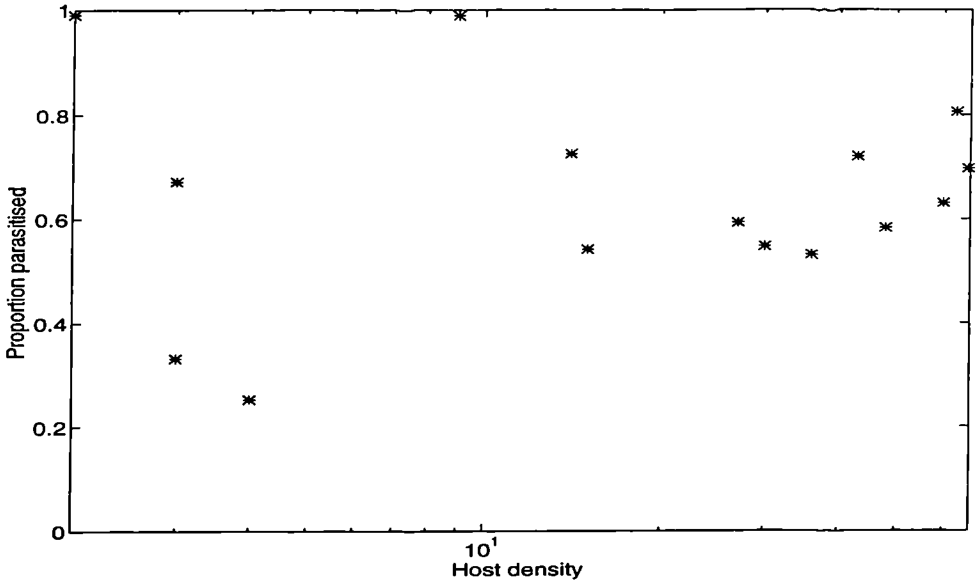


Figure 20: Percentage parasitism plot for set 2A

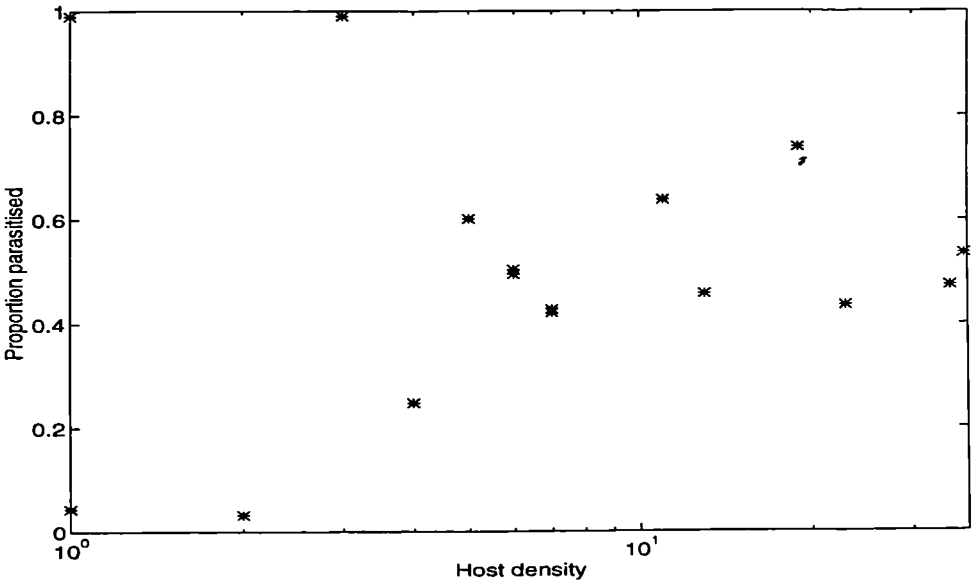


Figure 21: Percentage parasitism plot for set 2B

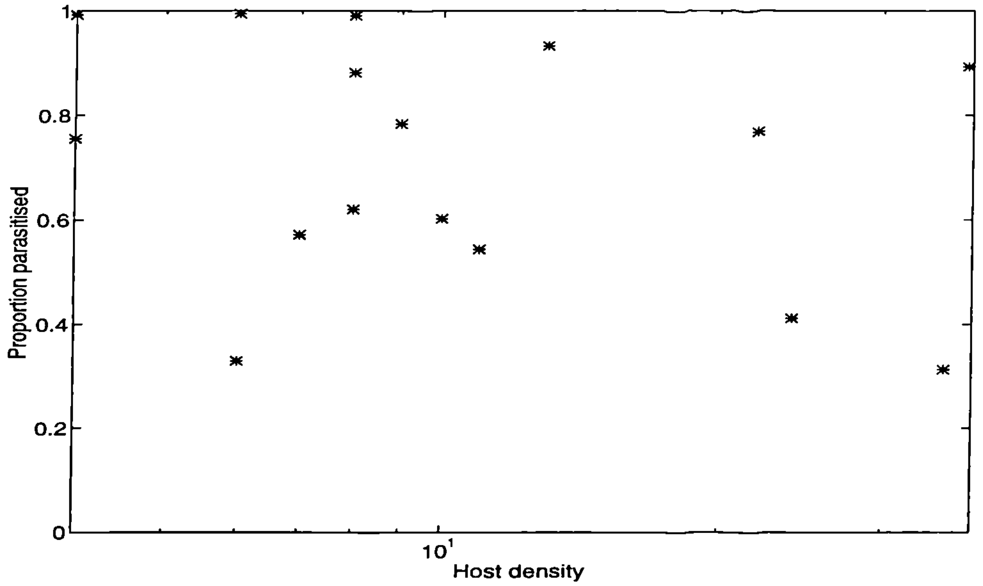
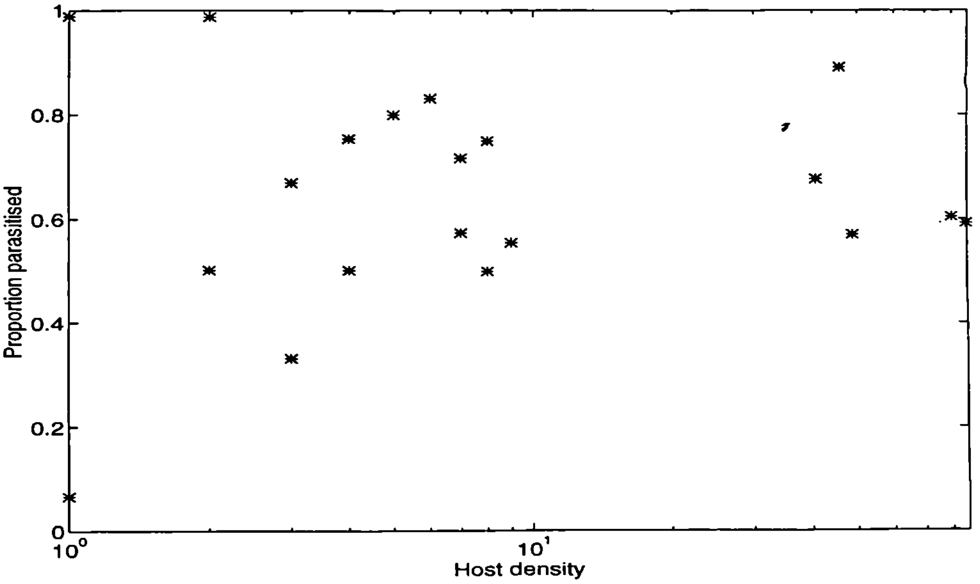


Figure 22: Percentage parasitism plot for set 3



dependence or, more simply, by assuming the parasites treat the entire experimental area as a single patch. This implies it may have been better to perform the experiment on a larger spatial scale in order to assess this.

6.4.2 Numerical considerations

We shall now consider the effect of assuming that the searching parasite density is a deterministic function of the host density within a patch when there is a random error component within the effect. In particular consider the effect on the previous model of introducing a gamma distributed random error term ϵ_i to the parasite density. The probability of an individual in the ith patch being parasitised is now $1 - \exp(-bn_i^{\mu}\epsilon_i)$

If we fit use a complementary log-log link function then the link gives

$$\begin{aligned} g(\pi_i) &= \log\{-\log(e^{-bn_i^{\mu}\epsilon_i})\} \\ &= \log(b) + \mu\log(n_i) + \log(\epsilon_i) \end{aligned}$$

If expectations are now taken of each side in order to remove the error term ϵ_i we get

$$\begin{aligned} E(g(\pi_i)) &= \int_0^{\infty}[\log(b) + \mu\log(n_i) + \log(\epsilon)]\frac{\Gamma(\alpha)}{\alpha^{\alpha}}\epsilon^{\alpha-1}e^{-\alpha\epsilon}d\epsilon \\ &= \log(b) + \mu\log(n_i) + \int_0^{\infty}\log(\epsilon)\frac{\Gamma(\alpha)}{\alpha^{\alpha}}\epsilon^{\alpha-1}e^{-\alpha\epsilon}d\epsilon \end{aligned}$$

The integral part of this expression can be solved using the expression given by Gradshteyn and Ryzhik (1980) equation 4.352(1) by substituting $1/\alpha = \sigma^2$

$$\int_0^{\infty}(\log(\epsilon))\epsilon^{\alpha-1}e^{-\alpha\epsilon}d\epsilon = \frac{\alpha^{\alpha}}{\Gamma(\alpha)}(\Psi(\alpha) + \log\alpha)$$

This gives the expression

$$E(g(\pi_i)) = \log(b) + \mu\log(n_i) + \Psi(\alpha) - \log(\alpha)$$

The Ψ function can be approximated using the asymptotic expansion given by Abramowitz and Stegun (1965), equation **6.3.18.**

$$\Psi(\alpha) \approx \log(\alpha) - \frac{1}{2\alpha} - \frac{1}{12\alpha^2} + \frac{1}{120\alpha^4} + \frac{1}{252\alpha^6}$$

Using this substitution now gives expression

$$E(g(\pi_i)) = \log(b) + \mu\log(n_i) - \frac{1}{2}\sigma^2 - \frac{1}{12}\sigma^4 + \frac{1}{120}\sigma^8 + \frac{1}{252}\sigma^{12}$$

There is only a small error provided that σ^2 is small. McCullagh and Nelder (1989), page 108 mention that the log-log link ($g(\pi) = -\log\{-\log(\pi)\}$) is unsuitable when $\pi < 1/2$. As the two links are related by

$$g_1(\pi) = -g_2(1-\pi)$$

where g_1 and g_2 are the complementary log-log and log-log links respectively (although the formula works the other way round as well), this implies that the complementary log-log link may not be suitable for systems where there is a high rate of parasitism.

6.5 Variable host vulnerability

In the usual host-parasitoid models it is assumed that every time a searching parasitoid finds a host that is free from parasitism then the host becomes parasitised. The number of hosts parasitised within any given patch follows a binomial distribution, with the probability of any one host being parasitised as a deterministic function of the searching parasitoid density.

If however we allow each host a probability of avoiding parasitism each time it is found by a searching parasitoid, and allow this probability to be a random variable with a suitable distribution, then this introduces a new source of variability.

6.5.1 Initial starting point

Initially, assume that the effective local searching density of the parasitoids in the patch that we are studying is w. If the individuals search randomly and independently within the patch then the number of attacks per host follows a Poisson distribution with mean w. The probability of k attacks upon a randomly selected host is therefore

$$p(k) = \frac{e^{-w}w^k}{k!}$$

If the probability of an individual not becoming parasitised after the first k attacks upon it is S_k then the overall probability of that host escaping parasitism is

$$\sum_{k=0}^{\infty} \frac{e^{-w}w^k}{k!} S_k \tag{6}$$

6.5.2 All hosts equally vulnerable

If each host has a fixed probability r of avoiding being parasitised on the kth attack if it has not been parasitised earlier, then the probability of avoiding becoming parasitised after k attacks is r^k. Thus the overall probability of becoming parasitised is

$$\begin{aligned} P(S|w) &= \sum_{k=0}^{\infty} \frac{e^{-w}w^k}{k} r^k \\ &= e^{-w} \sum_{k=0}^{\infty} \frac{(wr)^k}{k} \\ &= e^{-w(1-r)} \sum_{k=0}^{\infty} \frac{e^{-wr}(wr)^k}{k} \\ &= e^{-w(1-r)} \end{aligned}$$

Thus the effect of introducing a fixed resistance parameter r for each host is identical to reducing the per capita searching efficiency of the parasites by a factor of

$1-r$. This case is thus indistinguishable from the case where all attacks by parasites that have found a host automatically succeed.

6.5.3 Host Classification

We shall now look at the effect on the R/I/I model of host-parasite systems of subdividing the host population in each patch into several categories, assuming that the hosts in different categories have differing susceptibilities to parasitism. This will give model R/A/I.

Suppose that the host population can be divided without error into C discrete categories. For each host in the kth category, let the probability of escaping parasitism if it is found by a searching parasite be b_k. Let $\mathbf{b} = (b_1, \ldots, b_C)$ be the vector form of this. Let there be Q patches and in the ith patch let the number of hosts tested for parasitism be $\mathbf{Y}_i = (Y_{i1}, Y_{i2}, \ldots, Y_{iC})$ and number actually parasitised be $\mathbf{X}_i = (X_{i1}, X_{i2}, \ldots, X_{iC})$ where Y_{ik} is the number of hosts tested in the kth category and X_{ik} is the number of these that are parasitised.

If we take the approach of Pacala and Hassell then the probability of escaping parasitism for an individual in the ith patch and the kth category is $\exp(-b_k n_i^\mu \epsilon_i)$ where ϵ_i has a gamma distribution with unit mean.

If we assume that the hosts search randomly and independently within a patch then

$$P(X_{ik}|Y_{ik}, n_i, \epsilon_i) = \begin{pmatrix} Y_{ik} \\ X_{ik} \end{pmatrix} \{\exp(-b_k n_i^\mu \epsilon_i)\}^{Y_{ik}-X_{ik}} \{1 - \exp(-b_k n_i^\mu \epsilon_i)\}^{X_{ik}}$$

The likelihood for the vector X_i given Y_i and ϵ_i is therefore

$$P(\mathbf{X}_i|\mathbf{Y}_i, n_i, \epsilon_i) = \prod_{k=1}^{C} \begin{pmatrix} Y_{ik} \\ X_{ik} \end{pmatrix} \{\exp(-b_k n_i^\mu \epsilon_i)\}^{Y_{ik}-X_{ik}} \{1 - \exp(-b_k n_i^\mu \epsilon_i)\}^{X_{ik}}$$

Removing the conditioning on ϵ_i by multiplying by its density and then integrating with respect to ϵ gives

$$P(\mathbf{X}_i|\mathbf{Y}_i, n_i) = \int_0^\infty \prod_{k=1}^{C} \left[\begin{pmatrix} Y_{ik} \\ X_{ik} \end{pmatrix} \{\exp(-b_k n_i^\mu \epsilon)\}^{Y_{ik}-X_{ik}} \{1-\exp(-b_k n_i^\mu \epsilon)\}^{X_{ik}} \right] \gamma(\epsilon)\, d\epsilon$$

This gives the log-likelihood for the observed data set as

$$l = \sum_{i=1}^{Q} \log \left(\int_0^\infty \prod_{k=1}^{C} \left[\begin{pmatrix} Y_{ik} \\ X_{ik} \end{pmatrix} \{\exp(-b_k n_i^\mu \epsilon)\}^{Y_{ik}-X_{ik}} \{1-\exp(-b_k n_i^\mu \epsilon)\}^{X_{ik}} \right] \gamma(\epsilon)\, d\epsilon \right)$$

In order to simplify this expression we can perform the substitutions

$$\begin{aligned} A_i &= \sum_{k=1}^{C} (Y_{ik} - X_{ik}) b_k = (\mathbf{Y}_i - \mathbf{X}_i)^T \mathbf{b} \\ F &= \sum_{i=1}^{Q} \log \left\{ \prod_{k=1}^{C} \begin{pmatrix} Y_{ik} \\ X_{ik} \end{pmatrix} \right\} \end{aligned}$$

Notice that F is a function of the data but not the parameters and so can be left out of the process of maximising the likelihood if required.

The log-likelihood is now

$$\begin{aligned} l &= F + \sum_{i=1}^{Q} \log \left(\int_0^\infty \{\exp(-A_i n_i^\mu \epsilon)\} \prod_{k=1}^{C} \left[\sum_{j=0}^{X_{ik}} \begin{pmatrix} X_{ik} \\ j \end{pmatrix} \{-\exp(-b_k n_i^\mu \epsilon)\}^j \right] \gamma(\epsilon)\, d\epsilon \right) \\ &= F + \sum_{i=1}^{Q} \log \left(\int_0^\infty \{\exp(-A_i n_i^\mu \epsilon)\} \prod_{k=1}^{C} \left[\sum_{j=0}^{X_{ik}} \begin{pmatrix} X_{ik} \\ j \end{pmatrix} (-1)^j \exp(-j b_k n_i^\mu \epsilon) \right] \gamma(\epsilon)\, d\epsilon \right) \end{aligned}$$

In order to interchange the summation and product signs on the right hand side of the above expression it helps to introduce some new notation. Let $\{\mathbf{V}_i\}$ be the set of vectors of length C indexed by $l \in L_i$ such that

$$\mathbf{V}_{il} = \{W_{il1}, W_{il2}, \ldots, W_{ilc}\}$$

$$W_{ilk} \in \{0, 1, \ldots, X_{ik}\}$$

and $\{\mathbf{V}_i\}$ contains all possible permutations of the W_{ilk}.

It is useful at this point to introduce the following substitution

$$B_{il} = \prod_{k=1}^{C} \begin{pmatrix} X_{ik} \\ V_{ilk} \end{pmatrix} (-1)^{\sum_{k=1}^{C} W_{ilk}}$$

The form of the log-likelihood is

$$l = F + \sum_{i=1}^{Q} \log \left(\int_0^\infty \{\exp(-A_i n_i^\mu \epsilon)\} \sum_{l \in L_i} \left[B_{il} \exp\{- \left(\sum_{k=1}^{C} b_k V_{ilk} \right) n_i^\mu \epsilon\} \right] \gamma(\epsilon)\, d\epsilon \right)$$

This now gives

$$\begin{aligned} l &= F + \sum_{i=1}^{Q} \log \left(\int_0^\infty \{\exp(-A_i n_i^\mu \epsilon)\} \sum_{l \in L_i} B_{il} \exp(\mathbf{V}_{il}^T \mathbf{b} n_i^\mu \epsilon) \gamma(\epsilon)\, d\epsilon \right) \\ &= F + \sum_{i=1}^{Q} \log \left(\sum_{l \in L_i} B_{il} \int_0^\infty \exp\{-(A_i + \mathbf{V}_{il}^T \mathbf{b}) n_i^\mu \epsilon\} \gamma(\epsilon)\, d\epsilon \right) \\ &= F + \sum_{i=1}^{Q} \log \left(\sum_{l \in L_i} B_{il} \int_0^\infty \exp\left\{-(A_i + \mathbf{V}_{il}^T \mathbf{b}) n_i^\mu \epsilon\right\} \frac{\alpha^\alpha \epsilon^{\alpha-1} e^{-\alpha\epsilon}}{\Gamma(\alpha)}\, d\epsilon \right) \\ &= F + \sum_{i=1}^{Q} \log \left(\sum_{l \in L_i} B_{il} \frac{\alpha^\alpha}{\Gamma(\alpha)} \int_0^\infty \exp\left\{- \left[\left\{(A_i + \mathbf{V}_{il}^T \mathbf{b}) n_i^\mu\right\} + \alpha\right] \epsilon\right\} \epsilon^{\alpha-1}\, d\epsilon \right) \end{aligned}$$

The form of the integrand is that of a Gamma density.

$$\int_0^\infty x^\nu e^{-\mu x}\, dx = \frac{1}{\mu^\nu} \Gamma(\nu)\ \mu > 0\ \nu > 0$$

Then after performing the following substitutions

$$\begin{aligned} \mu &= T_{il} = \left\{(A_i + \mathbf{V}_{il}^T \mathrm{b}) n_i^{\mu}\right\} + \alpha \\ \nu &= \alpha \end{aligned}$$

The form of the log-likelihood is

$$\begin{aligned} l &= F + \sum_{i=1}^{Q} \log \left\{ \sum_{l \in L_i} B_{il} \frac{\alpha^{\alpha}}{\Gamma(\alpha)} \frac{\Gamma(\alpha)}{T_{il}^{\alpha}} \right\} \\ &= F + Q\alpha \log(\alpha) + \sum_{i=1}^{Q} \log \left\{ \sum_{l \in L_i} \left(\frac{B_{il}}{T_{il}^{\alpha}} \right) \right\} \end{aligned}$$

If there is assumed to be no host-density independent parasitism, then we can proceed as in the the case where $\sigma^2=0$ except that the scalar b is replaced by the vector b, where b_k is the relative rate of parasitism for the kth category (Model D/A/I). We can again express this in terms of a generalized linear model by replacing b with b_k in equation 4. Therefore the form of the estimating equation for the parasitism rate for the kth category in the ith patch is now

$$\begin{aligned} g(\pi_k) &= \log[-\log\{1 - (1 - e^{-b_k n_i^{\mu}})\}] \quad , && (7) \\ &= \log(b_k) + \mu \log(n_i) && (8) \end{aligned}$$

Thus the model can be fitted using the GLIM package by fitting a binomial model with a log-log link, regressing the parasitism rate against the log of the host density and the class of the host. The statistical significance of the age catches can be assessed by looking at the change in the deviance that occurs when b_k is replaced by b.

In the Pacala and Hassell approach the effective host density is estimated by the number of hosts recovered from each patch. This is fine if all patches are the same size and all hosts equally vulnerable. If however the rate of parasitism among different groupings of the host within a patch varies then the estimate of the host density ought to take this factor into account. A possible method of doing this is to consider the mean parasitism rate for each category k taken over all the patches i. Let this be R_k. If the host density for the kth category in the ith patch is n_{ik} then the effective host density in that patch is the weighted average $\sum_{k=1}^{C} n_{ik} R_k$.

6.5.4 Uniform Vulnerability

Now consider the simple case where the probability of a host resisting an attack is r where r is drawn from the uniform distribution independently for each host and is the same for all the attacks upon that host (Models R/I/U, D/I/U, E/I/U and I/I/U). If there are k attacks then the probability of surviving all k attacks given r is r^k. If we integrate with respect to r then the probability of surviving all k attacks is

$$S_k = \int_0^1 r^k dr = \frac{1}{k+1}$$

The overall probability of not being parasitised is thus

$$\begin{aligned} P(S|w) &= \sum_{k=0}^{\infty} \frac{e^{-w} w^k}{k!} \frac{1}{k+1} \\ &= \sum_{k=0}^{\infty} e^{-w} \frac{w^k}{(k+1)!} \\ &= \frac{1}{w} \sum_{k=0}^{\infty} \frac{e^{-w} w^{k+1}}{(k+1)!} \\ &= \frac{1}{w}[1 - e^{-w}] \end{aligned}$$

One advantage of this approach is that there are no extra parameters that need estimating. The corresponding disadvantage is that it is inflexible, with no method of estimating the degree of heterogeneity in the host population. This is dealt with in the next section.

6.5.5 Beta Distribution

If a more flexible approach is required then it can be assumed that the resistance r of each individual is drawn from a Beta distribution with parameters α_1 and α_2. This gives the models ?/?/E, ?/?/H and ?/?/V. Then the probability of surviving k attacks is

$$\begin{aligned} S_k &= \int_0^1 r^k \frac{r^{\alpha_1 - 1}(1-r)^{\alpha_2 - 1}}{Be(\alpha_1, \alpha_2)} dr \\ &= \int_0^1 \frac{r^{\alpha_1 + k - 1}(1-r)^{\alpha_2 - 1}}{Be(\alpha_1, \alpha_2)} dr \\ &= \frac{Be(\alpha_1 + k, \alpha_2)}{Be(\alpha_1, \alpha_2)} \int_0^1 \frac{r^{\alpha_1 + k - 1}(1-r)^{\alpha_2 - 1}}{Be(\alpha_1 + k, \alpha_2)} \\ &= \frac{Be(\alpha_1 + k, \alpha_2)}{Be(\alpha_1, \alpha_2)} \end{aligned}$$

Thus the probability of not being parasitised is

$$\begin{aligned} P(S|w) &= \sum_{j=0}^{\infty} \frac{e^{-w} w^j}{j} \frac{Be(\alpha_1 + j, \alpha 2)}{Be(\alpha_1, \alpha_2)} \\ P(S|w) &= \frac{e^{-w}}{Be(\alpha_1, \alpha_2)} \sum_{j=0}^{\infty} \frac{w^j Be(\alpha_1 + j, \alpha_2)}{j} \end{aligned}$$

A problem with this approach occurs if α_1 and α_2 become large. In this case there is little heterogeneity among the hosts and the situation is very close to that in section 6.5.2. The ratio $\alpha_1/(\alpha_1 + \alpha_2)$ is highly correlated with w, possibly leading to problems of parameter estimation in the model. This can be solved if the restriction $\alpha = \alpha_1 = \alpha_2$ is introduced. In this case the degree of heterogeneity in the host population with a high value of α can be estimated by $1/\alpha$ with $\alpha = \infty$ corresponding to a homogeneous population. The expected probability of a host being parasitised on the first attack is 1/2, so the estimate of effective searching density of the parasites will be greater in this model when compared to that from models where all attacks automatically succeed.

This approach can be combined with the approach of categorising the data in section 6.5.3 with different α_1 and α_2 for each group, but with w being common. If this gives too many parameters to be estimated accurately, or numerical problems arise, then some restrictions could be placed on the values of α in order to reduce the dimensionality of the problem.

If the only interest is in the relationship between parasitism rate and age category then we could add a vector parameter **F** to take account of the searching parasite density in each patch and then look at the relationship between the parasitism rates for age groups within each patch. (Models F/A/I, F/A/U, F/A/E etc.)

6.6 Stability considerations

An important consideration for a system is whether or not it is stable. Instability implies there may be outbreaks of the host population, or local extinction of both host and parasite. If the parasite disappears locally then the host population from either the original population or immigrants can cause an unchecked outbreak.

In order to study stability Hassell *et al.* (1991) looked at the following simple general model model of a discrete generation host-parasite system.

$$N_{t+1} = \lambda N_t F(N_t, P_t) P_{t+1} = \omega N_t [1 - F(N_t, P_t)]$$

where N_t is the host and P_t the parasite density in the tth generation, $F(N_t, P_t)$ is the fraction of hosts N_T that escape parasitism, λ is the rate of population increase of the host in the absence of parasitism and ω the mean number of female parasitoids emerging from each parasitised host which was assumed to be 1 for all of the models. If there is a single patch containing all the hosts and the parasites search independently and randomly within it then this is a Nicholson-Bailey system (Nicholson and Bailey, 1935) and the system gives rise to unstable oscillations.

This model has a point of local equilibrium (N^*, P^*) when

$$1/\lambda = F(N^*, P^*)$$

$$P^* = N^*(1 - 1/\lambda)$$

Necessary and sufficient conditions for local stability are

$$\frac{\lambda^2}{\lambda - 1} P^* \left[\frac{\partial F(N_t^*, P_t^*)}{\partial P_t}\right] < 1$$

$$\frac{\lambda - 1}{\lambda}\left(\frac{-\partial F(N^*, P^*)}{\partial P_t}\right) > \frac{\partial F(N^*, P^*)}{\partial N_t}$$

They went on to discuss when these stability criteria were met for a variety of models. In these models the host has been assumed to occupy discrete patches within each generation and in the first four models there was complete redistribution of both hosts and parasites between generations. The coefficient of variation (CV^2) of searching parasitoid density per host was found to be an approximate guide to the behaviour of the system, with a value $CV^2 > 1$ indicating stability in the population dynamics of a variety of host-parasite models.

When the parameter estimates from the cottony-cushion scale system are examined, the system appears, from the $CV^2 > 1$ criterion, to be highly unstable, with neither host density dependent effects, as measured by μ, nor host density independent effects, as measured by σ^2, contributing significantly to the coefficient of variation

CV^2. This system in the wild also appears to be unstable, with experimenters (Thorarinsson, 1990) finding patches containing only the remains of hosts where 100% parasitism has occurred.

There may be other stabilising influences in the system due to the differential rate of parasitism with host age and the possibility of density dependence at a larger scale. In any case the assumptions underlying the Nicholson-Bailey equations do not hold in this case because the parasitism rate varies with host age and the generation time of the parasite is only one third of that of the host (Quezada, 1969). Also the number of parasitoids emerging from each parasitised host varies with usually one parasitoid emerging from a first or second instar and up to 18 emerging from an adult. There is also a possible stabilising effect from the presence of the rarer parasite *R. cardinalis*. Therefore if the Nicholson-Bailey model is not a fair description of the population dynamics, criteria for stability based on it might not be a good guide to the stability of the system in nature.

Even if the dynamics are locally unstable, the movement of the host could lead to large scale stability even if there are local extinctions. In this case the outbreaks of the host appear to be at a very low level and not to have any major economic importance.

Murdoch *et al.* (1987) found that for a continuous time model with two age classes (juvenile and adult) and overlapping generations for both host and parasitoid the introduction of an invulnerable age class for either juvenile or adult hosts could stabilise the population dynamics. Presumably partial invulnerability, as suggested by models of the form ?/A/? could result in a slightly smaller stabilising effect than complete invulnerability.

Murdoch and Stewart-Oaten (1989) have challenged the emphasis in the literature on the discrete-time models and the effect of aggregation as a stabilising influence on population dynamics. They concluded that for their continuous-time discrete space model, parasite aggregation independent of host density had no stabilising effect on the model, and that direct density dependence of parasitism rates on host density was a destabilising influence. Godfray and Pacala (1992) criticised their model on the grounds that they did not have true spatial element in the movement of either the hosts or the parasites. The assumption that parasitoids respond instantaneously to changes in the host population without any attempt to specify rules for this behaviour leads to a biologically untenable model. Models that have realistic criteria for movement tend to lead to systems of equations that are too complicated to be useful in this field.

6.7 Further work on host-parasite systems

A problem when deciding to set up an experiment such as a host-parasite study is deciding what spatial scale to use. If the area chosen for the experiment is too large then it may become difficult to manage, whereas if it is too small then the searching parasites may regard the entire experimental area as a single patch. If this is the case then the rate of parasitism across the experiment, once factors such as the age of the hosts in each patch are taken into consideration, is uniform. This can be tested by the standard techniques of assessing the goodness of fit of a simple binomial model. If the perceived patch size is larger than the gap between the patches as laid out by the experimenter but smaller than the overall experimental area then the analysis of the experiment becomes more difficult, as the correlation between the rates of parasitism needs to be taken into account. It may be possible to detect the presence of this effect by looking for correlations between the residuals after a fit has been made to the model. Attempting to model this effect would be considerably more difficult, especially if a non normal model is used. If the data are transformed to a Gaussian distribution then approaches such as Watkins (1990) can be used. It may be possible to minimise this effect by choosing a more suitable design for an experiment, such as a balanced nearest neighbour latin square rather than an ordinary latin square (Freeman, 1979). The perceived patch size could also be affected by the local vegetation with a piece of monoculture hedge being seen as a single patch but a set of separated trees over the same area being viewed as different patches. Indeed the dynamics of the population within a small patch such as a single tree could be different from those occurring within a large hedge.

It may be possible to break down the extra variability in the Pacala and Hassell model that is compensated for by the extra variable σ^2 into components using a generalized linear mixed model (Anderson and Hinde (1988), Preisler (1988), Im and Gianola (1988), Jansen (1990)) These combine the extension of the distribution of the response variable to the exponential family of generalized linear models (McCullagh and Nelder, 1989) with the correlated error structure of a linear mixed model (Rao, 1972). In linear models the response variable $\mathbf{y} = (\mathrm{y_1}, \ldots, \mathrm{y_n})$ is assumed to have a systematic component, which is a linear function of the known design matrix $\mathbf{X}$ and the parameter matrix β and an error component $\mathbf{e} = (\mathrm{e_1}, \ldots, \mathrm{e_n})$ with the $e_i^{\prime}s$ being independently and identically distributed normal random variables mean 0. That is

$$\mathbf{y} = \mathbf{X}^{\mathrm{T}}\beta + \mathbf{e}$$

In a LMM there is an extra error component $\mathbf{u} = (\mathrm{u_1}, \ldots, \mathrm{u_p})$ and an error design matrix $\mathbf{z}$ so that

$$\mathbf{y} = \mathbf{X}^{\mathrm{T}}\beta + \mathbf{z}^{\mathrm{T}}\mathbf{u} + \mathbf{e}$$

An example would be split-plot experiment where z_j represents the jth whole plot and u the error from the jth whole plot. In a generalized linear model y_i can be distributed according to any member of the exponential family, such as the binomial or Poisson distributions. The expected value μ of $\mathbf{y}$ is related to the design matrix X by a link function g so that

$$g(\mu) = \eta = \mathbf{X}^{\mathrm{T}}\beta$$

and the variance of y by a known function V of μ so

$$var(y) = \phi V(\mu)$$

Overdispersion or underdispersion can be taken into account by multiplying ϕ by an overdispersion parameter σ^2 In a generalized linear mixed model (GLMM) the LMM and GLM are combined as follows. The linear predictor η now has an error component $\mathbf{z}^{\mathrm{T}}\mathbf{u}$ added where $\mathbf{z}$ is known and u is an error term with mean 0. Thus the linear predictor is now

$$g(\mu) = \eta = \mathbf{X}^{\mathrm{T}}\beta + \mathbf{z}^{\mathrm{T}}\mathbf{u}$$

If we assume each component of $\mathbf{u}$ has a normal distribution then the maximum likelihood estimates u can be obtained by numerical integration. Unfortunately this can involve cumbersome high-dimensional numerical integration which, even for two crossed random effects, is impracticable. Engel and Keen (1993) suggested using methods without the full distributional assumptions about u, in which case Quasi-likelihood (Wedderburn, 1974) and MINQUE (Minimum Norm Quadratic Unbiased Estimation) (Rao, 1973) were combined.

The threshold model developed by Engel and Buist (1993) for binary data may be particularly useful. In this model we assume there is an underlying random variable r such that $y = 1$ when $r > \theta$ and 0 otherwise. θ is a threshold value which we can conveniently fix at 0. If $E(r|u) = \eta$ and the residual $\epsilon = r - \eta$, which has distribution F independent of u then

$$r = \eta + \epsilon = \mathbf{X}^{\mathbf{T}}\beta + \mathbf{z}^{\mathbf{T}}\mathbf{u} + \epsilon$$

The link function is $g(\mu) = -F^{-1}(1-\mu)$. This is a subject specific model (Zeger *et al.*, 1988).

If the parasitism rate was thought to vary with host age and there was more than one patch then u_j might represent the (unknown) error in parasite density associated with the jth patch. Another application could be for series of samples from sets of patches where one error could be included for each patch and another for variation in mean parasite density over time. This could also be extended into space by looking at, say, parasitism rates on high and low branches or twigs on the same plant and considering between-plant variability as an error.

This method has the advantage over incorporating large numbers of extra parameters into the systematic part of the model that, instead of estimating the parameters (as part of β), they are integrated out. They should not be included in the overdispersion effect because the errors are correlated.

A full investigation of the stability of a host-parasite system in the field would require a study over several generations. One problem with this approach is that if large numbers of hosts are repeatedly removed from each patch then this is likely to upset the dynamics of the system. A method of getting around this might be to replace these individuals with approximately equal numbers of laboratory hosts of whom a known proportion have already been parasitised.

6.8 Conclusion

The results from section 6.4 show that for three of the data sets there seemed to a constant level of parasite activity in all the patches with neither systematic variability with host density, as measured by μ, nor extra random variability, as measured by σ^2. Only in data set 2B did the data indicate significant deviation from a simple binomial model of uniform parasitism rates. Even in this case it appeared that the variability in the parasitism rates was not related to the host density.

In all of the models presented here it has been assumed that searching parasite behaviour is related to the relative, not absolute, host density. It seems more reasonable, particularly if the host population tends to fluctuate, to try to relate parasite behaviour to the absolute host density. Also the parasitism rate in each patch is a function of the searching female parasitoid density, but not of the host density. This model assumes that the handling time for each attack is negligible and that the parasites never run out of eggs. If the number of available hosts per parasite is high then this could affect parasite behaviour, with individuals becoming more choosy when the remaining egg supply is low. If the parasitism rate among hosts encountered by the parasite is high then it could, in order to avoid superparasitism (Daley and Maindonald, 1989), leave the patch. This would tend to even out the parasitism rates among the patches.

Chapter 7

Mark-recapture

7.1 Introduction

This chapter deals with the use of ring-recovery data to estimate survival rates and parameters for dispersal models. There has been much interest in using the data from mark-recapture experiments to estimate total populations, survival probabilities and rates of movement. Much of this work has involved splitting the data up into geographic strata. Transition probabilities between strata are then estimated, along with survival rates, which may vary with the area as well as other variables such as age, sex and weather. See, for example, Nichols *et al.* (1992), Darroch (1961) and Brownie *et al.* (1993). There has been considerably less interest in models where the model has not been stratified but the distance between mark and recapture point has been taken into account explicitly, although Kareiva (1983) and Manly and Chatterjee (1992) have done some work in this area.

A good reason for wishing to measure rates of movement, and associated parameters, is that the stability of an animal population is affected by the rate of movement of animals from one area to another. Thus the population can be unstable in each area taken individually but the overall populations may be stable if the fluctuations in the different areas are not correlated with one another.

Another motive for studying rates of movement lies in the estimation of genetic drift in populations. In this case the effect of a few individuals that breed far from their original area may have a disproportionate effect on the rate of movement of genes through the population. Because of this effect it is necessary to estimate not only the mean dispersal distances for each generation but also to measure the amount of extreme dispersal going on. This is because even a small number of individuals in the population that disperse a long way can prevent differentiation between populations. Numbers down to one individual every other generation may be enough to prevent populations in different areas becoming genetically incompatible (Wright, 1931).

Therefore if a model based on simple diffusion is used to model genetic change within a sample population then it is necessary to check whether or not the assumption of a simple random walk for the individuals under study is a reasonable one. If it is not then it is the degree of deviation from a simple diffusion model that must be estimated and this factor taken into account in the modelling of the gene pool.

This could be mathematically very awkward as models for genetic drift in two dimensions, even those based on a simple diffusion model, are difficult to analyse mathematically (Slatkin, 1985).

In section 7.2 a ring-recovery data set for the blackbird (*turdus merula*) in the UK is described. A survival model is fitted to this data in section 7.3. The fitting of a model combining survival with a Weibull distribution for dispersal distances by Manly and Chatterjee (1992) using least squares is discussed in section 7.4 along with the fit of a Weibull distribution for movement, conditioning on survival. Section

7.5 fits this model to dispersal distances of the common grackle (*Quiscalus quiscula*). Sections 7.6 and 7.7 introduce new models for dispersal distances. The estimation of the distribution of dispersion distances by Kareiva (1983) is discussed in section 7.8. The chapter concludes with a discussion of further work required in section 7.9. Some technical details are given in Appendix B.

7.2 Blackbird ring recoveries in the UK, 1953-1975

Greenwood and Harvey (1976) extracted from the files of the British Trust for Ornithology (BTO) the records of ringing and recovery for blackbirds where both the ringing and recovery positions were known. Only birds that were sexed and banded as nestlings during the breeding season (March-July) (Myers, 1955) and recovered during a subsequent breeding season were considered for analysis. Both ringing and recovery positions were given to the nearest minute of latitude and longitude. This approximates the positions by boxes measuring approximately 1.1km east-west and 1.8km north-south.

When the raw data were examined two obvious outliers and five transcription errors were noticed and these are shown in table 54.

The first two birds that had been ringed in mainland Britain were recovered in western Ireland. They were deleted from the data set for three reasons. Firstly it seems unlikely that members of a terrestrial species would normally move across a large body of water such as the Irish Sea. This implies that they were probably blown across during a storm. Also there were no reports of birds that had been ringed in the Republic of Ireland being recovered at any point. Including birds recovered in

Table 54: Observations deleted from Blackbird data set

	Ringing		Recovery		Ringing		Recovery	
Sex	Day	Year	Day	Year	Long.	Lat.	Long.	Lat.
Male	193	1969	93	1970	54.34	3.25W	54.04	8.28W
Fem.	170	1958	78	1960	55.38	2.05W	52.50	8.59W
Male	210	1966	70	1968	54.22	0.58E	54.21	0.53E
Male	165	1966	83	1969	53.24	2.54E	53.24	2.54E
Male	210	1955	210	1955	55.53	3.09W	55.53	3.09W
Male	151	1971	88	1977	53.46	0.22W	53.46	0.22W
Male	172	1971	120	1922	52.39	1.25E	52.39	1.25E

the Republic of Ireland when there were no reports of any being ringed there would bias the data set. Also the recovery rate in the Republic of Ireland may not be the same as in the UK. The next pair of observations were deleted because they were recovered from locations in the North Sea, probably oil rigs. The other three deleted observations had transcription errors in either the ringing or recovery dates.

All seven observations were deleted before the final maps of the ringing and recovery positions were drawn and before any analysis was done.

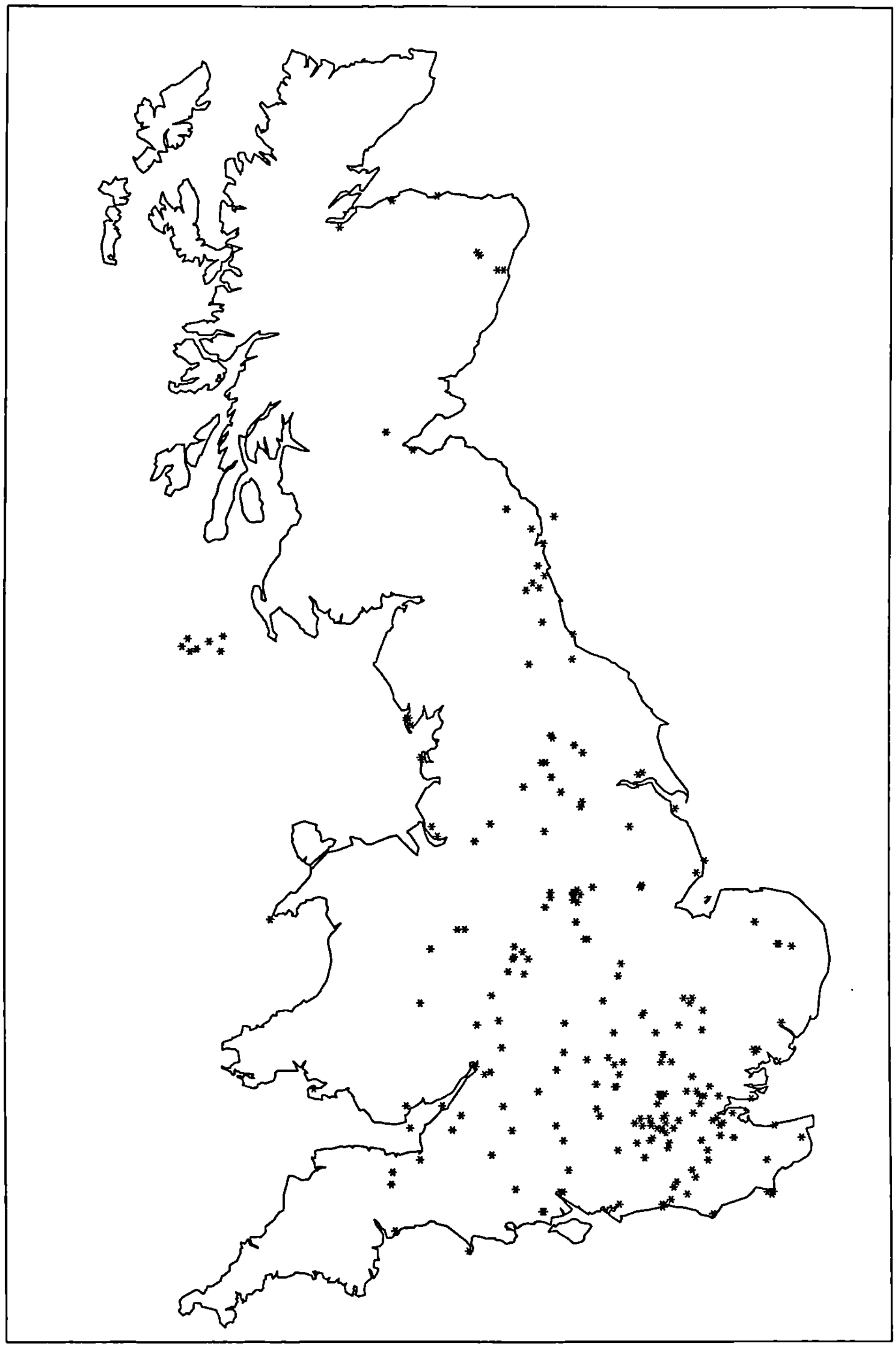
There were also discrepancies between the raw data, the tabulation given by Greenwood and Harvey (1976) and the tabulation given by Manly and Chatterjee (1992). The work here is based on the the raw data given by Greenwood and Harvey (1976).

In order to get a picture of the spread of the blackbird population across the United Kingdom the ringing positions of the birds were plotted in figure 23.

It appears from these maps, as well as from the maps of the recovery positions that neither ringing nor recovery positions are uniformly distributed. This is discussed more fully in section 7.9.

The recovery positions are shown in figure 24. In addition to this the tracks of

Figure 23: Ringing positions for blackbirds in UK 1953-1974



the dispersions were plotted for all dispersion distances exceeding 3 kilometres (figure 25).

In order to estimate the distances moved from the latitude and longitude data the individuals were all assumed to have been ringed in the centre of the ringing box and recovered from the centre of the recovery box. This approximation, which is used throughout this chapter is a quick and easy approach to the problem of the discrete nature of the data. A more complex approach is briefly described in section 7.9.

Individuals were classified as dispersed if the ringing and recovery boxes were different. The dispersed individuals were further categorised as short distance (moved less than 3km) or long distance (more than 3km) birds. In order to see if area of ringing was important the data set was divided up into Northern birds (ringed at 51 degrees 48 minutes or more north and southern birds ringed further south. This line was chosen because it was the median ringing latitude.

In order to find out if there was a significant difference in the dispersion distances of dispersed birds (excluding the non-movers for the moment) for males and females a Mann-Whitney test for similarity of distribution of the dispersion distance was performed. The P-value from the test,which was performed using the MINITAB package, was 0.48, which indicates no significant difference between the groups.

Similarly the Mann-Whitney test was performed to see if there was any significant difference between the dispersion distances for first year birds and older birds and between the Northern and Southern birds. No difference was detected for the age classes (P=0.18) but there was a significant difference between the north and the south (P=0.03) with the median dispersion being greater in the north (3.86km) than the south (2.18km).

In order to initially explore the data set and to get a feel for the factors and

Figure 24: Recovery positions for blackbirds in UK 1954-1975

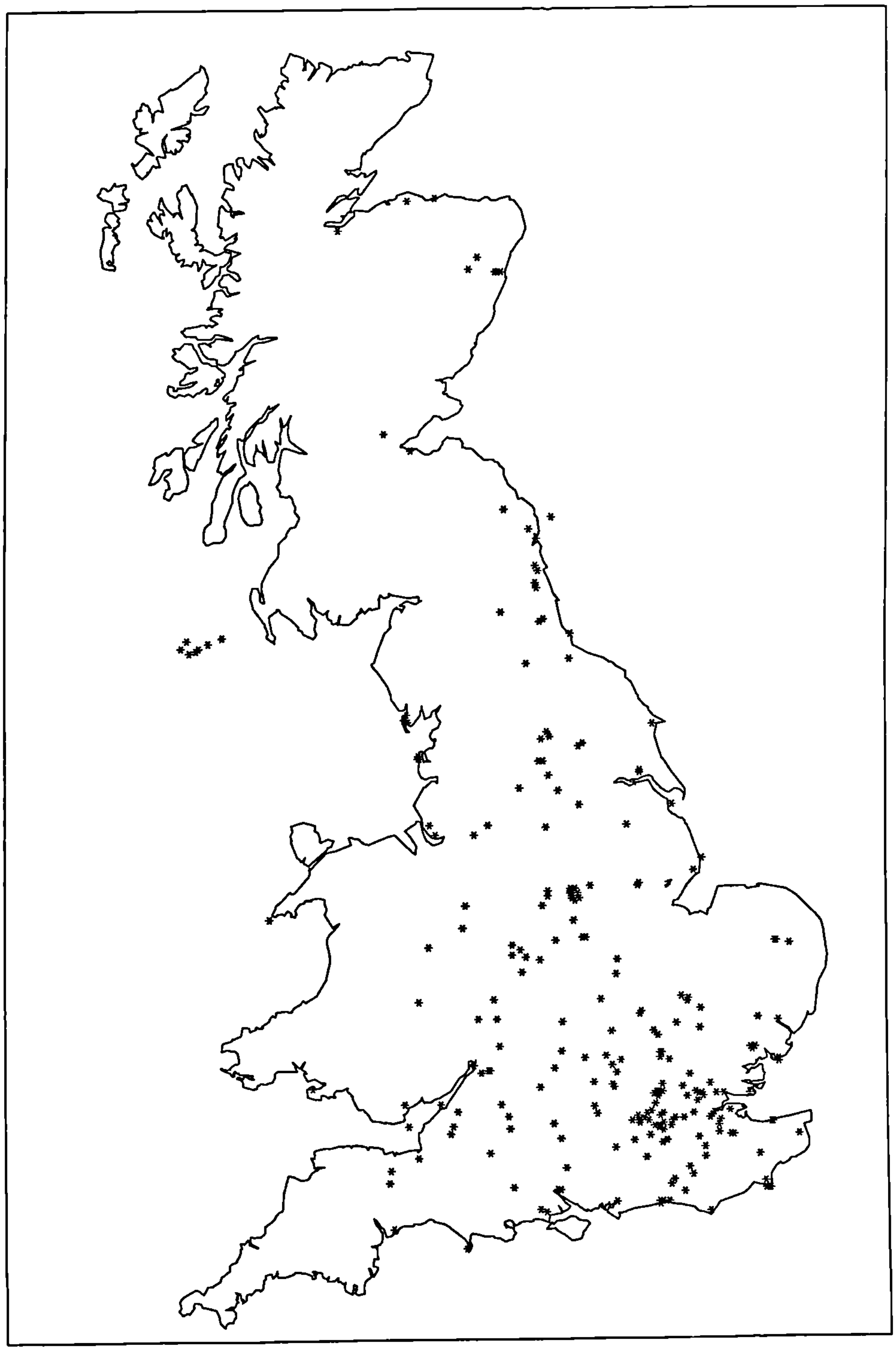


Figure 25: Moves over 3km recorded for blackbirds, 1953-1975

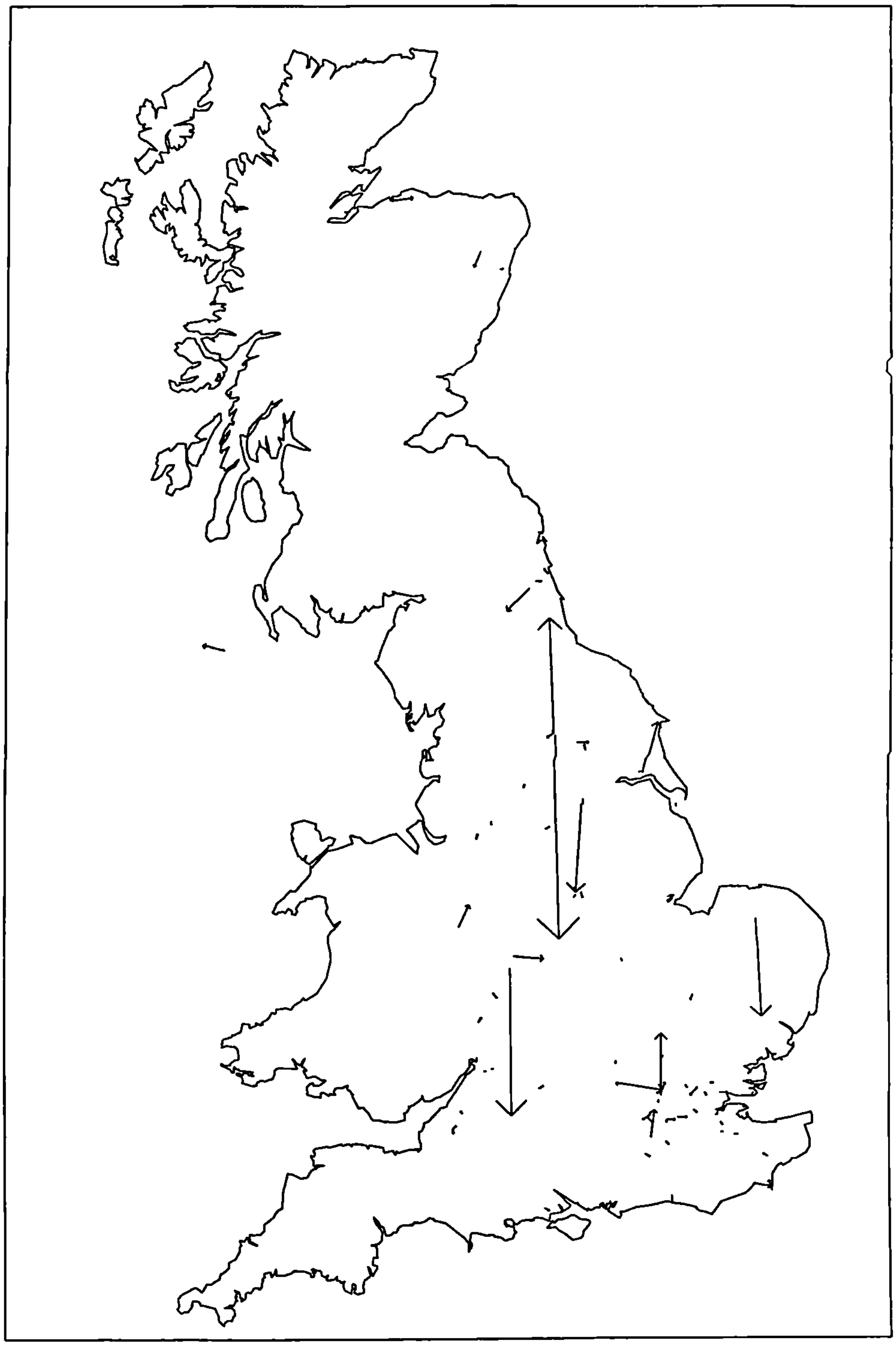


Table 55: Summary table for dispersion of blackbirds

		1st year			2nd year			Older			All		
Sex		M	F	All	M	F	All	M	F	All	M	F	All
Area	Dist												
North													
	Not	24	20	44	13	6	19	41	16	57	78	42	120
	Short	3	3	6	2	3	5	4	4	8	9	10	19
	Long	6	5	11	3	3	6	4	5	9	13	13	26
	ALL	33	28	61	18	12	30	49	25	74	100	65	165
South													
	Not	25	13	38	14	4	18	24	17	41	63	34	97
	Short	4	6	10	6	3	9	12	5	17	22	14	36
	Long	8	3	11	3	1	4	1	3	4	12	7	19
	ALL	37	22	59	23	8	31	37	25	62	97	55	152
All													
	Not	49	33	82	27	10	37	65	33	98	141	76	217
	Short	7	9	16	8	6	14	16	9	25	31	24	55
	Long	14	8	22	6	4	10	5	8	13	25	20	45
	ALL	70	50	120	41	20	61	86	50	133	197	120	317

interactions that were likely to be important a contingency table was constructed. The data were divided up by sex, age on recovery, distance dispersed and geographical location.

To see if the proportion of birds dispersing was affected by any of the above three factors 2 by 2 contingency tables of the numbers dispersing compared with area (north/south),age(1st years and older) and sex were formed. It was found that none of these factors had a significant effect on the numbers dispersing. Thus, apart from the increased dispersal distance for northern birds that are dispersed, it seems that survival and distance dispersed are independent of each other, sex and area.

The possibility of similarity between siblings hatched in the same year is not a problem for this data set because no pairs with the same ringing dates and locations occurred.

7.3 Survival rates for blackbirds

In this section the use of the blackbird recovery data for the estimation of survival rates is discussed. A model for estimating survival rates in the presence of censoring is developed, fitted and the fit assessed.

The numbers of individuals ringed and recovered by year of ringing and age on recovery are given in table 56, with the numbers by year of recovery and age given in table 57.

The total numbers of birds ringed in each year is not known so it is not possible to estimate the recovery rate for dead individuals. There appears to be an anomaly in the 1975 recoveries, with only six recoveries reported, as against a value of over 30 for each of the preceding six years. The last recovery for 1975 was on day 85 (out of a possible range 60 to 213). This implies that not all the recoveries for the 1975 were available when the data set was published. Including this data while taking this censorship into account would involve making assumptions about the reporting rate and seasonal mortality. Therefore this data was excluded from the analysis. Another factor which needs to be taken into account is that the recovery record for individuals ringed towards the end of the study period is time-censored by the lack of recoveries beyond day 85, 1975. This censorship must be taken into account if the survival rate estimates are not to suffer from severe downward bias. The ringing date from 1973 was also excluded as all the recoveries now included from that year were from 1974.

Table 56: Number of blackbirds recovered by age and year of ringing

Age Ringing year	1	2	3	4	5	6	7	8	9	10	11	ALL
1953	0	1	0	0	0	0	0	0	0	0	0	1
1954	0	0	1	1	0	0	0	0	0	0	0	2
1955	1	0	2	0	0	0	0	0	0	0	0	3
1956	2	1	0	0	0	0	0	0	0	0	0	3
1957	4	1	1	0	1	0	0	0	0	0	0	7
1958	1	4	0	2	0	0	0	0	0	0	0	7
1959	3	2	1	1	0	1	1	0	0	0	0	9
1960	0	0	2	0	0	0	1	0	1	0	0	4
1961	1	1	1	1	2	1	0	1	0	0	0	8
1962	9	2	0	0	3	0	0	1	0	0	0	15
1963	7	4	1	0	3	0	1	0	0	0	1	17
1964	6	3	0	0	0	0	0	0	0	0	0	9
1965	3	0	7	3	3	0	1	0	0	0		17
1966	5	3	6	2	1	4	0	2	0			23
1967	15	7	6	12	4	2	3	1				50
1968	13	8	4	6	2	1	0					34
1969	14	6	8	7	3	0						38
1970	9	9	7	5	1							31
1971	4	5	2	0								11
1972	8	4	1									13
1973	12	0										12
1974	3											3
ALL	120	61	50	40	23	9	7	5	1	1	317	

Table 57: Numbers of blackbirds recovered in each year by age

Age	1	2	3	4	5	6	7	8	9	10	11	Total
Recovery year												
1955	0	1	0	0	0	0	0	0	0	0	0	1
1956	1	0	0	0	0	0	0	0	0	0	0	1
1957	2	0	1	0	0	0	0	0	0	0	0	3
1958	4	1	2	1	0	0	0	0	0	0	0	8
1959	1	1	0	0	0	0	0	0	0	0	0	2
1960	3	4	1	0	0	0	0	0	0	0	0	8
1961	0	2	0	0	0	0	0	0	0	0	0	2
1962	1	0	1	2	1	0	0	0	0	0	0	5
1963	9	1	2	1	0	0	0	0	0	0	0	13
1964	7	2	1	0	0	0	0	0	0	0	0	10
1965	6	4	0	1	0	1	0	0	0	0	0	12
1966	3	3	1	0	2	0	1	0	0	0	0	10
1967	5	0	0	0	3	1	1	0	0	0	0	10
1968	15	3	7	0	3	0	0	0	0	0	0	28
1969	13	7	6	3	0	0	0	1	1	0	0	31
1970	14	8	6	2	3	0	1	1	0	0	0	35
1971	9	6	4	12	1	0	0	0	0	0	0	32
1972	4	9	8	6	4	4	1	0	0	0	0	36
1973	8	5	7	7	2	2	0	0	0	0	0	31
1974	12	4	2	5	3	1	3	2	0	0	1	33
1975	3	0	1	0	1	0	0	1	0	0	0	6
Total	120	61	50	40	23	9	7	5	1	0	1	317

We will now develop a model for survival rates involving maximum likelihood that takes these effects into account. We start off by assuming that the probability of an individual surviving to age $t+1$ given it was alive when it reached age t is ϕ_t, independent of the year of ringing of the individual. We therefore exclude the possibility of the mortality varying from year to year. The probability of an individual that dies during a year of full recoveries being included in the study (i.e. recovered during March-July and the ring returned with the positional information) is assumed to be s, independent of age and year.

The probability of dying and being recovered at age t, M_t, is therefore

$$M_t = s(1-\phi_t)\prod_{k=1}^{t-1}\phi_k$$

The probability of dying before reaching the age e is

$$C_e = s\sum_{j=1}^{e-1}(1-\phi_j)\prod_{k=1}^{j-1}\phi_k$$

The likelihood of being recovered at age t for an individual that was recovered despite there only being e years of the study left when it hatched is therefore

$$L(t|e,s) = \frac{M_t}{C_e} = \frac{(1-\phi_t)\prod_{k=1}^{t-1}\phi_k}{\sum_{j=1}^{e-1}(1-\phi_j)\prod_{k=1}^{j-1}\phi_k)}$$

We can therefore remove the conditioning on s. If there were n individuals in the study with ages of death $\mathbf{t} = (t_1 \dots t_n)$ and corresponding years till end of study $\mathbf{e} = (e_1 \dots e_n)$ the likelihood would be

$$L(\mathbf{t}|\mathbf{e}) = \prod_{i=1}^{n}\frac{(1-\phi_{t_i})\prod_{k=1}^{t_i-1}\phi_k}{\sum_{j=1}^{e_i-1}(1-\phi_j)\prod_{k=1}^{j-1}\phi_k)}$$

The log-likelihood is

$$\begin{aligned} l(\mathbf{t}|\mathbf{e}) &= \sum_{i=1}^{n}\log\frac{(1-\phi_{t_i})\prod_{k=1}^{t_i-1}\phi_k}{\sum_{j=1}^{e_i-1}(1-\phi_j)\prod_{k=1}^{j-1}\phi_k)} \\ &= \sum_{i=1}^{n}\log(1-\phi_{t_i}) - \sum_{i=1}^{n}\sum_{k=1}^{t_i-1}\log\phi_k - \log\{\sum_{j=1}^{e_i-1}(1-\phi_j)\prod_{k=1}^{j-1}\phi_k\} \end{aligned}$$

In order to reduce the number of parameters that need estimating three variations of this model were fitted to the data. In the first model the mortality is assumed to be independent of age ($\phi = \phi_1 = \phi_2 = \phi_3 \ldots$). In the second the mortality for all birds over 1 year of age was assumed the same but the mortality was different for the first years. The third variant of the model was a beta-geometric one where the mortalility for each individual followed a beta distribution, independently of all other individuals.

All three survival models were fitted to the data using programs written in Fortran using the NAG library. In order to assess the possible effect of terms such as the area of ringing, sex of ringed individual and dispersal the data set was classified by sex, area (North and South) and dispersal distance (undispersed and dispersed) and the model fitted to all the subsets that were possible by combining these three factors. The model where the time censorship was also taken into account was also fitted to the data separately for individuals ringed before 1968 and those ringed either in 1968 or later. This was done in order to see if there was a change in the survival rate over time. The resulting deviances for both the one-rate and two-rate models, along with model degrees of freedom, are given in table 58.

The third model proved difficult to fit to the data due to the estimates of the parameters for the beta distribution having a tendency to diverge towards infinity, implying the mortality rate has negligible variance. Although the use of reciprocals might improve the numerical accuracy of the calculations for this model, the lack of support for this model from the data does not justify the amount of work required. Thus the use of a variable survival rate is not justified from the data. This implies the survival rate appears to be constant with age of individual. When the number of fitted parameters are taken into account it is clear the the most parsimonious model

Table 58: Table of deviances for blackbird survival models with censorship

	One Rate		Two Rates	
Model	Deviance	Resid. D.F.	Deviance	Resid. D.F.
Mean only	997.68	298	997.50	297
Sex	995.56	297	995.03	295
Area	997.36	297	997.23	295
Dispersion	997.63	297	997.38	295
Date	997.58	297	997.26	295
Sex*Area	994.70	295	993.98	291
Sex*Dispersion	995.30	295	994.10	291
Sex*Date	995.25	295	991.98	291
Area*Dispersion	997.05	295	996.40	291
Area*Date	994.02	295	993.26	291
Sex*Area*Dispersion	994.13	291	991.61	283
Sex*Area*Date	990.58	291	986.65	283

is just the constant survival rate over age, time, area and sex.

For this table we can seen that the estimate of the survival rate does not appear to differ significantly between any of the groups. Therefore there is no need to estimate the survival rates separately. The overall survival rate is estimated at 0.70 with a 95% confidence interval of $[0.66, 0.75]$ and a 99% confidence interval of $[0.65, 0.76]$.

The predicted numbers recovered by age group and year of ringing are given in table 59.

When the survival rate for the first year is calculated separately from that after the first year the rates are estimated as $\phi_1 = 0.70$ and $\phi_2 = 0.71$ with 95% confidence intervals of $[0.65, 0.75]$ and $[0.66, 0.76]$ respectively. The respective 99% confidence intervals are [0.63,0.76] and [0.64,0.78]. The similarity between the estimates confirms that there appears to be no difference in the survival rates with age.

The deviances for the models where censorship is ignored again point to constancy in the survival rate over time, area and sex, giving a value for ϕ of 0.62. A 95% confidence interval for ϕ is $[0.58, 0.65]$ and a 99% region is $[0.58, 0.66]$. The survival rate

Table 59: Predicted numbers of blackbirds recovered by age and year of ringing

Age	1	2	3	4	5	6	7	8	9	10	11
Ringing year											
1953	0.3	0.2	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
1954	0.6	0.4	0.3	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.0
1955	0.9	0.6	0.5	0.3	0.2	0.2	0.1	0.1	0.1	0.0	0.0
1956	0.9	0.6	0.5	0.3	0.2	0.2	0.1	0.1	0.1	0.0	0.0
1957	2.1	1.5	1.0	0.7	0.5	0.4	0.3	0.2	0.1	0.1	0.1
1958	2.1	1.5	1.0	0.7	0.5	0.4	0.3	0.2	0.1	0.1	0.1
1959	2.7	1.9	1.3	0.9	0.7	0.5	0.3	0.2	0.2	0.1	0.1
1960	1.2	0.9	0.6	0.4	0.3	0.2	0.1	0.1	0.1	0.1	0.0
1961	2.4	1.7	1.2	0.8	0.6	0.4	0.3	0.2	0.1	0.1	0.1
1962	4.5	3.2	2.2	1.6	1.1	0.8	0.6	0.4	0.3	0.2	0.1
1963	5.1	3.6	2.5	1.8	1.3	0.9	0.6	0.4	0.3	0.2	0.2
1964	2.7	1.9	1.4	1.0	0.7	0.5	0.3	0.2	0.2	0.1	
1965	5.3	3.7	2.6	1.8	1.3	0.9	0.6	0.5	0.3		
1966	7.2	5.1	3.6	2.5	1.8	1.3	0.9	0.6			
1967	15.9	11.2	7.9	5.5	3.9	2.7	1.9				
1968	11.5	8.1	5.7	4.0	2.8	2.0					
1969	13.6	9.6	6.7	4.7	3.3						
1970	11.8	8.3	5.8	4.1							
1971	5.0	3.5	2.5								
1972	7.0	5.0									
1973	12.0										

estimates are smaller for this model because it fails to take account of the censorship of the long-lived birds that were ringed towards the end of the study period. We can compare this last set of results to those obtained by Manly and Chatterjee (1992). They fitted a model to this data set, which included survival but ignored censorship, by least squares. Their final estimate of the survival rate was 0.638, with a standard error of 0.0223 which was approximately the same as that obtained in the model considered here when censorship was ignored. Their approach is discussed more fully in section 7.4.

In order to assess the goodness of fit of the survival model including censorship, the number of individuals recovered each year was compared to the numbers predicted, as shown in table 60.

When the χ^2 statistic was calculated based on frequency table 60 the value obtained, when the recoveries for 1954 to 1957 inclusive were amalgamated, was 20.75, with 16 degrees of freedom. This is not significantly large at the 5% level, implying that the annual mortality rate does not vary significantly from what the model predicts.

The survival rate, estimated for the entire data set, was also used to calculate the expected numbers dying in each age category. The expected and observed numbers in each age group are shown in table 61. The constant survival rate between the groups implies that it would be reasonable to assume a model where there is no change in the proportion of individuals that are dispersed as the age of the individuals increases.

The assumptions of the model can be questioned in several ways. In particular the rate of recovery of dead birds might not be constant over time. If there is, say, a steady increase in the recovery rate then this will lead to an upward bias in the survival rates. In order to check this assumption it would be necessary to know the

Table 60: Actual and expected recoveries for each year

Year of death	Expected	Observed
1954	0.38	0
1955	1.00	1
1956	1.77	1
1957	2.24	3
1958	4.07	8
1959	5.20	2
1960	6.67	8
1961	5.65	2
1962	6.56	5
1963	9.81	13
1964	12.59	10
1965	11.24	12
1966	13.52	10
1967	17.33	10
1968	30.09	28
1969	32.33	31
1970	35.92	35
1971	35.60	32
1972	27.49	36
1973	24.39	31
1974	27.04	33

Table 61: Actual and expected recoveries for each age group

Age at death	Observed	Expected
1	105	102.9
2	61	72.4
3	49	47.5
4	40	31.7
5	22	19.4
6	9	11.3
7	7	6.5
8	4	3.2
9	1	1.8
10	0	1.0
11	1	0.6
12	0	0.0

numbers ringed in each breeding season.

A full study of the survival rates of the blackbird would require information on the recoveries throughout the year. This could bring problems of its own if the recovery rate varies with the time of year.

7.4 Fitting the Weibull Distribution to Movement Distances

One of the simplest models for movement in a two dimensional framework is the diffusion model. This model arises from the assumption of Brownian motion which is itself the limiting case of an uncorrelated random walk.

For an uncorrelated random walk, consider the case of an individual starting at the origin and then a step, the size and direction of which follows a symmetric bivariate distribution with zero mean and variance σ^2. If N independent steps are taken, all with the same variance σ^2, then the resulting distribution of the position at the end of the walk is bivariate normal with mean 0 and variance $N\sigma$. In the limiting case where N tends to ∞, σ^2 tends to 0 and $N\sigma^2 = w$, the sample path of positions at times $1, 2, \ldots, N$ is the sample path of a point undergoing Brownian motion. Replacing discrete N by a continuous variable t and fixing σ^2 allows the model to be considered in continuous time. Freedman (1971) gives a fuller discussion of Brownian motion and diffusion.

The density function for a position $\{x, y\}$ at time t given a start at the origin is

$$p(x,y) = \frac{1}{2\pi\sigma^2 t} e^{-\frac{x^2+y^2}{2\sigma^2 t}}$$

Skellam (1973) switched this to polar co-ordinates and then integrating out the angle to give the following density for the absolute distance between start and finish points, r

$$h(r;t) = \frac{r}{2\sigma^2 t} e^{-\frac{r^2}{2\sigma^2 t}}$$

The shape of this distribution is constant over time, and the mean distance will increase as a linear function of $\sqrt{t}$.

If the survival rate is ϕ for each period then the probability of dying in the tth year follows a Geometric distribution. $\phi^t(1-\phi)$ If the individual also moves according to a simple random walk then the probability density function for dying in the tth year at distance r from the origin is

$$h(r,t) = \phi^t(1-\phi)\frac{r}{\sigma^2 t}\exp(-\frac{r^2}{\sigma^2 t})$$

Manly (1977) considered a generalisation of this model. In this model the dispersion distance follows a Weibull distribution with scale parameter σ^2 and shape parameter α. These parameters can be interpreted as saying the observed distance

z has the same distribution as $r^{1/\alpha}$ where r is the displacement from the origin of a point undergoing simple diffusion and σ^2 is the variance in each dimension of the displacement of r. The α parameter measures the kurtosis in the data with a value of 1 indicating simple diffusion is an appropriate model, values less than 1 indicating leptokurtosis and values greater than 1 indicating platykurtosis. Thus if α is estimated as significantly less than 1 then there is a degree of overdispersion in the dispersal distances and a value less than 1 implies the distances vary less than would be expected from a diffusion model.

Introducing the α parameter the density now becomes (Manly, 1977)

$$f(z,t) = 2\phi^t(1-\phi)\frac{\alpha}{\tau(t)}\left\{\frac{z}{\tau(t)}\right\}^{2\alpha-1}\exp\left[-\left\{\frac{z}{\tau(t)}\right\}^{2\alpha}\right]$$

where $(\tau(t))^{2\alpha} = 2\sigma^2 t$. z has a Weibull distribution with shape parameter 2α and scale parameter $\tau(t)$. Note that at this point calculating the maximum likelihood estimates can be done separately for the survival parameter ϕ and the movement parameters σ^2 and α. In this model the probability of dying at a distance greater than z away from the origin at time t is

$$F(z,t) = \phi^t(1-\phi)\exp\left[\left\{\frac{z}{\tau(t)}\right\}^{2\alpha}\right] ,$$

Thus the probability of being recovered between z_1 and z_2 ($z_1 < z_2$) in the tth year is

$$F(z_1,t) - F(z_2,t) = \phi^t(1-\phi)\left(\exp\left[\left\{\frac{z_1}{\tau(t)}\right\}^{2\alpha}\right] - \exp\left[\left\{\frac{z_2}{\tau(t)}\right\}^{2\alpha}\right]\right)$$

Manly and Chatterjee (1992) fitted this model to the data discussed in section 7.2. The frequency table that they used is repeated in table 62.

The fitting method that they employed throughout their paper was to calculate the expected frequencies for each of the cells in the above table based on the parameter

Table 62: Distance from ringing to recovery point for male blackbirds

Distance(km) Age	0-3	4-7	8-20	21-55	-148	-403	-1097
1	58	11	2	2	0	1	0
2	35	5	0	0	1	0	0
3	34	1	0	0	0	0	0
4	23	0	0	0	0	0	0
5	12	1	0	0	0	0	0
6	6	0	0	0	0	0	0
7	4	2	0	0	0	0	0
8	4	0	0	0	0	0	0
9	1	0	0	0	0	0	0
10	0	0	0	0	0	0	0
11	1	0	0	0	0	0	0

estimates and from those calculate the χ^2 goodness of fit statistic. The parameter estimates that minimised the χ^2 statistic were those finally chosen.

As the model did not appear to fit the data very well, it was generalised by allowing α to vary in a linear fashion with time so $\alpha(t) = \alpha_0 + \alpha_1 t$. This allows the shape of the distribution of distances to vary over time. Unfortunately this also affects the mean dispersion distance so that it is no longer possible to consider scale and shape separately.

This was then further extended by allowing the scale parameter $\tau(t)$ to be made more flexible by replacing $\sigma^2 t$ with $\sigma^2 t^\beta$. This form was preferred over a linear relationship because there is no chance of ending up with a negative scale factor. It is still not possible to directly estimate the changes in the scale of dispersion if the shape parameter is changing in time however.

The goodness of fit statistics for this and the other models that they fitted, together with the parameter estimates and the standard errors for the final model are

Table 63: Parameter Estimates for Weibull model fitted to male blackbird data using frequency table

Model	Shape constant	Shape varying	Shape varying, $\beta \neq 1$ (s.e.)
Parameter estimates			
Survival $\hat{\phi}$	0.821	0.638	0.638 (0.0223)
Movement			
Scale parameters			
$\hat{\sigma}^2$	0.615	0.292	0.432 (0.078)
$\hat{\beta}$	(1)	(1)	-0.284 (0.247)
Shape parameters			
α_0	0.0140	-0.0671	0.151 (0.054)
α_1	(0)	0.183	0.0160 (0.0294)
Goodness of fit			
χ^2 statistic	104.46	62.13	40.4
Degrees of freedom	73	72	71

given in table 63.

The fit of the model to the female data gave similar results. When the model was fitted for both sexes together the increase in the deviance compared to when parameters were estimated separately was not significant (χ^2,= 9.45 with 5 degrees of freedom), implying the sets are similar. However parameter estimates were not given either for the females separately or for the joint estimation.

The failure to take account of the censorship mentioned in section 7.3 results in severely biased survival rate estimates.

Examination of these estimates shows that they each represent radically differing descriptions of the data. When the shape parameter for the distance travelled with time is allowed to vary, the estimate of the death rate $(1 - \hat{\phi})$ doubles. This is particularly worrying in the light of the functional form for the log-likelihood for non-categorised data in equation 9, where survival parameters can be estimated separately from movement parameters.

That there appears to be some dependence of the dispersion values on age at death can be seen when we look at the mean age on recovery for the different distance classes. The mean decreases over time, the opposite of what we would expect from a model assuming constant survival rates and outward diffusive movement, as is the case with the original model. However, because of the highly skewed nature of the dispersal distances, measures such as the mean need to be treated cautiously.

When the value of $\hat{\beta}$ is allowed to vary from 1 then the maximum likelihood estimates for α_0 and α_1 do not appear, from their standard errors, to be different from those obtained when α was constant. Together with the closeness of the estimate of β to zero, this implies that it is reasonable to assume that the distribution of the dispersion distance is constant with respect to age of individual upon recovery.

As was noted by Manly and Chatterjee (1992), the χ^2 statistics are not valid because of the large number of zeroes present in the data, and although it was stated that χ^2 statistics based on amalgamating some cells so that the asymptotic assumptions are valid show the model did not fit well, these values were not given. If the cells are constrained to have a minimum of three individuals then when the data are examined there is a maximum of 13 such cells for the males data set, with only one cell representing individuals from beyond 7 km. It then becomes very difficult to measure the shape of the dispersal distances with any confidence.

The final χ^2 statistic of 40.4 on 71 degrees of freedom represents an extremely low test statistic compared to the χ^2 distribution with 71 degrees of freedom (P > 99.5%). This implies a high degree of overfitting to the data.

It was assumed that the recovery rate did not depend either on age of individual or the distance between mark and recovery points. This assumption has to be made as it is not known either how many individuals were marked or what the true spatial distribution of the individuals was. Testing the hypothesis of variable recovery rates could be done using an experiment based on marking and releasing birds which were older than juvenile. This would be more difficult that marking nestlings.

Instead of classifying the data into discrete distance classes and finding the expected number of individuals in each class, it is possible to use the distance data directly to calculate the likelihood for each observation. This has the advantage of more efficient use of the data and eliminates the problem of how to divide the categories so that sufficient numbers remain in each set to make the use of a χ^2 test valid. We now consider this approach in more detail.

The data from the original paper (Greenwood and Harvey, 1976) were transformed into survival time (in years) and actual distance from ringing to recovery point. As the ringing and recovery positions were only known to the nearest minute of longitude and latitude, individuals that had dispersed were assumed to have been ringed and recovered from the centres of the relevant boxes.

The form of the probability density function for the most complex model with α varying with time and $\beta \neq 1$ for the raw data is

$$h(z,t) = 2\phi^t(1-\phi)\frac{\alpha(t)}{\tau(t)}\left\{\frac{z}{\tau(t)}\right\}^{2\alpha(t)-1} \exp\left[-\left\{\frac{z}{\tau(t)}\right\}^{2\alpha(t)}\right]$$

where $\tau(t) = (2\sigma^2 t^\beta)^{1/2\alpha(t)}$ and $\alpha(t) = \alpha_0 + \alpha_1 t$. Thus the likelihood for observing recovery distances $z_1, \ldots, z_n$ and ages on recovery $t_1, \ldots, t_n$ is

$$L(z,t) = \prod_{i=1}^{n} 2\phi^{t_i}(1-\phi)\frac{\alpha(t_i)}{\tau(t_i)}\left\{\frac{z_i}{\tau(t_i)}\right\}^{2\alpha(t_i)-1} \exp\left[-\left\{\frac{z_i}{\tau(t_i)}\right\}^{2\alpha(t_i)}\right]$$

Expanding out the function $\tau(t)$ and taking logs to get the log-likelihood function, we get

$$\begin{aligned} l(\mathbf{z},\mathbf{t}) &= \sum_{i=1}^{n}(t_i-1)\log(\phi)+\log(1-\phi)+\log(\alpha(t_i))-\log(\sigma^2 t_i^{\beta}) && (9)\\ &\quad +(2\alpha(t_i)-1)\log(z_i)-\frac{z_i^{2\alpha(t_i)}}{\sigma^2 t_i^{\beta}}+\log(2) && (10) \end{aligned}$$

This can be maximised with respect to ϕ without taking any of the distance parameters into account. Thus we can split the problem up into the estimation of survival rates, as in section 7.3, and model the movement conditional on age at death.

Fortran programs have been written to calculate the maximum likelihood estimates for the log-likelihood of these observations based around NAG Fortran library procedures and to provide contour plots (figure 26) of the log-likelihood function.

Maximum likelihood estimates of the parameters for this model have been produced. The model represents a generalisation of the Weibull distribution, where $\tau(t)$ is the scale parameter and $\alpha(t)$ is the shape parameter. The parsimony of this model compared to slightly simpler models has been tested by setting the parameter $\alpha_1 = 0$, implying a constant shape, and setting $\beta = 1$, implying a random walk model, or $\beta = 0$, implying that the scale does not change with time.

7.4.1 Distance censorship

Individuals categorised as non-dispersed pose a problem for this approach. Apart from other considerations, the likelihood function has a singularity at 0, so they cannot simply be given a dispersion distance of 0. If the non-dispersed individuals are ignored then the parameter estimates will be biased. In order to see how big this effect is the model was still fitted, with an analysis of deviance given in table

65 and parameter estimates in table 66. This bias, in the case of the blackbird data where most of the individuals have not dispersed, is so large as to make this method unreasonable.

If we take this left-censorship of the data into account then the probability density function given the censoring distance was r_0 would be

$$h(z,t) = \frac{2\phi^t(1-\phi)\frac{\alpha(t)}{\tau(t)}\left\{\frac{z}{\tau(t)}\right\}^{2\alpha(t)-1}\exp\left[-\left\{\frac{z}{\tau(t)}\right\}^{2\alpha(t)}\right]}{p(z > r_0)}$$

If the non-dispersed individuals are ignored but the likelihood adjusted by assuming that no dispersion of less than the size of a box are included in the data then this problem can be sidestepped, although much of the data is then deleted. The results for this method are given in tables 69 and 70. The third approach is to assume the individuals have dispersed a short distance. The distance chosen here was (0.7km). This was chosen because it approximately represented the median dispersal distance for individuals distributed uniformly in a circle of radius 1.1km, the minimum dispersal distance for individuals that changed boxes. Results for this approach are given in tables 67 and 68. A better, but more complex, approach to the entire problem of the discretisation of the data is outlined in section 7.9.

There is also a question of whether the models for dispersal distance hold when the distance observed is small. If searching for a nest is first done via an intensive search around the place where the bird was hatched and then changes to a less intensive method if this fails then the form of the dispersion distance would be a mixture distribution, with all the birds that found a nest in the intensive search being classified as undispersed. Another reason why the form might not hold is that the individual may have moved temporarily in search of food during the day on which it died, so the recorded position does not represent the position of the nest it was inhabiting at the time of death. The bias resulting from this extra displacement may

Table 64: Weibull model variations

Model	α	α_1	β	Note
1	$\alpha > 0$	0	1	Original Manly Model
2	$\alpha > 0$	None	1	Second Manly model
3	$\alpha > 0$	0	0	Distance independent of age
4	$\alpha > 0$	None	0	Constant scale
5	$\alpha > 0$	0	None	Constant Shape
6	$\alpha > 0$	None	None	Final Manly model
7	$\alpha = 1$	0	0	Simple diffusion

be large if the foraging range is not negligible compared to the distance between the ringing and adult nesting positions. The effect of the foraging range is likely to be negligible if the individuals have dispersed a long way to find a nest as adults.

The model fitting was done by taking a series of variations on the Weibull model and seeing which of them would give the best fit in terms of the overall deviance when compared to the number of parameters that would be required to estimate the model.

The models were fitted in the order specified in table 64.

Because of the suspicion that rate of movement might be different for birds from different areas (due to migration) or that the males and females might disperse differently (due to males needing to hold territories) (Catchpole, 1972), the data were classified by area (north/south) and sex. The data set was additionally classified by age (1st years and older birds) and by date (ringed before 1968 and ringed during or after 1968). Deviance statistics obtained for models with at least two terms not in the optimal model are excluded.

Classifying the data by age on recovery (1st year and older birds) did not decrease the deviance sufficiently to justify estimating the parameters separately for each age group.

Table 65: Analysis of deviance table, with simple truncation

	$\hat{\beta} = 1$		$\hat{\beta} = 0$		$\hat{\beta}$ variable	
α	α_0	$\alpha_0 + \alpha_1 t$	α_0	$\alpha_0 + \alpha_1 t$	α_0	$\alpha_0 + \alpha_1 t$
	671.5(98)	654.2(97)	630.8*(98)	630.3(97)	630.8(97)	629.6(96)
Area	651.5(96)	611.4(94)	604.6(96)	598.8(94)	602.5(94)	598.2(92)
Sex	665.3(96)	638.1(94)	624.6(96)	621.6(94)	623.6(94)	621.2(92)
Sex*area	637.8(92)	601.3(88)	597.1(92)	591.6(88)	592.6(88)	588.1(82)

Table 66: Time independent Weibull model fit to blackbird data,simple truncation

Area	Deviance	σ^2	α
N	325.69	2.654	0.339
S	278.85	2.204	0.487
A	630.78	2.114	0.361

Table 67: Analysis of deviance table with truncated data, Likelihood adjusted for censorship

	$\hat{\beta} = 1$		$\hat{\beta} = 0$		$\hat{\beta}$ variable	
α	α_0	$\alpha_0 + \alpha_1 t$	α_0	$\alpha_0 + \alpha_1 t$	α_0	$\alpha_0 + \alpha_1 t$
Simple	580.9	541.5	537.1*	537.1	537.0	535.8
Sex	579.1	536.6	534.8	532.9	533.4	531.7
Area	572.1	528.1	526.0	524.9	525.2	524.2
Age	545.9	537.3	536.4	527.1	527.3	535.7
Date	579.7	525.3	532.0	526.2	525.6	523.0

Table 68: Time independent Weibull model applied to blackbirds (both sexes),truncation affecting likelihood

Area	Deviance	σ^2	α
N	293.83	0.387	0.142
S	232.13	0.311	0.197
A	537.09	0.213	0.115

Table 69: Analysis of deviance table, with arbitrary distance for non-dispersed data

	$\hat{\beta}=1$		$\hat{\beta}=0$		$\hat{\beta}$ variable	
α	α_0	$\alpha_0+\alpha_1 t$	α_0	$\alpha_0+\alpha_1 t$	α_0	$\alpha_0+\alpha_1 t$
	1406.0(315)	1372.8	1266.8	1266.6	1266.7	1265.8
Area	1380.3	1318.0	1231.9*	1222.0	1229.0	1221.7
Sex	1386.0	1335.8	1246.1	1238.0	1243.5	1237.7
Sex*area	1345.1	1286.2	1209.7	1197.4	1204.5	1196.7

Table 70: Time independent Weibull model with arbitrary distance for non-dispersed

Area	Deviance	σ^2	α
North	707.1	0.861	0.301
South	524.8	0.873	0.432
All	1266.8	0.850	0.335

In order to estimate the accuracy of the parameter estimates for the model 95% and 99% confidence limits were calculated using profile likelihoods. The intervals are all given in table 71.

From the way the parameter estimators change as the model becomes more complex it was decided to look at the covariances of the parameter estimators. This was done by computing the hessian matrix numerically for each model (using NAG routine E05XAF). This was then inverted to give the variance-covariance matrix which was used to calculate the correlation matrix. The correlation matrix could have been calculated analytically, but this approach was not taken. For the final model chosen, the correlation between $\hat{\alpha}$ and $\hat{\beta}$ was 0.980. This is shown graphically in figure 26.

In order to assess the degree of correlation between the parameter estimators when the more complex model was fitted, the correlation matrix between all four parameters was calculated at the maximum likelihood point. This was done when the fit was done separately for the Northern and Southern groups as well as for the

Table 71: Confidence intervals for Weibull models with likelihood adjusted for truncation

Intervals for time independent model

Area	Parameter	Estimate	95% interval	99% interval
All	σ^2	0.214	[0.152,0.290]	[0.140,0.322]
	α	0.115	[0.087,0.141]	[0.080,0.149]

Intervals for most complex model

Area	Parameter	Estimate	95% interval	99% interval
All	σ^2	0.484	[0.292, 0.890]	[0.257, 1.083]
	α	0.161	[0.113, 0.212]	[0.100, 0.226]
	α_1	-0.010	[-0.024,-0.007]	[-0.030,-0.012]
	β	-0.286	[-0.767,-0.349]	[-0.882,-0.566]

Table 72: Parameter Estimator Correlation Matrix(Weibull model)

	σ^2	α	α_1	β
σ^2	1.00	0.96	-0.67	-0.41
α	0.96	1.00	-0.63	-0.25
α_1	-0.67	-0.63	1.00	0.81
β	-0.41	-0.25	0.81	1.00

entire data set. This is shown in table 72.

Most of these correlations are quite high, implying that if the dispersion distances had varied with time the description of that variation would have been difficult with this parameterisation.

In order to assess the effectiveness of the optimisation feature and to see whether the functional form of the likelihood was likely to lead to any difficulties in the optimisation procedure the likelihood function was plotted against the values of σ^2 and α for the final model. This plot is given in figure 26.

The value plotted was standardised by subtracting the final deviance of the model from that obtained for each point.

Figure 26: Weibull model, likelihood for all Blackbirds in UK

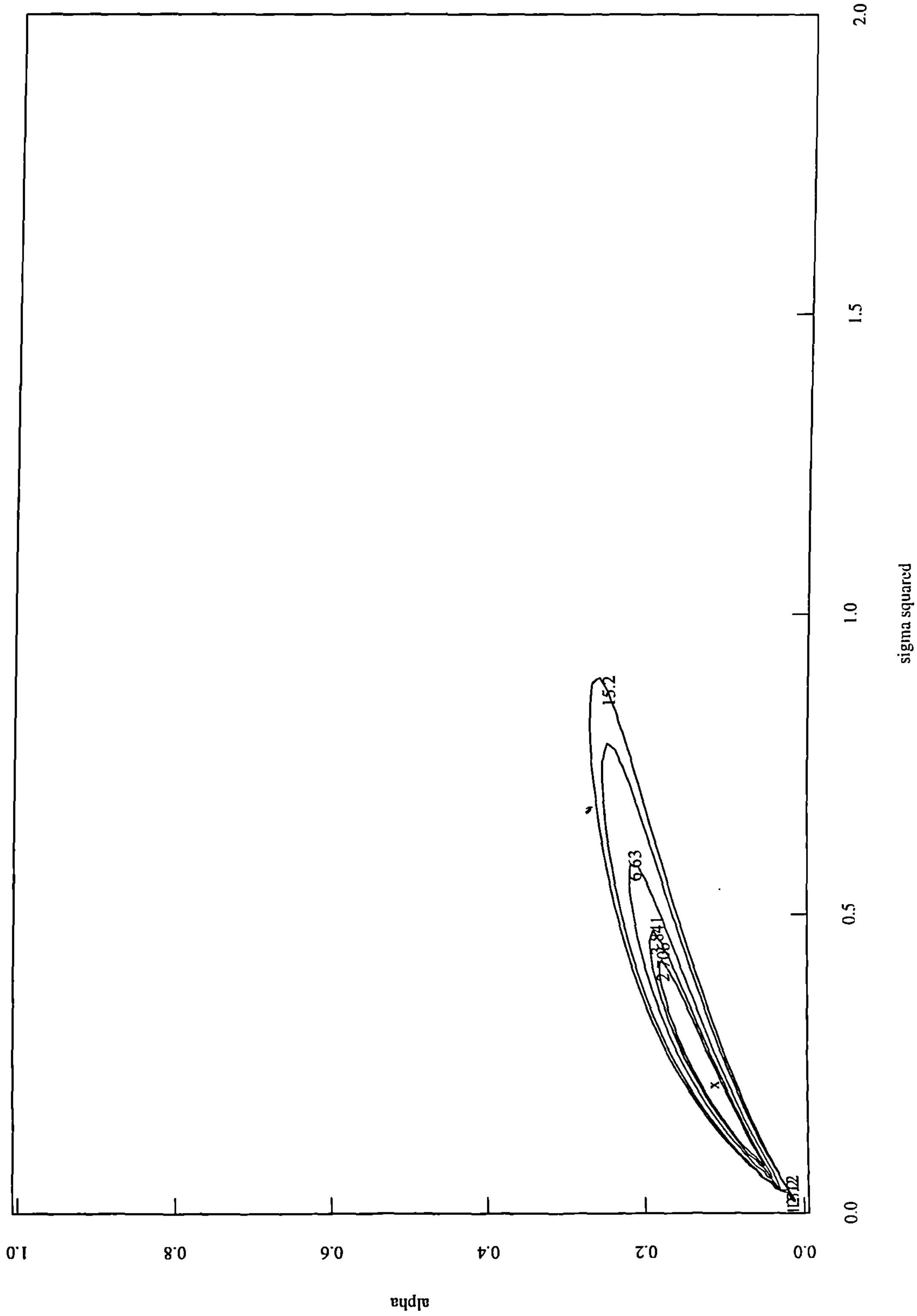


Table 73: Frequency table for northern birds

Interval(km)	Expected Frequency	Observed Frequency
Undispersed	108.7	120
[1.00,1.39]	4.5	0
[1.39,1.94]	4.5	4
[1.94,2.74]	4.5	13
[2.74,3.93]	4.5	8
[3.93,5.76]	4.5	6
[5.76,8.74]	4.5	2
[8.74,14.04]	4.5	2
[14.04,25.01]	4.5	4
[25.01,56.07]	4.5	1
56.07+	4.5	5

The very high correlation between some of these parameter estimators, in particular that between σ^2 and α_0 and between α_1 and β implies that a different parameterisation of the problem where the shape parameter estimator and scale parameter estimator are uncorrelated could give parameter estimates that can be more readily interpreted.

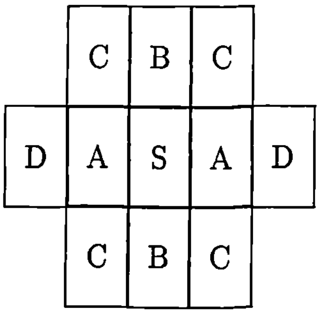
In order to get an overall measure of goodness of fit frequency tables 73,74 have been constructed based on the maximum likelihood estimates of the optimal model. These tables were constructed by having ten categories for the dispersed individuals each with identical frequencies.

The χ^2 statistics for the dispersed individuals in these tables are 28.11 for the first table and 45.78 for the second. These statistics imply that the model does not provide a good guide to the distribution of the individuals. The greatest observed frequency is in the $[1.8 - 2.4]$ km area. This can be explained by looking at the original form of the data. The ringing and recovery positions are not the exact points of the original nest and the place of death but are instead approximated to the nearest degree.

Table 74: Frequency table for southern birds

Interval(km)	Expected Frequency	Observed Frequency
Undispersed	106.4	97
[1.00,1.23]	5.5	7
[1.23,1.53]	5.5	0
[1.53,1.92]	5.5	7
[1.92,2.44]	5.5	19
[2.44,3.15]	5.5	3
[3.15,4.17]	5.5	8
[4.17,5.75]	5.5	1
[5.75,8.52]	5.5	7
[8.52,14.88]	5.5	0
14.88+	5.5	3

Figure 27: Layout of recovery boxes



This is best illustrated using picture 27. The boxes represent the areas represented by the original ringing point S, and the nearby recovery areas. Typical distances from the ringing box S to the recovery boxes are given in table 75.

This categorisation of the data, which is not taken into account in the model, may explain why it does not appear to fit the data well.

There are two immediately obvious solutions to this problem.

Table 75: Possible Ringing-recovery distances from box S

Recovery box	Distance	Number of boxes
A	1.155 km	2
B	1.852 km	2
C	2.183 km	4
D	2.310 km	2

The first method is to improve the accuracy with which the positional measurements are made. If the Ordnance Survey reference system is used then observations can be made to the nearest 100m. This would considerably reduce both the problem of the discretisation of the data, as the recorded distances would now be a good approximation of the true distances, and also enable the number of non-dispersed individuals to be drastically reduced. The distances moved by the individuals would include the distance from the current nest to the point of death, so the model may need to be amended to take this into account.

The other solution to this problem would be to calculate the probability density function for moving from the ringing to the recovery point in terms of the distance between them and then integrate over the areas of the ringing and recovery boxes. This would need to be done separately for each observation as the boxes get narrower in the East-West direction with increasing latitude. This is discussed further in section 7.9.

7.5 The dispersal of the Common Grackle

Moore and Dolbeer (1989) considered the distribution of the distance between the ringing and recovery points of the Common Grackle (*Quiscalus quiscula*) and of the Red-winged Blackbird (*Agelaius phoenicus*). In order to do this they extracted from the records of the United States Fish and Wildlife Service (USFWS) all the records of banding ring recovery for the two species for ringings and recoveries between 1924 and 1985.

In order to remove seasonal effects they then selected those records for which both ringing and recovery took place in the breeding season (21st April to 20th July) (Dolbeer, 1982) for which both ringing and recovery positions were known. Data from band *recovery stations and individuals* whose date of recovery were unclear were deleted from the set. The spatial blocking in the files is 10 minutes of longitude and latitude, so distances are known to approximately 20km. The data as they appeared in their paper is given in table 76.

The age was only broken down into young-of-year and adult birds, so it is not possible on the basis of this to estimate survival rates. Any survival analysis would have been complicated by the need to look at changes in banding methodology.

The majority of birds in each group are classed as non-dispersed and, as with the UK blackbird data, there are a few birds who have moved much further than the rest. In order to see whether the Weibull model might describe the data more accurately than a simple diffusion model, and to see if the dispersion parameters for the three groups might vary significantly, both Weibull and simple diffusion models were fitted to the data using maximum likelihood. Because the young-of-year birds were not classified by sex and the adult birds were not cited with age on recovery it is not possible to fit the time-dependent models from section 7.4. The dispersion distance was approximated by placing all the individuals at the midpoint of the band that they were occupying. Although any error that this may give is slight for the individuals that dispersed a long way this might have led to large errors when this procedure was followed for the first and second bands in particular. The Weibull

Table 76: Dispersal distances for Grackles

Distance		Young-of-year	Adult male	Adult female
0	20	729	1091	870
21	40	107	65	54
41	60	28	18	10
61	80	19	16	8
81	100	8	6	4
101	120	8	11	2
121	140	8	6	5
141	160	4	6	1
161	180	2	0	1
181	200	5	3	3
201	220	5	4	0
221	240	0	0	4
241	260	4	1	0
261	280	0	1	0
281	300	4	0	1
301	320	2	3	1
321	340	2	1	0
341	360	2	1	0
361	380	0	4	1
381	400	2	3	1
401	420	2	0	1
421	440	0	0	2
441	460	1	0	0
461	480	2	1	0
481	500	0	1	1
510	520	3	0	1
521	540	0	1	0
541	560	0	1	0
561	580	3	1	1
621	640	1	0	0
661	680	0	2	0
721	740	0	0	1
761	780	1	0	0
821	840	0	1	0
861	880	0	1	0
961	980	0	1	0
981	1000	0	1	0
1121	1140	1	0	0
1201	1220	1	0	0
1221	1240	0	0	1
2281	2300	0	1	0
2621	2640	1	0	0

Table 77: Analysis of deviance table for non-censored grackle data, Weibull model Weibull model

	Model		
Classification	Diffusion	Weibull	Censored Weibull
Base only	44486.0	26913.1	5292.0*
Age	44102.5	26838.7*	5291.4
Age+sex	43748.2	26806.9	5289.0

model was also fitted after the non-dispersed birds had been deleted from the data set and the likelihood adjusted to cope. The analysis of deviance table for these fits is given in table 77.

These results from these tables imply that the diffusion model is an extremely poor fit compared to the Weibull model. The results for the Weibull model without censorship imply that there is a significant difference between the groups based on age and sex, but the results from the censored data contradict this. Because the diffusion model fitted the entire data set so poorly it was not fitted to the censored data. However the parameter estimates for the two methods are also radically different so this could be an effect of one model fitting poorly.

In order to assess the absolute goodness of fit of the model frequency tables were constructed based on the expected numbers falling into each distance category for each model. This resulted in large numbers of cells at the longer ranges having very low expected values so these were amalgamated so that each cell had an expected count of at least 5. Then χ^2 goodness of fit tests were performed on the data. The parameter estimates and goodness-of-fit statistics are given in table 78. The frequency tables are given in tables 79, 80, 81 and 82.

The diffusion model gave completely the wrong shape for the distribution, predicting too many individuals in the centre of the distributional range and too few at either extreme. The extremely high χ^2 statistics reflect this. The same fault appears

Table 78: Parameter estimates and goodness-of-fit statistics for Grackles

Data	Model	$\hat{\alpha}$	$\hat{\sigma^2}$	χ^2(df)	Sig. level
Y-O-Y	Diffusion	(1)	8432.8	23206.9(13)	0.1%
Y-O-Y	Weibull	0.367	5.6170	378.3(9)	0.1%
Y-O-Y	Cens. Weibull	0.115	0.350	20.6(11)	NS
Male Adult	Diffusion	(1)	5403.7	25603.4(7)	0.1%
Male Adult	Weibull	0.385	5.210	544.2(7)	0.1%
Male Adult	Cens. Weibull	0.151	0.710	15.1(10)	NS
Female Adult	Diffusion	(1)	2356.4	8686.1(5)	0.1%
Female Adult	Weibull	0.427	6.018	470.4(5)	0.1%
Female Adult	Cens. Weibull	0.115	0.351	12.2(6)	NS
All Adult	Cens. Weibull	0.133	0.498	26.6(13)	5%
All	Cens. Weibull	0.125	0.423	46.5(18)	0.5%

Table 79: Observed and expected frequencies for young-of-year grackles, censored Wiebull model

Interval(km)		Observed	Censored Weibull
0	20	729	(3666.7)
20	40	107	88.1
40	60	28	38.5
60	80	19	22.1
80	100	8	14.5
100	120	8	10.2
120	140	8	7.6
140	160	4	5.9
160	200	7	8.4
200	240	5	5.8
240	300	8	5.8
300	400	8	5.8
400	580	11	5.3
580	1120	3	5.1
1120	2600	2	2.9

Table 80: Observed and expected frequencies for young-of-year grackles, Weibull model

Interval(km)		Observed	Weibull
0	20	729	527.6
20	40	107	176.8
40	60	28	93.1
60	80	19	54.5
80	100	8	33.8
100	120	8	21.7
120	140	8	14.4
140	160	4	9.7
160	180	2	6.7
180	220	10	8.0
220	280	4	5.2
280	2600	28	3.6

Table 81: Observed and expected frequencies for adult grackles

Interval(km)		Observed	Predicted
20	40	119	96.0
40	60	28	44.3
60	80	24	26.3
80	100	10	17.5
100	120	13	12.6
120	140	11	9.5
140	160	7	7.4
160	180	1	5.9
180	220	10	8.9
220	260	5	6.3
260	320	6	6.7
320	400	11	5.8
400	520	7	5.3
520	740	7	5.0
740	1460	5	5.0
1460	2600	1	2.3

Table 82: Observed and expected frequencies for all grackles

Interval(km)		Observed	Predicted
20	40	226	184.0
40	60	56	82.9
60	80	43	48.4
80	100	18	32.0
100	120	21	22.8
120	140	19	17.1
140	160	11	13.3
160	180	3	10.6
180	200	11	8.6
200	220	9	7.2
220	240	4	6.1
240	260	5	5.2
260	300	6	8.3
300	340	9	6.4
340	380	8	5.0
380	440	11	5.8
440	520	10	5.6
520	640	8	5.6
640	820	4	5.1
820	1200	5	5.1
1200	2600	4	5.9

Table 83: Confidence intervals for optimal Weibull model

Subset	Parameter	Estimate	95% interval	99% interval
Young-of-year	σ^2	0.350	[0.308, 0.400]	[0.298, 0.416]
	α	0.115	[0.107, 0.122]	[0.105, 0.125]
Males	σ^2	0.710	[0.611, 0.832]	[0.586, 0.872]
	α	0.151	[0.141, 0.161]	[0.138, 0.164]
Females	σ^2	0.282	[0.234, 0.344]	[0.223, 0.365]
	α	0.105	[0.094, 0.116]	[0.091, 0.119]
Adults	σ^2	0.497	[0.442, 0.562]	[0.428, 0.583]
	α	0.132	[0.125, 0.140]	[0.123, 0.142]
All data	σ^2	0.423	[0.387, 0.462]	[0.378, 0.474]
	α	0.124	[0.119, 0.129]	[0.117,0.131]

to occur with the non-censored model, although to a much smaller extent.

The model where the non-dispersed individuals are deleted displays a much better fit to the data, with insignificant χ^2 statistics for all three sets when considered separately. However when the fit is done jointly, as is implied by the value of the deviance from the model, the χ^2 statistic is significant. This could well be the result of the higher power of the test statistic when the number of cells is larger. The model appears to fit the distribution in the tail quite well, with the only significant deviation between the predicted and actual frequencies occurring in the first two bands, with the first band again having a predicted frequency that is too low and the second band having a predicted frequency that is too high.

The values of the parameters for the fit to the censored data, together with their 99% and 95% confidence intervals, are shown in table 83.

7.6 Movement with Capture

Models based on diffusion usually assume that individuals move at a constant rate with respect to time and that they are recovered while they are still moving. Thus the period of movement is the time between marking and recovery/recapture.

If the movement stops before recovery then this assumption is false. This may well be the case for bird movement, where individuals may nest in a single area, during one and possibly more summers.

The models considered here all consider movement to be a short hunt for a nesting site during, which the mortality is negligible, followed by a period of inhabiting that one site before being recovered at death. They do not take into account the possibility of more than one move.

Broadbent and Kendall (1953) considered a model for movement of the larvae of the helminth *Trichostrongylus retortaeformis* in two dimensions where the larvae wandered in a random manner until they came across a blade of grass which they would then climb. The rate of finding such stems was considered constant with respect to time, conditional on not having found a blade, so the overall distribution of the searching time was exponential. They considered what the distribution of these individuals would be after they had all found a stem to climb. They assumed that there was no mortality during the search for a stem.

If the individuals diffuse at a rate of ω, the rate of capture of individuals still moving is λ and the distance from the release point to the recapture point is r, then for

$$\rho = r\sqrt{\frac{2\lambda}{\omega}}$$

the probability density function for the final distribution is

$$K_0(\rho)\rho d\rho \tag{11}$$

where K_0 is a modified Bessel function, and the cumulative distribution function is

$$P(r < R) = K_1(\rho)\rho$$

This formula was then used to calculate expected numbers in concentric annuli away from a fixed starting point. Fitting a model by least squares was then suggested.

Yasuda (1975) studied the distribution of matrimonial distances, which is defined as the distance between the birthplaces of mates. A generalisation of the approach taken by Broadbent and Kendall was considered. Their model was generalised by looking at the situation that develops if the time that is spent in a random walk is distributed as a gamma random variable instead of the exponential.

The probability density for the amount of time spent until capture, T is

$$P(T) = \frac{c^{b+1}T^b e^{-cT}}{\Gamma(b+1)}$$

where c is a scale parameter and b a shape parameter. The mean of this distribution is $(b+1)/c$ and the second moment is $(b+1)/c^2$. If $b = 0$ then this is the same situation as was considered by Broadbent and Kendall. If the individuals perform independent random walks according to a simple diffusion model then the distribution of the dispersal distance r for an individual that is captured at time T is

$$\phi(r|T) = \frac{r}{\omega T}e^{-\frac{r^2}{2\omega T}}$$

The conditioning on the unknown stopping time can be removed by integrating the joint density of r and T with respect to T as follows.

$$\begin{aligned} m(r) &= \int_0^\infty \phi(r|T)p(T)dT \\ &= \frac{rc^{b+1}}{\omega\Gamma(b+1)}\int_0^\infty T^{b-1}\exp\left(-cr-\frac{r^2}{\omega T}\right)dT \\ &= \frac{h(rh)^{b+1}K_b(rh)}{2^b\Gamma(b+1)} \end{aligned}$$

where K_b is a modified Bessel function of the second kind, order b, and $h^2 = 2c/\omega$ is a scaling parameter.

Malecot (1967) described $m(r)$ as a $K-$distribution.

If $b < -0.5$ then the distribution is leptokurtic, otherwise it has a mode at 0. The mean is $\pi^{1/2}\Gamma(b+1.5)/h\Gamma(b+1)$ and the second moment is $4(b+1)/h^2$.

Yasuda went on to use maximum likelihood scoring to fit this distribution to an example data set. A series of intervals (r_k, r_{k+1}) were set up $(k = 0, \ldots n)$ with $r_0 = 0$ and $r_{n+1} = \infty$. The probability P_k of falling into the interval $[r_k, r_{k+1}]$ is

$$P_k = \int_{r=r_k}^{r=r_{k+1}} m(r)dr$$

The number of individuals falling into each interval (f_k) was then used in the following formula.

$$L = \frac{(f_0+f_1+\ldots,f_n)!}{f_0!f_1!\ldots f_n!}P_0^{f_0}P_1^{f_1}\ldots P_n^{f_n}$$

Here we will use direct estimation of the log-likelihood function instead. If the n individuals are observed at distances $r_i i = 1,\ldots,n$ from their original starting positions then the likelihood is

$$L = \prod_{i=1}^{n}\frac{h(r_i h)^{b+1}K_b(r_i h)}{2^b\Gamma(b+1)}$$

Therefore the log-likelihood is

$$
\begin{aligned}
l &= \log\left(\prod_{i=1}^{n}\frac{h(r_ih)^{b+1}K_b(r_ih)}{2^b\Gamma(b+1)}\right)\\
&= \sum_{i=1}^{n}(b+2)\log h + (b+1)\log r_i + \log K_b(r_ih) - b\log 2 - \log\Gamma(b+1)\\
&= n((b+2)\log(h) - b\log 2 - \log\Gamma(b+1)) + \sum_{i=1}^{n}(b+1)\log r_i + \log K_b(r_ih)
\end{aligned}
$$

In order to find the probability of ending up less than a given distance R away from the point of origin, the probability density function must be integrated between 0 and R.

$$
\begin{aligned}
P(r<R) &= \int_0^R m(r)dr\\
&= \int_0^R \frac{h(rh)^{b+1}K_b(rh)}{2^b\Gamma(b+1)}dr\\
&= \frac{h^{b+2}}{2^b\Gamma(b+1)}\int_0^R r^{b+1}K_b(rh)dr
\end{aligned}
$$

It is convenient at this point to introduce a change of variable into the integral. Substituting Rs for r gives the equation

$$
\begin{aligned}
P(r<R) &= \frac{h^{b+2}}{2^b\Gamma(b+1)}\int_0^1 (Rs)^{b+1}K_b(Rsh)Rds\\
&= \frac{(Rh)^{b+2}}{2^b\Gamma(b+1)}\int_0^1 s^{b+1}K_b(Rsh)ds\\
&= \frac{(a)^{b+2}}{2^b\Gamma(b+1)}\int_0^1 s^{b+1}K_b(as)ds
\end{aligned}
$$

where $a = Rh$. Gradshteyn and Ryzhik (1980) gives the following formula for the integral of the product of a modified Bessel function of the second kind with a power:

$$
\int_0^1 x^{\mu+1}K_\mu(ax)dx = s^\mu a^{-\mu-2}\Gamma(\mu+1) - a^{-1}K_{\mu+1}(a)
$$

If this formula is substituted into the above expression the result is

$$\begin{aligned}
P(r < R) &= \frac{h^{b+2}}{2^b\Gamma(b+1)} R^{b+2}[2^b(a)^{-b-2}\Gamma(b+1) - (a)^{-1}K_{b+1}(a)] \\
&= 1 - \frac{a^{b+1}K_{b+1}(a)}{2^b\Gamma(b+1)} \\
&= 1 - \frac{(Rh)^{b+1}K_{b+1}(Rh)}{2^b\Gamma(b+1)}
\end{aligned}$$

7.7 Heterogeneity

Leptokurtosis of data from movement experiments has been assumed for the purposes of this section to arise from heterogeneity in the population being studied. This section considers some models for ring recovery data that explicitly take into account this heterogeneity and attempt to model it in terms of a fitness parameter g which has a beta distribution with parameters α_1 and α_2. This will also be taken to be the survival rate for the individual which is constant over time for any individual. It is also assumed that all movement has ceased by the time of the first recoveries.

Initially consider the case where we are not interested in movement at all and only consider the survival probabilities. For an individual with survival rate g the probability of dying in the kth year is

$$p(k|g) = g^{k-1}(1-g)$$

If we now multiply this by the probability density function for g and integrate with respect to the parameter g

$$p(k) = \int_0^1 g^{k-1}(1-g)\frac{g^{\alpha_1-1}(1-g)^{\alpha_2-1}}{B(\alpha_1,\alpha_2)}dg$$

This simplifies to a ratio of beta functions.

$$p(k) = \frac{B(\alpha_1 + k - 1, \alpha_2 + 1)}{\mathrm{B}(\alpha_1, \alpha_2)}$$

For an initial model, it is assumed that each individual moves away from its ringing site in a straight line until it finds a suitable nesting site, at which it is recovered some time later. Let the probability of finding a nest between distance r and $r + \delta r$ given that the individual has not found one beforehand be $\lambda g \delta t$, for small δt. Then the probability density function for finding a nest at distance r is

$$P(r|g) = \lambda g r e^{-\lambda g r}$$

The probability of dying in the kth year is

$$p(k|g) = g^{k-1}(1-g)$$

The probability density for dying in the kth year at distance r is

$$p(r, k|g) = \lambda g r e^{-\lambda g r} g^{k-1}(1-g)$$

When these functions are multiplied together and then the parameter g is integrated out the density becomes after some algebra (see B.1 for details).

$$p(r, k) = \frac{\lambda r B(\alpha_2 + 1, \alpha_1 + k)}{\mathrm{B}(\alpha_1, \alpha_2)} M(k + \alpha_1, \alpha_1 + \alpha_2 + k + 1, -\lambda r)$$

where M is the confluent hypergeometric function.

Now consider what happens if movement takes place in two dimensions. This time start with a passive diffusion model where all movement occurs before the first recoveries are observed. Assume a diffusion rate σ^2/g that is inversely proportional to the fitness level. If all the individuals spend the same time t searching then we can subsume the searching time into the scale parameter σ^2

This gives a probability density at time t for an individual with fitness g of

$$h(r|t,g) = \frac{gr}{\sigma^2 t}\exp\left(-\frac{gr^2}{\sigma^2 t}\right)$$

Again assume a discrete time model for survival with probability g of surviving each year. If the individual dies in the kth year this leads to

$$p(r,k|g) = g^{k-1}(1-g)\frac{gr}{\sigma^2}\exp\left(-\frac{gr^2}{\sigma^2}\right)$$

If this is multiplied by the density function for g and integrated with respect to g then after some algebra (see B.2 for details) the joint density is

$$p(r,k) = \frac{rB(\alpha_2+1,\alpha_1+k)}{\sigma^2 \mathrm{B}(\alpha_1,\alpha_2)}M(\alpha_1+k,\alpha_1+\alpha_2+k+1,-r^2/\sigma^2)$$

This model was fitted to the movement distances of blackbirds in the UK. Because there did not appear to be any effect of age on distance between ringing and recovery point when the Weibull model was fitted, the age on recovery was conditioned upon in the calculations. The model has not been developed to the point where it is possible to calculate the probability of being recovered in any concentric annulus away from the origin. Thus it is not possible, as was done with the Weibull model to exclude the non-dispersed individuals and adjust the likelihood accordingly. Therefore they were arbitrarily positioned at a distance of 0.78 km from their ringing points. This may lead to bias in the estimates.

Because the values of α_1 and α_2 appeared to be very similar it was decided to fit a model where they were constrained to be equal. The analysis of deviance for both these models are given in table 84.

The table shows that there is no significant difference between the deviances when $\alpha_1 = \alpha_2$ than when they are estimated separately. The most parsimonious model is the simplest one, where the parameters are estimated jointly for both sexes and areas.

Table 84: Analysis of deviance for diffusion model with variable rate

	$\alpha_1 \neq \alpha_2$	DF	$\alpha_1 = \alpha_2$	DF
Simple	2561.66*	3	2566.44	2
Area	2533.36	6	2537.08	4
Sex	2553.06	6	2555.92	4
Sex*Area	2514.86	12	2519.54	8

The overall deviance is much greater than the value of 604.56 obtained when a four parameter model was fitted to the same data set using the Weibull distribution. This may be because the distribution of the individuals away from their ringing points is a long way from what would be expected under a simple diffusion model. However the models are not nested. This model provides another method of measuring departure from a simple diffusion model.

A model which integrates the Broadbent and Kendall model with the heterogeneity approach is now considered.

Again assume an annual survival probability of g. Let this also be the the trapping rate replacing λ in the density function for distance (Broadbent and Kendall, 1953). Thus the probability density function for distance to recovery point is

$$p(\rho|g) = K_0(\rho)\rho d\rho ,$$

where $\rho = r\sqrt{2f/\sigma^2}$.

If this is converted to a formula in terms of the distance r then we get

$$p(r|g) = K_0\left(r\sqrt{\frac{2f}{\sigma^2}}\right)\frac{r2g}{\sigma^2}$$

If the probability of dying in the kth year is included after some work we end up with a joint density

$$p(r,k|g) = K_0\left(r\sqrt{\frac{2f}{\sigma^2}}\right)\frac{r2g}{\sigma^2}g^{k-1}(1-g)$$

When the density function for g is included, and then the value of g integrated out of the expression, the density becomes

$$p(r,k) = \frac{5r\,B(\alpha_2+1,\alpha_1+k)}{\sigma^2 \mathrm{B}(\alpha_1,\alpha_2)}\,{}_1F_2(\alpha_1+k;1,\alpha_1+\alpha_2+k+1;v/4)$$

Where ${}_1F_2$ is a generalised hypergeometric series and $v = \frac{2r^2}{\sigma^2}$.

7.8 Estimation of Kurtosis from release recovery data

It is often the case that the simple diffusion model outlined in section 7.4 is not an adequate description of the data. One method of quantifying the degree of discrepancy between the expected distribution and the observed data set is to estimate the degree of kurtosis in the underlying bivariate distribution from which the distance from mark point to recovery/recapture point is calculated. Methods of doing this when only the overall dispersion distance are available are given by Okubo (1980). The estimation of the level of kurtosis from two studies is now considered.

Kareiva (1983) surveyed the ecological literature for examples of data sets that would be suitable for the estimation of movement models. He looked at data sets for herbivorous insects in order to concentrate on a set of species that fulfilled similar ecological roles. Of the sets that he found 12 that were suitable for further analysis.

A simple diffusion model was fitted to these sets and then assessed to see whether the model fitted adequately or if it showed significant deviation towards either leptokurtosis or platykurtosis. Leptokurtosis implies that there are more than the expected number of extreme observations, which could be due to heterogeneity of movement rates among individuals or heterogeneity in the environment. Platykurtosis, which occurs when there are fewer than the expected number of individuals with extreme values , is due to a higher than expected homogeneity in dispersal distances.

Data from 12 experiments on different species of herbivorous insects were analysed, 4 of which gave satisfactory fits for all the data, 4 had good fits for over half the data and the rest gave poor fits for most of the data. In general there were more data sets showing leptokurtosis than platykurtosis.

In their article Moore and Dolbeer (1989) considered the degree of dispersion and the kurtosis in the dispersal distances among Red-winged Blackbirds (Agelaius phoeniceus) and the Common Grackle (Quiscalus quiscula) using data obtained from the United States Fish and Wildlife Service.

Summaries of these data sets are shown in tables 85 and 76 .

The value of the Root Mean Square dispersal distances were calculated. In order to estimate the kurtosis of the underlying distribution, the data about longitude were ignored and the kurtosis of the north-south dispersion only was calculated. These statistics were corrected for bias using jackknife calculations which were also used for calculation of standard errors for the estimates. Confidence intervals were calculated based on these estimated standard errors. (See table 86 for details). The proportion of the sample with identical ringing and recovery boxes is given in the column labelled non-movers.

These confidence intervals are extremely large, especially for the estimate of the kurtosis. In particular the lower bound for the estimate of kurtosis for the young of the year female Common Grackles is less than the theoretical minimum for kurtosis of 1. For all the other data sets the lower bound for the kurtosis was much greater then the expected value of 3 derived from the normal distribution. Apart from for the adult female Red-winged Blackbirds the upper 95% confidence limit was more than

Table 85: Dispersal distances for Red-winged Blackbirds

Distance(km)	Young-of-year	Adult male	Adult female
0-20	100	202	49
21-40	8	18	0
41-60	3	5	2
62-80	1	5	1
81-100	1	2	0
101-120	1	3	0
121-140	0	4	0
141-160	1	0	0
161-180	2	1	0
181-200	0	2	0
201-220	1	1	0
221-240	1	0	0
241-260	1	1	1
321-340	1	0	0
501-520	0	1	0
521-540	1	1	0
581-600	0	1	0
621-640	0	0	1
681-700	1	0	0
921-940	0	1	0

Table 86: Dispersal statistics for Blackbirds and Grackles

Class	Non-movers	Sample size	Mean dispersal	RMS dispersal	Kurtosis Kurtosis
Red-winged Blackbird					
Young-of-year	81.3%	123	32.1	70.8	64.5
			(22.1,42.2)	(48.7,92.9)	(17.9,111.0)
Adult male	81.5%	248	26.6	67.6	131.9
			(19.7,33.4)	(47.0,88.1)	(29.5,234.4)
Adult female	90.7%	54	22.1	76.9	130.5
			(7.1,37.1)	(29.7,124.1)	(85.9,175.1)
Common grackle					
Young-of-year					
Male		89	17.1	32.6	77.5
			(11.9,22.3)	(19.9,45.3)	(18.6,136.4)
Female		71	29.8	50.2	23.0
			(16.5,35.1)	(36.8,63.5)	(0.3,45.6)
All	76.3%	955	33.7	94.8	632.0
			(28.8,38.7)	(66.3,123.4)	(57.2,1207.0)
Adult Male	87.1%	1252	21.3	76.8	749.3
			(17.8,24.9)	(54.7,98.9)	(55.4,1443.3)
Adult Female	89.3%	974	14.8	50.0	407.2
			(12.2,17.5)	(37.3,62.7)	(54.4,760.0)

5 times greater than the lower limit. This implies that there is very little precision in these estimates. The lack of accuracy in these estimates makes them of little value other than for drawing very broad conclusions about the data.

7.9 Mark-recapture conclusions

The dispersal rates for populations have strong effects on the degree of genetic variability between populations from different areas. Small numbers of individuals moving long distances, and then breeding with the local population, can have a disproportionate effect in preventing genetic drift and speciation. Thus any model of animal movement that is to be used to study genetic patterns must take not only the mean movement rates of the population into account but also the proportion of the population that travel long distances. A species in which large numbers of individuals moved moderate distances but few made long treks from their original area would be more likely to develop speciation than one in which most individuals hardly moved from their original position but a few travelled long distances.

We can use the α parameter from the Weibull model to measure the amount of heterogeneity in the movement distances compared to that from a simple diffusion model.

The parameter estimators for the Weibull movement model imply a very skewed distribution. This may be due to the individuals that have moved a long way having a large influence. This is despite the individuals that moved to Eire being deleted from the set. The effect of the distance censoring, which happens when the Irish data are removed, is to reduce the degree of skewness in the data. Including the data from Ireland would further decrease the already low estimate of α. The apparent lack of variability of the dispersal distance with age, sex and area of ringing are quite surprising. The need for males to take and hold a territory might have resulted in different distributions for the male and female dispersions but, when the data just for dispersed birds is considered, this does not appear to be the case.

From the plots of the ringing and recovery positions for the blackbirds in section 7.2 the positions appear to be clumped with some areas having very few recoveries. To some extent this may be due to differences in physical geography, with more mountainous areas having a lower bird population density. The human population density in these areas is also lower, so the chances of ringing and recovery may be less. The same arguments also hold when looking at possible differences between urban, suburban and rural areas. These factors may lead to some bias in the results due to different reporting rates. A full study of these effects would require classifying all the ringing and recovery positions by terrain type and human population density. It would then be possible to see if these factors, which have not been directly considered here, affect the survival and movement rates of blackbirds and whether, with changes in farming practices, the balance between urban and rural areas is changing. This could utilise a combination of the distance methods proposed here with the work on migration of Schwartz *et al.* (1993), although their method, based on a multinomial distribution, appeared to have low precision.

For all the data sets analysed here the exact ringing and recovery positions are not known. However for the blackbird data the positions are known down to a box of about 1.1km by 1.8km. However if we have a form for the pdf of the dispersion vector in terms of the distance between ringing and recovery points and the bearing, then given the ringing and recovery boxes, this function can be integrated to give a probability of having moved between the boxes. A possible approach to this is given in appendix B.4. This approach, if taken, removes at a stroke the problem of what to do with non-movers and individuals that moved a short distance. A full development of this model would allow hypotheses of radial symmetry (are north-south movements longer than east-west ones?) to be investigated.

Another area for further work is in the effect of weather conditions on dispersal. If it is assumed that birds only move to find a new nesting point during their first year and do not move again, as is implied by the constant dispersal with different ages of bird evident here, it would be interesting to regress the dispersal distance against a suitably chosen function of that year's weather to see if there was any effect. If the relationship was thought to be more complex, depending on overall population density and availability of food supplies as well as weather, then introducing a correlated error structure with the same error for each year, as was done for Generalized Linear Mixed Models in section 6.7, could well be a solution. There are too many years and not enough information for each year to have a regressor with a factor for each year of ringing. This could also be done, after suitable theory had been developed, for the estimation of the survival rates.

A problem with the Weibull model for movement is that it lacks any underlying biological motivation. Once the null hypothesis that $\alpha = 1$ (implying a diffusion model) is rejected there is no behavioural hypothesis to be tested. The models in sections 7.6 and 7.7 were attempts to do this but,again, there was no underlying *biological* model. A better model would be one where both survival and movement could be jointly and flexibly modelled with parameters that had real biological meaning. A reparameterisation of the Weibull distribution so that the mean dispersion and the shape parameter estimator were uncorrelated would lead to results that, at least, were easier to interpret.

Appendix A

An optimal algorithm for M_{rand}

This appendix contains an algorithm for calculating M_{rand} that will be optimal under all circumstances. A solution is optimal if there is no other method of arriving at randomness with fewer moves. The algorithm is based on the properties that an optimal solution must possess.

We assume that moves of any size, not just integer values, are allowed. We will also assume that the distance function D between all pairs of sample points forms a metric. The important properties of a metric that we use are

$$D_{ij} \geq 0$$

with equality if and only if $i = j$, and the triangle inequality:

$$D_{ij} \leq D_{ik} + D_{kj}$$

Consider points which have initial counts x_i, counts after all the moves have been made of x_i' and positions p_i. Let M be a matrix each element, M_{ij}, of which is the movement from p_i to p_j. Let D_{ij} be the distance from p_i to p_j. Let $T_{ij} = 0$ if M_{ij} is zero, and 1 otherwise. The cost of solution M is the elementwise sum of MD where the multiplication is also elementwise.

We will now show that if some point j is both a receiver and a donor then there is a solution with no greater cost where it is not both. If j is both a receiver and donor then there exist two points i and k such that

$$M_{ij} > 0 and M_{jk} > 0$$

The cost of the moves between i, j and k is

$$M_{ij}D_{ij} + M_{jk}D_{jk} + M_{ik}D_{ik}$$

If we replace M with M' which are identical apart from replacing the elements M_{ij}, M_{jk} and M_{ik} with

$$M'_{ij} = M_{ij} - \min(M_{ij}, M_{jk})$$
$$M'_{jk} = M_{jk} - \min(M_{ij}, M_{jk})$$
$$M'_{ik} = M_{ik} + \min(M_{ij}, M_{jk})$$

then the final counts are identical. However the new cost is

$$\begin{aligned}&M'_{ij}D_{ij} + M'_{jk}D_{jk} + M'_{ik}D_{ik}\\ &\quad = M_{ij}D_{ij} + M_{jk}D_{jk} + M_{ik}D_{ik} - \min(M_{ij}, M_{jk})\,[D_{ij} + D_{jk} - D_{ik}]\end{aligned}$$

By the triangle inequality the last term is strictly non-negative so we can replace M with M', thus eliminating either the move to j or the move from it. This can be done for all points that both donate and receive. Thus we can partition the data set into donors, receivers, and neutral points (which neither donate nor receive).

Define the gradient G_{ij} between two points i, j in a solution M to the moves to randomness problem as $G_{ij} = (x_i{}' - x_j{}')/D_{ij}$. We now show that for any optimal solution M there is a fixed value G_{max} such that $G_{ij} \leq G_{max}$ with equality if $M_{ij} > 0$. To see this, assume that there exists a solution M with two pairs of points (i, j) and (k, l), $M_{ij} > 0$ and $G_{ij} \leq G_{kl}$. If, for small δ we replace M_{ij} with $M_{ij} - \delta$ and M_{kl} by $M_{kl} - \delta(x_i' - x_j')/(x_k' - x_l')$, then the overall variance after the moves increases by a function which is of the order δ^2 but the overall cost changes by $\delta D_{ij}/G_{jl}[G_{ij} - G_{kl}]$. Therefore the original solution can only be optimal if G_{ij} G_{kl}.

This is a very strong condition, that we can impose if we wish to compute the optimal cost for M_{rand}, and suggests that a sensible method of computing M_{rand} in a rigorous manner would be to find the value of G_{max} that gives the required variance. This would need to be done iteratively.

This second restriction on a solution can be used to break down the problem of finding M into several smaller problems. Consider an n × n matrix K where $K_{ij} = 1$ if $(x_i - x_j)/D_{ik} > g$ and 0 otherwise. Then if rows and columns of K are rearranged so that it is of the form

$$\begin{pmatrix} K_1 & 0 & & 0 \\ 0 & K_2 & & 0 \\ & & \ddots & \\ 0 & 0 & & K_p \end{pmatrix} ,$$

where $K_1, K_2, \ldots, K_{p-1}$ are non-zero matrices that cannot be further split into empty blocks, and K_p is a block of zeroes, then because of the gradient rule above, no movement may take place between any of the members of different blocks, so the problem has now been broken down into finding a solution to the problem of reducing all the gradients to g in each block separately.

For this problem, consider the block K_1, dropping the subscript for notational convenience. If the donors in this block are d and the receivers are r with initial counts D and R respectively, cost function C, and movement matrix M then the problem is now how to minimise the cost function which is the elementwise sum of $M \otimes C$ subject to $(D - M1)(R + M'1)' \leq gC$ element-wise, with equality if $M_{ij} > 0$.

Appendix B

Derivations of mark-recapture models

B.1 Straight line movement with heterogeneity

Assume that we have survival time measured as a discrete variable and an annual survival probability f for each individual. If f has a beta distribution $beta(\alpha_1, \alpha_2)$ then the probability function for dying in the kth year, given f, is

$$p(k|f) = (f)^{k-1}(1-f)$$

If movement is in a straight line with constant stopping rate of λf then the probability of ending up at distance r is

$$p(r|f) = \lambda f r e^{-\lambda f r}$$

The probability density function for f is

$$p(f) = \frac{f^{\alpha_1 - 1}(1-f)^{\alpha_2 - 1}}{B(\alpha_1, \alpha_2)}$$

If we combine these together and integrate out f then the joint probability density function for r and k is

$$p(r,k) = \int_0^1 \lambda f r e^{-\lambda f r} (f)^{k-1}(1-f) \frac{f^{\alpha_1-1}(1-f)^{\alpha_2-1}}{B(\alpha_1,\alpha_2)} df$$

Collecting terms together this gives

$$p(r,k) = \frac{\lambda r}{B(\alpha_1,\alpha_2)} \int_0^1 f e^{-\lambda r f} f^{\alpha_1+k-2}(1-f)^{\alpha_2} df$$

The integrand has the same form as that in a representation of the confluent hypergeometric distribution function M given by Abramowitz and Stegun (1965) , equation 13.2.1

$$\frac{\Gamma(b-a)\Gamma(a)}{\Gamma(b)} M(a,b,z) = \int_0^1 e^{zt} t^{a-1}(1-t)^{b-a-1} dt$$

After the following substitutions:

$$\begin{aligned} a-1 &= \alpha_1 + k - 2 \\ b-a-1 &= \alpha_2 \\ z &= -\lambda r \end{aligned}$$

This representation is valid if a and b are both greater then zero. Substituting for the formula in the density function yields

$$p(r,k) = \frac{\lambda r}{B(\alpha_1,\alpha_2)} \frac{\Gamma(\alpha_2-1)\Gamma(\alpha_1+k-1)}{\Gamma(\alpha_1+\alpha_2+k)} M(\alpha_1+k-1, \alpha_1+\alpha_2+k, -\lambda r)$$

We can replace the Gamma functions with a beta function to get

$$p(r,k) = \frac{\lambda r B(\alpha_2-1, \alpha_1+k-1)}{B(\alpha_1,\alpha_2)} M(\alpha_1+k-1, \alpha_1+\alpha_2+k, -\lambda r)$$

B.2 Diffusion with Heterogeneity

The joint density for k and r for the case where the movement occurs by diffusion in two dimensions is

$$p(r,k|f) = f^{k-1}(1-f)\frac{fr}{\sigma^2}\exp\left(-\frac{fr^2}{\sigma^2}\right)$$

If we now multiply this by the density function for f and integrate out the value of f we get

$$p(r,k) = \int_0^1 f^{k-1}(1-f)\frac{fr}{\sigma^2}\exp\left(-\frac{fr^2}{\sigma^2}\right)\frac{f^{\alpha_1}(1-f)^{\alpha_2}}{B(\alpha_1,\alpha_2)}df$$

The integral here is of the same form as the integral representation of the confluent hypergeometric function (Abramowitz and Stegun, 1965), equation 13.2.1

$$\frac{\Gamma(b-a)\Gamma(a)}{\Gamma(b)}M(a,b,z) = \int_0^1 e^{zt}t^{a-1}(1-t)^{b-a-1}dt$$

where

$$\begin{aligned} a &= \alpha_1 + k \\ b &= \alpha_1 + \alpha_2 + k + 1 \\ z &= -r^2/\sigma^2 \end{aligned}$$

The probability density function is

$$p(r,k) = \frac{rB(\alpha_2+1,\alpha_1+k)}{\sigma^2 \mathrm{B}(\alpha_1,\alpha_2)}M(\alpha_1+k,\alpha_1+\alpha_2+k+1,-r^2/\sigma^2)$$

B.3 Diffusion with trapping and heterogeneity

The joint density for distance moved and year of death is

$$p(r,k|f) = K_0\left(r\sqrt{\frac{2f}{\sigma^2}}\right)\frac{2rf}{\sigma^2}f^{k-1}(1-f)$$

If this is multiplied by the probability density function for the heterogeneity factor f and then integrated with respect to f then when the value of f is integrated out we get

$$p(r,k) = \int_0^1 K_0\left(r\sqrt{\frac{2f}{\sigma^2}}\right)\frac{2rf}{\sigma^2}f^{k-1}(1-f)\frac{f^{\alpha_1-1}(1-f)^{\alpha_2-1}}{B(\alpha_1,\alpha_2)}df$$

After the substitution $v = 2r^2/\sigma^2$ and some tidying up this becomes

$$p(r,k) = \frac{2r}{\sigma^2 B(\alpha_1,\alpha_2)}\int_0^1 K_0(\sqrt{vf})f^{\alpha_1+k-1}(1-f)^{\alpha_2-1}df$$

This integral is given in Gradshteyn and Ryzhik (1980) Equation 6.592.2.

$$\begin{aligned}
&\int_0^1 x^{\lambda}(1-x)^{\mu-1}K_v(a\sqrt{x}) \\
= \;& 2^{v-1}a^{-v}\frac{\Gamma(v)\Gamma(\mu)\Gamma\left(\lambda+1-\frac{1}{2}v\right)}{\Gamma(\lambda+1+\mu-\frac{1}{2}v)}\,{}_1F_2\left(\lambda+1-\frac{1}{2}v;1-v,\lambda+1+\mu-1/2v;\frac{a^2}{4}\right) \\
+ \;& 2^{1-v}a^{v}\frac{\Gamma(-v)\Gamma\left(\lambda+1+\frac{1}{2}\mu\right)\Gamma(\mu)}{\Gamma\left(\lambda+1+\mu+\frac{1}{2}v\right)}\cdot{}_1F_2\left(\lambda+1+\frac{1}{2}v;1+v,\lambda+1+\mu+\frac{1}{2}v;a^2/4\right)
\end{aligned}$$

Substitution from this formula yields

$$p(r,k) = \frac{2r}{\sigma^2 B(\alpha_1,\alpha_2)}\frac{5}{2}\frac{\Gamma(\alpha_2+1)\Gamma(\alpha_1+k)}{\Gamma(\alpha_1+\alpha_2+k+1)}\,{}_1F_2(\alpha_1+k;1,\alpha_1+\alpha_2+k+1;v/4)$$

Where ${}_1F_2$ is a generalised hypergeometric series. We can simplify this a little to

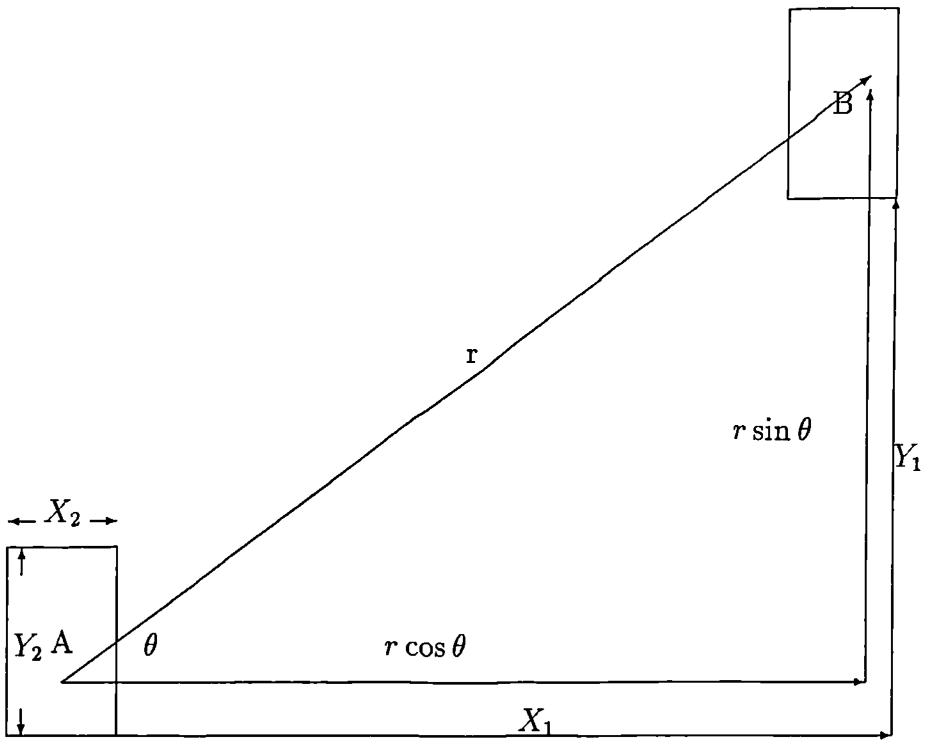
$$p(r,k) = \frac{5rB(\alpha_2+1,\alpha_1+k)}{\sigma^2 \mathrm{B}(\alpha_1,\alpha_2)}\,{}_1F_2(\alpha_1+k;1,\alpha_1+\alpha_2+k+1;v/4)$$

Further simplification may be possible but this has not been attempted yet.

B.4 Integrating the movement distance

For all the data sets analysed here the exact ringing and recovery positions are not known. For the blackbird data the positions are known down to a box of about 1.1km

Figure 28: Ringing and recovery boxes



by 1.8km. The ringing and recovery positions have been approximated by using the centres of the boxes. We will now remove that approximation by integrating over the areas of the two boxes. Initially, let's look at a move between two boxes A and B as shown in figure 28

Let the probability density function for ending up at a distance r from the ringing point be $p(r)$. Let the pdf (per unit area) for ending up at a randomly chosen position at a distance r and angle θ from the ringing point be $p_a(r,\theta)$. Note that if there is radial symmetry then $p_a(r,\theta) = \frac{p(r)}{2\pi r}$. Let the area of the recovery box where recoveries could occur if the displacement vector were (r, θ) be $A(r, \theta)$.

We will start off by looking at the situation where the ringing and recovery boxes are different. First we note that the set of possible recovery points for a given displacement vector is a rectangle. Therefore we need only calculate the dimensions of this rectangle to get $A(r, \theta)$. Along the x-axis the size is $(|X_2| - |X_1 - r\cos\theta|)$. Similarly along the the y-axis the distance is $(|Y_2| - |Y_1 - r\sin\theta|)$ Thus the area is $|(|X_2| - |X_1 - r\cos\theta|)(|Y_2| - |Y_1 - r\sin\theta|)|$

If ringing and recovery occurred in the same box then we can restrict out attention to moves where $\theta \in [0, \pi/2]$ and then multiply the result by 4.

In general these formulae can probably be simplified quite considerably, with θ being integrated out if we assume radial symmetry. It may be possible, with a suitable choice of $p(r)$, to get rid of the need to integrate with respect to r as well. If this were the case then a reliable and numerically accurate routine could be constructed with relative ease. All of the functional forms of $p(r)$ discussed earlier could be adapted to this approach.

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