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PART TWO

ROOK FLOCKS and FOOD FINDING: TESTS of FUNCTIONAL HYPOTHESES



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The following have been excluded at the request of the university:

The quotes on pages 209, 213 & 214.

Appendix 4.

Suddenly he begins to pour forth a flood of eloquence - facing them as he speaks: Will they come with him down to the field where the cows are grazing? There will be sure to be plenty of insects settling on the grass round the cows, and every now and then they tear up the herbage by the roots and expose creeping things. 'Come,' you may hear him say, modulating his tones to persuasion, 'come quickly; you see it is a fresh piece of grass into which the cows have been turned only a few hours since; it was too long for us before, but where they have eaten we can get at the ground comfortably....Or what do you say to the meadow by the brook? The mowers have begun and the swathe has fallen before their scythes; there are acres of ground there which we could not touch for weeks; now it is open, and the place is teeming with good food....Are you afraid? Why, no one shoots in the middle of a summer's day. Still irresolute? (with an angry shrillness). Will you or will you not?...You are simply idiots (finishing with a scream of abuse). I'm off!'

Seeing him start, the rest follow at once, jealous lest he should enjoy these pleasures alone....

Richard Jeffries (1879) Wildlife in a Southern County

Part Two Chapter One - Introduction

Part one compared the winter habitat use and foraging behaviour and ecology of the four corvid species regularly found in the open agricultural landscape of lowland southern Britain. The four species, as well as showing differences in those aspects just mentioned, also show marked differences in social organisation. Some general links between ecology and social organisation have been summarised by Waite (1978). The social organisation of these four species in winter has been summarised in chapter two of part one.

The possible relationships between aspects of social organisation and interspecific competition have been considered in part one. The present section tests an alternative hypothesis for one aspect of winter social organisation - whether flocking by rooks can increase the rate of encounter of patchily-distributed prey.

Part Two Chapter Two - Grouping by birds: a review of functional interpretations (*)

2.2.1 Introduction

The choice of rook flocking as an aspect of social organisation to investigate was not determined solely by its relevance to the general question of coexistence amongst the four corvid species under consideration. In addition, a major stimulus was the fact that at the time of instigation of the study only one convincing demonstration that flocking by a wild bird species increased the probability of locating a patchily-distributed natural prey, with a subsequent increase in prey intake rate, had been published (Krebs 1974). Thus an attempt was to be made to increase the number of comprehensive studies available from which an assessment might be made of whether social location of aggregated prey was the general phenomenon across the animal kingdom which it was held in many papers to be. Krebs had observed great blue herons (Ardea herodias) foraging for transient fish schools, whilst the rook forages for terrestrial invertebrates.

(*) This chapter is an expansion and update of one which appears in Waite (1978). Some repetition of material from that study is inevitable. The main viewpoint of the present chapter is similar to that of the earlier work.

Many less satisfactory investigations of this and other functional hypotheses concerning grouping by birds existed. Thus an investigation into the possible functional significance of rook flocking had a more general relevance. It was considered that a critical review of the literature had a place in such an investigation because of the general lack of rigorous testing of hypotheses current at the time. In fact the last few years have shown a considerable improvement in the quality of studies published in this area, which is reflected in the review given below. Even so, the author considers that problems still exist and the purposes of the current review are:

- (a) to demonstrate the diversity of ecological variables relevant to the behaviour of grouping through a comprehensive review of the literature;
- (b) to demonstrate the failure of many studies to adequately test functional hypotheses arising from the possible relationships between these ecological variables and behaviour; and
- (c) to present ways in which hypotheses may be tested by observation of birds in the wild, and thus dissuade the future production of a literature like that reviewed; and to demonstrate which hypotheses, by their nature, remain untestable.

2.2.2 Benefits and costs: a summary

The review will consider functional aspects of avian grouping ("why?"), and not causal ones ("how?"). Functions of aggregation by birds have mainly been related to two ecological events - the procurement of prey and the avoidance of becoming prey. A number of other benefits of aggregation have also been suggested, along with some costs. "Aggregation" and "group" are defined in this chapter as any association between two or more animals which involves some direct social behaviour on the part of at least one of the animals which brings about, or maintains, some behavioural interaction between them. The animals need not necessarily be of the same species, nor need every member of the group benefit equally or at all.

The following list summarises the main kinds of advantages and disadvantages which have been related to avian grouping behaviour.

BENEFITS

Prey

- a. Locating patches.
- b. Efficient exploitation of patchy environments.
- c. Defence of feeding areas.
- d. "Strength in numbers" enabling penetration into feeding areas unavailable to single birds.
- e. Flushing of prey into availability.
- f. Vigilance decrease allowing feeding rate increase.
- g. Social facilitation of feeding rates or prey types.
- h. Cooperative hunting.
- i. Food stealing from other flock members.
- j. Reduction of the risk of starvation.

Predation

- a. "Selfish herd" advantages.
- b. Detection of predators.
- c. Defence against predators.

Reproduction

- a. Access to opposite sex facilitates pairbonding, etc.
- b. Location of good nesting sites.
- c. Benefits related to communal breeding.

Reduction of Agonistic Encounters

Facilitation of Learning by Young

Synchronisation of Social Behaviour

Reduction of Energy Loss by Thermoregulation

Reduction of Energy Expenditure by Formation Flying

COSTS

Prey

- a. Competition.
- b. Agonistic encounters.
- c. Interference.

Predation

- a. Conspicuousness attracting predators.
- b. Increased predation rates.

Reproduction

- a. Competition for nest sites and materials.
- b. Competition for mates.
- c. Increased risk of cuckolding.
- d. Increased risk of misdirected parental care.
- e. Increased risk of inbreeding.
- f. Physical interference in breeding.
- g. Transmission of parasites and diseases.
- h. Cannibalism.

These costs and benefits may be experienced by birds in the dynamic situation of the flock, the more static situation of the breeding colony, or whilst coming as a flock to rest in one place for roosting.

2.2.3 Weak and strong function

Information about these proposed consequences of grouping has come mainly from observational study. Interpretation of the data in most of these studies is influenced by the assumption that the behaviour observed has been moulded by natural selection. It is conventional to distinguish between two different kinds of functional explanation - weak and strong (e.g. Hinde 1975, Williams

1966). A strong functional explanation of an observed behaviour seeks to define the ecological determinants which constituted the selective forces acting to shape the behaviour in the evolutionary past. A weak function describes a consequence or effect of behaviour which has some influence on present-day survival value, but which did not necessarily evolve through the action of the same ecological variable with which contemporary survival value has been linked, nor even necessarily through the action of natural selection at all.

Tinbergen was one of the first ethologists to make the consequences of this distinction clear - for example in 1963 he wrote that we must not confuse

1963).

There have been considerable fruitless attempts to define "the" strong function of avian grouping - e.g. the debate whether prey distribution (Murton 1971a) or predator pressure (Lazarus 1972) was the major selective force causing the evolution of bird flocking. There are at least three reasons why this is a dangerous process - firstly,

such arguments may be erroneous since they are based on the 'a priori' assumption that the behaviours are adapted; secondly, they can be fruitless if there is no possibility of distinguishing strong from weak function; and thirdly, they can lead to failure to study problems scientifically.

That the search for proof of a strong function is impossible is particularly well illustrated by studies relating grouping to a reduction of predation pressure. Showing that solitary birds suffer more predation than flocks is a valid process if one is concerned only to show a consequence of behaviour. But to conclude from such data that flocking is a strategy designed to reduce predation is not correct, for the comparisons of mortality have been made on solitary individuals of a species which is normally gregarious, and which may well display advertisement behaviour and flash-plumage. The true alternative strategy would be solitary behaviour linked with crypticity of behaviour and plumage. Of course one cannot perform this test for any bird species, since there are none which show different phases of behaviour and plumage corresponding firstly to crypticity, and then to advertisement, coupled with the corresponding changes in solitary or grouping behaviour. Predation rate data show the weak consequences of solitary or flocking behaviour, given that the species concerned is already a gregarious one; it cannot demonstrate that flocking is an evolved strategy which is better

than a solitary and cryptic one.

2.2.4 Adaptation by natural selection?

Since modern genetics is not the current author's field of study, no more will be done than to mention the fact that there are alternatives to the neo-Darwinian explanation of behaviour as the adaptive result of natural selection (e.g. see Feldman & Lewontin 1975, Gould & Lewontin 1979, Lewontin 1977). There are two related problems with this criticism of the adaptationist approach, however, which limit its effectiveness to combat the neo-Darwinian explanation.

Firstly, the proposition that some behaviours may not have evolved through the action of natural selection is as untestable as the alternative proposition it seeks to undermine. To propose that a behaviour is non-functional is effectively to propose the null hypothesis. The rejection of an alternative hypothesis (a functional one in this case) does not prove the truthfulness of the null hypothesis but only the (probable) falsity of the alternative (e.g. Winer 1971).

Secondly, the adaptationists will always be one step ahead - the disproving of one experimental hypothesis cannot prove the truthfulness of the null, but could only

lead to the proposition of another alternative hypothesis to test. As each functional hypothesis is disproved, another is erected in its place. For every one rejected, there would always be another possibility to propose as an alternative to the null hypothesis of no evolved function.

2.2.5 Strong function confuses the issue

The fruitlessness of the attempt to define strong functions may be compared to the old nature-nurture argument. The debate over whether flocking by birds primarily evolved in response to the distribution of prey or predation pressure is largely irrelevant to what kind of present-day advantage or disadvantage may be experienced as a result. If a bird, when vigilant, were looking for the whereabouts of a conspecific as an indicator of a good prey patch, it would not ignore a predator which it, or another flock member, happened to see approaching, just because it were not looking for a predator at the time.

The argument can also be reversed, of course; and it is even conceivable that a behaviour could be demonstrated to have a present-day disadvantage in relation to a particular ecological variable, and yet that same variable could have actually been the prime selective force acting to mould the evolution of the behaviour:

2.2.6 Strong function and scientific method

The final deleterious outcome of a non-critical acceptance of the adaptationist approach, or of a confusion between the identification of the evolutionary history of a behaviour and its contemporary effects, is a failure to study the problem scientifically. The literature is full of examples where a hypothesis is erected to explain the evolution of some observed behaviour and is then treated as sufficient. Even where such speculations are subjected to test to confirm whether the proposed evolutionary history remains a present-day effect, the tendency to think in terms of a particular evolutionary history to a behaviour seems to produce a failure (of which examples will be given below) to identify, and control for, the effect of possible confounding variables, or other explanations. As Deag says:

The best studies have abandoned the elusive search for the strong functional explanation of observed behaviour and followed the hypothetico-deductive method of most contemporary science:

- (a) observation of behaviour and its ecological setting;
- (b) erection of alternative, testable, hypotheses concerning the effects of ecology on behaviour;
- (c) test of the hypotheses by further observation, with possible confounding variables controlled for statistically, or by experimental control and manipulation of key variables.

This process is described in further detail below.

2.2.7 Optimal group sizes for different individuals

A further related problem has been the tendency to contrast benefits as mutually exclusive, and increasing linearly with group size. But many earlier studies have suggested that this need not necessarily be the case. For example, several studies have indicated that the balance of

benefit and cost to flocking differs for different members of a flock. Crook and Butterfield (1970), Hurton et al. (1971) and Ward (1965) are examples of early studies which indicated that some birds (subordinates or females, in these cases) received a cost by flocking (due to increased agonistic encounters or inefficiency of foraging) which outweighed the benefit gained. Many more recent studies have shown such a different balance of costs and benefits for different flock members (e.g. Baker et al. 1981, Barnard & Sibly 1981, Caraco 1979b, Jennings & Evans 1980, Rohwer & Edwald 1981).

A mixture of benefits and costs occurring at different flock sizes may also mean that the greatest return to a particular bird may come at an optimum rather than maximum flock size. Page & Whitacre (1975) and Siegfried & Underhill (1975) are two examples where the reduction in predation risk to a bird was lowest at an intermediate flock size due to the fact that the benefit of flocking versus predation (probably in these cases the benefits of increased vigilance or reduced likelihood of being the prey selected on any particular attack) began to be outweighed by increased costs at the highest flock sizes (probably increased conspicuousness of the groups attracting more predators, or the presence of many birds inhibiting escape movements). Caraco et al. (1980) have recently demonstrated that yellow-eyed juncos (Junco phaeonotus) altered

their flock sizes in response to increased predator presence, in a way which probably reflected the change in optimum flock size associated with changing the balance of the costs and benefits of flocking for individuals of this species.

2.2.8 Studies illustrating problems

Before describing ways in which the functional study of avian grouping can be carried out adequately, several common faults in the design, execution, analysis and interpretation of studies will be illustrated. These faults include the design of data collection to 'prove' one experimental hypothesis, not test between alternatives; the acceptance of the experimental hypothesis on insufficient data; poor design and interpretation due to a confusion between describing possible evolutionary pathways and demonstrating current advantage or disadvantage; the failure to demonstrate causal links between variables; and the acceptance of the experimental hypothesis in spite of contrary data which really dictates that the null hypothesis cannot be rejected. The studies cited here are simply single examples from a large potential pool, as will be indicated in the final section of this chapter.

One common problem is that a single possible explanation is fitted to data. The nature of the data is often

insufficient to allow alternative explanations to be examined and firmly rejected. In fact, data are often insufficient to adequately establish even the explanation proffered. It often seems as though studies were designed to demonstrate that the authors' prejudice for a certain functional explanation of some aspect of grouping behaviour by their particular subject species is correct.

Hoogland & Sherman (1976) produced a lengthy study of the possible costs and benefits of colonial nesting by the bank swallow (= sand martin), Riparia riparia. The authors conclude that the main benefit is reduced predation due to synchrony of the breeding cycle 'swamping' predators with an excess of prey, and cooperation in mobbing physically deterring predators from attack. They conclude that social foraging advantages were not operating or unimportant. They also list a number of disadvantages.

However, their data do not allow one to establish or reject any one of the considered costs or benefits reliably. The five disadvantages cited are supported only by very circumstantial evidence - for example it is stated that the risk of parasitic infestation by a flea (Ceratophyllus riparius) increased with increasing colony size. However, no data are given, or studies cited, to indicate whether the minimum and maximum number of fleas found in any burrow at the different colony sizes are sufficient to

affect reproductive success or adult survival differentially.

The advantage of social foraging is rejected on the statement that "the social facilitation of foraging never requires coloniality....Therefore, this explanation is not likely to be sufficient for the tight clumping of bank swallow burrows" (p.45). This illustrates the argument given above (section 2.2.5) that confusion between weak and strong function can cause a failure to examine hypotheses. The paper is entitled "Advantages and disadvantages of bank swallow...coloniality", and does not state that it wishes to trace the evolutionary history of coloniality. Whether or not social foraging requirements (the authors consider the possibility of social attraction to prey patches) could have caused the evolution of colonial breeding is irrelevant to a test of whether close nesting with neighbours can then subsequently allow a benefit to be gained from using nest neighbours to locate patches. The authors in fact give some data indicating that colony neighbours left to forage together, but these are the only data given regarding foraging behaviour. The reason given for the lack of data is that since the birds "ranged far from the colony while foraging, we could not examine grouping tendencies during actual foraging" (p.45). The social foraging hypothesis is therefore rejected without any data being collected to examine it - it is rejected because of a

confusion between weak and strong functional explanations.

The only other possible advantage considered is a reduction of the predation effect on breeding success. It is shown that considerable reproductive synchrony occurred. It is not shown that reproductive success differed between those breeding synchronously and asynchronously, though another study (Emlen & Demong 1974, 1975) is cited as demonstrating this. Despite the fact that Emlen & Demong found that the major cause of this differential mortality was due to starvation and not predation, Hoogland & Sherman conclude that the function of such synchrony is to increase breeding success by a selfish herd 'swamping' of predators. Thus they support a functional explanation without giving data of their own and without data on the frequency of occurrence or success rates of predators (Mead & Pepler 1975, a study not cited, give data which suggest a possible increase in predator attendance at colonies at the time of synchronous fledging).

A series of experiments are described which indicate that a mammalian predator's approach was detected quicker in larger colonies. Data are given to show that such mammalian predators could be deterred by mobbing. It is then stated that this should result in reduced predation in larger colonies, and even though their own data failed to demonstrate any systematic difference in the predation

rates on different sized colonies, the hypothesis is still accepted (p.54). A very few data are given on the mobbing of wild blue jays (Cyanocitta cristata) to suggest that mobbing deterred attacks on young placed at the burrow entrance but not at the bottom of the cliff face or in the centre of the gravel pit (p.49), a rather bizarre set of observations based on a total of only 17 observations which cannot be analysed for statistical significance, and whose relevance to naturally-occurring predation and its relation to colony size is difficult to understand. No data are given on the detection, or mobbing, of raptors, despite the fact that Mead & Pepler suggest that they are more important predators at the colony than mammals, and hunt by surprise appearance over the top of the colony in a manner which is difficult to reconcile with an early detection, followed by mobbing, hypothesis.

Thus a series of benefits and costs are appraised, and accepted or rejected on inadequate evidence, or on nil evidence but on a confusion of the difference between the evolutionary history of a behaviour and current survival value. The study was designed in a way which made distinguishing between any of the alternative hypotheses impossible.

The second example is of a study which is more carefully designed but which also fails to distinguish between

alternative hypotheses. Stinson (1980) assumed on the basis of other studies that flocking could reduce predation rates. He then proposed a model which predicted that when prey was scarce and not strongly clumped, the individuals of no species observed should be randomly distributed, but should clump. Further, if the densities of prey for which different species were foraging were positively correlated, then species should be non-randomly and positively associated with foraging individuals of other species.

Stinson tested his model's predictions by observing Charadrii foraging in winter (so food was probably scarce), and on uniformly sandy stretches of beach (so food, he assumed, was probably randomly or over-dispersed). The data supported the two predictions of his model - each of ten species observed was clumped in dispersion both intra- and inter-specifically.

However, Stinson considers no alternative hypotheses. For example, it is possible to build a complementary model related to social location of prey which is similar in nature and predictions except for one key factor - the dispersion of the prey. If prey were scarce and the prey densities of different species were correlated, but this time prey dispersion was clumped, then, if one makes (like Stinson) an initial assumption based on other work that flocking can facilitate the location of prey patches, the

same predictions follow: birds should be non-randomly distributed both intra- and inter-specifically. The crucial difference between the two models is that the first assumes that prey are randomly or over-dispersed, the other that they are clumped. Unfortunately Stinson did not measure this, but assumed that the prey in the areas of beach he observed were randomly dispersed. Without demonstrating that this was the case, no firm acceptance of his predation hypothesis can be made, especially since most invertebrate types in nature are known to be aggregated in dispersion (e.g. Southwood 1978). If Stinson had considered other alternative functional explanations during the design of the study, the crucial nature of the dispersion of the prey would have been identified, and it would have been clear that measurement of that variable was essential if alternative hypotheses were to be rejected.

The study by Patterson & Makepeace (1979) illustrates a similar, common fault. The study investigated the relationship between breeding success and colony size in shelduck Tadorna tadorna. It was found that breeding success decreased with increasing colony size. Patterson & Makepeace also established that the amount of time spent nest-prospecting also decreased significantly with colony size (due to increased mutual interference between different pairs of duck).

However, no causal link between the two was made to adequately suggest that it was the increase in mutual interference which caused the reduction in breeding success. Two circumstantial pieces of evidence were presented. Firstly there was no tendency for pairs which were successful in hatching broods to have been alone during prospecting (and thus not suffering from interference) more frequently than unsuccessful pairs (thus suggesting no link between interference and breeding success). Secondly, more dominant males during interactions while prospecting were more successful in hatching broods (thus suggesting a possible link between a subordinate's inability to combat interference, and a reduction in breeding success).

However, as Patterson & Makepeace themselves are aware (p.531), this is in no way adequate evidence to prove a causal link - for example the more dominant males could have held better quality territories and this could have been the cause of their increased breeding success. All three variables (breeding success, amount of interference, and colony size) could easily have been causally linked to some other, unidentified and unmeasured, variable. The authors in this instance were aware of the fault in their design, but as the final section of this chapter indicates, it is a common fault in studies of breeding success and colonial nesting.

The final example is not actually a study of avian grouping, but does serve to illustrate how the assumption of the adaptiveness of behaviour causes a refusal to reject unsupported hypotheses - the kind of attitude which has been criticised as unscientific by individuals from other disciplines (e.g. Bateson 1978, Lewontin 1977). This example is used, rather than a grouping one, since the study itself was very well designed and executed in its preliminary stages (design, data collection and analysis). It is only the final step (acceptance or rejection of the experimental hypothesis), which can be faulted. It is the interpretation of the study in an undergraduate text which will be considered, rather than that of the author of the study.

Zach (1979) found that the number of times northwestern crows (Corvus caurinus) needed to drop whelk shells before they broke open, and could be eaten, depended on the height from which they were dropped. By multiplying the number of drops required to break a shell at each height by that height, and by calculating the amount of energy expended in handling the prey compared to the energy gained from eating the different sized whelks available, Zach was able to make quantifiable predictions based on optimality theory. Zach predicted that if crows were trying to maximise energy intake and minimise energy expenditure when foraging, they should take only the largest

whelks and drop them from heights between about 4 and 11 metres.

The first prediction was upheld - the crows chose only the largest whelks when a choice was offered to them. The second prediction was partially supported - the most frequent drop was about 5m, but crows did not frequently drop from heights up to 11m. Zach himself considered that the crows might depart from his prediction if there were an unmeasured cost of dropping from the greater heights, for example the shell being lost.

This study is described in Krebs & Davies (1981) as their first example of a test of the exact predictions of an optimality model. This undergraduate text includes the usual few pages of warning about the dangers of designing studies and interpreting results (e.g. pp.27 and 34-8). They also state that it is their assumption that natural selection has produced maximally efficient animals (pp.57-8 and 66). The point of describing the Zach study, and Krebs & Davies' interpretation of it, is that the predictions of the optimal foraging model were not fully supported - it was predicted that the crows would drop from between 4 and 11m, but in fact dropped most frequently at just over 5m, and not at all heights.

Krebs & Davies give four reasons why an optimality model's predictions may not be supported by the data.

Firstly, some constraint may not have been identified (for example a need to achieve intake of different kinds of protein may require the adoption of a different diet than that which maximises energy intake). Secondly, the animal may have some other goal (for example minimising the risk of predator attack may be a more important goal which conflicts with behaviour which would be optimal for energy intake). Thirdly, some cost or benefit may not have been measured and built into the model (for example extra handling times for large prey, or in Zach's case an unmeasured cost could have been that shells may be lost from higher drops). Finally, the animal may be poorly adapted, not maximally efficient, for example because an animal has yet to respond to recent environmental change.

The conclusion from this is that, if a study designed to test quantitative predictions based on optimality theory does not produce results which support the predictions, then one explains the results away somehow, with a more or less glib 'explanation' - the theory of optimality itself cannot be wrong. The hypothesis which is supposed to be under test - that the animal forages optimally - is in fact not falsifiable, and the process is therefore not open to scientific inquiry. Zach may be right when he says that the reason the prediction was not supported was because of an unmeasured cost. That is not the point. Had he found that crows dropped only from c.10m, one could have

speculated that crows dropped from the highest heights because they would then have more time available for other things; or think of many other more or less plausible speculations to explain the particular results obtained. The point is that the experimental hypothesis of optimal foraging was not fully supported by the data. Instead of concluding that the null hypothesis (that the crows were not foraging optimally) could not be rejected, the experimental hypothesis is accepted anyway. This is not the usual scientific process. An experimental hypothesis which cannot be rejected is not open to scientific verification.

The example above was used because it is described in an undergraduate text. Both Krebs and Davies have of course produced functional studies of behaviour which were both equally well designed, and in which the results did in fact support their predictions, as will be described below. The fault common to all four of the examples described above was data which were not adequate to fully test the hypotheses in question, due to design faults often caused by muddled thinking about, or dogmatic belief in, the theories of natural selection and function. The following section attempts to set the limits to what best can be achieved at present in the scientific study of function - at any rate, they represent the guidelines within which the research reported in the later chapters of this thesis were

carried out.

2.2.9 Guidelines for research on the functions of avian grouping

The study of functional issues in behaviour should be no different to that of any other phenomena which are open to scientific inquiry. Any scientific study should proceed through a series of steps which may be summarised as:

1. Observe
2. Design
3. Predict
4. Test
5. Analyse
6. Interpret
7. If necessary, repeat 2-6

Observation should be the first step for any study of function, whether the study is to be carried out in the field or in the laboratory. A knowledge of the natural history of the animals concerned, along with familiarity with the literature, will suggest not only the possible functional hypotheses, but also all the relevant variables which must be taken into account. The design of the study can be aided by drawing flowcharts where the variables are linked by arrows in different possible networks of causality (examples can be found in chapter 2.4 below). All possible functional explanations of the behaviour in question should be considered, enabling all relevant variables

to be identified and measured. Just as in the design of laboratory experiments with only a single or few factors, close scrutiny of the design should be made to ensure that all possible confounding variables have been identified.

Relevant examples of confounding variables in avian grouping studies include a tendency for birds of a normally-gregarious species which behave in a solitary manner to be subordinates in poor or abnormal condition (e.g. Kenward 1978, Murton et al. 1971), or for birds breeding on the edge of colonies to be younger, less experienced breeders (e.g. Coulson 1968, review in Ryder 1980). Thus these variables of degree of grouping behaviour are confounded by parallel variations in fitness and age. It is not always obvious in which way variables will confound - for example, in carrion crows it is the flocking birds which are less fit, since they are the non-breeding surplus which have failed to gain a territory. A common method in the study of the function of communal breeding behaviour is the comparison of the performance of pairs breeding alone with those breeding in the presence of 'helpers'. However, the possibility that better-quality pairs, or pairs in better territories, attract additional birds must be disentangled from any true effect that the presence of those birds have on fitness. Brown & Brown (1981) is one study which could distinguish these two factors, but many studies cannot, as the relevant sections

in 2.2.10 below indicate. For someone trained in psychology where one is continually vigilant for confounding variables during experimental design, and where journal referees spend a high proportion of their time and ingenuity seeking out the effects of confounding variables on the experiments submitted to them, the behavioural ecology literature in general stands out very badly indeed in this matter.

The design stage of the study, including modelling of systems where possible, should produce hypotheses which are testable by further observation and measurement of behaviour. Measurement will enable the decision to be made of whether the null hypothesis (that sociality has no effect on fitness) may be rejected. Predictions alternative to the null hypothesis may be general (that sociality increases fitness via the particular mechanism specified), or particular (that under a certain level of environmental condition a given rate of behaviour will occur to alter fitness to a given degree), depending on whether or not the initial phases of the study included the quantification of variables which could be modelled to produce quantitative predictions. Examples of both kinds will be given below.

The test of the hypotheses will require the measurement of the relevant social behaviour and environmental variables, and of fitness. Strictly speaking the measure-

ment of an effect on current survival-value should be made in terms of inclusive fitness. An individual's inclusive fitness is the amount of its genetic material which it passes on throughout its life. Theoretically this would include behaviour which increased the survival of any kin which contained a proportion of identical genetic material, but realistically this would normally be measured as the total number of offspring produced during its active breeding life by an individual, which themselves survive to reproduce. Outside of laboratory conditions even this is rarely achieved and various other measures which are assumed to correlate with inclusive fitness are taken. These approximations to inclusive fitness include fledging success in one year, hatching success, clutch size, individual survival, prey intake rate and vigilance rates.

To some extent the nature of the grouping behaviour under consideration will determine the quality of the measure of fitness taken - many studies of the effects of cooperative breeding group size on fitness are able to measure fledging success in any one year, and some longitudinal studies have documented lifetime reproductive output (see the relevant sections in 2.2.10 below). Nisbet & Drury (1972) and Parsons et al. (1976) are two examples where some effects of colonial breeding in herring gulls (Larus argentatus) were measured in terms of survival of young birds during their first year, and many breeding

studies measure at least annual fledging success. However, when measuring the effects of behaviour which individuals alter in the short-term - for example, associating at various flock sizes - can only be achieved using some short-term measure of fitness, for example variations in prey intake rates.

Although the assumption that these other measures are correlated with inclusive fitness is probably in most cases reasonable, it is not always the case. For example, Ligon & Ligon (1978) were unable to show any systematic effect of group size on annual fledging success in green woodhoopoes (Phoeniculus purpureus), but it was found that when the offspring were followed to the end of their first year, differential survival of the young meant that yearling survival did increase with increasing group size. This was probably because, although fledging the same total number of young, those from the larger groups were heavier and in better condition at the time of fledging. Similarly, Vehrencamp (1978) was unable to find increased breeding success for groove-billed anis (Crotophaga sulcirostris) breeding in groups in any one season, but males which bred in groups did have higher total reproductive rates over their whole life.

As the approximations recede further from a direct measurement of inclusive fitness a time budget approach

becomes valuable - for example the amount of time spent foraging, vigilant, preening or involved in agonistic encounters may all make an independent contribution to fitness. If a situation appears to have several costs and benefits whose combined effect on fitness is to be assessed, then measurement of cost and benefit in the same currency (for example the amount of energy expended or gained) is required.

The analysis of behavioural systems which include many variables is greatly aided by the use of multivariate statistics. If the situation precludes the control of confounding variables by randomisation of allocation of their effects, as is often possible in the laboratory, then statistical control through the use of partial correlation in multiple regression, or the analysis of covariance becomes essential. Multivariate analyses can also quantify the combined effects of several approximations to fitness (for example those mentioned in the preceding paragraph).

Finally the interpretation phase should be straightforward. Can the null hypothesis be rejected? If so, can one choose between alternative experimental hypotheses? Were any quantitative predictions supported? If the null hypothesis cannot be rejected, then if some unmeasured cost (for example) seems to be responsible, redesign the study with new hypotheses and test again - do not accept the

experimental hypothesis if the data cannot support it.

Tinbergen et al. (1962) is often cited as a classic example of a semi-experimental test of some functional hypotheses regarding the contemporary survival-value of eggshell removal from the nest by black-headed gulls (Larus ridibundus). A good example of a test of a functional hypothesis regarding grouping behaviour by wild birds is Krebs (1974). Although earlier studies had concerned themselves with sociality, most of these studies failed to establish the hypotheses unambiguously, as the review below will indicate.

Krebs tested the hypothesis that great blue herons (Ardea herodias) used the presence of other feeding birds to indicate the location of dense, transient patches of estuarine fish. Current survival value of flocking was measured in terms of variations in short-term intake rate of prey. The hypothesis that birds in larger flocks would have higher rates of prey intake rate was supported. Possible alternative explanations of such an increase were rejected by further data - for example the possibility that birds in larger flocks had higher prey intake rates because they spent less time scanning for predators was discounted, since at any one prey density single birds did not have lower prey intake rates than flock birds. Krebs showed

that prey density influenced variations in prey intake rates, and that the largest flocks tended to occur on the densest prey areas by social attraction.

Caraco (1979a & b), Caraco et al. (1980), Pulliam (1976) and Pulliam et al. (1974) studied a situation where the costs and benefits of flocking were mingled in a somewhat more complex way. Yellow-eyed juncos had higher intake rates of prey in larger flocks due to a reduction in time spent scanning. However, levels of aggression were higher in larger flocks, and at the largest flock sizes led to a drop in prey intake rate. Thus the benefit of increased prey intake rate due to decreased vigilance was counterbalanced in the larger flocks by the reduction in prey intake rate through increased agonistic encounters. It was possible to demonstrate at what flock size this cost and benefit balanced to maximise prey intake rate.

However, two exogenous variables altered the balance of the cost and the benefit - at higher temperatures food was easier to come by and aggression rates increased in the flock; and when cover from predators was available, or when a predator was in the vicinity, vigilance rates were lower or higher (respectively) at any particular flock size. Thus it was possible to model the effect of three independent variables (temperature, predator-pressure and flock size) on a cost (reduction of prey intake rate due to

agonistic encounters) and a benefit (increased prey intake rate due to a reduction of time spent vigilant) of sociality. It was shown that optimum flock size varied under different combinations of these three variables. Barnard (1980), Barnard & Stephens (1981) and Barnard, Thompson & Stephens (1982) are similar examples of quantification of the effects of different variables in combination on short-term prey intake rate.

The study of grey-crowned babblers (Pomatostomus temporalis) by Brown & Brown (1981) and Brown et al. (1978) is a good example of the use of both statistical and experimental control of confounding variables. Increased group size was associated with increased breeding success in this cooperatively breeding species, but breeding success also showed simultaneous correlations with territory size and quality, and the age of the breeding female. However, multiple regression indicated that the partial contribution of group size was indeed the most important predictor of the observed variation in breeding success. This strongly suggested that the behaviour of 'helpers' at the nests (for example feeding the nestlings or joining in territory defence) did indeed contribute to the fitness of the breeders; rather than good quality breeders or territories simply attracting other birds into the territory whose effect on breeding success was neutral, but who joined the territory to (for example) learn how to raise broods or to

inherit a good-quality territory.

To test this, Brown & Brown (1981) removed the extra birds from some of the territories - if they, rather than territory quality (etc.) indeed caused increased breeding success for the breeding pair, then their removal from the territory should have resulted in a drop in breeding success. This is what was found, and this remains the only study so far published on cooperatively breeding groups where the possible effects of the confounding variables of territory size and quality, and breeding-pair quality, have been controlled for unambiguously.

Davies & Houston (1981) is a good example of where modelling of observed costs and benefits produced quantitative predictions about exactly when pied wagtails (Motacilla alba) would gain a benefit from allowing a second bird to occupy its winter territory and aid in its defence. The territorial birds studied exploited a renewing prey source. On days when food abundance in the territory was high, many birds attempted to intrude on the territory to feed. The authors were able to develop a model which quantified the benefits and costs of defending the territory alone or with a satellite (which helped in territorial defence) under different levels of food abundance and intensity of trespass. The model predicted that at a certain level of prey abundance the cost of increased

intrusions, without the aid of a satellite's contribution to territorial defence, exceeded the benefit of sole access to the prey resources of the territory. Below this key level of prey abundance intrusion pressure without the satellite present did not produce a greater cost than the cost of the satellite's share of the resources, and thus it was predicted that the territory owner should evict the intruder. Observation indicated that satellites were indeed accepted or displaced by the territory owners at levels of prey abundance very close to that predicted by the quantification of the model. These birds showed short-term switches between a solitary or a social strategy which served to maximise prey intake rates.

The work outlined in the following two chapters has attempted to follow the guidelines set out above. Field observations of rooks suggested that birds used others to locate the densest prey patches (chapter 2.3). Possible alternatives explanations are assessed and rejected. The key exogenous variable is then manipulated experimentally and further measurement is made to see whether the predicted changes in behaviour resulted (chapter 2.4). In addition Chantrey (1982) further tested the patch-location hypothesis by comparing the relative food-finding efficiencies of 'rooks' which showed social attraction with 'rooks' which did not (something not known to occur in nature) by

computer simulation, employing values for variables suggested by the naturalistic observations.

2.2.10 Functions of sociality

The review which follows lists all studies known to the author which have investigated functional aspects of bird sociality. It is thought to be comprehensive up until about 1980, but some studies will inevitably have been omitted from a literature so large, much of which is scattered in odd natural history journals and books. However, enough studies have been traced to provide a good sample of the kinds of functional categories which exist.

Each entry is classified not only by the type of sociality and ecological variables concerned, but also by the degree of certainty with which the hypotheses about behaviour may be accepted; and whether the study was conducted in the field or laboratory, or by theoretical considerations (including computer simulation of constructed models), or by comparisons between many species. The reason for this should be clear from the preceding sections of this chapter; many functional speculations have been made but relatively few hypotheses have been satisfactorily established empirically. (*) Thus within each

(*) It was decided not to break the kinds of categories of behaviour down systematically by bird family since it would be impossible to differentiate true patterns from the tradi-

behavioural/ecological category studies may be listed as reviews, comparisons of patterns of variation in social organisation and ecology between many species, or theoretical formulations or models, including tests of such models by computer simulation. Studies which actually investigate behaviour empirically are divided into those carried out in the wild or in the laboratory, and where the functional hypothesis was reasonably established or where evidence to support it is only circumstantial. Evidence may be circumstantial for a number of reasons - for example other possible explanations may not have been adequately tested and discounted; or causality may not have been reasonably established because some confounding variable remained unmeasured; or because no direct measurement of fitness (or approximation to it) was taken, but the cost or benefit was only assumed.

There seemed no other reasonable way to organise the review than to present each behavioural category and its

tion to investigate particular functional hypotheses if one is working on a particular species. For example, many gull and tern species (Laridae) have been investigated for possible anti-predator functions of colonial nesting, and few for possible food-related functions. It is not at present possible to tell whether this is because Laridae generally do not derive food-related benefits from coloniality, but mainly anti-predator ones - a true biological pattern; or whether it is simply the result of a tradition amongst workers studying Laridae to investigate anti-predator hypotheses, or perhaps because it is difficult to study the food-gathering behaviour of species which tend to have wide foraging ranges over an environment where it may be difficult to track them or their prey.

ecological setting as a separate entity - such a splitting of costs and benefits up into discrete units is not to encourage a research strategy which considers only one aspect of behaviour at a time. It is hoped that the preceding sections of this chapter will have emphasised the need for a multivariate approach to the multivariate universe with which functional study concerns itself. The costs and benefits described are not mutually exclusive, and hence one study can of course be referenced in more than one section below.

Reviews

No fully comprehensive review of the ecological factors involved in bird aggregation, or of studies concerned with these, has so far appeared. Those which have covered the range of social organisations and ecology have reviewed a limited number of studies, in the main uncritically. The present review is thus complementary to those already published in its aims. Some of the reviews listed cover the general question of the functions of bird sociality, others one aspect in detail (for example vigilance, Dimond & Lazarus 1974; information-centres for food-finding, Bayer 1982, Ward & Zahavi 1973; cooperative breeding, Brown 1978, Emlen 1978 & 1982b, Koenig & Pitelka 1981).

Alexander 1974; Allee 1931, 1938; Bayer 1982; Bertram 1978; Brockmann & Barnard 1979; Brown 1964, 1974, 1975, 1978; Brown & Orians 1970; Burger 1981a; Clutton-Brock 1974; Cody 1971b; Crook 1965, 1970a, 1970b; Crook & Goss-Custard 1972; Curio 1978; Darling 1952; Davies & Krebs 1978; Davis 1952; Dimond & Lazarus 1974; Emlen 1978, 1982b; Fisher 1954; Gochfeld 1980b; Graul et al. 1977; Hainsworth & Wolf 1979; Hamilton & Watt 1970; Harvey & Greenwood 1978; Humphries & Driver 1970; Koenig & Pitelka 1981; Krebs 1978a, 1979; Krebs & Barnard 1981; Krebs & Davies 1981; Lack 1966, 1968; Lazarus 1972; McKinney 1978; Mason & Lott 1976; Meinertzhagen 1959; Moriarty 1976; Morse 1977; Moynihan 1962; Murton 1971a; Orians 1969, 1971; Rand 1954; Rubenstein 1978; Schoener 1971; Selander 1972; Ward & Zahavi 1973; Welty 1962; Wiens 1976; Wiley 1974; E.O. Wilson 1975; Wittenberger 1981.

Benefit: Prey: Locating Patches

If the food supply is sufficiently patchy in space and time, there will be an increased probability of an individual finding food if it watches others foraging and joins any which locate a patch, rather than if it forages independently over the same area. The prey must of course be hard for an individual bird to detect and the patches unpredictable in occurrence. Individual prey intake rate must increase with increases in prey density or there will be no benefit from locating a patch in terms of short-term increases in prey intake rate, though it may be advantageous for prey intake rate to stay the same if the bird forages on a patch for longer, and food availability elsewhere is limited.

Social attraction must be shown to occur. Thorpe called this kind of social learning 'local enhancement', which he defined as "directing attention of associates to a particular object or environmental situation" (Thorpe, 1963, p.137). Social attraction may occur on a large scale (between flocks on patches some distance apart, for example between different fields or lakes, etc.); or within a single foraging flock (for example to a particular bird on a particular branch of a tree, in a foraging flock of woodland passerines), to maximise the efficient exploitation of 'fine-grain' variation in prey patchiness.

These two types of learning do not differ qualitatively but represent the same kind of behavioural response by individuals to environments at either end of a prey patch size spectrum. Birds showing 'fine-grain' local enhancement will be observing and responding to others within a foraging flock, but birds showing only 'coarse-grain' social attraction may forage quite independently from other birds once at the feeding site.

Few studies have demonstrated the existence of local enhancement, with a consequent increase in individual prey intake rate, unambiguously. Barnard (1980) has done so for house sparrows (Passer domesticus) feeding on patches of spilt barley grain, and Krebs (1974) for great blue herons foraging for estuarine fish schools; while Bertin (1977) and Gochfeld & Burger (1982) have probably demonstrated it in less complex situations where no other explanations of increased prey intake rate following local enhancement seemed possible. (*)

(*) To detail all the possible prey and predator situations, and the different kinds of behavioural processes involved, which have been described in the literature, would require a thesis-length production in itself. Hence only those studies which have provided reasonable support for functional hypotheses, or which illustrate particular problems in a particular field, have been described in any detail. Needless to say, the titles of each study referred to appear in the reference list at the end of the thesis, and will often be the only guide to the reader of this review as to the subjects and situation of any particular study.

No studies have unequivocally demonstrated 'fine-grain' local enhancement within a foraging flock. However, it might be noted that Herrera's data are interesting in that the feeding rate of species which were usually to be found in mixed-species flocks was twice as high when in flocks than when in single-species associations, but the feeding rate of species which did not frequently associate with other species was not different whether in single or multi-specific groups. In addition, niche overlap increased when in mixed groups for those species which were frequently found in such flocks (and whose feeding rate was increased), but the niches of infrequently associating species (whose feeding rate did not increase) was, on the contrary, reduced. An interpretation of these data could be that those species with increased niche were copying the feeding areas of members of other species, and that this was the cause of the increase found in their prey intake rates.

Many other studies have described probable local enhancement, but have failed to prove an increase in prey intake rate, or failed to emphatically discount other possible explanations of observed increases in prey intake rate. The many circumstantial accounts of local enhancement (and the suggestions of common sense) suggest that it is probably of widespread occurrence in many species; but the onus is on the researcher to demonstrate that it not

only occurs, but is clearly a superior strategy to individual search and exploitation of prey.

Social attraction to prey patches by following experienced birds out of a colony or roost (the 'information-centre' hypothesis) is a special case of local enhancement. De Groot (1980) has demonstrated that the learning mechanisms necessary can occur, with a series of experiments using red-billed weaver birds (Quelea quelea). A number of birds were trained to find food in a number of different areas. Subsequently, hungry birds followed birds which had recently fed in the test arena to feeding areas which contained food (which was not visible from the start box), in preference to entering other areas where they had also had previous experience of finding food.

However, evidence for its operation in natural situations is lacking. A number of studies demonstrate that departures of birds to feed from colony or roost is clumped but, although this is necessary, it is certainly not sufficient to prove the existence of the mechanism. For example Andersson et al. (1981) demonstrated that departures from a black-headed gull colony were clumped, but field experiments proved beyond reasonable doubt that the information-centre hypothesis was not operating for this colony at that time, at least to artificially-provided food dumps. In this instance clumped departures were caused by non-

breeders arriving and departing in groups, and local enhancement to new naturally-occurring food supplies visible near to the colony. It is necessary to show not only that departures from the colony are clumped; but that the birds which follow others out go to a new food source, positioned such that the following bird could not have seen birds foraging on it from its position within the colony or roost (i.e. they were not simply showing straightforward local enhancement); and that the follower's prey intake rate was higher as a result of following another bird to that patch than on its previous foraging bout.

LOCATING LARGE-SCALE PREY PATCHES

Comparisons between species

Broom et al. 1976; Buskirk 1976; Crook 1964, 1965; Custer & Osborn 1978; De Vos 1979; Dilger 1960; Erwin 1977, 1978; Fry 1972; Karr 1971; Lack 1966; Newton 1967, 1972, 1976, 1979; Schoener 1968b; Simmons 1967; Stacey & Bock 1978; Walsberg 1977; Ward & Zahavi 1973; Watling 1975; Verbeek 1973; Zahavi 1971a.

Theoretical

Chantrey 1982; Krebs 1974; Kiester & Slatkin 1974; Waltz 1982.

Empirically established - field/flock

Barnard 1980; Krebs 1974; chapter 2.3 of this thesis; (Bertin 1977; Gochfeld & Burger 1982.)

Empirically established - laboratory/roost

De Groot 1980.

Circumstantial - field/flock - competing hypotheses not eliminated.

Hafner et al. 1982; Vines 1981.

Circumstantial - field/flock - passing birds land near foraging flocks, rather than elsewhere or by non-foraging flocks, and begin to forage with them.

Anderson & Horwitz (1979); Armstrong 1946, 1947, 1951, 1971; Ashmole 1963a, 1971; Balda & Bateman 1972; Caldwell 1981; Crook 1964, 1965; Fisher 1954; Frings et al. 1955; Greig-Smith 1978b; Hamilton & Gilbert 1969; Harrington 1978; Hickling 1957; Hinde 1959, 1961; Hinde & Fisher 1951; Hoffman et al. 1981; Houston 1974; Jackson 1938; Kahl 1964; Kushlan 1977; Leck 1971b, 1972; Ligon 1971; Loman & Tamm 1980; Marshall 1961; Meinertzhagen 1959; Murton 1971a; Murton, Coombs & Thearle 1972; Murton & Isaacson 1962; Murton, Isaacson & Westwood 1966; Murton & Westwood 1977; Newton 1967, 1972; Nichols 1912; Pinowski 1959; Thorpe 1951, 1963; Tristram 1899; Verbeek 1973; Vuillemeir 1967; Walsberg 1977; Ward 1965; Willis 1972a.

Circumstantial - field/flock - passing birds are attracted to flocks after changes in the calls, or other behaviour, of birds in the flock.

Frings et al. 1955; Hoffman et al. 1981;

Marshall 1961; Nichols 1912; Pinowski 1959;
Willis 1967, 1972a.

Circumstantial - field experiment/flock - passing birds
land near models (a) increase in number landing with
increasing model flock size.

Drent & Swierstra 1977; Krebs 1974; Murton 1974.

Circumstantial - field experiment/flock - passing birds
land near models (b) increase in number landing with
increasing model flock density.

Murton 1974.

Circumstantial - field experiment/flock - passing birds
land near models (c) increase in number landing with
increasing proportion of models in foraging postures.

Drent & Swierstra 1977; Inglis & Isaacson 1978;
Krebs 1974; Murton 1974.

Circumstantial - field/flock - feeding flocks occur in open
country where flying birds can see others foraging in
fields, but not in densely-wooded areas.

Pinowski 1959.

Circumstantial - field/flock - flocking occurs (or flock
size increases) as food becomes scarcer and/or more patchy.

Balda & Bateman 1972; Cody 1971a; Crook 1965;
Fogden 1972; Hinde 1952; Lovari 1978; Morse
1970; Moynihan 1962; Newton 1967, 1972; Powell
1980; Pulliam et al. 1974; Siegfried 1971a;
Snyder & Snyder 1970; Watling 1975; Williamson &
Gray 1975.

Circumstantial - field/colony - colony members, and/or neighbours within colonies, forage together.

Balda & Bateman 1972; J.W.F. J.W.F. Davis 1975; Erwin 1977; Feare et al. 1974; Horn 1968; Hunt & Hunt 1976a; Krebs 1974; Lack 1966; Newton 1967, 1972; Walsberg 1977; Ward & Zahavi 1973.

Circumstantial - field/colony - colony members leave colony synchronously to forage.

Andersson et al. 1981; Custer & Osborn 1978; Emlen 1971; Evans 1982; Feare et al. 1974; Gaston & Nettleship 1981; Hoogland & Sherman 1976; Horn 1968; Krebs 1974; Ward & Zahavi 1973.

Circumstantial - field/colony - synchronous breeding maximises the number of birds available for local enhancement effects.

Diamond 1976; Emlen 1971; Emlen & Demong 1975; Ward & Zahavi 1973.

Circumstantial - field/colony - colonial breeding occurs (or colony size increases) as food becomes scarcer and/or more patchy.

Crook 1965; Kushlan 1976a, 1976b; Mader 1975; Newton 1967, 1972; Walsberg 1977; Ward & Zahavi 1973.

Circumstantial - field/roost - dispersion patterns from the roost indicate that roost members could be following others to good feeding areas.

Broom et al. 1976; Feare et al. 1974; Ffrench 1967; Hamilton & Gilbert 1969; Hamilton et al. 1967; Houston 1976; Murton et al. 1972; Siegfried 1971a; Ward 1965; Ward & Zahavi 1973; Zahavi 1971a.

Circumstantial - field/roost - roost members switch feeding sites; members of different roost sometimes use the same feeding sites; etc.

Broom et al. 1976; Feare et al. 1974; Murton et al. 1972.

Circumstantial - field/roost - communal roosting occurs (or roost size increases) as food becomes scarcer and/or more patchy.

Broom et al. 1976; Fogden 1972; Gyllin & Kallander 1976, 1977a; Hamilton & Gilbert 1969; Hamilton et al. 1967; Kushlan 1976a; Lack 1966; Newton 1967, 1972; Siegfried 1971a; Ward 1965; Ward & Zahavi 1973; Zahavi 1971a.

LOCATING SMALL-SCALE PREY PATCHES

Theoretical

Chantrey 1982; Morse 1978; Thompson & Vertinsky 1975; Thompson, Vertinsky & Krebs 1974.

Empirically established - field experiment

Roell 1978.

Empirically established - laboratory

Barnard & Sibly 1981; Brockman & Barnard 1979; Krebs 1973; Krebs et al. 1972; Sasvari 1979.

Circumstantial - field/flock - birds observed to change area of foraging in response to another's discovery of food

Alvarez 1975; Austin & Smith 1972; Barnard et al. 1982; Grieg-Smith 1978a; Herrera 1979; MacDonald & Henderson 1977; Morse 1978; Rowley 1978.

Circumstantial - laboratory/flock birds observed to change area of foraging in response to another's discovery of food

Barnard 1978; Barnard & Sibly 1981.

Circumstantial - field/flock - within mixed-species flocks, species overlap more in feeding niche than when in single-species flocks; and therefore may be tending to move to forage where other species are foraging.

Buskirk 1976; Heaney, cited Krebs 1973; Herrera 1979; Krebs 1973 (laboratory); Morse 1978; Ogasawara, cited Krebs 1973; chapter 1.6, this thesis.

A number of studies have investigated situations where initial observations suggested that local enhancement for food-finding might be operating, but failed to find evidence that this was in fact so; or whose evidence suggests that a prey patch-finding interpretation of behaviour may be incorrect. For example, Kruijt et al. (1972) found that black grouse (Lyrurus tetrix) were more attracted to models as their number and density increased; however, this was carried out near lek grounds during the breeding season, and thus serves as an example that to show attraction to conspecifics or models (to show that local enhancement does

occur) is necessary, but not sufficient, to demonstrate that the attraction is to denser prey patches. As well as an attraction to potential mating sites, demonstrated by Kruijt et al., birds which flocked to reduce predation risk (for example) would also be expected to show local enhancement.

Similarly, Davis (1970) found that although starlings (Sturnus vulgaris) did tend to flock more as food became scarcer or patchier, this was also the time of the year when hormone levels were lowest and territorial behaviour least pronounced; Davis speculates that this reduction in hormone level may be the reason flocking occurs and that the fact that food is scarcer and patchier in winter may be coincidentally, and not causally, related to degree of sociality. In some species flock sizes are reduced at times when food is scarcer (Clutton-Brock & Harvey 1978).

The kinds of evidence required to test the 'information-centre' hypothesis have been described in the introduction to this section of the review; there have also been several attempts to test the hypothesis which have failed to find supporting evidence. Andersson et al. 1981, Fleming 1981 and Loman & Tamm (1980) all failed to find recruitment to artificially provided food in black-headed gulls, pied wagtails, and ravens and hooded crows, respectively. Bayer (1981) and Pratt (1980) have questioned

Krebs' (1974) data which claimed to have shown that birds left the colony in groups for the feeding grounds. Snapp (1976) and Counsilman (1974) found that colonially breeding swallows (Hirundo rustica) and communally roosting Indian mynas (Acridotheres tristis) foraged independently of one another and not in flocks.

The food-finding function of mixed-species flocks has also been questioned in some instances. Moynihan (1962) and Willis (1972a) are two examples where the species in the flocks took very different prey whose distributions were unlikely to be correlated. Willis also found that some species left flocks to feed when a good area of prey was located elsewhere (this of course does not necessarily disprove that these species could not have been benefitting previously from the location of other food sources which did correlate in distribution with those of other flock members). Finally, Austin & Smith (1972) and Morse (1970) found that feeding niche overlap decreased when some species came together in flocks, thus reducing the likelihood that they were using other species to locate prey patches.

Benefit: Prey: Efficient Exploitation of Patchy Environments

Apart from social location of prey patches, it is possible to imagine increasing the efficiency with which the total resources of an area are exploited in two further ways. Firstly, if prey patches shift their position in space, then the average distance flown by a bird to gain a given amount of food will be less if all birds fly out from a central 'refuge', than if each flies from a separate fixed territory within the total area (Horn 1968 has demonstrated this simple energy-saving concept mathematically). Secondly, a single flock of birds foraging systematically over an area will decrease the likelihood of individuals foraging in areas recently exploited by another bird. This strategy will be particularly valuable when prey is renewing.

However, simple and intuitively likely as these concepts are, there is as yet no convincing evidence that either definitely occurs in the wild. The best evidence so far has been provided by Drent's (1980) study of barnacle geese (Branta leucopsis). Drent demonstrated a regular, periodic return to different areas. The return time between areas closely matched the time needed for the grass crop to renew its growth. On each visit to a site the geese cropped c.35% of the blade of the main prey (Plantago spp.), and experiments showed that this crop renewed its growth fastest when between 30 and 50% of the blade was cropped. Finally, birds crossing a plot after a flock of

at least five other geese had grazed there stayed for less time than the first flock.

Comparisons between species

Andersson & Gotmark 1980; Pleasants 1979; Stacey & Bock 1978; Walsberg 1977.

Theoretical

Cody 1971a; Hamilton & Watt 1970; Horn 1968; Schoener 1968b; Wiens 1976.

Circumstantial - field/flock - effect on fitness not proven, though behaviour is consistent with the hypothesis.

Balda & Eateman 1971, 1972; Cody 1971a, 1974b; Drent 1980; Emlen 1971; Hamilton & Gilbert 1969; Hamilton et al. 1967; Henty 1979; Horn 1968; MacDonald & Henderson 1977; Morse 1970; Miller 1922; Powell 1980; Short 1961.

Morse (1970) has suggested that members of a species may exploit an environment more efficiently by learning about other species' niches through watching them while foraging in mixed-species flocks, and then avoiding using that niche. This would be of benefit if the other species was superior in terms of either exploitation or interference competition. But no evidence to suggest that this really does occur has yet appeared.

Benefit: Prey: Defence of Feeding Areas

Aggregation could enable birds to defend food resources from other birds of the same species or from dominants of another species. Davies & Houston (1981) have demonstrated that this effect occurs in pied wagtails on winter territories (this study has been discussed in detail in section 2.2.9 above). Other studies of stable groups defending food supplies have failed to demonstrate unequivocally that a single bird could not also defend the resources if it were required to do so.

Theoretical

Schoener 1971.

Empirically established - field/flock

Davies & Houston (1981).

Circumstantial - field/flock - defence observed, but no proof of increased effectiveness of defence at larger group sizes

Birkhead 1981.

Circumstantial - field/colony - defence observed, but no proof of increased effectiveness of defence at larger group sizes

Kinnaird & Grant 1982; Lack 1954; MacRoberts

1970; MacRoberts & MacRoberts 1976; Stacey & Bock 1978; Wolfenden 1978.

Vehrencamp (1978) provides one example where increased group size did not cause an increase in the effectiveness of territory defence; hence the onus is on workers to demonstrate not only that communal defence of resources occurs, but that it is also more effective than solitary defence.

Coombs (1961) and Patterson et al. (1971) are examples which show that some species (in this case the rook) do not actively defend feeding areas but show a certain degree of overlap in range without active defence behaviour observed.

Benefit: Prey: 'Strength in Numbers' Enabling Penetration into Feeding Areas Unavailable to Single Birds

This behaviour may be seen as the converse of the one described in the previous section. A group of one species may be able to penetrate the territory of an individual of another, dominant species, to feed where a single bird is unable to do so. This may perhaps also occur between dominant territory-holding members and the subordinate 'surplus' members of a single species.

Empirically established - field/flock

Moore 1977, Scott 1980.

Circumstantial - field/flock - groups penetrated feeding areas, but no proof is given that prey intake rates improved as a consequence, compared to foraging elsewhere without time spent in agonistic encounters.

Bossema et al. 1976; Dow 1977b; Fisler 1977;
Kodric-Brown & Brown 1978; Roell 1978; Rowley
1978; Stiles 1973; Stiles & Wolf 1970; Wolf 1975.

Benefit: Prey: Flushing of Prey into Availability

Birds may follow other animals and exploit food disturbed by their movements. Such cases are often commensal, and do not necessarily require the presence of conspecifics in a flock for the individual to gain its advantage (indeed, the area immediately around the animal which is flushing the prey may be defended against conspecifics).

The definition of this category is not straightforward. Kleptoparasitism of prey already procured by another bird has been omitted (see review by Brockmann & Barnard 1979) but prey taken which has been flushed, but not yet procured, is included, even if this is prey which the flushing animal could have eaten itself. Also, prey must have been disturbed into availability somehow to be included; associations where birds find prey in faeces or

take parasites from another animal are not defined here as social behaviour, any more than taking invertebrates from cracks in a tree's bark would normally be defined as commensalism.

Examples of this type of association are many, but mainly fall into three categories: terrestrial invertebrates disturbed by grazing ungulates; benthic fauna or flora disturbed to the water surface by diving or wading birds or animals; or flying invertebrates disturbed from foliage. A particular problem with this area (though the same applies to other areas too) is that while many studies document the occurrence of this behaviour, perhaps because it is fairly unusual and conspicuous when it occurs, few give any indication of whether a significant enough proportion of the bird's time is spent in the activity to make it a biologically important phenomenon to the species concerned. Charnov et al. (1976) have modelled some of the parameters involved, while Burger & Gochfeld (1982) is the most comprehensive study yet which attempts to investigate such issues.

Theoretical

Charnov et al. 1976.

Empirically established - field

Burger & Gochfeld 1982; Dinsmore 1973; Emlen & Ambrose 1970; Grubb 1976; Heatwole 1965; Kushlan 1978b; MacDonald 1981; Oniki 1972; Rand 1953; Russell 1978; Siegfried & Batt 1972; Smith 1971.

Circumstantial - field/flock - association observed, but no evidence that prey intake rate increased as a result.

Anderson 1974; Ashmole et al. 1956; Bailey & Batt 1974; Balph & Balph 1977; Bartholomew 1942; Belt 1874; Bent 1923; Beven 1980; Blaker 1969; Boswall 1970; Brosset 1969; Burger & Serruti 1977; Cantello & Gregory 1975; Charnov et al. 1976; Chapin 1939; Cottam et al. 1942; Croxall 1976; Cunningham-van Someron 1970; Custer & Dinsmore 1975; Dawn 1959; Dawson 1975; Davis 1926; Fraser 1974; Gatenby 1968; Gerard 1975; Gochfeld 1978; Greig-Smith 1978a; Grimwood 1964; Halley & Lloyd 1978; Harrison 1979; Hobbs 1958, 1959; Hoffman et al. 1981; Ingram 1944; Jackson 1945; Jones 1975; King 1963; Leck 1971a; MacDonald & Henderson 1977; Mackworth-Praed 1946; Madge 1965; Morse 1970; Mueller et al. 1972; Neave 1910; North 1944; Parks & Bressler 1963; Paulson 1969; Pearse 1950; Pettet 1975; Rand 1954, 1967; Rice 1963; Robson 1975; Rowley 1978; Scott 1972; Short 1961; Siegfried 1971b; Skead 1951, 1966; Swynnerton 1915; Tebbutt 1961; Turcek 1956; Vinnicombe 1976; Watson 1977; Wiese & Crawford 1974; Willis 1966, 1968; Winterbottom 1943, 1949; Zaret & Paine 1973.

Benefit: Prey: Vigilance Decrease Allowing Feeding Rate Increase

Membership of a group may enable a decrease in individual vigilance (for example for predators - see below), and thereby give more time for feeding. Caraco (1979a) has

modelled the operation of such a system based on the earlier work of Pulliam (1973, 1976); fieldwork stemming from this approach has been described in detail in section 2.2.9 above.

It should be noted that demonstrating correlations between group size, vigilance and time spent feeding is necessary, but again by no means sufficient to prove that it is the decrease in vigilance which causes increased prey intake rate. It is also possible that decreased prey intake rate (for example because the bird is on a poor patch) causes an increase in looking up for the whereabouts of better feeding areas. Both behaviours are correlated with flock size because smaller flocks tend to occur on the poorer prey areas. Barnard (1980), Krebs (1974), and chapter 2.3 of this thesis present evidence that this indeed seems to be happening in three instances where simultaneous correlations between flock size, vigilance and feeding rates were found. To prove that it is vigilance rates which cause variations in prey intake rates, and not the other way round, a predation effect on vigilance, mediated through flock size, must be demonstrated - for example by demonstrating that birds in lower flock sizes are always more vigilant than larger flocks, no matter what prey density they are feeding on; or by demonstrating that equal flock sizes have different average vigilance rates when in the presence or absence of a predation threat (for

example, at different distances from cover, or when a hawk is in the vicinity). Barnard (1980), Caraco (1979b) and Caraco et al. (1980a) are examples of studies where such control is found in studies of wild birds; laboratory studies do not encounter the same problem since prey densities are usually held constant in these studies.

Theoretical

Caraco 1979a, 1980a & b, 1981; Dimond & Lazarus 1974; Lazarus 1979a; Pulliam 1973, 1976; Treisman 1975b.

Empirically established - field

Barnard 1980; Caraco 1979b; Caraco et al. 1980a; Feare et al. 1974.

Empirically established - laboratory

Lazarus 1979a, 1979b; Powell 1974.

Circumstantial - field/flock - direct measurement of flock size, vigilance rates and prey intake rates, but direction of causality not established.

Abramson 1979; Bertram 1980; Burger & Howe 1975; Buskirk 1976; Fairchild et al. 1977; Jennings & Evans 1980; Kenward & Sibly 1978; Murton 1968; Murton, Isaacson & Westwood 1971; Rubenstein et al. 1977; Silliman et al. 1977; Smith & Evans 1973.

Circumstantial - field/flock - no quantification of either vigilance or prey intake rates (or both) is made.

Austin & Smith 1972; Dimond & Lazarus 1974; Feare & Inglis 1979 (laboratory); Lack 1954, 1968; Lazarus 1972; Lazarus & Inglis 1978; Morse 1977, 1978; Morton & Shalter 1977; Murton & Isaacson 1962; Pulliam et al. 1974; Siegfried & Underhill 1975; Willis 1972a.

Many studies demonstrate that individual vigilance rates decrease with increasing group size, but prefer to relate this only (or mainly) to a predator-detection advantage. These studies are listed in that section, but an increase in time available for feeding is one possible consequence in these studies also.

Benefit: Prey: Social Facilitation of Feeding Rates or Prey Types

It may be more advantageous for an individual to concentrate its search on the most abundant of several available prey types; it may be more efficient to concentrate on a specific type of feeding action to exploit a particular prey type; or a prey-type may be most efficiently exploited by a certain ratio of pecks to paces or a certain number of paces per unit time. Birds recently arrived within the flock, or inexperienced birds, may increase their feeding efficiency by copying the behaviour of birds already foraging within the flock. The

behavioural response concerned is termed social facilitation, and differs from local enhancement by involving the elicitation of a particular behavioural response, rather than merely the directing of the individual's attention to part of the environment (Thorpe 1963).

Effects of these kinds operating within flocks have not frequently been studied outside of laboratory conditions. Murton, Isaacson & Westwood (1971) provide detailed observational data of individually-marked woodpigeons (Columba palumbus) which suggested that some birds attempted to copy the foraging rates of others. In winter these birds foraged in stably structured flocks in which the same individuals were usually found either in the centre of the flock or on the edge. 'Edge' birds weighed less, lost weight faster, showed evidence of adrenal stress, and had lower rates of survival. They had lower feeding rates and changed flocks more frequently than 'centre' birds. They watched centre birds while foraging, and their pacing rates were correlated with those of centre birds; but their foraging was disrupted by the progress of the centre birds displacing them. The result of copying the centre birds' pacing rate did not, however, always increase feeding efficiency, since the disruption experienced by displacement and watching resulted in a lower proportion of clover leaf ingested compared to the ingestion of poorer quality species, and also to a higher

proportion of larger, older (and therefore less nutritious) pieces of clover leaf - the edge birds were less selective in their feeding. Subsequent field experiments, with baited plots (Murton 1971c), showed that birds foraging in flocks switched to foraging for the most profitable of the prey types offered in a way which suggested they were copying the foraging preference of birds experienced at foraging for that prey type, resulting this time in increased efficiency of prey exploitation.

Any further direct demonstration of such social facilitation of feeding in the wild has not appeared, though the description of the spread of milk-bottle feeding by wild tits (Parus spp.) and, subsequently, other species, suggests that the phenomenon may occur more frequently than the lack of research suggests. Clayton (1978) provides a recent review of the topic.

Empirically established - field experiment

Murton 1971a.

Empirically established - laboratory

Alcock 1969a; Dawson & Foss 1965.

Circumstantial - field/flock - copying demonstrated, but no evidence given to show that feeding rates are increased as

a result compared to individual foraging.

Fisher & Hinde 1949; Hinde & Fisher 1951; MacLean 1970; Morse 1973; Hurton, Isaacson & Westwood 1966, 1971.

Circumstantial - laboratory/flock - copying demonstrated, but no evidence given to show that feeding rates are increased as a result compared to individual foraging.

Allee 1931, 1938; Evans & Patterson 1971; Feare & Inglis 1979; Klopfer 1959, 1961; Krebs 1973; Krebs et al. 1972; Lazarus 1979b.

In addition, Alcock (1969b), Turner (1965) and E.O. Wilson (1975) have produced some circumstantial evidence to suggest that new microhabitats, as well as foraging rates or prey types, may be exploited through social facilitation.

Benefit: Prey: Cooperative Hunting

The true cooperative hunting of prey is an advanced form of social behaviour not frequently found in birds (or at least, not frequently documented). The prey may be too large or elusive for single animals to catch, or else of a type which can only be taken less efficiently by singletons. It is only the former situation in which advanced cooperative behaviour is seen. This type of behaviour has only been described anecdotally for birds, the most remark-

able being the descriptions by Gurney (1861) and Meinertzhagen (1959) of ground hornbills (Bucorvus abyssinicus) killing large snakes. The latter, for example, describes an incident where seven birds surrounded a nine foot long black mamba and made darting pecks at the snake for about twenty minutes. The snake struck at the birds, which put their wings down to take the bites, and as the snake was striking at one bird, the others were able to peck at the snake's body. The snake in the end was exhausted; the birds then pulled the snake to pieces and fed on it. Similar anecdotes have been published (for example Dixon 1933, Sharp 1951) describing magpies dodging in to peck at an eagle kill alternately; while the eagle was striking at one bird its 'partner' could feed.

Of course the problem with such anecdotes is that they do not prove that the birds concerned were truly cooperating, or merely performing normal, individual feeding actions which were successful with the particular prey item concerned only because other individual birds were also doing the same thing at the same time. This latter situation is clearly what happens when gulls or skuas (*Stercorariidae*) chase other birds as a group, and the chased birds disgorge more frequently as more birds join the chase; or where one crow is able to steal an egg because the brooding bird is chasing off another crow which has attempted to take the egg itself. In fact such behaviour

might be seen as a kind of 'strength in numbers' type of behaviour, the difference between that category and the present one being that in the former case grouping was required not to feed on the prey itself, but simply to allow access to the area within which to feed.

Similarly, several species of water birds have been claimed to form into lines to herd fish into a confined semi-circle in front of the flock. However, these studies have not shown that the birds cooperate to form a semi-circle; it could be that birds individually move to the back edge of an elliptical school which is moving away. A semi-circle of birds would then form as an aggregation in response to the shape and movements of the prey, and not as a device to manipulate the distribution of the fish.

The studies cited in the 'empirically established' section below are all examples where birds performed feeding actions which were part of their normal repertoire, but where the presence of others doing the same thing directly caused increased feeding success.

Empirically established - field

Andersson 1976; Arnasson & Grant 1978; Furness 1978; Hatch 1970, 1975; King 1980; Montevecchi 1979; Munro & Bedard 1977; Taylor 1979; Verbeek 1977.

Circumstantial - field/flock - descriptions of apparent group hunting, but no evidence produced to show that feeding rate is increased compared to solitary foraging.

Bratholomew 1942; Cottam et al. 1942; Dixon 1933; Emlen & Ambrose 1970; Friedmann 1967; Gurney 1861; Meinertzhagen 1959; Miller 1979; Rand 1954, 1967; Sharp 1951; Taylor 1978.

It should be noted that not necessarily all members of the foraging group will benefit from an increase in intake rate of prey - for example Arnasson & Grant (1978), Hatch (1970, 1975), Taylor (1979) and Verbeek (1977) all show that only a proportion of optimally-positioned birds increased their prey intake rates. In fact in these studies although the success rate of foraging attempts increased with increasing group size, the average prey intake rate for a group member was not greater, and in some cases was less, than when foraging alone. Of the studies cited above only King (1980), Munro & Bedard (1977) and Taylor (1979) have shown that not only is the success rate of a group attack higher as group size increases, but also that prey intake rate is increased for the average flock member.

Benefit: Prey: Food Stealing from Other Flock Members

Dominant individuals may benefit from joining a flock

by stealing prey items which other flock members have already procured. As stated above in the 'flushing' of food section, kleptoparasitism or other interspecific predatory behaviours are not included.

Theoretical

Parker 1974.

Empirically established - laboratory

Baker 1978; Baker et al. 1981; Barnard & Sibly 1981; Feare & Inglis 1979.

Conversely, Kushlan (1978a) found that great egrets (Egretta alba) who robbed other egrets or herons were actually less successful, in terms of short-term energy intake, compared to birds which adopted the more normal stand-and-wait foraging technique of this species.

Benefit: Prey: Reduction of the Risk of Starvation

There is some evidence that foraging in a flock can reduce the likelihood of starvation (or satiation) due to a reduction in the variance of feeding rates occurring during different foraging bouts. This may perhaps be due to flocks tending to occur more frequently on patches of a

certain minimum content, due to birds on a good patch having a longer stay-time and therefore allowing a flock of birds to build up on a patch rather than individuals continually moving to forage elsewhere. The increased number of birds present may mean that mean intake rate of prey does not increase, but the chances of arriving on a patch which does not contain enough food for survival is less.

Theoretical

Caraco 1981; Chantrey 1982; Thompson et al. 1974.

Circumstantial - field/flock - reduction in variance of feeding rate demonstrated, but no evidence that the risk experienced by single birds is sufficient to reduce fitness.

Krebs 1974.

Circumstantial - laboratory/flock - reduction in variance of feeding rate demonstrated, but no evidence that the risk experienced by single birds is sufficient to reduce fitness.

Baker 1978; Baker et al. 1981.

Benefit: Predation: 'Selfish Herd' Advantages

The more animals there are in a group, the less is the likelihood of any one individual being taken on each separate attack by a predator. Similarly, many animals breeding all at the same time will reduce the period over which eggs and young are available to a given number of predators, 'swamping' the predators and leading to decreased levels of predation. Hamilton (1971) coined the phrase 'selfish herd' to describe such simple statistical consequences of an increase in group size.

Of course, whether or not an individual benefits from such a reduction in the likelihood of being taken depends on other things - for example whether different sized aggregations attract the same number of predator attacks, or whether the success rate of predator attacks is equal on groups of different sizes. Only when these factors are also quantified can an accurate assessment be made of the true relative 'selfish herd' advantages of different group sizes. Page & Whitacre (1975) provide an example where such quantification was made, and the advantage of flocking over solitary behaviour established.

A problem which is often illustrated by studies of colonially breeding birds is a failure, having demonstrated a significant difference in breeding success between birds in different group sizes or densities, to adequately

establish that the cause of such differences is differential predation pressure. Possible confounding variables (for example age or experience differences correlating simultaneously with colony size and breeding success) are usually unmeasured and often not even considered; and most of these studies do not even quantify predation rates but merely assume that observed predation varies in it's rate between different colony sizes, and no quantitative elimination of other possible causes of differential success (e.g. starvation) is made.

Relatively few studies have shown pure 'selfish herd' advantages, possibly because many animals show active behaviour towards predators (see the following two sections on defense and detection); these animals may also be enjoying 'selfish herd' advantages simultaneously, but it would be very difficult to separate the effects of active behaviour from those connected with the 'selfish herd' mechanism.

Comparisons between species

Buskirk 1976; Crook 1964, 1965; Lack 1968; Pulliam & Mills 1977; Wiley 1974; Willis 1972b, 1973.

Theoretical

Charnov & Krebs 1975; Hamilton 1971; Treisman 1975a, b; Trivers 1971; Vine 1971, 1973; Williams 1964.

Empirically established - field/flock

Page & Whitacre 1975.

Empirically established - field/colony size

Fautin 1941; Robertson 1973.

Empirically established - field/colony centre versus edge

Andersson & Wiklund 1978 (field experiment); Fuchs 1977 (field experiment); Kruuk 1964 (field experiment); Siegel-Causey & Hunt 1981.

Empirically established - field/colony density

Cody 1971b.

Empirically established - field/colony synchrony of breeding

Birkhead 1977; Dyrce et al. 1981; Fautin 1941; Parsons 1971; Robertson 1973; Vermeer 1970 (field experiment);

Circumstantial - field/flock - individual likelihood of being taken by a predator decreased with increasing flock size, but no quantification of frequency of attacks on

different flock sizes, etc.

Munro & Bedard 1977.

Circumstantial - field/flock - no quantification to prove that predation rate decreased with increasing flock size.

Bedard & Munro 1975; Bertram 1980; Bourne 1980; Goss-Custard 1970b; Grant 1971; Hamilton 1971; Lazarus 1972; Owens & Goss-Custard 1976; Willis 1972a, 1972b, 1973.

Circumstantial - field/flock - birds approached by a potential predator move closer to other birds, but no quantification that this reduces individual likelihood of predation.

Ainley 1972; Buckley & Buckley 1972; Kruijt et al. 1972 (field experiment); Willis 1972a.

Circumstantial - field/colony - breeding success increased with increasing colony size, but no quantification to prove that this was due to risk of individual predation decreasing with increasing colony size.

Burger 1979; Darling 1938; Fisher 1952; Gaston & Nettleship 1981; Langham 1974; MacLean 1973; Nelson 1966; Veen 1977.

Circumstantial - field/colony - breeding success increased in the colony centre, but no quantification to prove that this was due to risk of individual predation decreasing in the colony centre.

Balda & Bateman 1972; Cullen 1960; Dexheimer & Southern 1974; Emlen 1952b; Feare 1976; Gochfeld 1980a; Langham 1974; Orians 1961a; Patterson 1965; Penney 1968; Reid 1964; Siegfried 1972; Spurr 1975; Taylor 1962; Tenaza 1971; Veen 1977.

Circumstantial - field/colony - breeding success increased with increasing colony density, but no quantification to prove that this was due to risk of individual predation decreasing with increasing colony density.

Birkhead 1977; Darling 1938; Harris 1980.

Circumstantial - field/colony - breeding success increased with increasing breeding synchrony in the colony, but no quantification to prove that this was due to risk of individual predation decreasing with increasing colony synchrony.

Birkhead 1977; Brown 1967; Burger 1979; Darling 1938; Erwin 1971; Feare 1976; Harris 1969b; Kadlec & Drury 1968; Kruuk 1964; Langham 1974; Nelson 1966; Parsons 1975; Patterson 1965; Veen 1977; Vermeer 1970.

Circumstantial - field/colony - breeding synchrony exists in the colony, but no quantification to prove any effect on fitness.

Balda & Bateman 1972; Davis & Dunn 1976; Elgood & Ward 1963; Hoogland & Sherman 1976; Schaller 1964; Windsor & Emlen 1975.

Circumstantial - field/roost - no quantification to prove that predation rate decreased with increasing roost size.

Fleming 1981; Gadgil 1972.

It was stated in the introduction to this section that the simple statistical truth behind the 'selfish herd' concept - that as group size increases any individual's chance of being taken on any one predator attack decreases

- will only be of true benefit if the frequency and success-rate of attacks on larger group sizes does not increase too much. A large number of studies have looked for, but failed to find differential individual predation rates between different group sizes (or have even found increased individual predation risk with increasing group size - these latter references are discussed in the disadvantages sections below). Though most of these have not quantified why this should be so, it is most likely to be the result of larger groups attracting more predators to them.

Rudebeck (1950-1) found that predators did not have a greater success rate when attacking smaller flocks or solitary birds, but did not quantify the relative frequency with which different flock sizes were attacked. Lutz (cited Kenward, 1978) found that predator success was actually higher on larger flocks of corvids because flock members got in one another's way as they tried to escape. Hoogland & Sherman (1976), Knopf (1979), Lohrl & Gutscher (1973), Smith (1943), Snapp (1976) and Vehrencamp (1978) all found no relation between breeding colony size and individual rate of predation suffered by nests. Ashmole (1963b) found that predation rates were so high in certain sooty tern (Sterna fuscata) colonies that only c.1-2% of chicks fledged, and that frigate birds (Fregata aquila) appeared to be attracted to attack only at colonies where a

large number of chicks were available. Coulson (1968, 1971, 1972), Montevecchi (1978) and Ryder (1980 - review) all found increases in breeding success in larger colonies, but were able to show that these were due to age or habitat differences, and not to individual predation rate.

Balda & Bateman (1972), Horn (1968), Knopf (1979), and Montevecchi (1977) found that there was no consistent difference in predation rates suffered by individual nests on the edge or in the centre of colonies. Penney (1968) found an effect in one season, but not in a second. Emlen (1971) found that breeding success was lower on the edge of a colony of sand martins, but this was due to a greater tendency to abandon nest sites for other reasons - individually suffered predation rates did not differ.

Buckley & Buckley (1972), Butler & Trivelpiece (1981), Dexheimer & Southern (1974), Goransson et al. (1975), Hunt & Hunt (1975), Patterson (1965) and Tinbergen et al. (1967) all found that predation was higher in denser colonies, sometimes as the result of cannibalism, but also perhaps because increased interference from neighbours left eggs exposed more frequently. Cody (1971b) is of particular interest - he showed that predation rates were reduced in denser colonies (thus they enjoyed a 'selfish herd' advantage), but this benefit was outweighed by the cost of increased conspecific interference, to the extent that

fledging rates actually decreased in the denser colonies. Thus this study emphasises once again the way in which different mechanisms may be operating together in any one situation.

In a rather similar vein Brown (1967), Erwin (1971), Harris (1969b), Nisbet & Drury (1972), Orians (1961), Parsons et al. (1976) and Smith (1943) have shown a seasonal decline (or increase) in breeding success which does not correspond to the pattern of breeding synchrony seen in colonies; these studies have shown that even if a 'selfish herd' advantage exists in breeding synchronously, birds could still be better off breeding asynchronously since the advantages of breeding earlier (or later, as the case may be) more than outweighed any cost which may have been incurred from increased predation.

Bryant (1975), Coulson & White (1956, 1960, 1961), Emlen & Demong (1975), Harris (1969a) and Parsons (1975) found that asynchronous breeders did suffer lower breeding success, but demonstrated that this was due not to predation but to other factors (starvation or age/experience differences). Thus the danger of not measuring such possible confounding variables is once again emphasised.

Burger (1974b) and MacRoberts & MacRoberts (1972) found that synchrony of breeding did not exist at the colonies studied, and thus could not contribute a 'selfish

herd' effect. The latter is interesting in that the colonies studied were those of herring gulls and lesser black-backed gulls (Larus argentatus and L. fuscus), species which have quite frequently been shown to display synchrony at other colonies (Darling first recorded synchrony within herring gull colonies).

Finally, one may note that even if synchronous breeders do suffer lower individual predation rates, the direct cause of this is not necessarily the result of a 'selfish herd' reduction in the statistical likelihood of suffering a predator attack, but possibly because asynchronous breeders may (for example) find food harder to collect, and thus leave the nest unguarded from predator attack for longer periods.

Benefit: Predation: Detection of Predator Approach

As well as the rather passive advantages offered by the 'selfish herd', birds may show active behavioural means of reducing the effect of predation upon them or their nests; the advantages offered by some of these behavioural mechanisms may increase with increasing group size.

If each bird is vigilant for a standard time; if the vigilance bouts of any one individual are randomly distri-

buted in time; and if the bouts of any one individual are independent of the timing of those of other birds; then the probability of at least one bird being vigilant when a predator approaches will increase with increasing group size. If the vigilant bird alerts the others when it detects a predator approach; if earlier detection leads to earlier escape reactions; and if earlier reactions means increased likelihood of a predator's attack failing; then individual predation risk can be reduced as group size increases. Only one study (Kenward 1978) has produced evidence to show that all of these conditions are fulfilled; and even this study employed falconry techniques, and did not study naturally-occurring predation (woodpigeons under attack by trained goshawks, Accipiter gentilis, were studied). Other studies, at best, show only that detection or reaction likelihood is increased; no other study also demonstrates quantitatively that earlier detection or reaction definitely reduces the probability of the predator making a kill.

Elgar & Catterall (1981) and Treherne & Foster (1980), building upon Pulliam (1973), have shown by simulation that the increased likelihood of detection of an approach very quickly reaches an asymptote. The exact group size past which increased likelihood of detection becomes negligible will of course vary depending on the value of certain parameters (for example the probability that any bird will

detect the predator; the time the predator takes to make its final detectable approach; or the length of the individual bouts), but their simulations employing values from field studies suggest that detection probabilities for many foraging flocks will not increase meaningfully once flock size exceeds around 10 birds.

However, because the asymptote is so quickly reached, it is the case that individual vigilance rates may drop as group size increases without any meaningful drop in the probability of a predator's approach being detected. A drop in the amount of time spent in individual vigilance leaves more time for other activities, for example feeding - as has already been described above. Studies which show such a relationship between group size and individual vigilance rates, but which do not attempt to quantify what the increased time is used for, nor quantify the effect of such a relationship upon actual detection of a predator approach, have been included in this section rather than any other. However, it will be clear from what has been written above that such data are insufficient to demonstrate an advantage from increased likelihood of predator-detection.

Theoretical

Elgar & Catterall 1981; Lazarus, cited Dimond & Lazarus 1974; Pulliam 1973, 1976; Stinson 1980;

Treherne & Foster 1980; Treisman 1975a, b.

Empirically established - field experiment/flock

Kenward 1978.

Circumstantial - field experiment/flock - faster reaction times to predator appearance as group size increases, but no proof of predation rate decrease.

Grieg-Smith 1981; Kenward 1978; Siegfried & Underhill 1975.

Circumstantial - laboratory/flock - faster reaction times to predator appearance (or novel stimulus) as group size increases, but no proof of predation rate decrease.

Lazarus 1979a, b; Powell 1974.

Circumstantial - laboratory/flock - faster reaction times to a conspecific taking flight as group size increases, but no proof of predation rate decrease.

J.M. Davis 1975.

Circumstantial - field/flock - individual vigilance decreases as group size increases, but no proof that predator-detection rate or reaction time increases, or predation rate decreases.

Abramson 1979; Burger & Howe 1975; Dimond & Lazarus 1974; Drent & Swierstra 1977; Elgar & Catterall 1981; Inglis & Isaacson 1978; Jennings & Evans 1980; Lazarus 1978; Lazarus & Inglis 1978; Murton 1967, 1968; Smith 1977; Willis 1972a.

Circumstantial - laboratory/flock - individual vigilance decreases as group size increases, but no proof that predator-detection rate or reaction time increases, or predation rate decreases.

Powell 1974.

Circumstantial - field/flock - individual vigilance probably decreases with group size increases, but no quantification of this.

Allee 1938; Balda et al. 1972; Bates 1863; Boswall 1970; Feare et al. 1974; Galton 1883; Goss-Custard 1970b; Lack 1954, 1968; Lazarus 1972; Morse 1970, 1977, 1978; Moynihan 1962; Murton & Isaacson 1962; Murton et al. 1971; Newton 1967, 1972; Owens & Goss-Custard 1976; Powell 1980; Rowley 1978; Willis 1972a.

Circumstantial - field experiment/flock - fewer birds land at model flocks with increased proportion of the models in vigilant posture.

Inglis & Isaacson 1978.

Circumstantial - field experiment/colony - faster reaction times to predator appearance as group size increases, but no proof of predation rate decrease.

Hoogland & Sherman 1976; Neuchterlein 1981.

Circumstantial - field/colony - individual vigilance probably decreases with group size increases, but no quantification of this.

Lack 1954; Newton 1967, 1972; Ricklefs 1981.

Circumstantial - field/colony - frequency of alerting calls probably increases with group size increases, but no quantification of this.

Hoogland & Sherman 1976; Watson & Dickson 1972; Windsor & Emlen 1975.

Circumstantial - field/roost - individual vigilance probably decreases with group size increases, but no quantification of this.

Balda et al. 1972; Broom et al. 1976; Counsilman 1974; Gadgil 1972; Gadgil & Ali 1976; Lack 1954; Newton 1967, 1972; Zahavi 1971.

A number of studies related to this question have shown, yet again, the importance of identifying and quantifying all relevant and confounding variables. Kenward (1978) and Murton et al. (1971) identified an important confounding variable by demonstrating that solitary woodpigeons weighed less and were suffering from adrenal stress; thus it is impossible to know whether the greater success of predator attacks on solitary birds was due to their slower detection and reaction to the predator approach, or to the fact that their poorer condition made them easier prey. Birds in flock sizes greater than one did not differ systematically in condition, and hence Kenward's data showing increasing predator success with increasing flock size (whilst omitting singletons from the analysis) are not contaminated by the confounding variable of condition.

Grieg-Smith (1981), and Siegfried & Underhill (1975)

found that flock size was not unambiguously related to reaction times to a predator appearance. Both studies found that single birds, or very low flock sizes, reacted to a predator's appearance as quickly as some of the medium sized flocks, because they were much more vigilant. This will have reduced the amount of time left for other things, of course, and thus have been disadvantageous - but simply in terms of the predator detection hypothesis, they were not at a disadvantage by being in a small group size. The latter study also found that the largest groups reacted slower than some of the smaller ones - this time because they spent less time vigilant due to a rise in time spent in agonistic encounters.

Patterson & Makepeace (1979) found that although vigilance rates of male shelducks (Tadorna tadorna) were related to colony size, detection rates of a predator's appearance were not. Barnard (1980), Bertram (1978), Hardy (1976), Krebs (1974), Lazarus & Inglis (1978), Smith (1974, 1977) and chapter 2.3 of this thesis, either show no relation between group size and vigilance, or that at least some of the vigilance has functions other than the detection of a predator. Gaston (1977) found that the 'sentinel' behaviour of jungle babblers (Turdoides striatus) was not correlated with predator activity. These studies show that the assumption that vigilance is necessarily for predator detection can be incorrect.

Broom et al. (1976), Cheke (1977), Gurr (1968), Shaw (1979), Siegfried (1971a), and Ward (1965) show that a predator can take an individual from a group without group members other than those immediately adjacent being alerted. Thus the detection of a predator will not necessarily be communicated to other group members.

Benefit: Predation: Defence against Predator Attack

There are a number of behavioural ways in which grouping might increase the effectiveness of a bird's defence against predator attack. Mobbing of a predator may be more effective when performed by a group than by a single bird; calls or behaviour may help to coordinate a group escape response; aggregations may serve as more passive defences by presenting a physical deterrent to a fast-moving predator which may risk injury if it attacks a close-packed group; or the presence of many prey may confuse a predator and prevent it from concentrating its attention on the chase and capture of one individual bird.

There is more than one way in which mobbing behaviour may reduce predation rates. This section lists studies which have investigated whether communal mobbing affects predation rates, but does not attempt to split them according to the exact behavioural mechanism, since none of the

studies offers more than circumstantial evidence to support the relevance of one mechanism over any other. Curio (1978) lists the following possible mechanisms, and lists the studies which support each speculated mechanism:

1. Mobbing silences nestlings so that predators are not attracted to the nest.
2. By joining a group, rather than mobbing singly, a bird will entail 'selfish herd' advantages.
3. More birds mobbing means increased confusion for the predator, and less effective attack.
4. A large number of birds mobbing may persuade a predator to leave an area and try elsewhere.
5. Mobbing may indicate to a predator that it has been detected, and that an attack will be ineffective.
6. Mobbing may alert other birds to a predator's presence.
7. Mobbing may attract an animal to prey on the predator.
8. An inexperienced bird may learn by observation of others mobbing which animals or places are dangerous.
9. Mobbing may cause a predator to drop a bird which it has already caught.

This area is possibly one of the worst for inadequate quantification or control of confounding variables. To list a large number of these studies as offering even circumstantial evidence to support a causal link between the behaviour observed and any effect on predation rate, is to be very generous. Not one study exists which establishes with reasonable certainty that observed differences in predation rate are due to the action of group defence, and many do not quantify predation rates at all. Andersson (1976) probably has the strongest evidence: the number of kittiwakes (Larus tridactylus) mobbing great skuas (Catharacta skua) was significantly higher before unsuccessful than successful attacks.

Circumstantial - field/flock - Communal mobbing occurs, but no proof that predation rates are reduced.

Alison 1976; Bourne 1977; Curio 1978; Emlen 1973; Ficken & Witkin 1977; Fry 1977; Galef 1976; Lack 1954; Lazarus 1972; Lorenz 1966; Perrins 1968; Rohwer et al. 1976; Smith & Holland 1974; Swynnerton 1915; Wiley 1971; other references in Curio 1978.

Circumstantial - field/flock - calls and/or behaviour occur which appear to coordinate escape responses, but no proof that predation rates are reduced.

Balphy & Balphy 1977; MacDonald & Henderson 1977; Marler 1955, 1956; Morse 1970; Owens & Goss-Custard 1976; Thake 1981; Wiley 1971.

Circumstantial - field/flock - confusion of a predator increases with increasing group size; no proper quantification of this or of predation rates.

Cody 1974a; Crook 1960; Davis 1980; Grinnel 1903; Humphreys & Driver 1970; Lazarus 1972; Lorenz 1966; Marler 1955, 1956; Miller 1922; Morse 1970; Owens & Goss-Custard 1976; Powell 1974; Sharp 1951; Willis 1972a; Wynne-Edwards 1962.

Circumstantial - field/flock - effectiveness of a group as a physical deterrent increases with increasing group size; no proper quantification of this or of predations rates.

Crook 1960; Hamilton 1971; Humphreys & Driver 1970; Kruuk 1964; Lack 1954; Lazarus 1972; Meinertzhagen 1959; Owens & Goss-Custard 1976; Tinbergen 1951.

Circumstantial - field/colony - communal mobbing occurs, predation rate decreases (or breeding success increases) with increasing group size, but no strong demonstration than other possible explanations have been discounted.

Alvarez 1975; Andersson 1976; Clark & Robertson 1979; Dyrce 1977; Dyrce et al. 1981; Kinnaird & Grant 1982; Mountford 1957; Olsson 1951; Patterson 1965; Slagsvold 1980b; Veen 1977; Vehrencamp 1978; Wiklund 1979; Wiklund & Andersson 1980; Wolfenden 1978.

Circumstantial - field experiment/colony - communal mobbing occurs, predation rate decreases with increasing group size, but no strong demonstration than other possible explanations have been discounted.

Fuchs 1977; Goranson et al. 1975; Kruuk 1964; Slagsvold 1980b.

Circumstantial - field/colony - Communal mobbing occurs,

but no proof that predation rates are reduced.

1977;

Balda & Bateman 1972; Buckley & Buckley 1979; Burger 1974a; Burger & Hahn 1977; Collias & Collias 1964; Cullen 1960; Erwin 1979; Hoogland & Sherman 1976; Horn 1968; Kruuk 1976; Lack 1968; Lohrl & Gutscher 1973; Mader 1975; Heinert-zhagen 1959; Newton 1967, 1972; Rand 1967; Sears 1979; Slagsvold 1980a; Snyder 1974; Walsh & Walsh 1976; White & Springer 1965.

Circumstantial - field/roost - Communal mobbing occurs, but no proof that predation rates are reduced.

Braestrup 1963; Counsilman 1974; Gadgil 1972; Gadgil & Ali 1976; Lack 1968.

Circumstantial - field/roost - aerial convolutions occur, but no proof that predation rates are reduced.

Dickson 1979.

A number of studies show that communal defence is not shown: Burger & Hahn (1977), A numr (1967), Burger & Hahn (1977),

Krebs (1974), Milstein et al. (1970), Roskaft (1980), Snapp (1976) and Taylor & Wodzicki (1958). Others have shown that it may occur, but be ineffective in reducing predation rates: Ashmole (1963b), Blem (1979), Burger (1974b), Burger & Lesser (1978), Chandler (1979), Cody (1971b), Emlen et al. (1966), Hardy (1976), Horn (1968), Lemmetyinen (1971), Smith (1943) and Windsor & Emlen (1975). Widsor &

Emlen (1975) also found that mobbing tended to be most intense in solitary nesting swallow (Hirundinidae) species, rather than the other way round.

Benefit: Predation: Aggregated Prey are More Difficult to Locate

Taylor (1976) has shown experimentally in the laboratory that grouping can reduce predation rates by making the available prey of an area more difficult for a predator to locate. Trivers (1971) and Vine (1973) have considered this theoretically. However, Taylor (1977) has shown that by making the experiments somewhat more realistic, aggregated prey can be heavily penalised once the first patch has been located (references have already been given above to field studies which showed that denser colonies could suffer greater predation rates).

Benefit: Reproduction: Access to Opposite Sex

That regular access to the opposite sex in winter flocks or early gatherings at the breeding colony actually increases fitness has only fairly weak circumstantial evidence to support it. Some studies (e.g. Ekman 1979) show that individuals tend to mate with a member of the winter group; but of course this does not provide any evidence to show that the winter group is necessary for, or increases the likelihood of, finding a suitable mate.

Circumstantial - field/flock, colony or roost - various kinds of weak circumstantial evidence only.

Brown 1975; Ekman 1979; Emlen 1973; Goodwin 1976; Gurr 1968; Kruijt et al. 1972 (field experiment); Lorenz 1966; Siegfried et al. 1977; Smith 1977; Watson & Dickson 1972; Willis 1972b.

Benefit: Reproduction: Location of Good Nesting Sites

As with the preceding section, there is really no proper evidence on this proposed effect of grouping. For example, Patterson & Makepeace (1979) provide a variety of circumstantial evidence to suggest that this occurs in shelducks - for example, successful breeders in the previous year tended to land in unoccupied areas more frequently, and were more often seen alone. The authors

suggest that this may be because they already know of good sites and do not need to land near other birds, or associate with them, in order to find one. However, some of the relationships were not supported statistically, and it does not require much imagination to think up alternative possible explanations for the data.

Circumstantial - field/flock, colony or roost - various kinds of weak circumstantial evidence only.

Klopfer & Hailman 1965; Koskomies 1957; Patterson & Makepeace 1979.

Benefit: Reproduction: Communal Breeding

Group breeding (where non-breeding birds are involved to varying extents in parental care or territory maintenance) can have varying consequences for different members of the group. This area is one where possible cause and effect between group size and fitness is difficult to establish, since there is a particular problem with the confounding variables of age and experience of the breeding birds, and/or territory size and quality, confounding any observed relationship between group size and fitness. This has already been described in some detail in section 2.2.9 above, and the best study so far demonstrating control of

confounding variables (Brown & Brown 1981) described.

The proposed effects of group breeding are numerous, but the most frequently cited include greater production of nestlings, sharing of the work load increasing the breeders' survival, maintenance of a larger or better territory through increased effectiveness of territorial defence, experience at breeding gained by the non-breeders, and likelihood of inheriting a territory increasing for non-breeders. The increased production of offspring may occur through faster feeding rates, better nest protection, sharing of work load, or maintenance of a better quality territory. As with the section on communal mobbing above, no attempt is made to list which studies favour which mechanism, since in most cases no real evidence is produced to support one interpretation over another. Brown et al. (1978), Tarboton (1981), Vehrencamp (1978) and Verbeek & Butler (1981) all show that feeding rates were not faster in groups, yet breeding success did increase; thus at least some studies have eliminated one of the possible mechanisms, even if it is difficult to strongly establish the true mechanism(s) involved.

Theoretical

Brown 1978, Emlen 1978, 1982b.

Empirically established - field

Brown et al. 1978.

Empirically established - field experiment

Brown & Brown 1981.

Circumstantial - field - Lifetime personal fitness increases with increasing group size; possible causes other than group size probably not operating, but confounding variables not actually quantified.

Kinnaird & Grant 1982; Vehrencamp 1978.

Circumstantial - field - Annual breeding success increases with increasing group size; possible causes other than group size probably not operating, but confounding variables not actually quantified.

Wolfenden 1981.

Circumstantial - field - Annual breeding success increases with increasing group size; possible causes other than group size not considered adequately at all.

Alvarez 1975; Dyer & Fry 1980; Emlen 1981; Faaborg & Patterson 1981; Lawton & Guindon 1981; Ligon & Ligon 1978; Rowley 1965a & b; Stallcup & Wolfenden 1978; Tarboton 1981; Verbeek & Butler 1981; Wolfenden 1975, 1978.

Circumstantial - field - Nestlings fed quicker, but effect on breeding success not quantified or not proven.

Birkhead 1981; Collias & Collias 1978; Graul et al. 1977; Kinnaird & Grant 1982; Mader 1979.

Circumstantial - field - Nestlings not fed quicker, but breeders share of the work-load is decreased; however, effect on breeding success not quantified or not proven.

Brown & Brown 1981; Brown et al. 1978; Gaston 1973; Ligon & Ligon 1978; Parry 1973; Rowley 1978

Circumstantial - field - Breeding pairs in larger groups live longer, but possible confounding variables not actually quantified.

Stallcup & Wolfenden 1978.

Circumstantial - field - Non-breeders in larger groups live longer, but possible confounding variables not actually quantified.

Stallcup & Wolfenden 1978; Verbeek & Butler 1981; Wolfenden 1981.

Circumstantial - field - Non-breeders increase chance of breeding earlier (or at all) as group size increases, but possible confounding variables not actually quantified.

Birkhead 1981; Brown 1974, 1975; Foster 1977; Kinnaird & Grant 1982; Ligon 1981; Selander 1964; Stallcup & Wolfenden 1978; Wolfenden 1981; Wolfenden & Fitzpatrick 1978.

Group breeders do not always have increased breeding success. Birkhead (1981, and Warui cited therein) found that breeding success was less in groups, while Faaborg & Patterson (1981) found that breeding success increased in groups, but that the the number of offspring produced per individual male was greater in monogamous pairs. Kin selection, though perhaps more likely in group breeding

than in any other situation for birds, has however not been demonstrated or properly investigated (see e.g. Koenig & Pitelka 1981).

Lekking and Other Polygynous Mating Systems

Some males, and perhaps all the females, of lekking species presumably benefit from this form of social organisation. Most of the possible consequences appear in other sections (for example, reduction of predation); Selander (1972) and Wiley (1974) give reviews.

Polygyny or polyandry seem often to be a response to favourable environmental conditions which allow increased breeding success through a chance to breed again, rather than stay as a monogamous pair when conditions are such that one parent is able to raise the brood without assistance (see e.g. Gaul et al. 1977, Orians 1969, Selander 1972).

Benefit: Reduction of Agonistic Encounters

If birds must come into proximity at localised food sources, then agonistic encounters are a potentially disrupting force (see food disadvantages, below). It is possible that grouping might enable individuals to become familiar with one another, and as a consequence reduce the frequency of agonistic encounters. It may also be that flocked birds relieve themselves of the considerable energy expenditure involved in the defence of type A territories, partly held through agonistic encounters.

Balph & Balph (1977) found that agonistic encounters were more frequent and intense with strangers than with familiar flock members in dark-eyed juncos, while Barash (1974) showed that flocked black-capped chickadees (Parus atricapillus) were subjected to fewer agonistic encounters than solitary birds with other unfamiliar birds in the vicinity. However, in neither of these cases was any evidence produced to show that the level of aggression experienced by single birds was sufficient to affect fitness.

Benefit: Facilitation of Learning by Young

The presence of other conspecifics in addition to the

parents may facilitate the learning by young birds of places or objects to avoid if they offer danger, or to approach if they offer some resource; or to learn skills, for example foraging techniques, by observational learning. Only circumstantial evidence has been produced to suggest that such learning is facilitated by flocking:

Croxall 1976; Emlen & Demong 1975; Fogden 1972; Smith 1977; Stefanski & Falls 1972.

Benefit: Synchronisation of Social Behaviour

The status of this proposed benefit is much the same as that of the previous two. That some behaviour is synchronised within groups has been demonstrated, but effects on fitness compared to solitary behaviour have not been demonstrated:

Bergman & Donner 1964; Brodie 1976; Crook 1961; Evans & Patterson 1971; Gould & Heppner 1974; Griffin 1974; Hamilton 1967; Hamilton & Gilbert 1969; Lorenz 1966; Moynihan 1962; Rabol & Noer 1973; Sabine 1956; Thake 1980; Wallraff 1977, 1978; Ward 1978.

Balcomb (1977) and Keeton (1970) - the latter by experiment - have demonstrated that flocking does not improve the coordination of migration flights compared to solitary behaviour, in contrast to what several of the studies listed above have claimed.

Wynne-Edwards (1962) suggested that coordinated display flights functioned to advertise population size, and thus lead to control through group selection; however, no evidence is produced to support this speculation, and the theory of population control by group selection as Wynne-Edwards formulated it has been heavily criticised (e.g. Maynard Smith 1976, Williams 1966, 1971, E.O. Wilson 1975). Crook (1965), Lack (1966) and Ward (1965) provide naturalistic observations which are incompatible with Wynne-Edwards speculation than display flights may have been advertising population size for group selection effects to operate.

Benefit: Reduction of Energy Loss by Thermoregulation

Aggregation may reduce the energy expenditure of an individual through reduction of heat loss. Again, there is no firm demonstration of the effects of aggregation upon fitness, though some studies have shown quantitatively that there can be some saving on energy-loss.

Circumstantial - field/colony - Energy loss reduced in larger compound nest, but no quantification of the effect of this upon breeding success.

Bartholomew et al. 1976; White et al. 1975.

Circumstantial - field/colony - Energy loss probably reduced in larger compound nest, but no quantification of this or of its effect upon breeding success.

Collias & Collias 1977.

Circumstantial - field experiment or laboratory/roost - Energy loss reduced as roosting flock size increased, but no quantification of the effect of this upon individual survival.

Brenner 1965 (laboratory); Whitlock 1979 (field experiment).

Circumstantial - field/colony - Energy loss probably reduced in larger roost, but no quantification of this or of its effect upon individual survival.

Balda et al. 1977; Braestrup 1963; Brodie 1976; Francis 1976; Lack 1956; Tast & Rassi 1973; Whitlock 1979; Yom Tov et al. 1977; Zahavi 1971.

A number of studies have illustrated that care is necessary before concluding that grouping affects heat-loss - for example Broom et al. (1976), Fleming (1981), Kelty & Lustick (1977), Shaw (1979) and Thompson & Coutlee (1963) demonstrate that heat loss experienced is not dependent on the presence of other birds, since huddling does not occur, but is only a consequence of the choice of the particular site. Counsilman (1974), Siegfried (1971a) and Ward (1965) have shown that communal roosting occurs in climates in which protection from heat loss is not required, whilst Summers Smith showed that some house sparrows switched from communal roosting to roosting on their own in small

crevices when the weather became very cold. Swingland (1977) found that some subordinates were forced by aggression from others to roost in exposed parts of the roost where energy loss could be very severe - more severe than if they roosted solitarily elsewhere. Gyllin et al. (1977) and Yom Tov et al. (1977) show that the energetic saving in heat loss reduction was less than the energetic cost of flying a long distance to the roost. All of these studies demonstrate that in some species thermoregulation either does not occur, or is subordinate to other requirements satisfied by communal roosting.

Benefit: Reduction of Energy Expenditure by Formation Flying

Lissaman & Shollenberger (1970) showed in the laboratory that the V-formation flight of many species of birds could reduce energy expenditure; however no effect on fitness was demonstrated, and Gould & Heppner (1974), Higdon & Coursin (1978) and Williams et al. (1976) all showed either no saving, or a saving which would have a negligible effect on survival.

Cost: Prey: Competition

In general the costs of grouping are not as well documented as the advantages, presumably for the simple reason that if a bird is permanently receiving a heavy cost from grouping, it will cease to group. However, there are costs to grouping which will act to reduce the extent of any advantage received by grouping.

Theoretical

Pulliam 1976.

Circumstantial - field/flock - Subordinates lose weight faster and have reduced survival as food becomes poorer; but no convincing proof that competition for prey is the cause of this.

Crook & Butterfield 1970; Ward 1965.

Circumstantial - field/flock - Increased competition occurred as flock size increased, but no quantification of the effect of this upon prey intake rate.

Ashmole 1963a; Barnard 1978 (laboratory); Lorenz 1966; Moynihan 1962; Murton 1965; Murton et al. 1966; Newton 1967; Schoener 1968b; Wiley 1971; Wynne-Edwards 1962.

Cost: Prey: Agonistic Encounters

Increased aggression when foraging in a flock may

reduce the time available for feeding.

Empirically established - field/flock - Feeding rates of losers of agonistic encounters were reduced; cause and effect link reasonably established.

Mallory & Schneider 1979; Recher & Recher 1969;
Silliman et al. 1977.

Circumstantial - field/flock - No quantification of the effect of increased agonistic encounters on feeding rates.

Crook & Goss-Custard 1972; Feare & Inglis 1979;
Goss-Custard 1977a; Lockie 1956b.

Feare & Inglis (1979, laboratory experiment) and Patterson (1975) have shown that an increase in agonistic encounters need not necessarily affect prey intake rates if the encounters are brief and relatively infrequent.

Cost: Prey: Interference

Aggregation of predators may result in reduced intake through disturbance of the prey, leading to anti-predator reactions on the part of the prey reducing their availability to the predators; alternatively physical interference with each other's foraging actions (but not agonistic encounters) may reduce feeding efficiency.

Empirically established - field/flock - prey intake rate reduced, weight lost faster, and survival reduced for subordinates due to displacement by foraging movements (not aggressive displacements) of other flock birds.

Murton et al. 1971.

Empirically established - field/flock - prey intake rate reduced due to increased mutual physical interference while foraging; causal link reasonably established.

Kruuk 1964.

Empirically established - field and field experiment/flock prey intake rate reduced due to increased interference causing prey to show anti-predator reactions while foraging; causal link reasonably established.

Goss-Custard 1970a, b (field experiment); Hafner et al. 1982.

Circumstantial - field/flock - No quantification of the effect of increased physical interference of foraging movements on feeding rates.

Alison 1976; Crook 1960; Crook & Goss-Custard 1972; Feare & Inglis 1979; Lazarus 1972; Morse 1970; Summers Smith 1963.

Circumstantial - field/flock - no quantification of the effect on feeding rates of increased interference while foraging causing prey to show anti-predator reactions.

Buskirk 1976; Crook & Goss-Custard 1972; Goss-Custard 1970a, 1970b, 1976a, 1977b; Hoffman et al. 1981; Lazarus 1972; Murton 1971a.

Cost: Predation: Conspicuousness Attracting Predators

The possibility that 'selfish herd' or other anti-predator benefits of might be offset by the greater conspicuousness of groups attracting predators to them, has been mentioned above. Only circumstantial evidence has been produced to suggest that this can occur:

Alison 1976; Charnov & Krebs 1975; Odum 1942; Thompson & Coutlee 1963; Ward & Zahavi 1973; Wiley 1971.

Cost: Predation: Increased Predation Rates

Bedard & Munro (1975), Campbell (1975), Lutz (cited Kenward 1978) and Williams (1974) have shown that predation rates increased as foraging flock size increased; while Bartholomew et al. (1976), Blem (1979), Burger (1974b), Burger & Lesser (1978), Freer (1973), Lemmetyinen (1971), MacLean (1973), Scolaro & Kovacs (1978), Tinbergen et al. (1967), White et al. (1975) and Vehrencamp (1978) have shown that predation rates increased as breeding colony size increased. None of these studies were able to demonstrate unequivocally the cause of this increase, but in most cases it was probably increased conspicuousness or the close proximity of individuals to one another reducing predator search-and-travel time, once it had made initial contact with the aggregation.

A number of other studies describe, without exact quantification, higher predation on larger groups:

Ashmole 1963b; French 1967; Gyllin & Kallander 1976; Kepler 1967; Heinertzhagen 1960; Morley 1953; Patterson 1977; Veen 1977; Ward 1972; Ward & Zahavi 1973; Windsor & Emlen 1975.

Cost: Reproduction: Competition for Nest Sites and Materials

With this, and all of the other proposed costs associated with breeding, only a little circumstantial evidence is available, of varying quality. Most studies simply document the occurrence of a cost, without considering whether this is really substantially greater in colonies than for birds breeding in type A territories.

Burger (1978a & b) showed that competition was often seen, and that the biggest species in mixed-species heronries nested highest in the colony, but no effect of this on breeding success was measured. See also Hoogland & Sherman (1976) and Siegfried (1972).

Cost: Reproduction: Competition for Mates

No serious evidence has been produced that colonial breeding produces more competition for mates. See Hoogland & Sherman (1976).

Cost: Reproduction: Increased Risk of Cuckoldry

Bray et al. (1975) have shown that matings may occur outside of the pair - the mates of vasectomised red-winged blackbirds (Agelaius phoeniceus) laid fertile eggs.

Although it is reasonable to suppose that the risk of this is higher in colonies, this has not actually been quantified. See also Hoogland & Sherman (1976).

Cost: Reproduction: Increased Risk of Misdirected Parental Care

See Hoogland & Sherman (1976). This is not well documented compared to the evidence that colonial species have well-developed capacities for individual recognition of offspring in species where chicks may wander between nests (e.g. Beer 1970, Stevenson et al. 1970, Thorpe 1968, White et al. 1970).

Cost: Reproduction: Increased Risk of Inbreeding

Although there is some evidence that inbreeding can have deleterious effects in wild birds (e.g. Greenwood et al. 1978), no evidence exists to suggest that this is more likely to occur in colonial or group breeding species (the study cited was on an A-type territorial species). Many species have quite well-developed inbreeding-avoidance mechanisms (e.g. Bateson 1978a, Rockwell & Cooke 1977).

Cost: Reproduction: Physical Interference in Breeding

This potential cost is better documented. Hamerstrom & Hamerstrom (1960) showed that 37% of prairie chicken (Tympanuchus cupido) mating attempts were interfered with at the lek, and 17% disrupted (cf. Hogan-Warburg 1966). It seems likely that this is a higher figure than that suffered by A-type breeders, but whether such levels affect fitness is unknown. Kruijt et al. (1967) found much lower levels of interference at blackcock leks - only 8% of mating attempts were interfered with, and only 4 % disrupted.

Burger (1978a & b), Butler & Trivelpiece (1981) and Patterson & Makepeace (1979) found reduced breeding success and increased levels of interference in larger colonies, though the causal link between interference and breeding rate was not unambiguously established. See also Hoogland & Sherman (1976).

Cost: Reproduction: Transmission of Parasites and Diseases

That this is sufficiently more frequent amongst colonial breeders to affect fitness has not been established. See Hoogland & Sherman (1976) and Meinertzhagen (1959).

Cost: Reproduction: Cannibalism

High levels of cannibalism can occur. At some Larid colonies it can be the highest source of mortality. Studies finding high rates of cannibalism at Larid colonies include:

Brown 1967; Davis & Dunn 1976; Emlen 1956; Harris 1964; Hunt & Hunt 1975, 1976b; Monaghan 1979; Paludan 1951; Parsons 1971, 1976; Paynter 1949; Tinbergen 1953; Tinbergen et al. 1962.

Hunt & Hunt (1976), Monaghan (1979) and Parsons (1976) found that the rate of cannibalism increased in higher density colonies. Cannibalism does not occur in some of the smaller Laridae - e.g. Burger (1974a) did not record cannibalism amongst Franklin's gull (Larus pipixcan).

Since a good proportion of the studies cited here showed overall breeding success increases (see relevant 'benefit' sections above), it can only be assumed that for these colonies the cost of increased cannibalism was outweighed by whatever benefits accrued from colonial nesting.

Non-adaptive Behaviour or Epiphenomena

As mentioned in section 2.2.4 above, the assumptions that all behaviour must be functional and/or must have some

consequence may be incorrect. As mentioned in section 2.2.4, a problem with proposing that a behaviour is non-adaptive or neutral in consequence is that it is very difficult to prove this. It is not possible to know whether one has tried all possible experimental hypotheses, or whether one has perhaps tested the right one but failed to design a test sensitive enough to reveal a true consequence of the behaviour in question.

The following is a list of studies which have failed to demonstrate a positive or negative consequence of some aspect of avian grouping. No attempt is made to comment on the quality of the evidence produced in each case for these reasons.

Bedard & Munro 1975; Brosset 1975; Cruz 1974;
Emlen 1982a; MacRoberts & MacRoberts 1976;
Pleasants 1979; Snapp 1976; Stacey 1979; Stacey
& Bock 1978; Terborgh & Diamond 1970; Walsberg
1977; Walters & Walters 1980; Wiens 1976;

Chapter Three - Local enhancement for food finding by rooks foraging on grassland in winter (*)

Rooks spend much of their foraging time in flocks. The large number of categories in the preceding chapter suggests that the consequences of the interactions between ecological variables and social behaviour are diverse; that there is likely to be no single aspect of ecology associated with variation in social behaviour. However, while it is of course true that selective pressures acting to mould social organisation and behaviour will be multi-form, it is possible to investigate with which of such pressures a species' behavioural repertoire is particularly associated now. It has already been shown that the possible selective pressure of interspecific aggression - whatever its influence in moulding social behaviour in the past may or may not have been - cannot be related to the situation as it exists now, at least in lowland Britain.

Three previous studies (Feare et al. 1974, Murton 1971a, Pinowski 1959) suggested that an advantage of flock-

(*) A summary of this research has been published (Waite 1981). A copy is bound in as appendix four. A pilot study was conducted (Waite 1978); none of the material produced here (except some aspects of interpretation) appears in the earlier thesis. Whenever data or material appearing in the earlier report are cited, specific reference is made to that study.

ing for rooks might be to increase an individual's chances of finding patchily-distributed prey by watching where other birds foraged. Hurton and Feare et al. noted the fact that earthworms constituted a major part of the diet of rooks, and that such prey were probably variable in occurrence in the top levels of the soil, although they did not go on to measure either the dispersion of earthworms or the responses of rooks to this dispersion.

Pinowski noted the occurrence of social attraction by birds flying over an area to those already foraging on the ground. The attraction was principally visual, but observation and a play-back experiment suggested that calls could also attract birds to a field. He also found a tendency for larger flocks to occur in sparsely-wooded areas where birds could be seen foraging from some distance and thus be joined by others; whilst smaller flocks occurred in fields within more densely wooded areas where restricted vision perhaps prevented flying birds from locating foraging birds so easily. Large flocks only occurred in wooded areas on abundant and long-lasting food sources. This may suggest that rooks could learn the whereabouts of such areas and gather in large flocks, whereas the more transient visits of birds to other fields left insufficient time for flocks to build up, given the increase in the time needed to locate such birds, due to the restriction on vision in wooded areas. Pinowski also

described the break-up of a foraging flock, when it took flight, into smaller groups and individuals which flew off in different directions and began the build-up of foraging flocks once more - a phenomenon familiar to anyone who watches rooks, which he interpreted as a process of continually sampling a variable and changing food supply.

The mere occurrence of social attraction is not suggestive of a food-related advantage of flocking, of course - were the birds enjoying, for example, reduced-predation advantages from flocking, they would require social attraction mechanisms to keep the flock together. However, the three studies taken together are suggestive of the possibility that flocks might function to increase the probability of locating transient aggregations of soil invertebrates. This follows the correlation noted across many species, cited in the previous chapter (e.g. Crook 1965), which suggests a general link between avian grouping and aggregated prey resources.

A predator could increase its probability of finding prey by foraging in a group if the prey were aggregated in dispersion; if these aggregations were difficult to locate; and if they were unpredictable in occurrence. Under such conditions the probability of any prey patch being located would increase as the number of predators searching the area increased. If the other group members

could approach when one of their number had located a patch, and if each prey patch contained a certain minimum amount of prey, then each predator could also increase its individual intake rate of prey by foraging in a group.

The type of simple social learning involved is termed local enhancement, which has been defined by Thorpe (1963) as "Directing an animal's attention to a particular object or to a particular part of the environment." (The phrase social attraction is used interchangeably with local enhancement to relieve monotony! Its definition in this case is considered identical.) Its involvement in food finding has been demonstrated experimentally in the laboratory in two studies of Parus spp. (Krebs et al. 1972, Krebs 1973). At present only two reports have been published which provide substantial evidence of local enhancement behaviour increasing both the efficiency of prey-patch location and individual prey intake rate in birds foraging for natural prey - Krebs' (1974) study of great blue herons Ardea herodias and Barnard's (1980) of house sparrows Passer domesticus. (*)

These previous studies have suggested that local enhancement behaviour can occur on two different scales.

(*) As stated in chapter two above, the former study was a model and stimulus for the present one; Barnard's study was conducted concurrently and independently of the present one but was published while a report of the research under discussion here was in press.

Firstly, birds can use the presence or absence of flocks as indicators of large-scale areas of prey (Krebs 1974); and secondly, once within the flock, birds can use the behaviour of individual members of the flock as indicators of smaller-scale prey areas (Krebs et al. 1972, Krebs 1973).

Data from the current study are examined to test two hypotheses:

- (a) individual rooks could increase their chances of encountering large-scale patches of prey by watching where flocks were or were not foraging; and
- (b) if the prey were further aggregated within the area over which any one flock were foraging, that an individual could increase its chances of encountering small-scale patches of prey by local enhancement behaviour within the foraging flock.

Ideally, one would like data on inclusive fitness as the measure of the relative benefits from different forms of social behaviour (see section 2.2.9 above). However, this was not possible during the present study. Because of this it was necessary, as so often in similar studies of functional issues in animal behaviour (see e.g. Krebs & Davies 1978), to adopt short-term changes in the intake rate of prey as the measure of the advantage to be gained

from a tendency to join flocks and to interact in certain ways within a flock.

Given this measure, the following steps were necessary to test the hypotheses by field observation (for the justification of these steps as necessary and sufficient see chapter two):

- (1) Determination of what prey types were taken and in what proportion.
- (2) Measurement of the dispersion of the prey types:
 - (a) was the prey aggregated?
 - (b) was it hard to find?
 - (c) were the patches unpredictable in occurrence?
- (3) Did local enhancement behaviour (individuals tending to move near to other birds) occur?
- (4) Did an individual leave an area to forage elsewhere less frequently as prey density increased?
- (5) Did prey intake rate increase with increasing prey density?
- (6) Did prey intake rate increase:
 - (a) with increasing flock size (for large-scale prey patches)?
 - (b) following local enhancement to other birds within

the flock, i.e. with increasing flock density
(for small-scale prey patches)?

- (7) Was the increase in prey intake rate with increasing flock size or density the result of an increase in the occurrence on higher prey densities of larger or denser flocks?
- (8) Could the increase in prey intake rate with increasing flock size or flock density be explained by other food-related social behaviours (e.g. those listed in chapter two)?
- (9) Was the increase in prey intake rate outweighed by any concurrently increasing costs?

Once the prey types being taken were known, it was necessary to determine whether the prey was aggregated in dispersion. If prey were randomly or evenly dispersed, then there would have been no advantage in an individual bird showing local enhancement to others in terms of locating better areas of prey - individual search would have been an equally efficient method of locating prey. Further, if prey were easy to locate, or the patch locations were easy to learn and did not shift in location, then local enhancement to others would not increase the efficiency of exploiting the prey.

It was necessary to determine whether the birds were

showing social attraction to one another, or whether groups occurred simply as the result of individual attraction to some feature of the environment - i.e. to determine whether the birds were truly flocking or merely aggregating.

It was then necessary to determine whether two relationships existed between individual behaviour and prey density - firstly whether a bird left an area of higher prey density to forage elsewhere less frequently than an area of lower prey density; and secondly whether a bird's intake rate of prey increased with increasing prey density. The former was necessary since if birds left areas of differing prey densities at similar rates, then local enhancement to others would not have resulted in birds tending to group on the areas of higher prey density, and hence the presence of birds could not have served as an indication of areas of higher prey density to incoming birds. The latter relationship should have existed for there to have been a benefit in locating areas of higher prey density (of course birds could benefit by staying longer on higher prey densities, if time were not needed for other activities - however, this relationship is necessary if short-term intake rate of prey is the measure used in the study).

Since local enhancement to a flock could have been for

other, non-food related reasons (e.g. some of the other possible advantages associated with flocking cited in chapter two), it should have been the case that prey intake rate increased when birds were in larger or denser flocks.

If all the preceding steps were proven, then it should have been the case that larger and denser flocks occurred on areas of higher prey density. This would have been the result of individuals tending to land near others to forage, and tending to leave areas of higher prey density less frequently. Finally, the gain in increased prey intake rate must not be outweighed by some increased cost, for example in the energy required to show social attraction rather than choose any prey patch, increased predation pressure on flocks, aggression, interference with foraging movements or disturbance of prey.

If all the above steps were proven, then it must be shown that the relationship between flock size or density and prey intake rate could not have been produced by the operation of one of the other social mechanisms connected with the exploitation of prey (again, these are listed in chapter two).

2.3.1 The Prey

The relative contributions of grain and of the different kinds of invertebrate prey have been indicated in

part one of the thesis. Rooks selected grassland over arable and over 80% of their foraging time was spent on grassland (table 1.4.1). Given this inequality of total foraging time on the two habitat types, grassland therefore represented a more important source of prey in both calorific and nutritional terms (table 1.4.3 lists the relative intake rates per minute from grassland and arable).

When on grassland birds were observed to take only invertebrate prey. Some prey types taken may be determined by direct observation using a powerful telescope (see Methods chapter), but small invertebrates cannot be identified in this manner. However, earthworms were one major prey type which was readily identified through the telescope. When on grassland earthworms represented 79.3% of intake in terms of calorific value and 84.3% of protein-containing material (table 1.4.5). This figure is likely to be a minimum indication of the importance of earthworms to the diet, since some very small earthworms were probably mis-classified as other invertebrate types, depending on weather conditions and distance of the observer from the subject bird. Since not all of the other prey items were identifiable in every case, and since earthworms were clearly important to the diet, the dispersion of earthworms only, and the behaviour of rooks with regard to this dispersion, is analyzed below. (*)

(*) Some additional information on the important influence

A. Local Enhancement to Varying Prey Densities between Different Grass Fields

Results

2.3.A.1 Earthworm Dispersion

The densities and dispersion of earthworms at Keele in winter is described in section 1.3.8. Earthworms were highly aggregated between fields (section 1.3.8.1 and figure 1.3.8). These prey were probably hard to find by birds, though there is no direct evidence on this.

Although sward appearance differed between the three crop types, within any one crop type the human sampler was unable to discover any differences in the physical appearance of the sward which predicted earthworm densities.

Observation of foraging rooks suggested that earthworms were detected either by sight from a distance of only a few inches, or discovered on probing into the soil surface.

Patch-quality is unlikely to advertise itself, of course, unless there is an advantage to the organism providing the food being eaten (e.g. nectar-producing plants) (Mainsworth

of earthworms on rook biology is given in appendix five; given this influence, we might expect a similarly strong influence on social behaviour.

& Wolf 1979).

Section 1.3.8.3 and figure 1.3.7 indicate that earthworm densities did shift between fields over the winter.

2.3.A.2 Social Attraction

The numbers of rooks landing on one field and the numbers flying on without stopping were counted during a two-week period. (*) It was hoped that environmental conditions would be unlikely to change significantly during this period, and that differences in the numbers of birds landing and passing on would reflect social attraction and not individual attraction to some environmental variable - i.e. that the rooks were truly flocking and not merely aggregating.

The data (table 2.3.1a) indicated that rooks were significantly more likely to land on the field if conspecifics were already present, and more likely to fly on if no birds were present on the field. It was further the

(*) Experiments on attraction to models were begun. However, the behavioural plasticity of Corvids tends to make them investigate any novel situation. They would probably local enhance to a sky-blue pink elephant if you put one in the middle of a field, but the attraction would not necessarily tell you anything relevant about social food finding. Experiments with models in different postures (cf. e.g. Drent & Swierstra 1977, Inglis & Isaacson 1978, Krebs 1974, Hurton 1974) would probably be valuable.

Table 2.3.1

Tendency for passing rooks to land on a field and the absence, presence, flock size and density of birds already on the field

Partial gammas in (b) and (c) were calculated with the effects of mean NND and flock size, respectively, controlled for; there is some contaminating effect in each case, but gammas remain substantially greater than zero.

a)

	Passing Rooks	
	Fly On	Land
Rooks Present on Field	66	173
No Rooks Present	184	117

b)

Flock Size of Rooks on Field	Fly On	Passing Rooks	
		Land	% Landing
1 - 2	25	36	59.0
3 - 6	60	122	67.0
7 - 11	3	24	88.9
12 - 20	5	59	85.3
21 - 30	3	34	91.9
> 30	1	16	94.1

c)

Mean NND of Rooks on Field	Fly On	Passing Rooks	
		Land	% Landing
0 - 3 m.	15	84	84.8
4 - 6	15	77	83.7
7 - 10	10	42	80.8
> 10	35	13	27.1

a) $\chi^2 = 61.52$, $df = 1$, $p < 0.001$.

b) $\chi^2 = 36.1$, $df = 2$, $p < 0.001$ (last 4 rows combined); Zero-order Gamma = 0.563; Partial Gamma = 0.418.

c) $\chi^2 = 66.82$, $df = 3$, $p < 0.001$; Zero-order Gamma = -0.627; Partial Gamma = -0.536.

case that birds were more likely to land as the flock size of birds already on the field increased (table 2.3.1b). Such behaviour would be advantageous if larger flocks were indicative of better feeding areas (see below).

In addition, it was observed that rooks continually left and joined flocks foraging on a particular field; and that when an entire flock left a field, its members usually broke up into smaller groups which flew off in various directions.

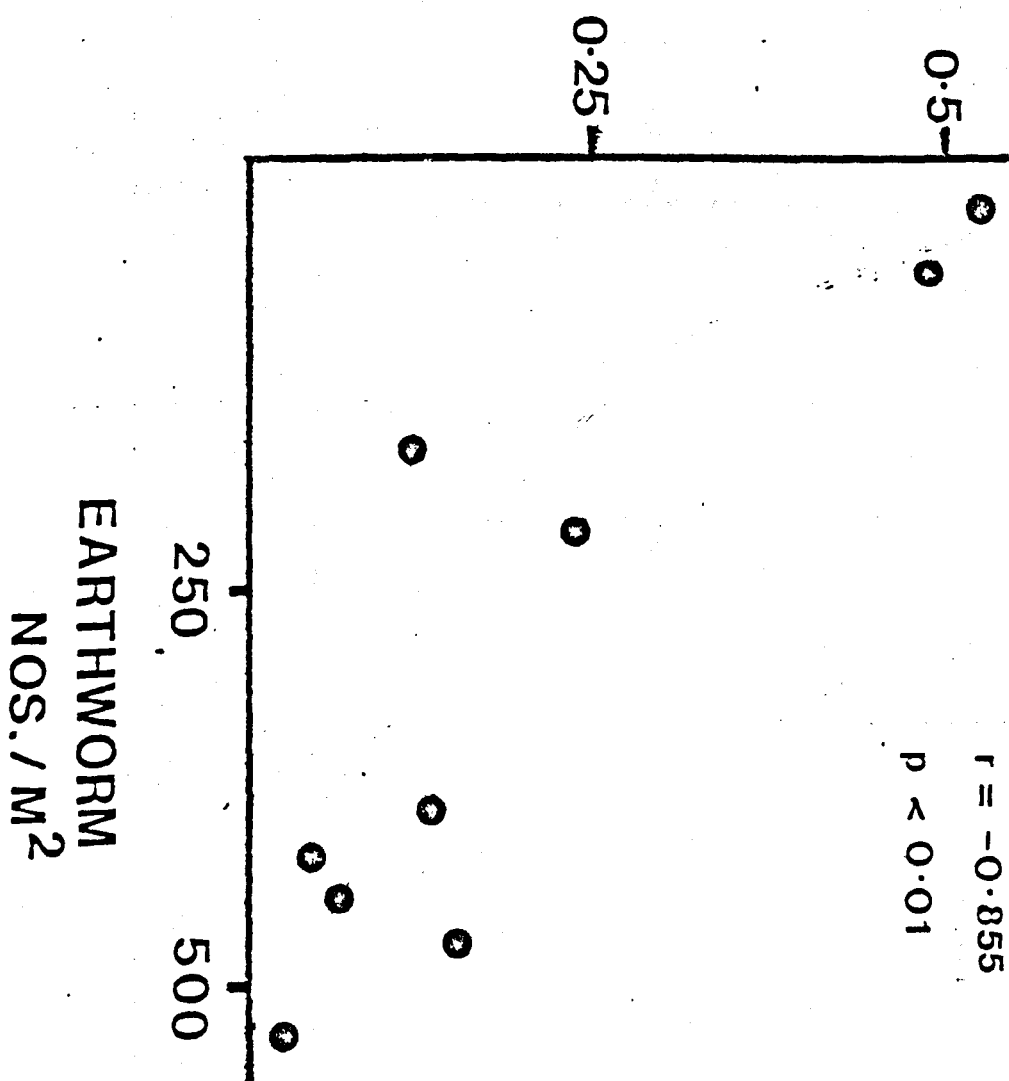
2.3.A.3 Relationships with Prey Density

Figure 2.3.1 indicates that rooks tended to leave grass areas with lower earthworm densities at a faster rate than areas with higher earthworm densities. Figure 2.3.2 indicates that earthworm intake rate increased with increasing earthworm densities. Although this may seem trivially likely, in fact it is not necessarily so - for example Goss-Custard (1970a) demonstrated that consistent variation of the rate of number of items ingested did not occur with increases in the density of one particular prey of redshanks (Tringa totanus). This was because as prey density increased, not only did the numbers of prey per unit area increase, but the size of each prey item also increased. Thus redshanks could increase the calorific value of their intake rate without increasing the number of

Figure 2.3.1

Relationship between earthworm density and tendency for rooks to stop foraging and move elsewhere

MEAN NO. ROOK FLIGHTS / MIN.



MEAN NO. ROOK FLIGHTS / MIN.

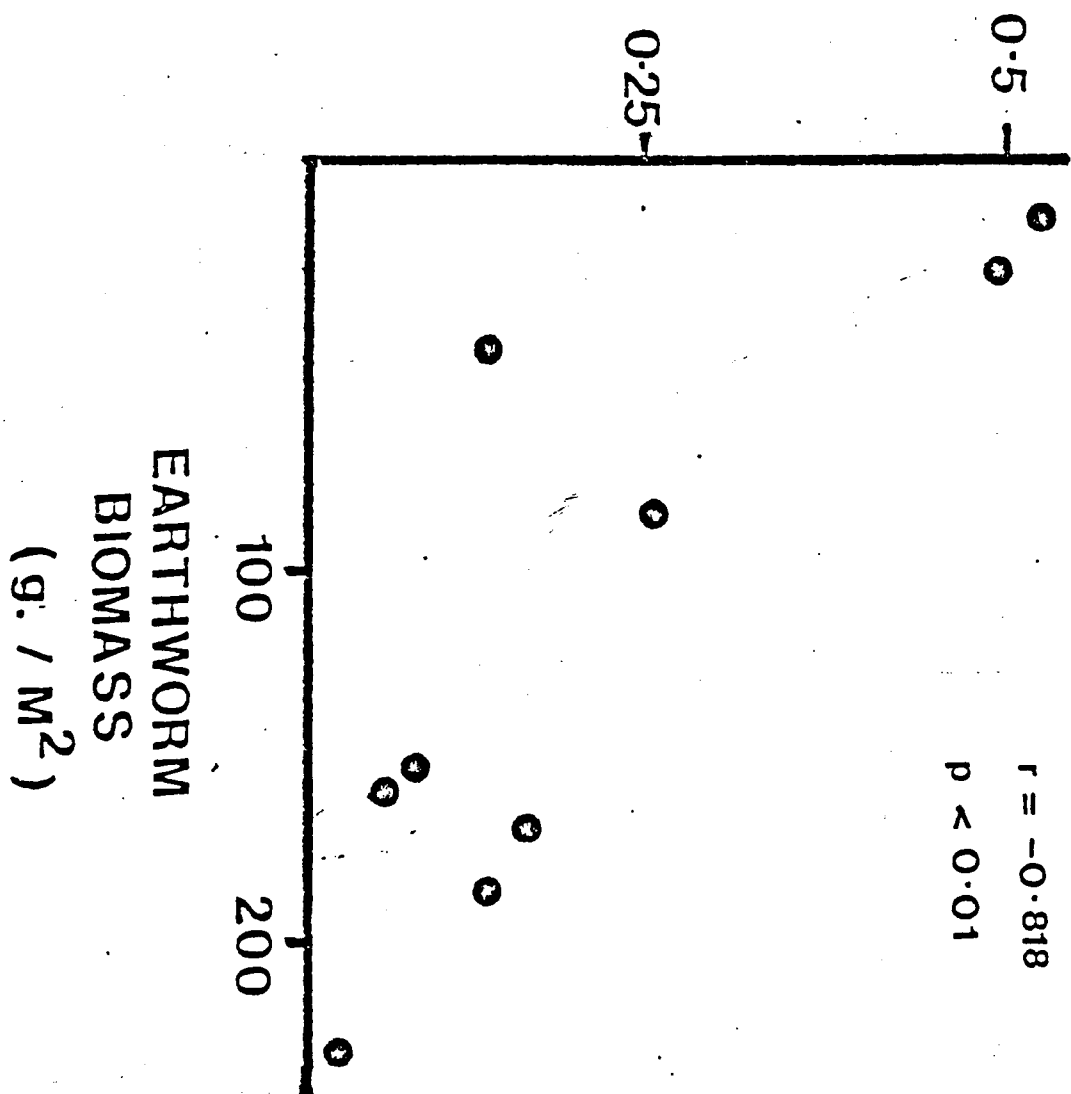
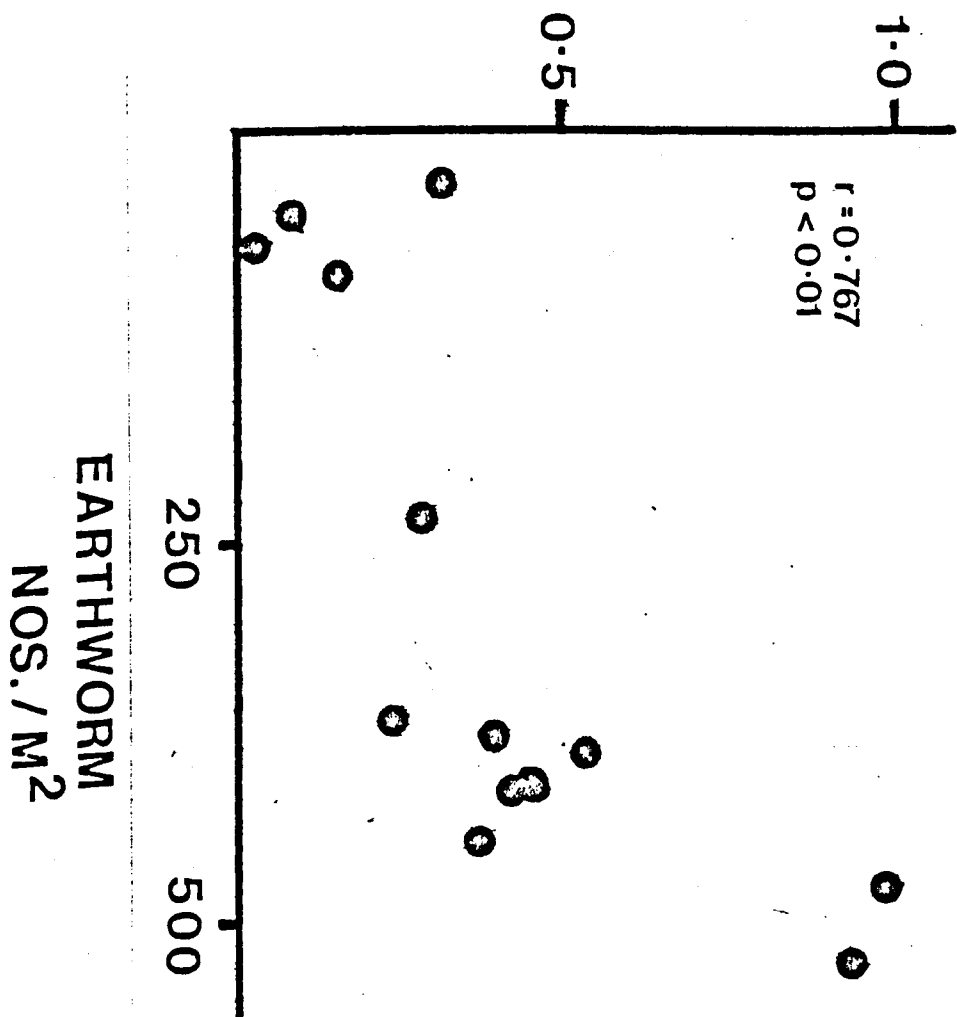


Figure 2.3.2

Relationship between earthworm density and earthworm intake rate of rooks

MEAN NO. WORMS EATEN / MIN.



MEAN WEIGHT WORMS EATEN

(g. / MIN.)

0.4

0.2

$r = 0.631$
 $p < 0.05$

EARTHWORM
BIOMASS

(g. / M²)

100

200

(9)

items ingested.

Secondly, if data were collected at the lowest or highest prey densities possible, then if birds demonstrated a type C functional response (figure 2.3.4), a linear relationship might not be revealed. The data in figure 2.3.2 suggest that an asymptote of rook capture rate of earthworms was not reached at Keele in winter, and the required relationship did hold. Since some food-related hypotheses suggest a direct influence of group size on prey intake rate, data were collected so that, at each prey density, approximately equal sample sizes were taken from higher and lower flock sizes. This ensured that larger flock sizes would not tend to be sampled more often at the higher prey densities, and that any relationship revealed between prey intake rate and prey density could not be explained, for this step, by a direct relationship between group size and prey density.

A census of rooks occurring on the fourteen grassland areas sampled for soil invertebrates in winter 1979 (see chapter 1.3) was conducted during the 26-day period of the sampling period. Table 2.3.2 and figure 2.3.5 indicate that larger flocks - whatever the measure of bird-use adopted - tended to occur on higher earthworm densities.

Fig. 2.3.4 - Three types of functional response of a predator to prey density

- (A) Lotka-Volterra linear response
- (B) Response typical of an invertebrate predator feeding on one prey type; asymptote due to ceiling on handling-time or satiation
- (C) Response of a vertebrate predator with more than one prey type available; response becomes linear only when prey reaches a certain level, due to either difficulty of locating low prey levels, or low prey levels being too costly to search for and collect compared to the alternate prey types available

(B and C after Holling 1965)

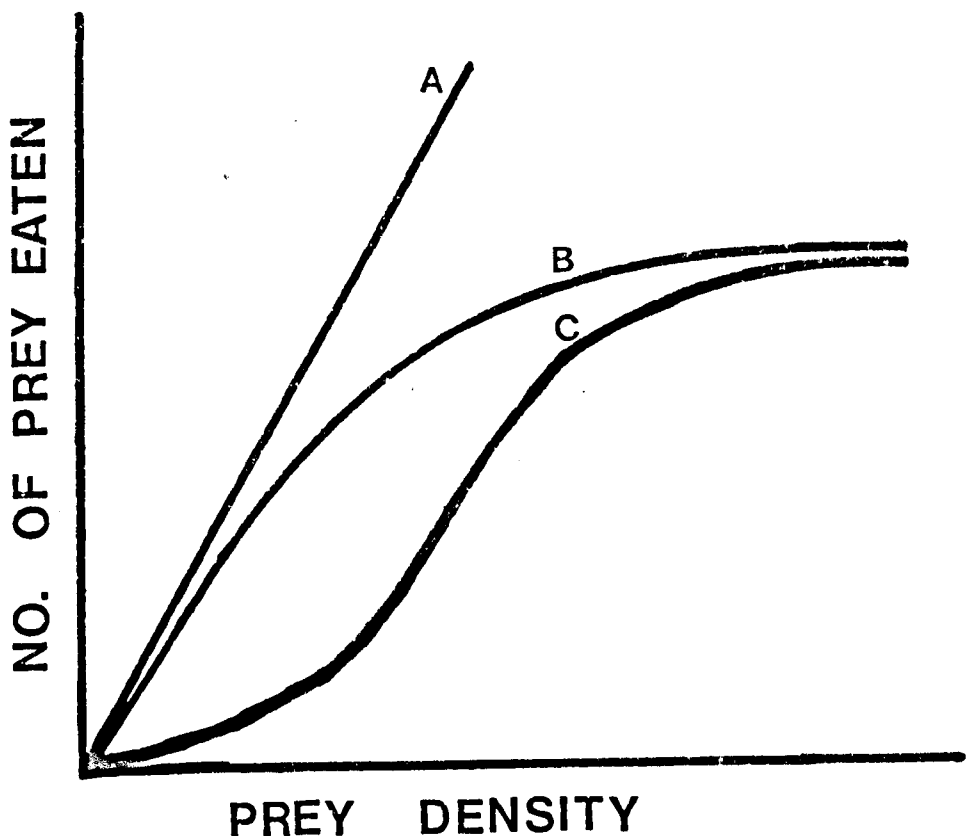


Table 2.3.2 - Relationships between earthworm density and measures of rook use and group size

(Obs. = Observations; FS = Flock Size)

INDEPVAR.	DEPVAR.	RHO	SIG. LEVEL
EARTHWORM NUMBERS / m ²	% OBS. ROOKS PRESENT	.872	***
	F.S. inc. NOUGHTS	.878	***
	F.S. exc. "	.864	***
	MEDIAN FS inc. "	.823	***
	MEDIAN FS exc. "	.959	***
EARTHWORM BIOMASS (g / m ²)	% OBS. ROOKS PRESENT	.835	***
	F.S. inc. NOUGHTS	.732	**
	F.S. exc. "	.701	**
	MEDIAN FS inc. "	.650	*
	MEDIAN FS exc. "	.804	**

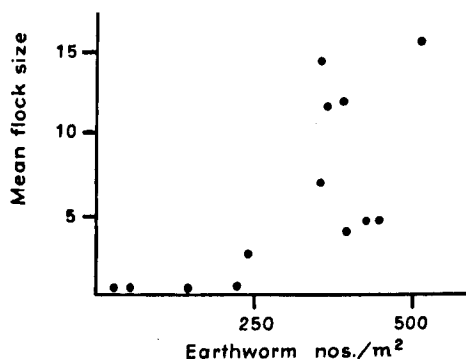


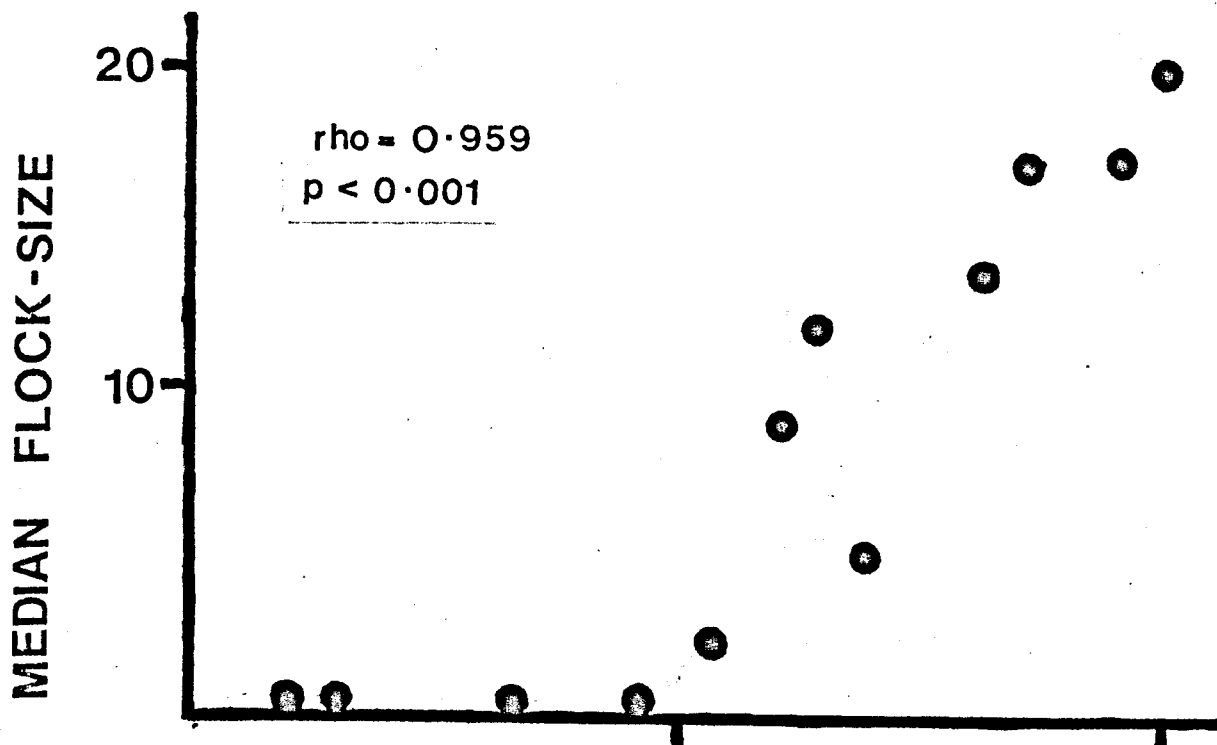
FIGURE 2.3.5 (a)

$Rho = 0.730, p < 0.01.$

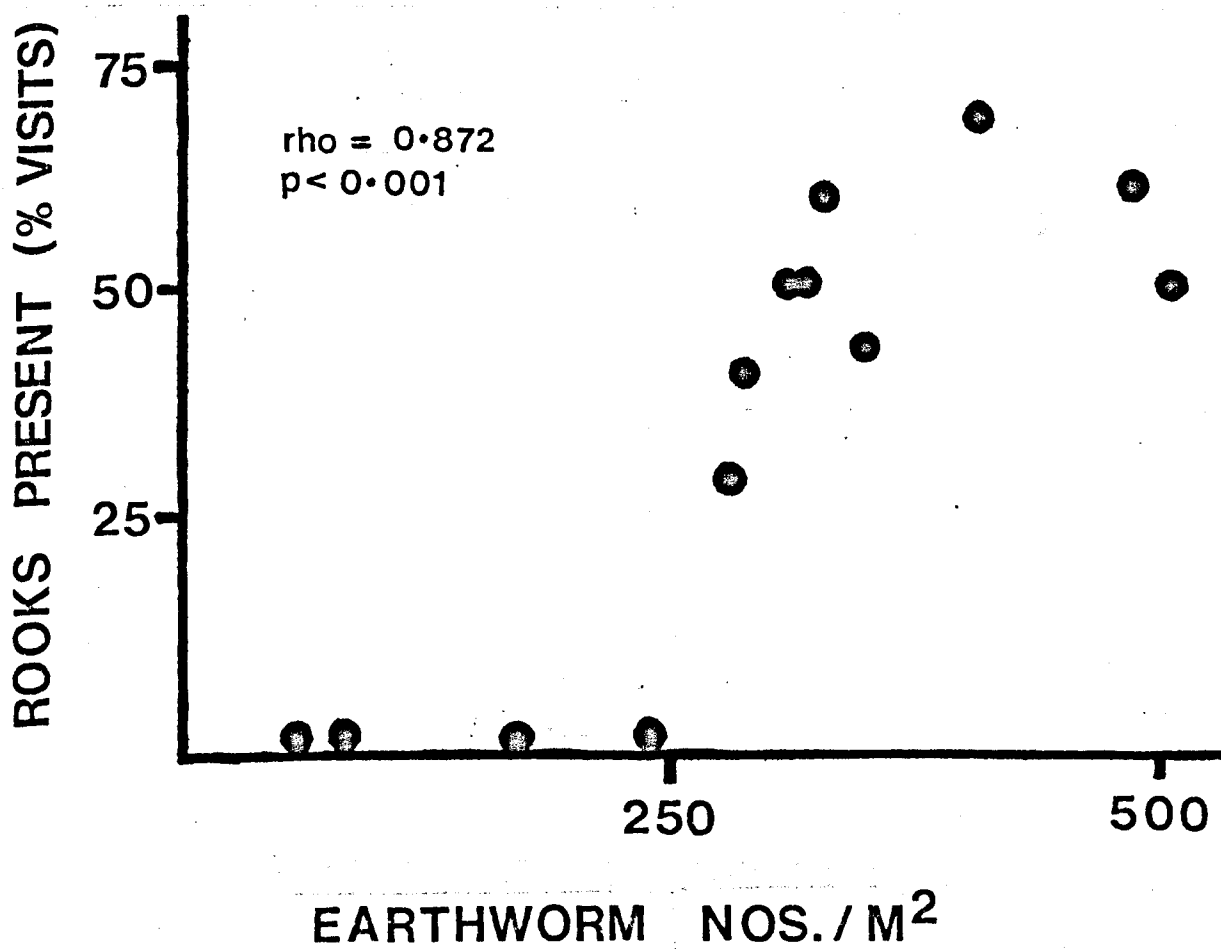
(Relationship with earthworm biomass:

$rho = 0.876, p < 0.001$)

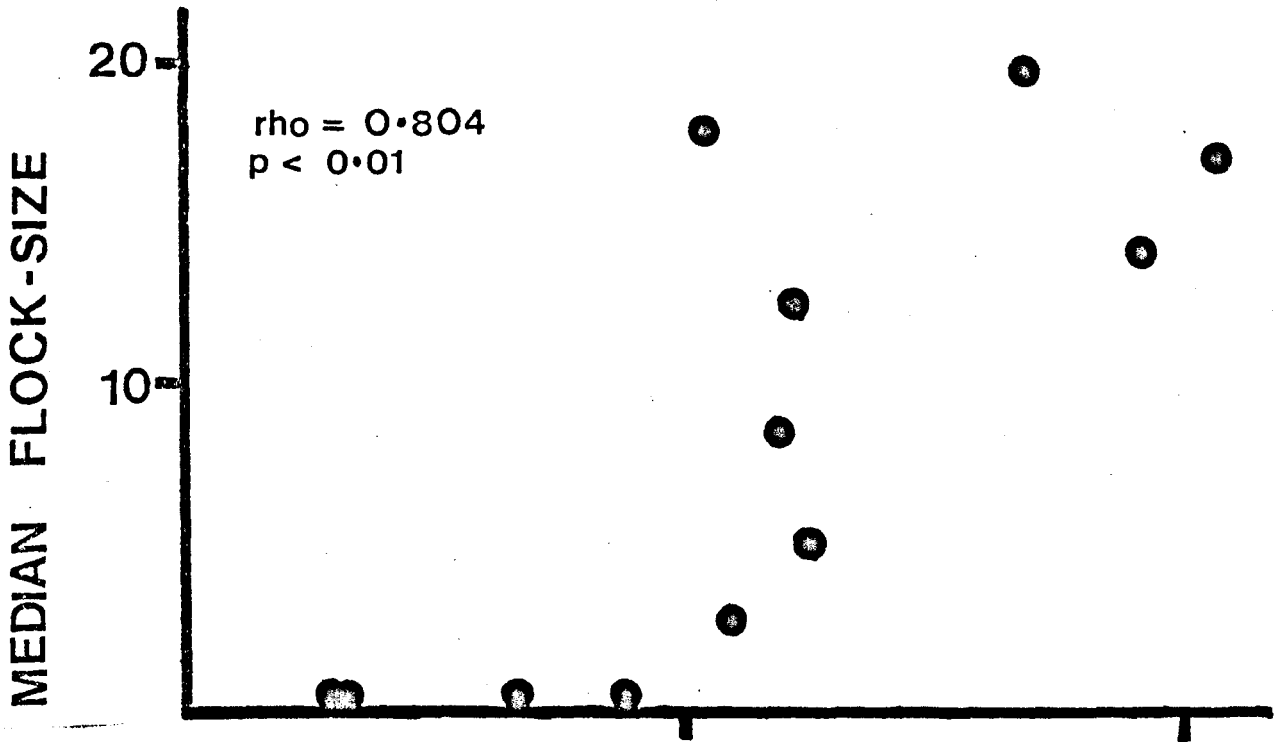
(b)



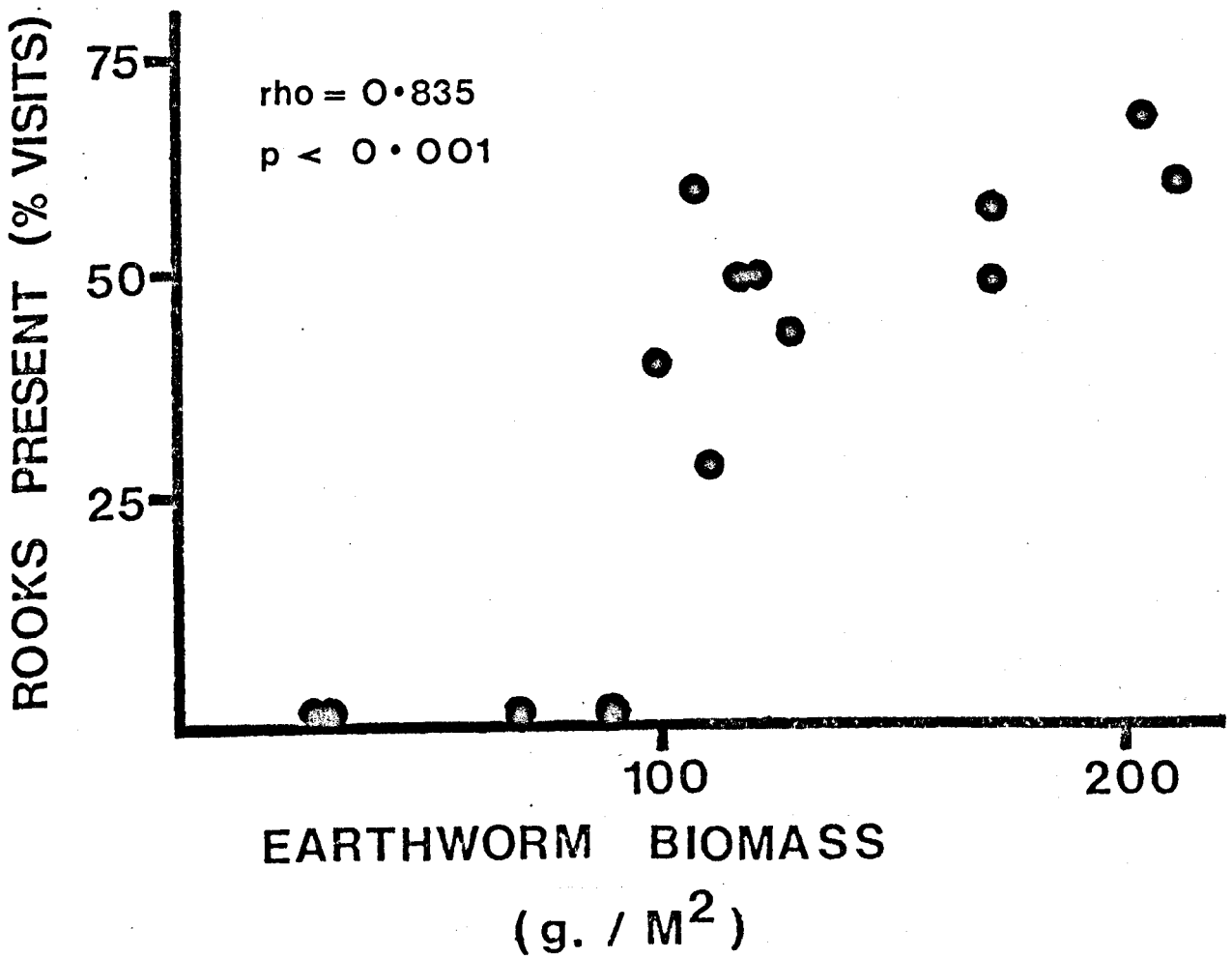
(c)



(d)



(e)



2.3.A.4 Relationships with Flock Size

Figure 2.3.6 illustrates two relationships with flock size - intake rates of earthworms increased, and vigilance rates decreased, with increasing flock size. Figure 2.3.7 illustrates mean vigilance rates of four Corvid species foraging on grassland at different flock sizes. Rooks and jackdaws on their own or in pairs had significantly higher vigilance rates (post analysis of variance comparisons by Scheffe test, $p < 0.10$, the appropriate level for this test) than carrion crows or magpies on their own or in pairs., while vigilance of rooks in flocks did not differ significantly from that of carrion crows or magpies on their own or in pairs.

Figure 2.3.8 demonstrates that there was no tendency for birds at lower flock size to have lower earthworm intake rate at any particular earthworm density. When the earthworm intake rates of approximately equal numbers of rooks in small and large flocks were recorded at each of 13 separate earthworm densities, there were no significant differences between different flock sizes in earthworm intake rates (table 2.3.3c), with no tendency for earthworm intake rate to increase as flock size increased (table 2.3.3a).

Figure 2.3.6

Relationships between rook flock size, earthworm intake rates, and vigilance

(a) Flock size and feeding rate ($\rho = 0.335$, $N = 67$, $p < 0.01$); (b) flock size and vigilance ($\rho = -0.631$, $N = 139$, $p < 0.001$).

Data for several flock sizes have been blocked together for the figure (mean \pm s.e.) but statistical analysis was performed on the original points.

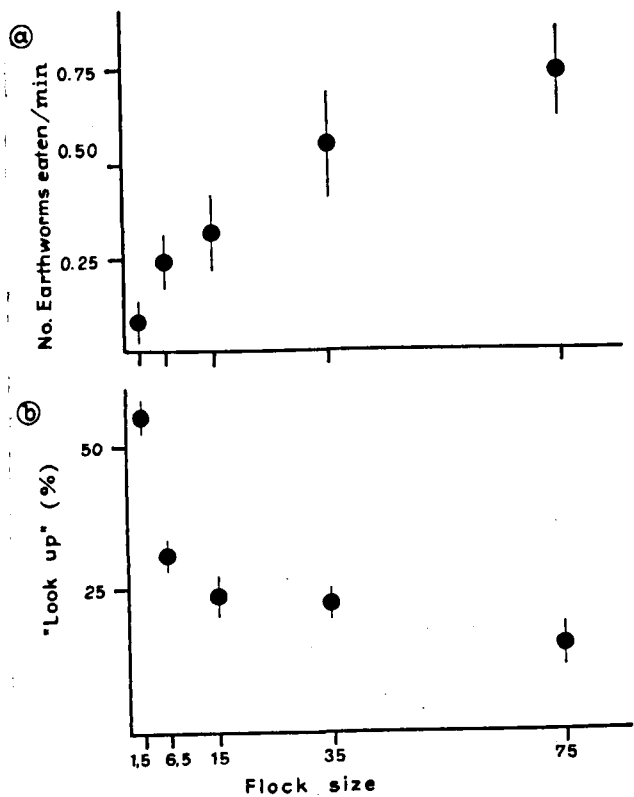
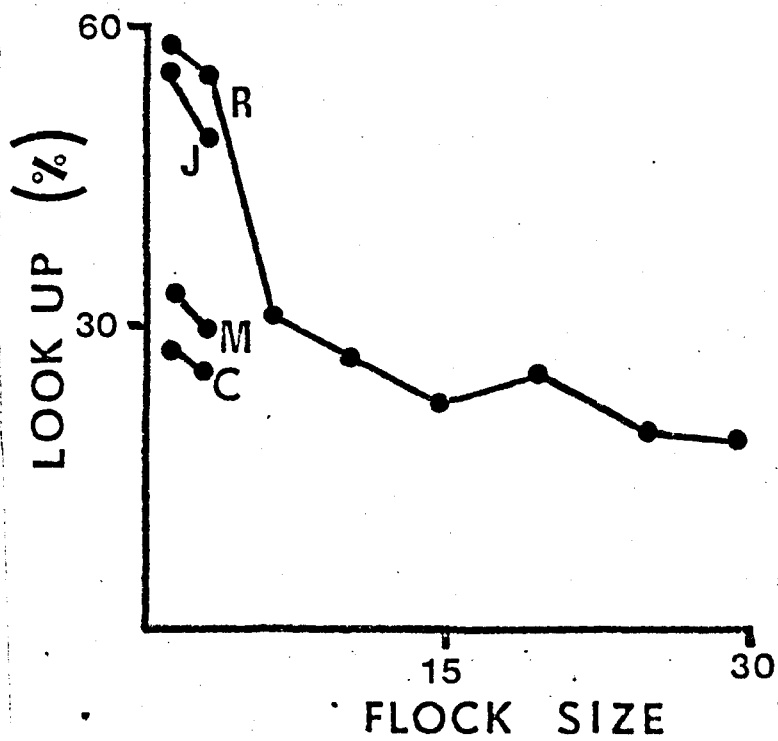


Figure 2.3.7

Relationship between flock size and vigilance for four Corvid species on grassland



$F = 67.28$; $df = 4, 139$; $p < 0.001$

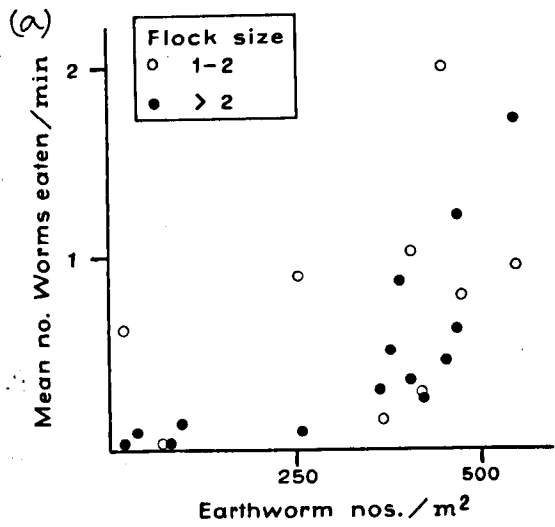
Scheffé Test:

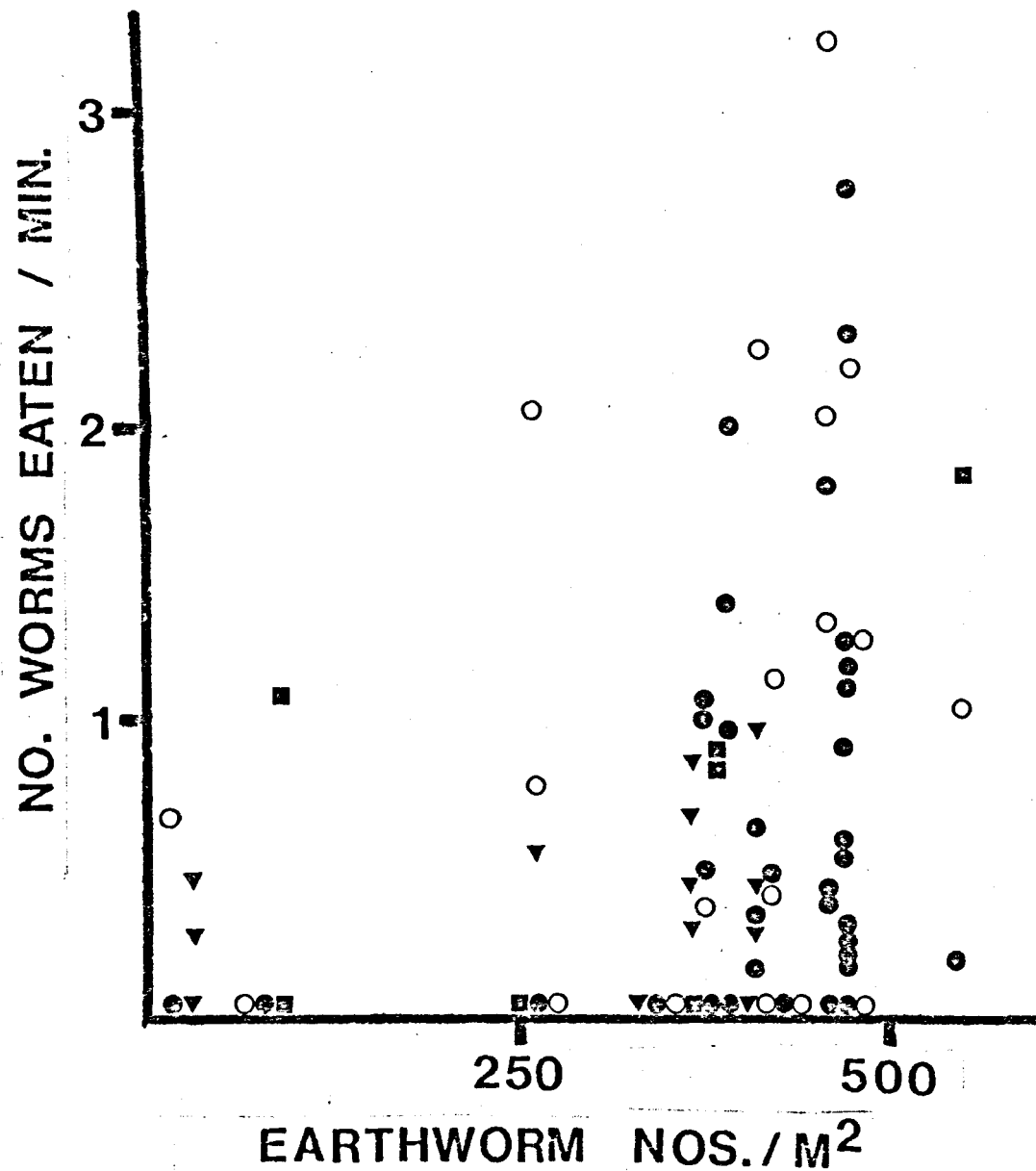
	R1-2	R > 3	J	M	C
ROOK 1-2	-				
ROOK >3	**	-			
JACKDAW 1-2	*	**	-		
MAGPIE 1-2	**	NS	**	-	
CROW 1-2	**	NS	**	NS	-

Figure 2.3.8

Number of earthworms eaten per minute by flocking and non-flocking rooks at different earthworm densities

(a) Summary figure for rooks on their own or in pairs compared to birds at any other flock size; (b) Same relationship for four different flock size categories.





% POINTS
ABOVE / BELOW
 \bar{X} NO. WORMS EATEN / MIN.
AT EACH WORM DENSITY

<u>flock size</u>	<u>% points Ab./Bel.</u>
○ 1-2	67 : 33
● 3-10	42 : 58
▼ 11-20	63 : 37
■ >21	57 : 43

Table 2.3.3

Flock size and earthworm intake rate at different earthworm densities

(a) mean intake rate (numbers / min.) for the different flock size categories in the ANOVA; (b) mean intake rate for the different earthworm density categories in the ANOVA; (c) 2-way ANOVA table of earthworm intake rate by flock size and earthworm density. When equal numbers of the different flock sizes are recorded at the different prey densities, rather than recording from flocks encountered in the frequency with which they naturally occur, then there is no increase in earthworm intake rate with flock size.

(a)	Mean EW Intake Rate	(b)	Earthworm Numbers per Square Metre	Mean EW Intake Rate
Flock Size	-----		-----	-----
1 - 2	0.74		0 - 100	0.10
3 - 10	0.25		101 - 300	0.27
11 - 20	0.17		301 - 400	0.41
> 21	0.56		> 400	0.94

(c)	F	df	P
	----	-----	-----
Flock Size	2.46	3, 96	N.S.
Earthworm Numbers per metre square	2.98	3, 96	< 0.05
FS x EN	0.97	9, 96	N.S.

Discussion

2.3.A.5 Earthworm Dispersion

Although the data indicated that earthworm densities shifted, they could not indicate how often such shifts occurred, nor whether they were predictable by rooks. The implications of different kinds of shifts are summarised in table 2.3.4. If prey patches were shifting unpredictably and often, then all members of a predator population could benefit from local enhancement behaviour facilitating location of the best patches. If patches shifted rarely, but also unpredictably, then all of the predator population could benefit from local enhancement when the shifts occurred. In the meantime there might be no benefit from grouping in local enhancement terms, if the predators were able to individually learn where the prey patches were; however, if when the prey patches shifted was unpredictable, then grouping behaviour might continue to be necessary as an insurance for when the shift came (cf. Ward & Zahavi 1973), or grouping might persist because of other possible benefits (e.g. those listed in chapter two), or merely as a neutral behaviour without any current positive or negative effects, an epiphenomenon of the behaviour which previously had a function (see chapter 2.2).

If prey patches shifted predictably, and individual

Table 2.3.4

Prey patch predictability and members of the predator population benefitting from local enhancement behaviour

Prey Patch Predictability	Who Benefits from Local Enhancement?
UNPREDICTABLE - shift in location often	ALL
UNPREDICTABLE - shift in location rarely	ALL when shift occurs (in between shifts flock persists for: insurance? other benefits?)
PREDICTABLE	YOUNG and/or IMMIGRANTS (ignorant of local conditions)

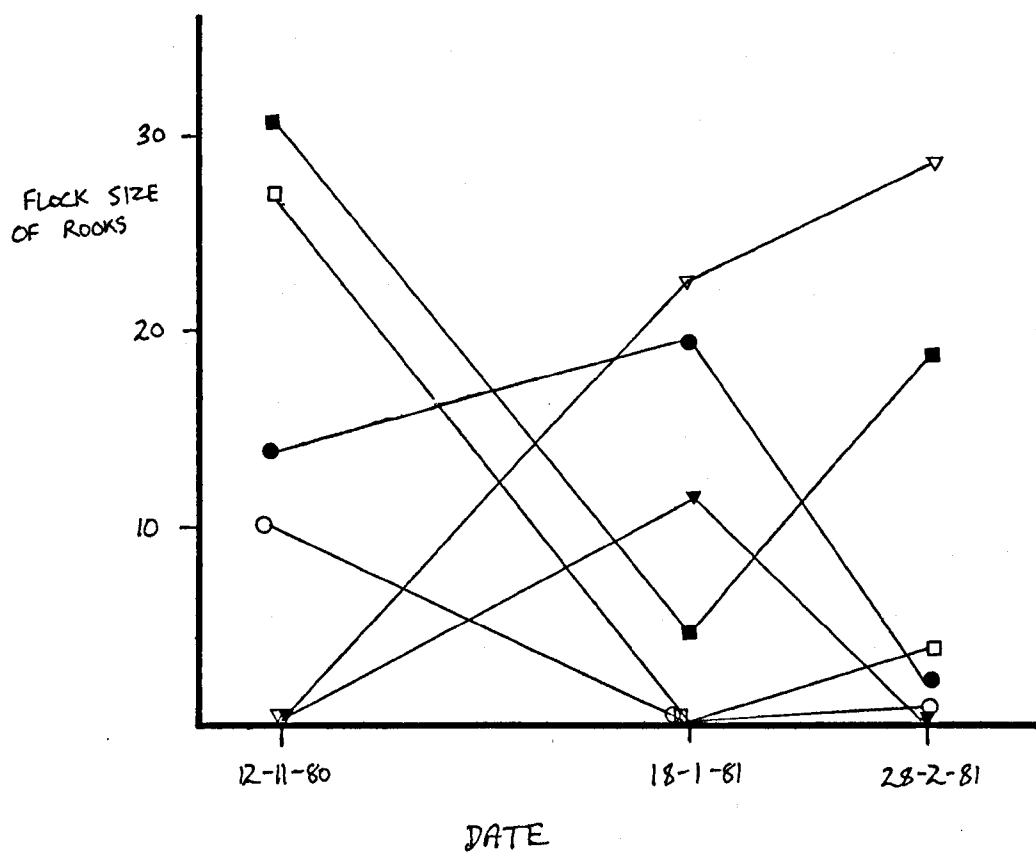
birds were capable of learning this, then there would be no benefit to such birds from local enhancement. However, inexperienced young or immigrant birds could benefit by following others - in winter there is both immigration into Britain from the continent (e.g. Busse 1969, Hurton 1971b) and some dispersal of British birds within the country (e.g. McKilligan 1980, Munro 1975).

Which of these situations existed during the present study cannot be answered by the data available. More detailed analysis of the pattern of prey patch shifts would be required, followed by experiments with captive birds on the capacity to learn such patch-shift patterns (recent interest in optimal foraging has stimulated research into the ability of birds and other animals to assess and remember patch quality - see e.g. Hainsworth & Wolf 1979). Observations of marked birds would be needed to determine which members of the rook population were benefiting by local enhancement.

Although it is not known exactly how birds reacted to the observed shifts, we can at least demonstrate that birds did not regularly occur in the same fields at the same flock sizes. Although figures 1.4.1a to f show that there were some fields which almost always held rooks, figure 2.3.9 indicates shifts in flock sizes for six of the fields sampled for soil invertebrates twice during the winter

Figure 2.3.9

Shifts in rook flock size between six different grass fields
over a winter



1979-80. The census dates in the figure are unfortunately from the next winter and so cannot be related directly to shifts in earthworm densities - but comparison with figure 1.3.7 indicates that the kind of criss-cross shifting pattern of earthworm densities between fields at different times was mirrored by similar flock size shifts. The figure illustrates that flock sizes shifted around - one field did not always hold a flock whose membership was stable, as occurs in, for example, woodpigeons foraging for clover in winter (Murton et al. 1966, 1971).

2.3.A.6 Prey Density, Flock Size and Behaviour

Table 2.3.1 indicates that birds were showing social attraction to one another, and groups did not occur simply as the result of individual attraction to some feature of the environment - i.e. the birds were truly flocking and not merely aggregating.

If a bird's intake rate of prey did not increase when on higher prey densities, then there would be no benefit in locating higher prey densities, at least in terms of short-term intake rate. Similarly, if an individual rook "gave up" and moved on to forage near another flock as often when it was on a good prey patch as when it was on a poor prey patch, then local enhancement would not result in larger flocks eventually building up on the higher prey densities.

Hence the presence of a flock would not be an indication to a passing bird of high prey density. Figures 2.3.1 and 2.3.2 indicate, however, that these two conditions were fulfilled.

Following on from this, since birds stayed longer on better prey areas, then on average a bird which gave up elsewhere will have arrived on a better prey area when it showed social attraction to a bird which was still foraging. If this process repeated itself continuously, then larger flocks will have tended to build up on the best prey densities (table 2.3.2 and figure 2.3.5). Birds in larger flocks had higher feeding rates (figure 2.3.6a) because feeding rate increased with prey density (figure 2.3.2). Thus whether or not there was a "selfish herd" (for example), or any other advantage from joining flocks, there was an advantage for rooks in terms of an increase in individual prey intake rate.

However, an increase in prey intake rate with increasing group size could have occurred through the operation of behavioural mechanisms other than local enhancement. Other ways in which flocking could affect prey exploitation include:

- (a) increasing the efficiency with which the total resources of an area are exploited; for example by group foraging reducing individual flight distances to

shifting prey patches, or by group foraging decreasing the likelihood of individuals foraging in areas recently exploited by another bird;

- (b) social facilitation of the most efficient feeding rate, feeding action or choice of prey type;
- (c) the movements of other animals flushing prey into availability;
- (d) cooperative hunting of prey too large or elusive for single birds to catch;
- (e) communal defence of feeding areas against competitors or, conversely, membership of a group enabling penetration into feeding areas unavailable to single birds because they are defended by a dominant animal;
- (f) membership of a group enabling a decrease in individual vigilance (e.g. for predators), and thereby giving more time for feeding.

Most of these other possible mechanisms are either irrelevant, given the nature of the prey involved (flushing of prey, cooperative hunting); or not competing hypotheses, in the sense that even if they were also operating, local enhancement for food finding could still also be operating and be of advantage simultaneously (exploiting shifting prey resources, social facilitation).

Of the remainder, there is no evidence that flocking by rooks constituted group defence of a feeding area. Groups of rooks were not observed to defend feeding areas against conspecifics or other species. Birds belonging to one rookery tend to forage in particular areas, but there is overlap between rookeries (Phillipson 1933, Coombs 1961, Patterson et al. 1971, P.T. Green, pers. comm.).

It has been proposed that grouping may enable rooks to feed within the territories of carrion crows in Holland, by reducing the effect of carrion crow attacks (Bossema et al. 1976, Roell 1978). However, flocking did not reduce the frequency of successful carrion crow attacks nor the frequency of attacks suffered per individual rook (Waite 1978 and chapter 1.7).

Finally, vigilance decreased with increasing flock size (figure 2.3.6b). Such a relationship, along with an increase in feeding rate with increasing flock size, has often been taken as evidence that being in a flock reduces individual vigilance (due to there being "more eyes" available to look out for predator attack), and that this gives more time for feeding (many references, see chapter 2.2). If the relationship between flock size and feeding rate was due to lower vigilance levels of less "nervous" or "wary" flock birds allowing more time for feeding, then it should have been the case that birds in larger flocks had higher

feeding rates than birds in smaller flocks, at any particular prey density. Feare et al. (1974) found that single rooks did have lower feeding rates than flock birds at each particular stubble grain density, suggesting that single birds were unable to feed as efficiently as flock birds, presumably because they spent more time looking around (figure 9 in Feare et al. 1974). However, in the present study of rooks foraging on grassland, there was no tendency for birds at lower flock size to have lower earthworm intake rates at any particular earthworm density (figure 2.3.8). Thus single birds, or birds at low flock size, did not have lower prey intake rates simply because being in a low flock size meant that they had less time for feeding.

The patch-locating hypothesis under consideration in this chapter predicts that feeding rates should increase with increasing flock size only when data are collected at random, because larger flocks tend to occur on higher prey densities more frequently than smaller flocks. But at any particular prey density, flock size should not necessarily be related to feeding rate. This is supported by the present data, while the data do not support the prediction of the vigilance hypothesis that the flock size \times feeding rate correlation occurred because of higher vigilance levels of birds foraging in smaller flocks. The flock size \times look up negative correlation seems therefore interpretable in the following way. Birds at lower flock size have

higher look up levels because they tend to occur more often on poorer prey areas; look up is therefore interpreted not only as vigilance for predators, but also as vigilance for other rooks as indicators of better prey areas (cf. Krebs 1974).

This interpretation receives circumstantial support from comparative vigilance data from three other Corvid species also foraging on grassland. These four related species are probably open to approximately similar predation pressures when foraging on open grassland areas in lowland Britain. There is no relation between the weight of the species and tendency to flock on grassland (Waite 1978), and the species appear equally conspicuous. To a human 'predator' they appear equally palatable (Cott 1946, Cott & Benson 1970), and are preyed upon by the same kinds of ground and aerial predators (e.g. Coombs 1978, Davies & Davis 1973, Davis & Davis 1981, Roskaft 1980, Rudebeck 1950/51). Yet vigilance levels of the carrion crow and magpie on their own or in pairs were similar to those for rooks in flocks; whilst vigilance levels of rooks when on their own or in pairs were significantly higher than either those of the carrion crow or the magpie. Vigilance of jackdaws, also a normally gregarious species, when solitary or in pairs, was also significantly higher than that of carrion crows or magpies.

The normal social organisation of the breeding population of carrion crows and magpies is characterised by A-territoriality (see chapter 1.2), two (or sometimes, outside of the breeding season, several) birds to each area. They forage on their own or as pairs. It seems that carrion crows and magpies do not require flocking to locate their prey on grassland (appendix 8). It seems likely, then, that the different vigilance levels of the species are related to the differences in social organisation connected with the exploitation of prey, given the apparent similarity in vulnerability to predation. Thus the most reasonable interpretation must be that rooks did not flock to reduce vigilance levels, but that being at low flock size caused an increase in looking up for other rooks as indicators of better feeding areas.

2.3.A.7 Conclusion

None of the observations of wild rooks foraging for a natural prey contradicted the predictions of the hypothesis that local enhancement could increase food-finding efficiency with a consequent increase in individual prey intake rate. However, the data were not sufficient to demonstrate whether shifts in the location of earthworm densities were predictable or not. The capacity of rooks to learn predictable patterns of prey-shifting (should they exist)

also remains unknown.

2.3.2 Digression: a Cost of Flocking

The preceding discussion (and Waite 1981) assumed that the feeding benefit of being in a flock increased continuously with flock size, since the relationship between flock size and earthworm intake rate did increase, though at different rates, up to all flock sizes recorded (figure 2.3.6a). However, although the relationship was statistically significant, the proportion of variance in intake rate explained by the relationship with flock size was low (r -squared = 0.112). There are several methodological reasons for expecting a large error variance, and thus a reduction of the correlation coefficient and an underestimation of the true strength of the relationship. Firstly, data were taken over a long period of time, and thus a field containing a high prey density at one time (and thus containing a large flock size) might actually be a rather low prey density compared to other times when data were collected. Since earthworm intake rate was related to prey density (figure 2.3.2) it was therefore quite likely that a low flock size on one occasion would yield similar prey intake rates to a high flock size at another time, since the same prey density could on one occasion be the lowest

ranked prey density available in the area (and thus attract small flocks), but at another time the highest ranked prey density (and thus attract large flocks). Although there is no reason to suppose this would induce any systematic bias to obscure the true relationship, it will have introduced scatter to the relationship and reduced the value of the correlation coefficient.

Secondly, some low flock sizes will have come to good prey densities by chance whereas, because of the relationship between prey density and tendency to take flight and show local enhancement (figure 2.3.1 and table 2.3.1), few large flocks will have occurred on low prey densities. Thus some degree of systematic bias may introduce scatter at one end of the graph (while reducing the value of the correlation coefficient this tendency is, of course, a true biological cause and not an addition to error variance).

Thirdly, there are likely to be large individual differences in motivation, skill, etc., all of which, though not expected to introduce systematic bias, will have introduced scatter to the overall relationship even if each individual bird's intake rates were perfectly positively correlated with prey densities. Similarly, intake rates vary with differing climatic conditions (appendix 8).

However, the addition of more recent data and the analysis of the species interactions reported in part one of the thesis have suggested yet another contributory reason for the low coefficient. Figure 2.3.6a presented the data for all earthworm size classes combined. Figure 2.3.10a presents the relationships, for the increased sample size now available, for small earthworms separately from medium and large earthworms. Intake rates of small earthworms were significantly positively related to flock size, both in terms of numbers and calorific value ingested, but those of medium/large earthworms were not.

Given the evidence produced in chapter 1.6, where a negative relationship was described between the intake rate of large earthworms by carrion crows and the flock size of all other birds present in a field, this suggests that large flocks of rooks, though finding themselves on denser patches of earthworms, could not feed on the larger size classes efficiently. (*) This was probably because they were disturbed down their vertical burrows by the increased activity of the birds, whereas the smaller, non-permanent

(*) Given that the proportion of medium/large earthworms did not decrease at higher earthworm densities, the relationship between flock size and intake rate of medium/large earthworms may have been neutral, rather than negative as it was for carrion crows, because of the effects of decreased intake rates due to disturbance at higher flock sizes, and of increased location of denser areas of earthworms due to local enhancement effects at higher flock size, cancelling one another out. However, field work designed to test both this and the proposed disturbance explanation are required.

Figure 2.3.10

Relationship between prey intake rates of rooks and flock size

(a) Intake rates of different size classes of earthworms by numbers and calorific value. Correlations of flock size with intake rates of:

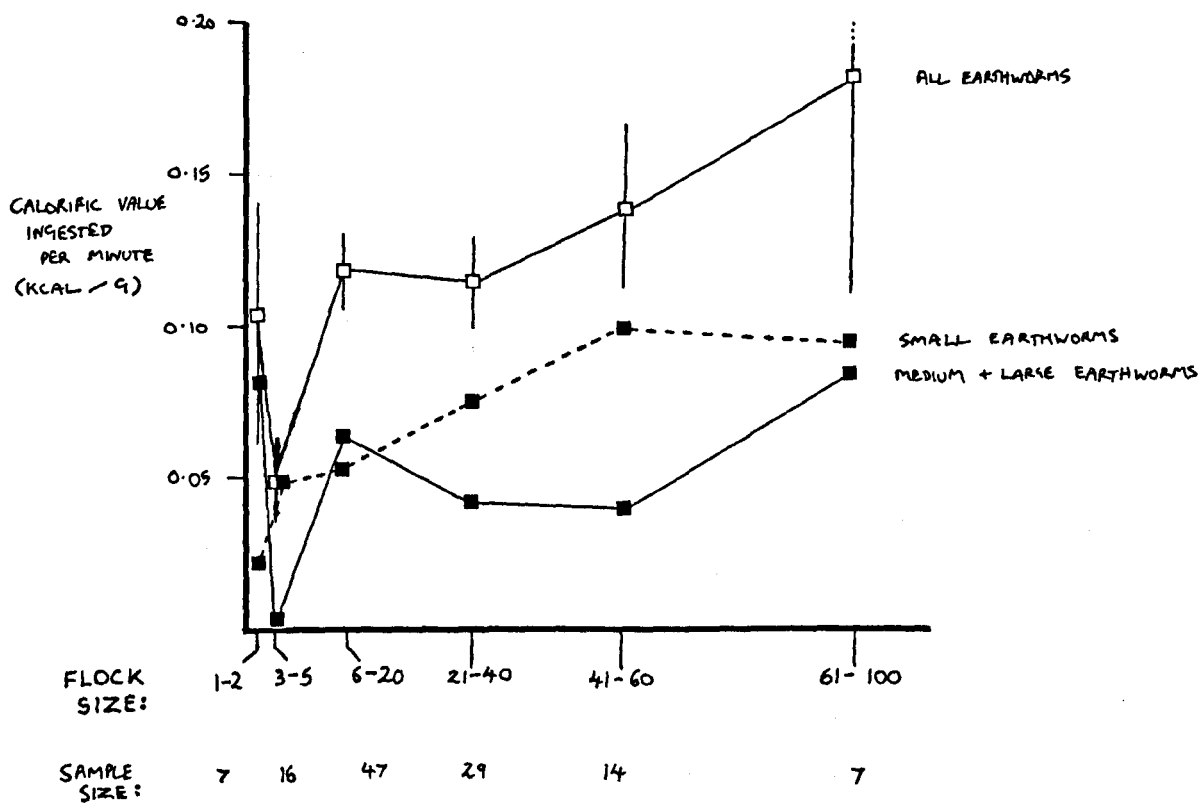
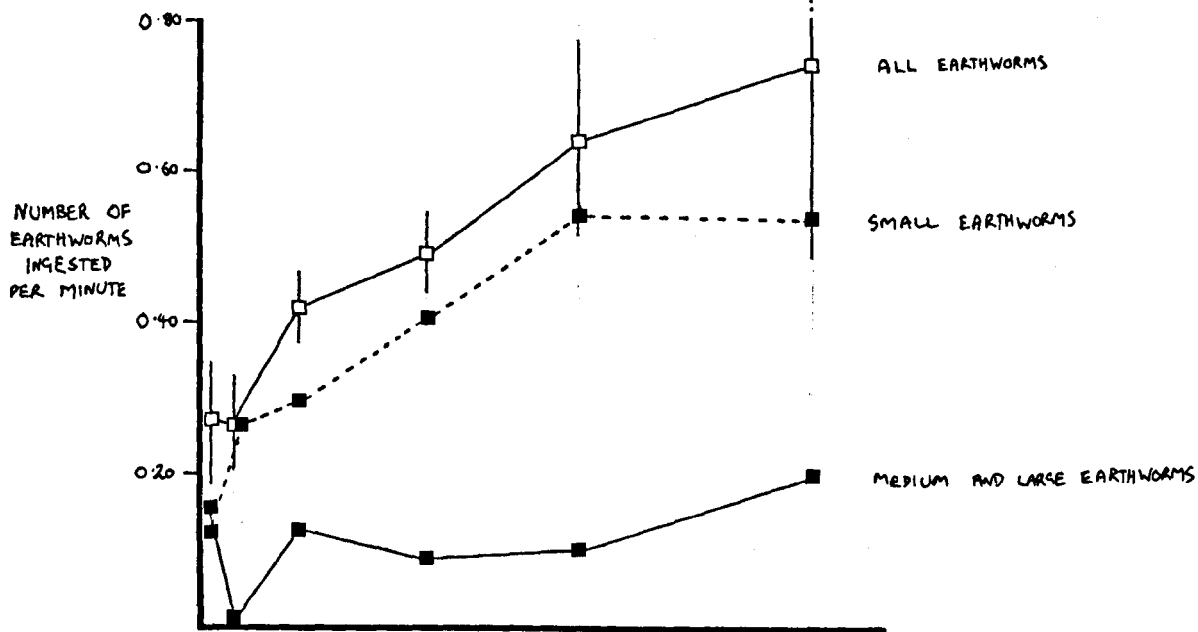
	<u>Rho</u>	<u>n</u>
small earthworms:	0.282	**
medium and large earthworms:	0.039	NS
all earthworms:	0.227	*
small ew calorific value:	0.282	**
med./lge. ew calorific value:	0.040	NS
all ew calorific value:	0.185	*

(b) Intake rates of earthworms and other invertebrates by numbers and calorific value. Correlations of bird numbers with intake rates of:

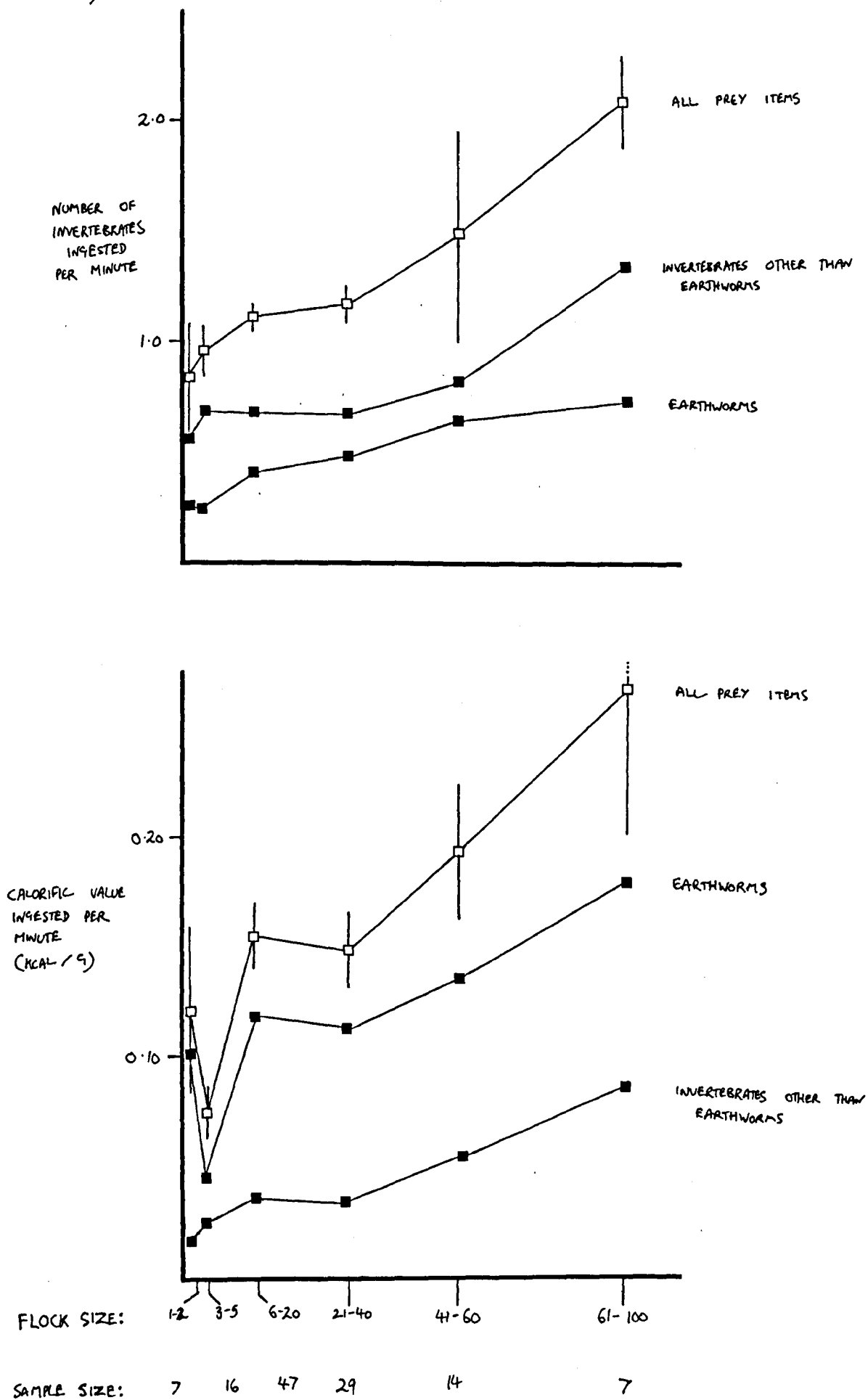
	<u>Rho</u>	<u>n</u>
earthworms:	0.227	*
other invertebrates:	0.153	NS
all invertebrates:	0.276	**
ew calorific value:	0.185	*
other inv. calorific value:	0.133	NS
all invert. calorific value:	0.236	**

Points for different bird numbers have been grouped together and the mean plotted (+/- s.e.) for ease of interpretation, but correlations were carried out on the original data.

(a)



(b)



burrowing earthworms inhabiting the root layer, could not show a similar anti-predator response (or at least, could not show a response which made them completely unavailable to birds in the same way as the larger size classes could). The fact that intake rates of other classes of invertebrates, also probably limited in their disturbance by the flock size of predators foraging for them, increased significantly with flock size (figure 2.3.10b), further suggests that the lack of relationship for medium/large earthworms was due to disturbance.

The fact that small earthworms formed the major part of the earthworm diet at all flock sizes meant that the overall effect was for an increase in total earthworm intake rate (and of total invertebrate intake rate) with increasing flock size, because smaller earthworms were by far the commonest prey type available in the soil in winter (chapter 1.3). Thus the disturbance cost of flocking was more than offset by the benefit in terms of increased intake rates of small earthworms and other invertebrate types, due to the increased efficiency of location of denser prey patches brought about by flocking behaviour, as just described.

Rooks had higher total earthworm intake rates than the solitary carrion crows foraging on undisturbed large earthworms (figure 1.6.2), suggesting that the evolution of

flocking behaviour and a probing bill was in general advantageous not only in terms of enhancing ecological separation from carrion crows, but in allowing the efficient exploitation of an abundant prey. Rook exploitation of this prey is almost certainly connected with the high abundance of rooks compared to the other three Corvid species under consideration in lowland Britain (chapter 1.7).

The data suggest that the greatest benefits accrue at the highest flock sizes, yet table 1.2.2 indicates that rooks were most frequently found foraging at medium flock sizes (50% were in flocks of 6-40 birds). Rather interestingly, figure 2.3.10b indicates that in terms of calorific value of intake, it was actually worse for a rook to be in a very small flock (3-5 birds) than to be on its own or as a pair - possibly because the disturbance effect had begun to operate but was not overcome by any local enhancement benefit at such low flock size. Another possibility is that some solitary birds were on their own because they had discovered some particularly good area on a previous visit, and had flown directly there to forage - and thus had high prey intake rates - whereas small flocks may almost always have been searching flocks which had yet to settle at a high prey density area. These different possibilities should be tested.

Medium/large earthworm intake rates dropped at flock sizes of 3-5 birds, but intake rates of small earthworms and other invertebrates had not yet risen sufficiently to compensate for this drop. Table 1.2.2 indicates that in fact more birds foraged on their own or in pairs (20.9%) than in small flocks (17.4%). Only 11.6% of rooks were found at flock sizes where the greatest benefits accrued, suggesting that conditions were not often such that rooks could maximise their prey intake rates in winter at Keele.

B. Local Enhancement to Varying Prey Densities within Single Grass Fields

The difference in the form and behaviour of flocks of different species of birds can be as striking to the observer as the difference between species which adopt a solitary way of life (or indeed other members of the same species) which adopt gregariousness. Foraging flocks of rooks on grassland in winter were not compact, with flock members moving together in a closely integrated fashion as can be the case with, for example, some winter flocks of starlings (*Sturnus vulgaris*) (pers. obs.), or with woodpigeons (*Columba palumbus*) feeding on clover (Murton et al. 1971). Rather, rooks foraged at times seemingly independently of other birds, but occasionally flew over to land near others, sometimes briefly interacting with the birds they landed near, and then continued foraging. "Flocks" in the same field could contain birds foraging within a few feet of one another and birds fifty or more yards apart. In addition, as flocks moved over a field, time-lapse plotting indicated that flocks of the same number of birds "expanded" and "contracted", as time passed, thus varying in the total area of the field which they covered (Green 1977).

It was considered that if variations in prey densities

existed on a small scale within a single grass field over which a flock was foraging, then birds which gave up foraging on an area with poorer prey density, and showed social attraction to flock neighbours which had located a denser prey area within the field, could gain an advantage in food-finding efficiency once foraging within a flock. If birds showed local enhancement and also tended to leave areas of higher prey density less frequently, then birds would begin to congregate on the denser prey areas within the field, resulting in a "contracted" flock with a lower mean nearest neighbour distance and a higher mean intake rate of prey. Flocks would "expand" again as the prey were depleted and birds foraged wider in search of other denser prey areas.

Results

2.3.B.1 Earthworm Dispersion

Data described in section 1.3.8.2 indicate that c.75% of grass fields showed signs of aggregation over the kind of area which flocks could occupy. The data in section 1.3.8.4 showed that aggregations could shift in location within a field, though this was supported statistically only for earthworm numbers and not biomass.

2.3.B.2 Social Attraction

Although, as described above, rook flocks were not as coherently compact as some bird flocks, yet time-lapse plotting of birds on large grass fields indicated that birds kept closer together when foraging than was necessary given the size of the field available to them. Plotting of flocks on a 10.5 hectare grass field at Keele indicated that flocks covered on average 17.7% of the field ($N = 51$ flocks plotted, mean FS = 24.6), calculated by drawing lines between perimeter birds so that all birds were within the boundary. Birds foraged independently for the most part, but were observed to lift off and re-land nearer to other birds at times during foraging bouts. A number of flocks were selected arbitrarily and observed for five minutes each; birds taking flight to re-land within the same field were recorded as landing within or further than 5 metres from a conspecific. This constituted a fairly rigorous definition of choice of landing by a conspecific, since mean nearest neighbour distance for winter flocks was c.10 metres. The results indicated that 59.9% of birds landed within 5 metres of another rook ($N = 206$ flights observed). It is unknown what proportion of birds would be expected to land within or greater than 5 metres from another bird if landings were at random, since the area flocks covered on the fields used for these data were not measured. But for each flock observed the area of field

available greater than 5 metres from another bird (and often subsequently foraged over by the flock) was certainly considerably greater than the area of field available within 5 metres of any conspecific. Even if a very conservative estimation of the expected proportions for random landing is taken (50:50), the observed proportion of birds landing within 5 metres of another rook indicates a significant tendency to land near another conspecific (binomial test, $z = 3.28$, $p < 0.01$).

2.3.B.3 Relationships with Prey Density

It would be difficult, but not impossible, to map out the variations in earthworm densities accurately within a field and then to collect behavioural data from birds recognised as foraging on these different densities. However, such a comprehensive invertebrate sampling programme was not possible during the present study. There were significant relationships between earthworm intake rate, flight rate, flock size and earthworm densities when the overall density of earthworms within separate grass fields was measured (see A). It is necessary to assume that these relationships would also hold were the measurements of behaviour and flock density from within the same field.

2.3.B.4 Relationships with Flock Density

Figure 2.3.11a indicates that earthworm intake rate tended to increase with decreasing mean nearest neighbour distance. Flock size is also negatively correlated with mean NND (Waite 1978, Chantrey & Waite 1979). However, a partial correlation for those observations of earthworm intake rate when both flock size and nearest neighbour distance were recorded indicated that both variables were still significantly correlated with earthworm intake rate when the other was controlled for (partial correlation coefficients: FS x earthworm IR, $r = 0.287$, $p < 0.05$; mean NND x earthworm IR, $r = -0.203$, $p < 0.05$, 1-tailed; the simultaneous relationship is illustrated in figure 2.3.11b). Thus neither the relationship between flock size and earthworm intake rate, nor that between flock density and intake rate, could have been entirely caused by the relationship between flock size and density.

Figure 2.3.12 indicates that the relationship between flock density and earthworm intake rate was due to small earthworm intake rate and not medium/large earthworm intake rate. The extra data in this figure compared to figure 2.3.11 provide a smoother negative relationship between flock density and overall earthworm intake rate. The figure further indicates that intake rates of all invertebrate types other than earthworms were not related to

Figure 2.3.11

Relationships between rook flock density, flock size and earthworm intake rates

(a) Flock Density and feeding rate ($\rho = -0.442$, $N = 76$, $p < 0.001$); (b) Flock size, density and earthworm intake rates.

Data for several flock sizes have been blocked together for the figure (mean \pm s.e.) but statistical analysis was performed on the original points.

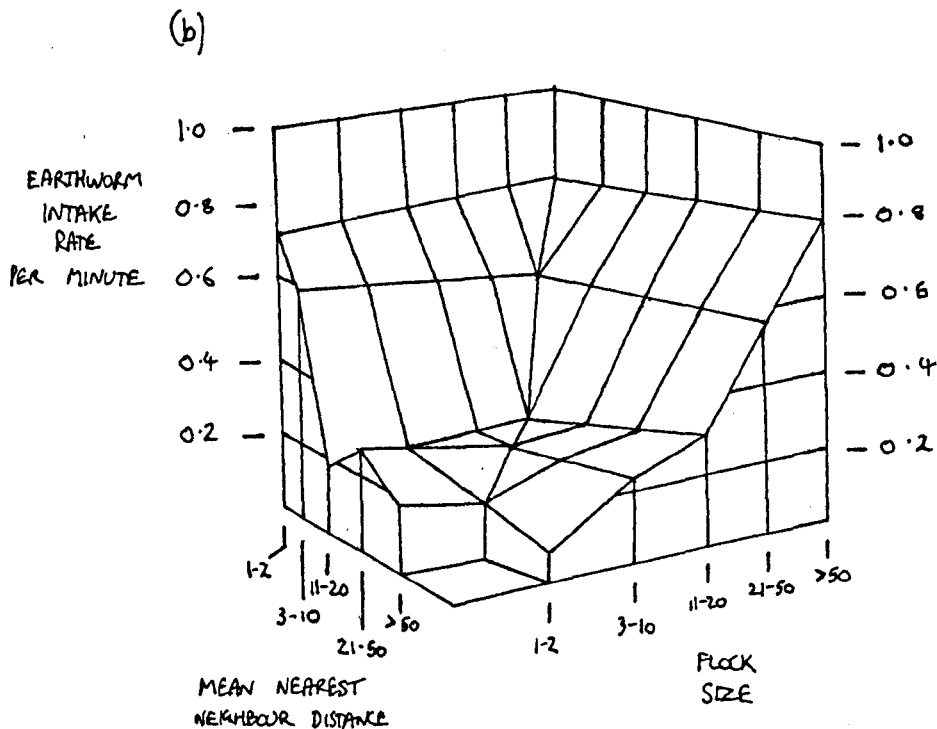
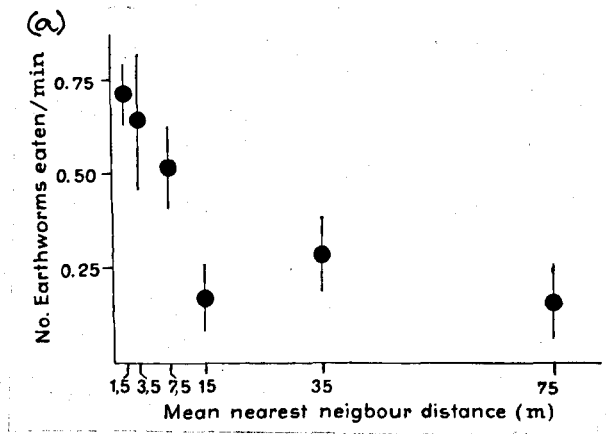


Figure 2.3.12

Relationship between prey intake rates of rooks and flock density

(a) Intake rates of different size classes of earthworms by numbers and calorific value. Correlations of mean nearest neighbour distance with intake rates of:

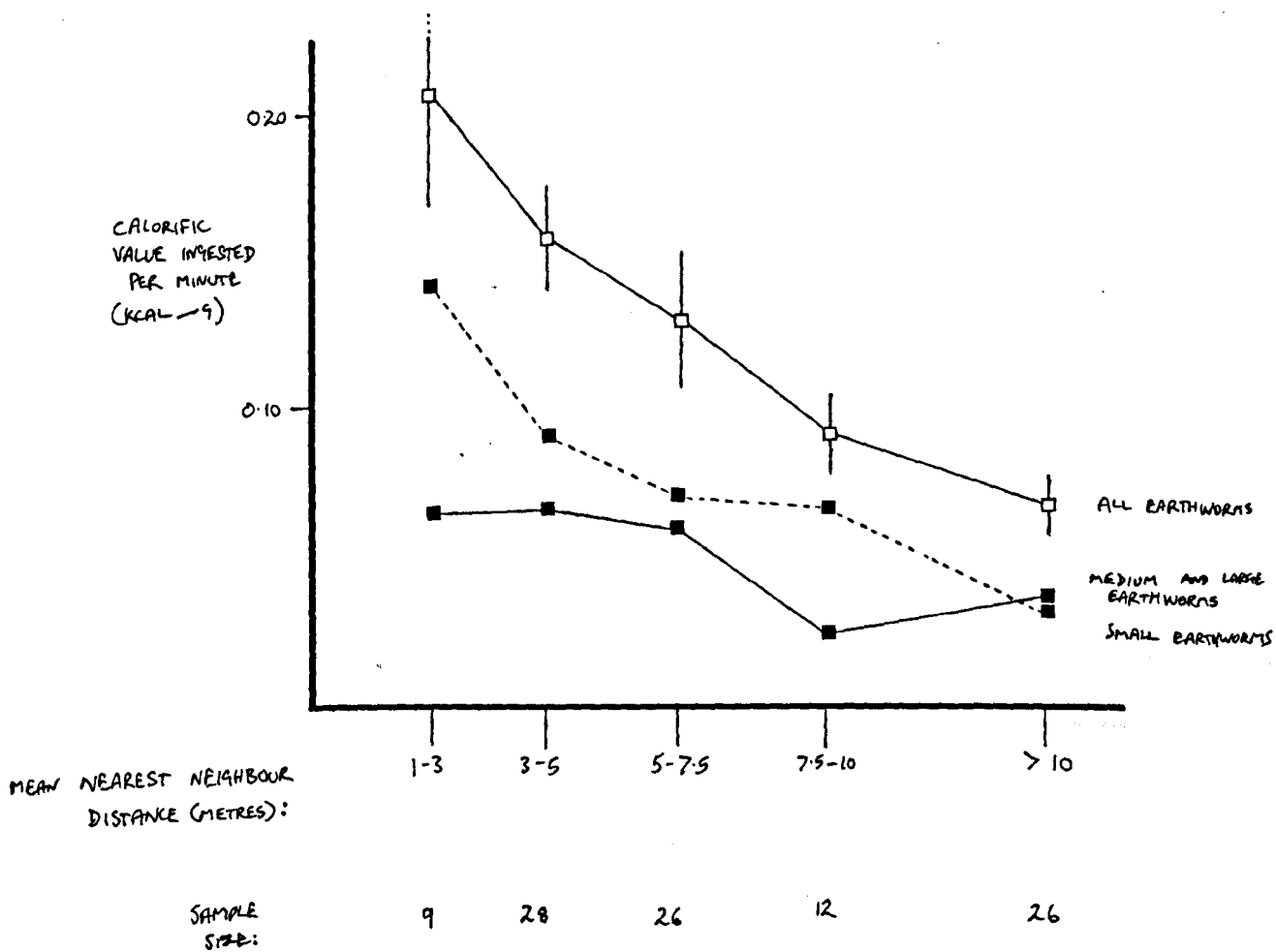
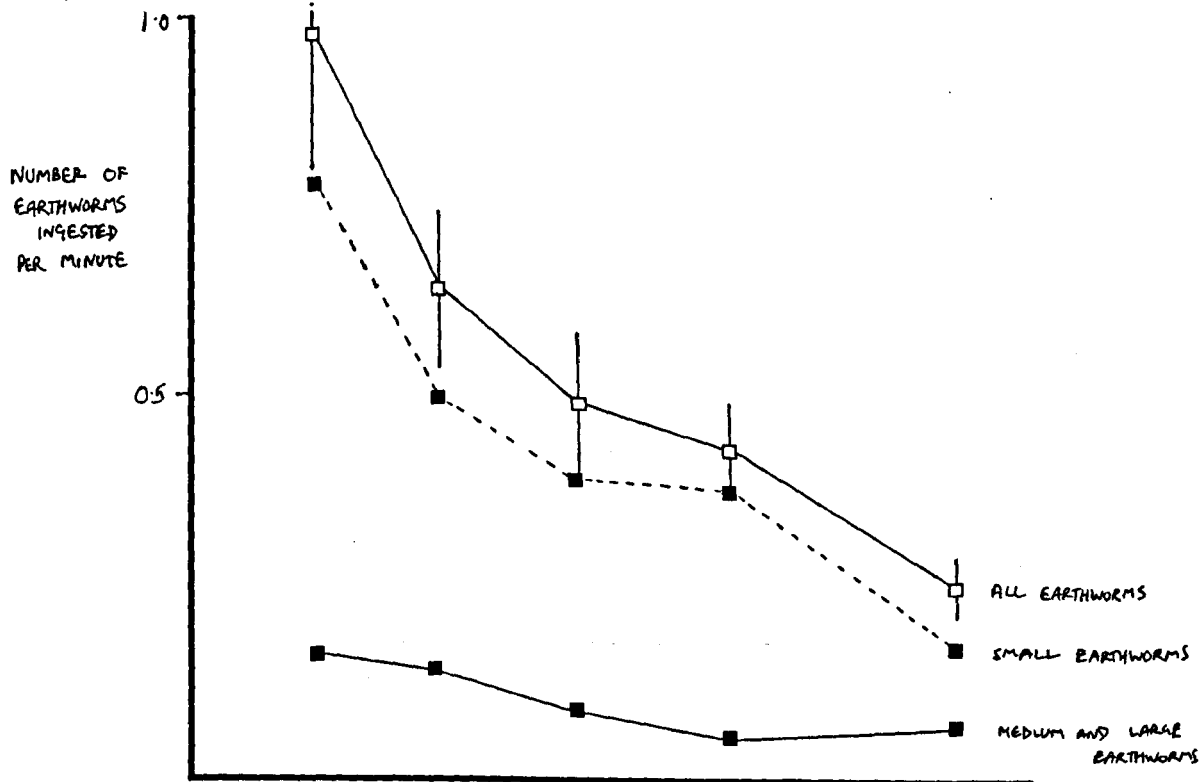
	<u>Rho</u>	<u>n</u>
small earthworms:	-0.357	***
medium and large earthworms:	-0.107	NS
all earthworms:	-0.334	***
small ew calorific value:	-0.357	***
med./lge. ew calorific value:	-0.105	NS
all ew calorific value:	-0.296	***

(b) Intake rates of earthworms and other invertebrates by numbers and calorific value. Correlations of mean MND with intake rates of:

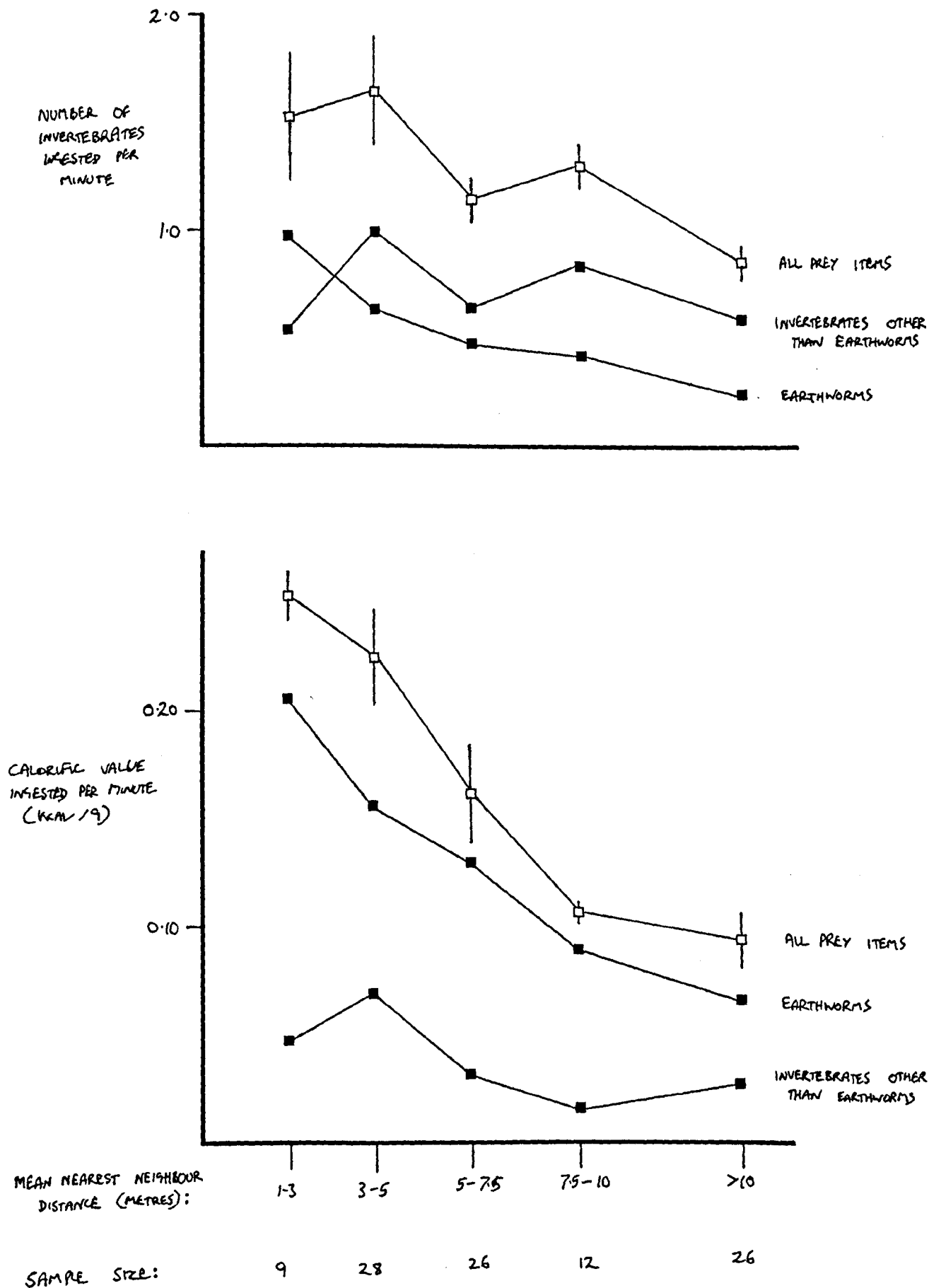
	<u>Rho</u>	<u>n</u>
earthworms:	-0.334	***
other invertebrates:	-0.104	NS
all invertebrates:	-0.361	***
ew calorific value:	-0.296	***
other inv. calorific value:	-0.102	NS
all invert. calorific value:	-0.374	***

Points for different bird numbers have been grouped together and the mean plotted (+/- s.e.) for ease of interpretation, but correlations were carried out on the original data

(a)



(b)



flock density.

No significant relationship was found between flock density and vigilance in the present study ($\rho = -0.056$, $n = 35$, N.S.).

Discussion

2.3.B.5 Earthworm Dispersion

The data have indicated that earthworms were aggregated within single fields (i.e. within the area over which a single flock could forage) in a high proportion of cases. In addition, earthworms were probably hard to find (see A). Lastly, the data indicate that earthworm densities could shift in location within fields, but for two fields sampled this relationship was significant for earthworm numbers only and not biomass. The fact that earthworm densities were shown to be aggregated within cowpats is further evidence that the location of earthworm aggregations will shift within single fields if these are grazed, since earthworm densities beneath pats have been shown to vary with the age of the pat (e.g. Boyd 1958, Holter 1979). The higher areas of earthworm density beneath pats will shift about the field as each pat builds up to its maximum

earthworm density then declines again as it disintegrates. As in (A), however, the data cannot indicate to what extent such patterns were predictable, nor whether rooks could learn such shift patterns.

2.3.B.6 Prey Density, Flock Density and Behaviour

Rooks showed local enhancement within single grass fields (within a flock) since (a) though not foraging as a compact group all of the time, birds moved towards others at intervals, and (b) birds generally kept closer to others than the size of the field demanded. It is assumed that the effect in (b) resulted from the behaviour in (a).

Data were not available to establish whether the necessary relationships between prey density variations within a single field and prey intake rate, tendency to leave a patch, and flock density existed. Given that these relationships existed between larger scale prey areas (A), then perhaps an assumption that, if measured, they would be found to exist between smaller scale areas is not unreasonable.

With regard to the relationship between prey density and flock density, two pieces of circumstantial evidence might be offered. Firstly, rooks flying over a field during a two-week period in November 1979 tended to land

significantly more often, and fly on less often, if birds already on the field were at lower mean NNDs (table 2.3.1c). This response would be advantageous if denser flocks tended to occur on higher prey densities. (It should be noted that this response could also have "selfish herd" benefits; Hamilton 1971).

Secondly, the variance in mean NND for rook flocks foraging on a randomly dispersed prey type (stubble wheat) was significantly less than that for rooks foraging on an aggregated prey type (earthworms in grassland). Time-lapse photographs were taken, with an interval of 30 seconds between frames, of rook flocks foraging under the two prey conditions. The mean NND for each frame was measured, and it was found that the variance in mean NND for flocks on grass was significantly greater than for flocks on stubble (variance-ratio test: $F = 2.87$, $df = 19, 19$, $p < 0.05$). An interpretation of these data could be that the greater variation in flock density on grassland was the result of birds coming together on areas of higher earthworm density, and scattering wider on areas of lower earthworm density.

Since local enhancement could be for other, non food-related reasons, it should be the case that birds showing social attraction within a foraging flock had increased feeding rates. If birds showed local enhancement and were less likely to give up as frequently on better prey densi-

ties, then birds will have congregated on the better prey areas; thus it should have been the case that feeding rates increased with increasing flock density. Figures 2.3.11 and 2.3.12 indicate that earthworm intake rate did tend to increase with increasing flock density. Thus there was an advantage for rooks in having shown social attraction to other members of the foraging flock in terms of an increase in individual prey intake rate.

Clearly, if MND were to drop to very low levels birds would become restricted in movements and agonistic interactions might increase in frequency. However, the lowest mean MND recorded when grassland foraging occurred was one metre. Figure 2.3.12a indicates that medium/large earthworm intake rate was not significantly negatively related to increasing flock density, as might have been expected on the prey-disturbance hypothesis. However, as already stated, MNDs were never very low on grassland (mean MNDs on stubble were usually much lower) and thus it would seem that down to these MNDs prey were not disturbed - it seems that the disturbance effect is not connected with distance between birds so much as a large number of birds continually criss-crossing the area to be searched (as mentioned earlier, flocks did not cover the ground in a coordinated fashion such that ground covered by one bird was always ignored by others).

The fact that flock size was positively related to the intake rate of all invertebrates other than earthworms (figure 2.3.10b), but flock density was not (figure 2.3.12b), strongly supports the suggestion that the flock density relationship with earthworm intake rate was due to birds building up on denser patches of earthworms. All other invertebrates were aggregated between fields (chapter 1.3) and individual invertebrate types were aggregated within fields - however, each type was not necessarily aggregated in the same place within a field, producing a random distribution for all other invertebrate types combined (see figure 1.3.3); thus a measure of intake rate of all these types combined would not expect to be related to variations in flock density, which would reflect behavioural responses to the distribution of the most important, aggregated, prey type (earthworms).

If vigilance increased with increased mean NND, then the hypothesis could be advanced that the negative correlation between mean NND and earthworm intake rate was the result of a decrease in vigilance allowing more time for feeding as mean NND increased. However, no significant relationship was found between mean NND and look-up in the present study. It is possible that the measure of vigilance defined was not sufficiently sensitive to detect true levels of vigilance for other foraging conspecifics at

close distances between birds. Without any way of knowing whether the lack of relationship was valid or the result of inadequacy of measurement, it would be unfruitful to present data of the kind given in (A) above. It is therefore impossible to make any firm conclusions on this point with the data currently available. The observations relating to the other possible food-related social mechanisms have been given in (A).

2.3.B.7 Conclusion

For local enhancement to small-scale variation in earthworm densities within single grass fields (i.e. within the area over which a single flock might forage), all predictions were supported by the data with the following qualifications and exceptions:

- (a) Earthworm densities were not significantly aggregated within all grass fields sampled (or at least within the area of the field sampled); hence social attraction could only have been advantageous in terms of the location of denser prey patches when rooks were foraging on a certain proportion of the available fields.
- (b) That earthworm densities shifted in location within single fields was established for two fields sampled in terms of earthworm numbers only and not earthworm

biomass.

- (c) The data were not sufficient to demonstrate whether or not such shifts in location of earthworm densities as did occur were predictable, nor to demonstrate the capacity of rooks to learn any such patterns as might exist.
- (d) It was not possible during the present study to map out the varying earthworm densities within a single grass field and to measure flight rate, earthworm intake rate and mean MMD of birds foraging on these different densities.

2.3.3 Final Conclusion

It is concluded that the field observations of rooks foraging on grassland have provided fairly convincing evidence that individual rooks could gain an advantage, in terms of short-term increase in prey intake rate, by showing social attraction to conspecifics already foraging on different grass fields. Food-finding by local enhancement has been demonstrated for three different genera of birds feeding on three quite different prey types: great blue herons foraging for estuarine fish schools (Krebs 1974), house sparrows foraging on patches of spilt barley grain

(Barnard 1980), and rooks foraging for grassland earthworms.

The field observations have also provided evidence consistent with the view that individual rooks could gain a similar advantage (increase in prey intake rate) by showing social attraction to other members of the flock when foraging on a proportion of the grass fields available to them in winter. However, a more detailed programme of invertebrate sampling would be required before any firmer conclusion could be made either for or against the hypothesis. Such a detailed programme, by providing more information on the frequency and predictability of prey patch shifts, could also help to determine which members of the rook population could benefit from local enhancement both to and within flocks.

The different hypotheses of the kinds of food-related advantages, which might accrue from flocking, predict different causal relationships between variables. A direct influence of group size on prey-catching ability is hypothesised by, for example, cooperative hunting. Variations in prey intake rate are seen as the direct result of group size and behaviour, and no other variables are necessarily involved. The hypothesis that vigilance decrease at higher group size allows more time for feeding predicts a

direct effect of group size on vigilant behaviour, and a direct influence of vigilant behaviour on prey intake rate. Group size as such has only an indirect influence on prey intake rate, and this hypothesis makes no predictions about the relationships of variables with prey density.

The local enhancement hypothesis predicts that all variables are responses to variations in prey density, except for social attraction itself, the rate of which is indirectly mediated through variations in group size and density (see tables 2.3.1b and c). The only social influence is, therefore, one of a tendency when moving from one area to another, to land in the vicinity of other foraging birds. Group size as such has no influence, direct or indirect, on prey intake rate, but is itself a consequence of (a) the influence of prey density on frequency of leaving a prey patch, and (b) the tendency to local enhancement. Prey intake rate is influenced directly by prey density and not by group size. Group size is involved only in the sense that local enhancement to a larger group will result in higher prey intake rate because larger groups tend to occur on higher prey density. The food patch locating hypothesis therefore involves only a simple form of social behaviour.

Since the hypothesis states that the social and behavioural variables are all causally related not to each

other, but to prey density, variables from the field observations would have been more fruitfully treated by multivariate analyses. Unfortunately, however, for practical reasons it was not always possible to record all the variables at the same time for each separate bird observed. Thus it was necessary to treat the variables as independent of one another and to analyse by simple bivariate techniques. It might be noted that the variables, even though often measured independently of one another, show curvilinear relationships which are to some extent similar.

Barnard (1980) was able to make observations of all relevant variables on the same individuals, and similar conclusions to those of the current study were reached (in an independent and parallel study). In a situation where predation pressure was apparently inconsequential, partial correlation indicated that house sparrows in larger flocks had higher intake rates of barley grains not because of a direct influence of group size on behaviour, but because larger flocks tended to occur on areas of greater barley-grain density. As in the current study of rooks, larger flocks tended to occur on denser prey areas because of local enhancement and the tendency to leave areas of denser barley less frequently.

Since correlational evidence of the kind available from field observations cannot prove causal relationships,

it would be fruitful to control levels of the key exogenous variables identified (in this case prey density) experimentally, and measure variations in the social and behavioural variables in question. The results of such an experiment are reported in the next chapter. A similar approach is to quantify variables and run tests of different hypotheses by computer simulation. Chantrey (1982) reports the results of such an approach employing values derived from the field observations reported in this chapter. Chantrey found that birds which showed local enhancement behaviour both to foraging flocks, and to birds within foraging flocks, increased their intake rates of patchy prey and reduced the risk of finding too little prey.

Part Two Chapter Four - Rook flocks and food finding: test by field experiment

2.4.1 Introduction

The last chapter suggested that wild rooks feeding on a patchily distributed natural prey (such as earthworms, Lumbricidae) foraged essentially independently of one another; but when giving up to move elsewhere, showed social attraction and chose to start foraging again in the vicinity of other conspecifics.

Individual birds probably foraged 'optimally' (ie made decisions on how long to forage in any particular prey patch on the basis of their intake rates of prey in that patch compared to the average in the habitat as a whole). This is an assumption - the data available are actually only sufficient to show that birds spent less time foraging on areas with lower prey densities. It could be that birds simply had an invariable search time associated with any particular prey density, rather than the ability to remember average patch value at any particular time and adjust search times to these changing values. It will be noted that the assumption does not in this case qualitatively alter the arguments, it simply makes the birds more efficient. Evidence is accumulating that animals can

forage in this way - see e.g. Krebs (1978b) for a review, Hodges (1981) for some recent experimental evidence.

Since birds stayed longer on better prey areas, on average a bird coming to land near another bird which was still foraging would move to a better prey area. If all birds behaved similarly, then flocks would tend to build up on the better prey patches. It was suggested that rooks could, therefore, use local enhancement to increase the efficiency with which denser prey patches were located.

Comparable models have been derived from observation in natural settings by, for example, Barnard (1980), Burger (1981), Caraco (1979a & b), Caraco et al. (1980a), Krebs (1974), Pulliam (1976), and Pulliam et al. (1974). Krebs' situation was very similar, with prey density variations influencing behaviour, and predation on the birds inconsequential as a controlling variable. In Barnard's study also prey density influenced variations in the other variables in the system, though the presence of a predation-threat introduced another exogenous variable in one of the two situations observed. (These two studies have been described in the last chapter.)

The studies on yellow-eyed juncos (Junco phaeonotus) by Caraco, Pulliam and co-workers were somewhat different in that, in addition to predation threat, intraspecific aggression (influenced by temperature and prey density) was

an important variable influencing prey intake rate. In these studies aggression increased with increasing flock size (and this acted to reduce prey intake rates), thus counterbalancing the advantage of higher flock size in terms of reducing individual vigilance for predators (which acted to increase the time available for feeding). Thus optimal flock size (in terms of maximising prey intake rate) was not equivalent to maximum flock size.

In the present study, however, predation was not an important factor (see section 2.3.A.6 above, and the non-significant influence of human disturbance described below in section 2.4.3.2); and neither did intraspecific aggression occur at levels high enough to influence prey intake rates (chapter 1.7 and section 2.4.3.1 below). Maximum flock size in the natural setting was associated with maximisation of prey intake rate (figure 2.3.10), and the proposed model includes no conflicting costs and benefits of the kind defined by Caraco and Pulliam.

During normal field observation in the present study it was not possible to obtain all relevant measures simultaneously, and all of the variables were observed and none manipulated. Since the interpretation offered by the last chapter hypothesised that all behaviours were direct or indirect consequences of changes in but one exogenous variable (i.e. the density of prey in the different

patches), an experiment was designed using wild rooks foraging for an artificially provided prey. All measures could then be readily taken simultaneously, and the hypothesised exogenous variable manipulated by the experimenter.

The model proposed here is, therefore, not simply analysed by naturalistic observation, but is tested by a new set of data gathered in a semi-experimental way. In addition the data are analysed by a statistical method (path analysis) which can test not only whether the changes in behaviour predicted by the model occurred, but also help to develop modifications to take into account unpredicted relationships.

2.4.2 Method

Wild rooks were attracted to clearly visible bait on a large pasture field on the campus of the University of Keele, Staffordshire (field 1 of figure M.1b), for a week prior to the start of the experiment. When birds were visiting the bait reliably a grid of nine separate, but contiguous, plots (each 2m x 8m) was marked out on the field. The plots were marked only by white posts at each corner, and thus the observer was required to judge, by tracing imaginary lines, which plot a bird was foraging on. This will have introduced some error. The size of the

experimental area was a compromise between a readily observable area, and the need to produce plots big enough to allow the maximum number of birds which were likely to arrive on the test grid to forage normally. Flock sizes at any one time were generally quite small - the maximum recorded on one plot was 15 birds at a mean nearest-neighbour distance of 0.4 metres. The rate of aggression was higher than in the natural situation, but no systematic effects were found between aggression rates and the other measured variables. No systematic effects of high bird density were detected on prey intake rate (compare naturalistic observations in figures 2.3.11 & 12). Plots, selected randomly, were seeded with one of nine different densities of de-husked oat groats (a palatable food with a short handling time of low variability). Within each separate plot the groats were scattered as evenly as possible. Figure 2.4.1 illustrates the experimental area.

For local enhancement to be a more efficient method of locating prey than individual search, the prey patches must be hard to locate and unpredictable in occurrence (cf. Barnard 1980, Krebs 1973, 1974, Krebs et al. 1972, chapter 2.3). After scattering, the plots were brushed over by hand to settle the groats down into the grass root-layer. Subsequent observation of birds suggested that the areas of differing prey density could only be discovered by close search of each plot. Prey patches in the experiment were

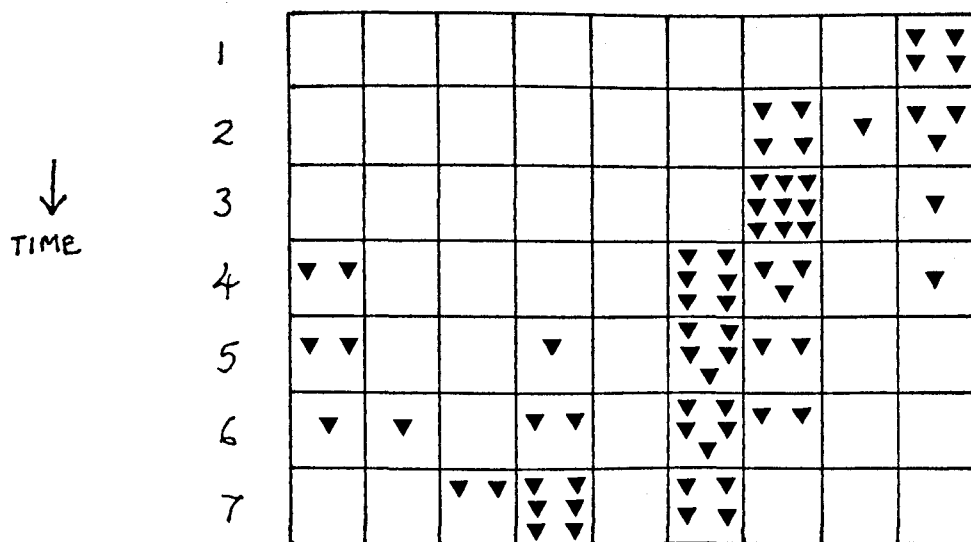
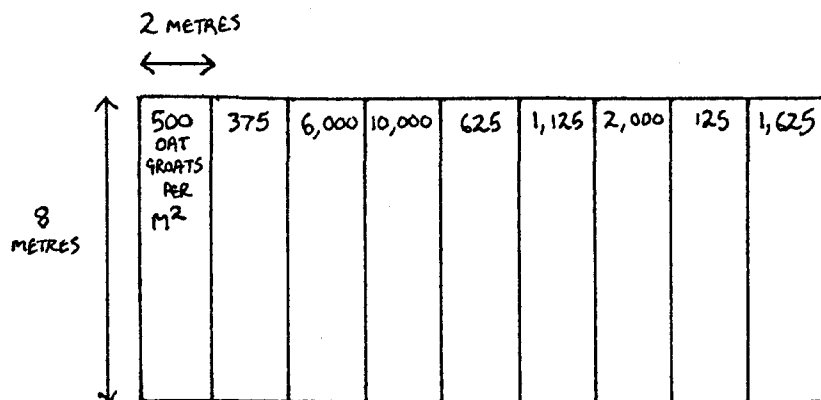
Figure 2.4.1

Layout of the seeded experimental area, and depiction of a seven minute foraging sequence

The top figure shows the dimensions and prey densities within the experimental area, and the bottom figure shows the number of rooks on each plot at different times through seven minutes of foraging time on the grid.

- (1) 0m00s to 2m30s: four rooks land to the right of the grid and move on to the edge plot 1625 to forage.
- (2) 3m00s to 3m40s: four more birds landed near to those already foraging; one bird discovered plot 2000 and three others quickly moved to forage there also.
- (3) 3m50s to 4m10s: two more birds land to the right of the grid and move on to forage; one immediately joins the other birds, which have all now reached plot 2000.
- (4) 4m10s to 4m28s: two birds land to the left of the grid and move onto edge plot 500; six of the other birds have now moved across from plot 2000 to plot 1125.
- (5) 5m02s to 5m13s: one of the plot 1125 birds has foraged across plot 625 to plot 10000; two birds have left the grid.
- (6) 5m47s to 5m53s: one bird has moved from plot 500 to plot 375; one bird has moved from plot 1125 to plot 10000; one bird has flown in to plot 1125.
- (7) 6m10s to 6m55s: a series of moves, arrivals and departures has led to the majority of birds feeding on the highest plot, 10000, with two more on the second highest plot; four birds are still on plot 1125.

At this point the birds were disturbed and all flew off the grid. This was the fullest sequence recorded illustrating the process of location of the best prey areas. Almost all birds which moved by flying into the grid or from plot to plot landed near to another bird (see text).



thus hard to find. At the start of the experiment the location of the patches was also unpredictable, due to the random allocation referred to above. However, if a single bird made more than one visit to the experimental area, on subsequent visits the patches would not have been unpredictable if the bird had visited all available prey plots on the previous visit and could remember their locations. This could have introduced some error into the results (see below).

Prey in the experiment were non-renewing. Since predation-induced changes in densities could not readily be monitored, uneven depletion of prey in different plots could have introduced further error. The experiment was stopped when a large proportion of the prey was still available in an attempt to reduce this error.

Data were recorded on the 8th and 9th March 1981. The test area was watched continuously from 1500 on the 8th (when the grid was seeded) until nightfall, and from dawn until 0930 on the 9th, when the experiment was stopped.

Visits to the grid were recorded on videotape from a building near the field, and later replayed repeatedly to enable the following variables to be recorded for each bird:

(a) Prey Density - the number of oat groats per m² in the

plot on which the bird was foraging.

- (b) Flock Size - the number of birds within the prey plot (not the entire grid) on which the subject was foraging.
- (c) Prey Intake Rate - the number of oat groats ingested during the subject's stay on that prey plot, expressed as the rate of ingestion per minute.
- (d) Looking Up Rate - the frequency with which rooks 'looked up' (see section M.11.7 for further definition of this measure of vigilant behaviour).
- (e) Length of Stay - the duration (in seconds) of the visit to that prey plot.
- (f) Human Disturbance - unfortunately a number of records may have ended prematurely due to disturbance. When people walked across the field near to the experimental grid, this was recorded and subsequently entered as a dummy variable into the regressions to measure the extent of this source of error.
- (g) Local Enhancement Behaviour - when entering the experimental grid, and when moving between plots, it was recorded whether or not birds landed within two yards of another conspecific. This was a conservative definition of social attraction, given the size of the

entire experimental space (135 square metres) available to incoming and moving birds which was free of other birds.

A few carrion crows, jackdaws, magpies and starlings visited the grid, but data were recorded only from rooks. Though the numbers of these other species were far fewer than those of rooks, some depletion will have occurred and may have introduced some error into the analyses.

Each separate prey density plot was, for the purposes of this experiment, deemed a separate 'field'. Hence an observation ended when a bird either left the grid completely, or simply moved onto another of the prey plots within the grid. A total of 146 rook visits were recorded during the course of the experiment, but missing data reduced the number of recordings with complete data for all variables to 41. Logarithmic or arcsine transformations were appropriate for several non-normal variables and to correct curvilinear relationships.

Data were analysed using techniques associated with path analysis (Blalock 1971, Kim & Kahout 1975, Wright 1921). Most frequently used in econometrics and sociology (Duncan 1966, Johnston 1972), path analysis is of particular value in disciplines where quasi-experimentation is of necessity the rule rather than the exception (Blalock 1964, Cook & Campbell 1979, Heise 1975). A relevant recent

biological example is Myers et al's (1979) analysis of the relative roles of prey density and number of intruding birds as proximate causes of variations in territory size of wintering sanderlings (Calidris alba).

Path analysis' main value lies in its ability to test the fit of hypothesised models to a set of data and to indicate where new hypotheses need to be generated. The study of flowcharts, with path coefficients labelled, is the usual way in which this is achieved. The calculation, in simple recursive systems, of path coefficients (usually expressed as standardised beta values derived from multiple regression equations), correlations between exogenous variables, and disturbances associated with endogenous variables, is straightforward (e.g. Duncan 1966, Kim & Kahout 1975). However, unbiased estimates of coefficients in reciprocal, non-recursive systems require the use of two stage least squares regression (Duncan et al. 1968, Namboodiri et al. 1975).

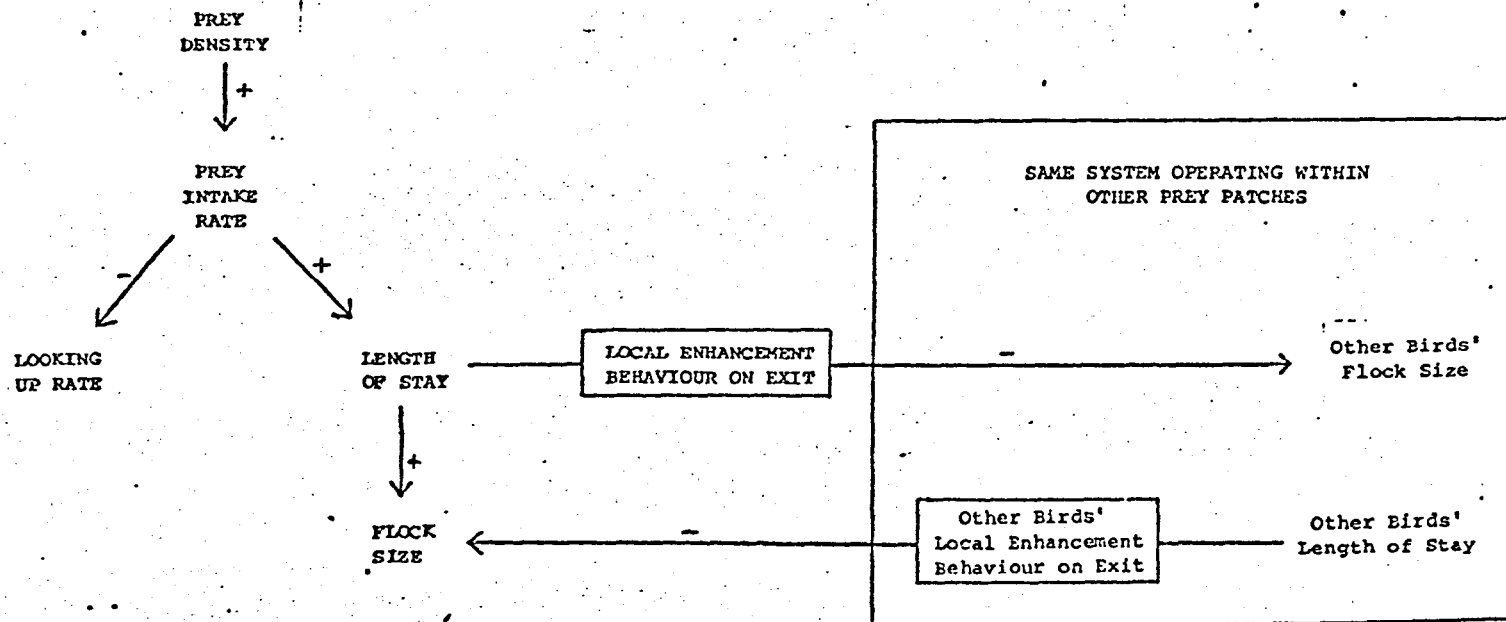
2.4.3.1 Model I - Description

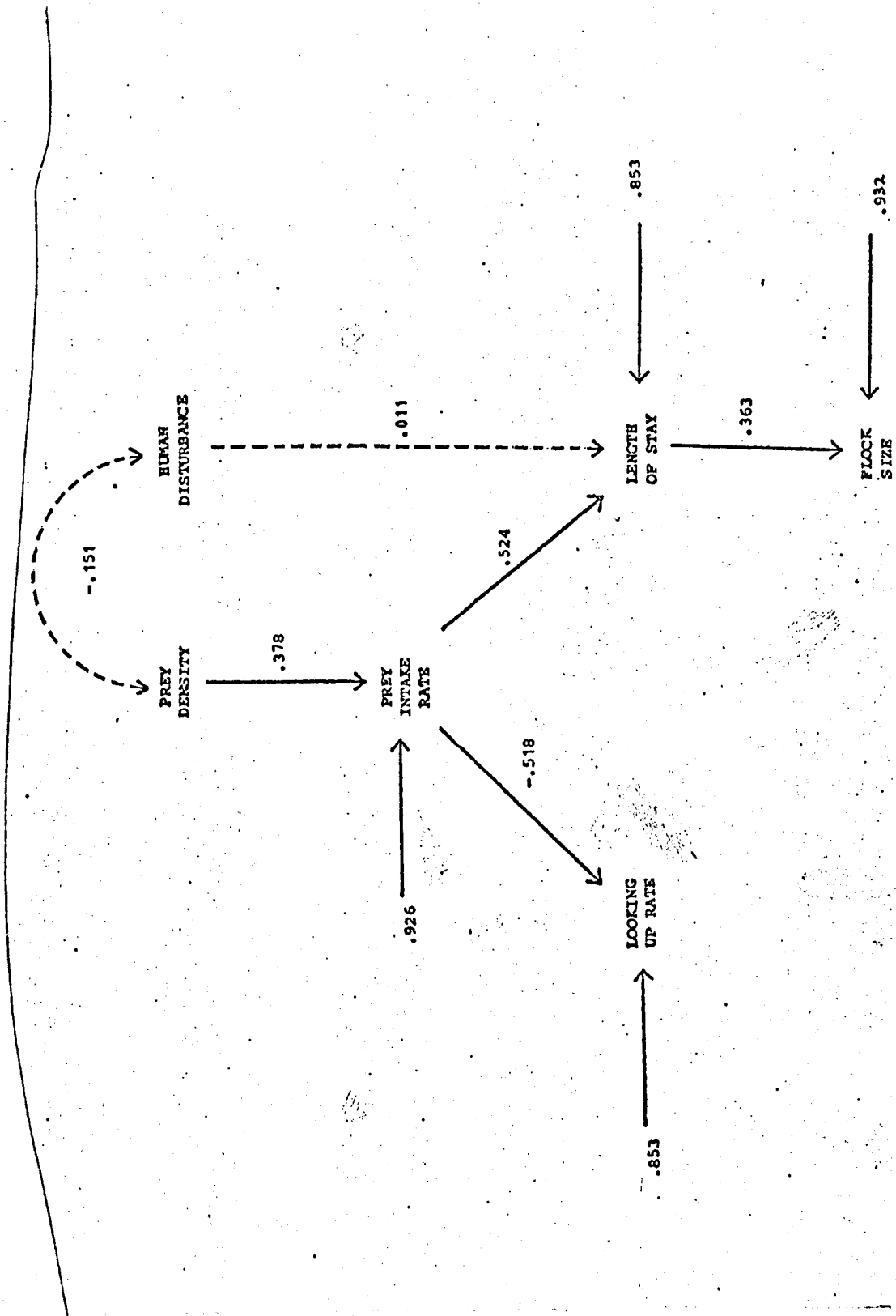
The first causal model, derived from field observations of rooks foraging for natural earthworm prey (chapter 2.3), is presented in figure 2.4.2a. There is a positive relationship between prey density and prey intake rate.

Figure 2.4.2

Causal model drawn from predictions in section 2.3.3 above, based on observations of wild rooks foraging for natural earthworm prey

- (a) This model predicts that birds forage 'optimally' and then, when moving to forage elsewhere, always choose to land near other birds (see text for further explication).
- (b) Test by path analysis of part of this model, using data gained by attracting wild rooks to artificial prey provided at varying densities ($N = 41$ bird visits). Paths are labelled with their coefficients (standardised beta values); the curved, double-headed arrow (labelled with the simple r value) indicates an unanalysed correlation not part of the model as defined; and disturbances (error terms) associated with each endogenous variable are calculated as the square root of $(1 - R\text{-squared})$.





Birds with low intake rates tend to look up more, scanning for other feeding areas and the presence of other birds as indicators of them; and birds with low intake rates of prey leave to forage elsewhere sooner. Length of stay will vary positively with flock size through the incidence of social attraction, since the longer a bird remains on a prey area, the higher the probability that other birds will be attracted to feed with it, having given up elsewhere. Thus the model states that larger flocks will build up on higher prey densities through the mediation of a series of behavioural responses.

Intraspecific aggression was not very frequent, and is not in the natural situations studied (chapter 1.7, Lockie 1956b, Patterson 1975). No meaningful (or significant) relationships were found between rates of agonistic encounters and any of the other variables in the present experiment, and thus aggression rate has been omitted from the figures to reduce unnecessary complication.

2.4.3.2 Model I - Results

The model is generally supported by the data from the experiment. Birds arrived independently or in small groups and foraged over the experimental area. One feeding sequence is described in figure 2.4.1. Birds did show local enhancement (95% landed within two yards of another

bird when entering the grid, and 72% did so when moving between prey plots). It is unknown what proportions would be expected by chance, but if we take a conservative estimate of 50% (conservative because in each observation there was certainly more space available within the test grid greater than two yards from another bird than space available within two yards), then the observed proportions indicate significant tendencies to land near another conspecific (incoming birds: binomial test, $z = 8.9$, $N = 101$, $p \ll 0.001$; birds moving between prey plots: $N = 25$, $p = 0.022$; both 1-tailed).

The results of path analysis of that part of the model for which data are available from the current experiment are presented in figure 2.4.2b. Path coefficients (standardised beta values) are given alongside their respective paths; the correlation coefficient (simple r) between the two exogenous variables is drawn with a curved, double-headed arrow to indicate an unanalysed relationship with causes outside of the model as defined; and the disturbances (error terms) associated with each endogenous variable listed (conventionally calculated as the square root of $(1 - R\text{-squared})$ with each directly causally prior variable in the predictor list).

All path coefficients are significant (5% level or better, 1-tailed) with the exception of that between Human

Disturbance and Length of Stay, which was not in any case a predicted part of the model, but introduced to measure a possible source of error. The correlation between the two exogenous variables is also not significant. In addition, a significant proportion of the variability of each of the endogenous variables was predicted by the model (table 2.4.1).

A further test of the completeness of the model is an analysis of the strength of relationships between variables between which the model predicted no direct relationship. If the model were complete, correlations between variables where no path has been predicted should be nil when the effect of causally prior variables has been partialled out (Nachmias & Nachmias 1976). There are, however, several non-predicted relationships substantially greater than zero. These are between Human Disturbance and Looking Up Rate ($r = -0.219$) and three involving Flock Size: with Prey Density (0.218), Prey Intake Rate (0.226) and Looking Up Rate (-0.254). Although substantial, only the last of these partial correlations actually reaches statistical significance.

2.4.3.3 Model I - Discussion

The relationship between Human Disturbance and Looking Up Rate may indicate that some birds were detecting a human

Table 2.4.1

Amount of variability in the endogenous variables explained by model I (R-squared x 100)

<u>Endogenous Variable</u>	<u>Predictors</u>	<u>Variability Explained (%)</u>
Prey Intake Rate	Prey Density	14.3
Looking Up Rate	Prey Intake Rate	26.9
Length of Stay	Prey Intake Rate Human Disturbance	27.3
Flock Size	Length of Stay	13.2

approach before leaving (or without leaving) and that some looking up was directed at the person approaching. The relationships between Flock Size and Prey Density, and Flock Size and Prey Intake Rate, may also be specific to the test situation. The former suggests that some birds may have been able to recognise the areas of greater prey density directly. This could either have been due to the oat groats being more visible to some birds from a distance or (perhaps more likely), due to some birds making more than one visit to the grid and remembering where they had foraged previously - possible in the experimental situation since the location of the prey patches did not shift during the course of the experiment.

The latter relationship, between Flock Size and Prey Intake Rate with the influence of other variables partialled out, has two possible interpretations: the operation of some form of cooperative hunting, or social facilitation. Cooperative hunting is usually of benefit with prey too large or elusive for a solitary animal to exploit (eg. Kruuk 1972, Schaller 1972; chapter 2.2). Given the nature of the prey in the present experiment (oat groats) cooperative hunting seems an unlikely explanation. However, given that the prey was a novel one (at least novel when on grassland) it is possible that some birds new to the test grid were stimulated to feed on the groats by the presence of other birds doing so. Several observers shown

the video-tape agreed that some birds' behaviour suggested this may have occurred.

The significant relationship between Flock Size and Looking Up Rate also suggests a direct social influence on behaviour - birds in lower flock sizes were tending to look up more, irrespective of their prey intake rates, and irrespective of the density of prey on

which they were foraging. Since Flock Size was defined as flock size on that prey plot, and not on the entire experimental grid of prey plots, an interpretation of this relationship in terms of birds at lower flock size looking up more for predators (e.g. Dimond and Lazarus 1974; chapter 2.2) seems unlikely - birds in other 'flocks' on adjacent prey plots were in fact only a few metres away, as close as members of the same flock foraging for natural prey would be (chapter 2.3). Thus birds at low 'flock size' on one prey plot were not necessarily, in terms of their normal foraging dispersions, at a low flock size; and therefore, one might assume, be unlikely to respond to the threat of predation as if they were in a low group size. It seems more likely that in the test situation birds foraging in an plot with a lower 'flock size' tended to look up more to observe the behaviour and/or whereabouts of birds on other plots within the test grid or outside.

Whatever the true explanation, model I was clearly

inadequate in failing to posit any direct effects of flock size on behaviour. A new model is therefore proposed.

2.4.4.1 Model II - Description

The modification in the new model must be to incorporate direct effects of Flock Size on behaviour. It seems that the assumption of model I that "The only social influence is ... one of a tendency when moving from one area to another, to land in the vicinity of other foraging birds" (section 2.3.3 above) is incorrect. The experimental data suggest rather that a social influence on behaviour can occur before a move-on decision is taken. As stated above, explanation of group size effects in relation to defence against predation seem unlikely in the present experiment (and section 2.3.A.6 above gives evidence that such an explanation can at best only partly explain similar relationships in a natural situation). There is, however, a way in which a direct social influence on behaviour could increase the efficiency with which prey patches are located; and it is this modification which is incorporated into model II and then tested.

In the natural situation, it was observed that birds tended to show social attraction more frequently to larger flocks (table 2.3.1b). Since larger flocks tended on

average to build up on better prey densities (figure 2.3.5), it was suggested that a tendency to choose larger flocks, rather than simply any other conspecific, when moving on, would on average increase the efficiency with which the densest prey patches were located. Since it is the case that larger flocks tend to occur on the densest prey areas, then a continuous monitoring of the size of one's own flock relative to the sizes of flocks available elsewhere could result in an increase in the efficiency with which the best prey patches are found. If a larger flock became available, then a bird which gave up sooner than it normally would if it were simply obeying optimal foraging criteria, and went to forage with that flock, would on average move to a denser prey area. Optimal foraging theory states that decisions on when to

give up and move to another patch are made on the basis of a comparison of intake rates of prey on that patch compared to the average intake rate experienced in the habitat as a whole (eg. Krebs 1978). If, however, a giving-up decision based on a comparison of one's own flock size with other flock sizes available on other prey patches took precedence, then such a system could be more efficient than one based solely on optimal foraging criteria, since the time needed to sample the different prey levels available in the habitat would be reduced.

Such a concept is comparable to the reduction in

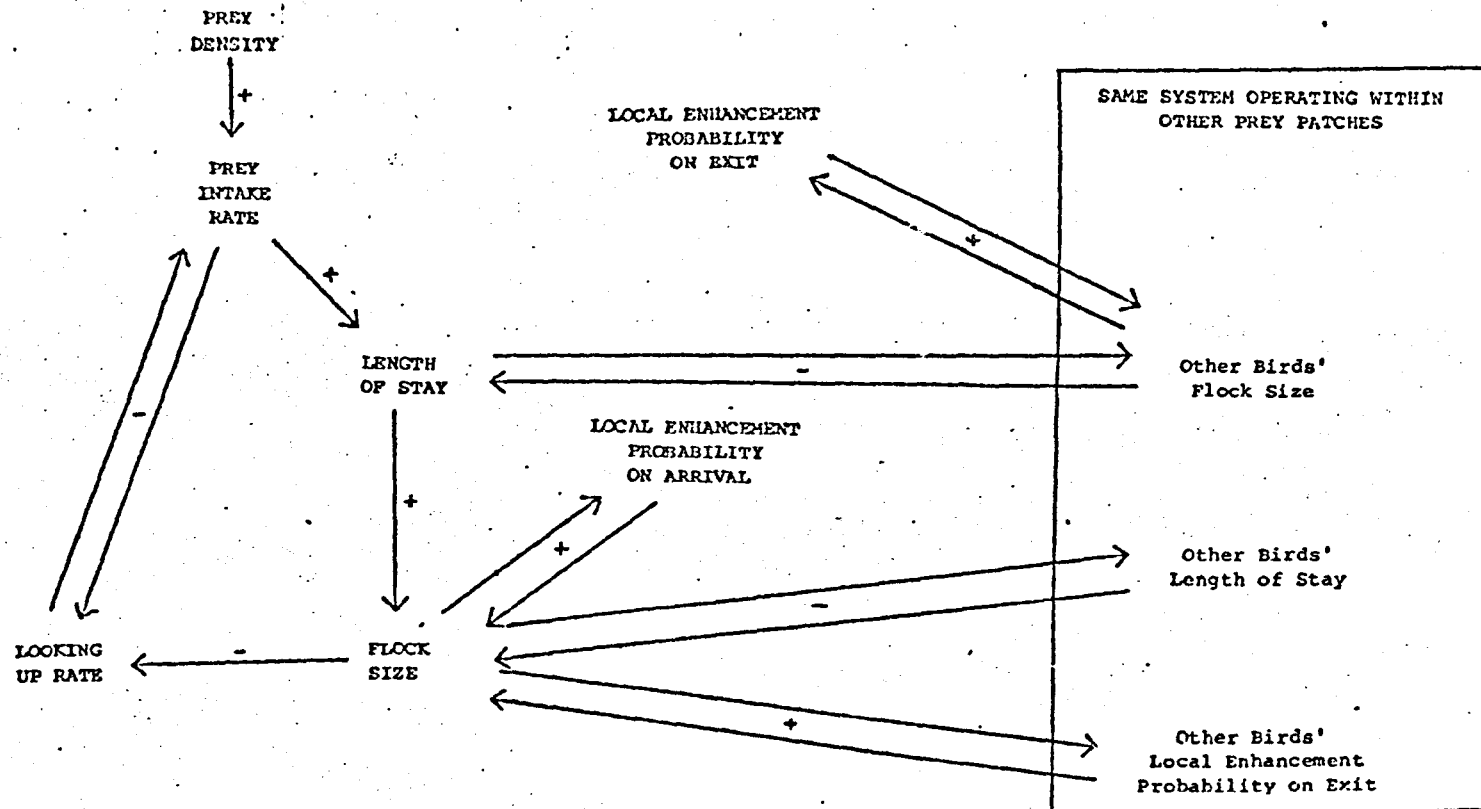
'risk' associated with flocking found in several studies (Caraco 1981, Chantrey 1982, Krebs 1974, Thompson et al. 1974). Birds which foraged in flocks were less likely to starve (or grow fat) - on average they did better by reducing their risk of suffering an extreme of low (or high) prey intake rates. Correspondingly, rooks which moved when a bigger flock size was available elsewhere might move from a bad patch to a good one and sometimes might move from a good patch to an equal or poorer one - but on average, because of the tendency for flocks to build up on the best prey areas, the move would be to a better prey patch.

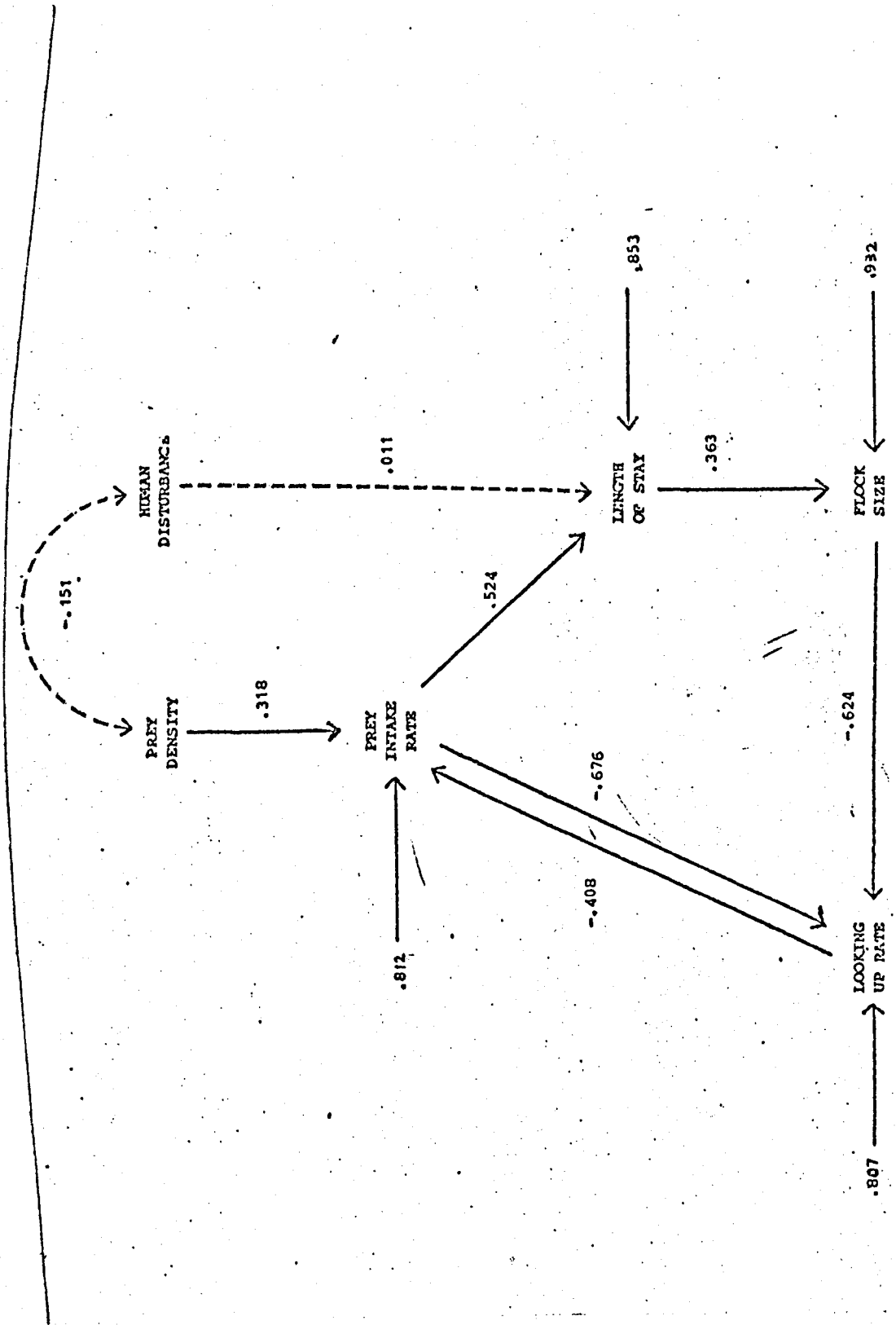
The implications of this hypothesis for the model are illustrated in figure 2.4.3a. Flock size, in addition to being determined by variables in the model, now becomes involved in a reciprocal system. Flock size has a negative effect on looking up rate - if a bird is in a small flock, then on average it will not be on the best prey patch available, and a larger flock is likely to be available elsewhere. Hence it looks up more to monitor the whereabouts of other flocks. An increase in looking up reduces the amount of time available for feeding and hence looking up rate can cause variations in prey intake rate as well as be the result of changes in prey intake rate. Flock size will not necessarily, however, affect length of stay since the vigilance for a larger flock will not always

Figure 2.4.3

Explication (a) and test (b) of model II

This model differs from the first in predicting a social influence on behaviour before move-on decisions are made, creating a system involving several reciprocal relationships.





be successful, if no such larger flock is available. Being in a small flock will, then, always increase looking up and therefore decrease intake rate, but will not always result in a change in how long the bird will forage on that patch. It is not one's own flock size which will determine length of stay, but the size of other flocks available elsewhere.

In addition, a series of reciprocal relationships will exist between a bird's own and other flock sizes, local enhancement probabilities, and lengths of stay - for example, the probability of showing social attraction when moving on will be influenced by the size of the flocks available (the probability increasing with the size of the flocks available); and reciprocally, a higher probability of showing local enhancement will therefore increase the size of that flock when the bird joins it.

In summary, then, model II states that birds adopt a mixed strategy for deciding when to move on from a prey patch, based sometimes on optimal foraging criteria, and sometimes on social stimuli. The hypothesised model states:

- (a) Move on to forage elsewhere when intake rate of prey falls below the mean intake rate for the habitat as a whole.
- (b) When moving, always land near another conspecific, and

choose a larger flock rather than a smaller one.

- (c) But when a larger flock than the one in which you are foraging at the moment is seen to be available, then move on to that prey patch regardless of present prey intake rate.

2.4.4.2 Model II - Results

Strictly speaking the new model, produced by a scrutiny of the result of testing the original one, should now be tested by a new experiment manipulating both prey density and the size of other flocks available (or by the relevant observations of naturally occurring flocks). However, as a first step to testing the adequacy of the new model, path analysis may be applied to the original data set. This test of model II is of course 'ad hoc' in the sense that it was developed from a test of the previous model, but is itself tested by the same data set. It is stressed again that the method is only quasi-experimental, a way of analysing mainly observational (correlational) data which can help to suggest new hypotheses. A more formal test of the new model would be produced by repeating the experiment, but this time also manipulating the new key exogenous variable identified - i.e. the size of other flocks available on other prey areas.

The results of path analysis for that part of the revised model for which data are available from the present experiment are presented in figure 2.3.3b, reciprocal paths having been estimated by two-stage least squares regression. All of the new predicted paths are significant. It should be noted that some key paths were not calculable with the data available (in particular those between behaviour and the size of other flocks in the area), and that the disturbance terms associated with the endogenous variables might be further lessened were these data available.

There is an improvement in the amount of variability in each endogenous variable predicted compared to model I (table 2.4.2). Finally, only one non-predicted path now appears which is substantially greater than nil, that between flock size and prey intake rate with other causally prior variables partialled out ($r = 0.226$). It is not, however, statistically significant, and may be the result of an error specific to the experimental situation (see discussion of the same relationship in model I, section 2.4.3.3 above).

2.4.4.3 Model II - Discussion

The modified model does provide a better fit to the data gained from the field experiment. However, data are

Table 2.4.2

Amount of variability in the endogenous variables explained by model II (R-squared x 100)

<u>Endogenous Variable</u>	<u>Predictors</u>	<u>Variability Explained (%)</u>
Prey Intake Rate	Prey Density Looking Up Rate	34.1
Looking Up Rate	Prey Intake Rate Flock Size	34.9
Length of Stay	Prey Intake Rate Human Disturbance	27.3
Flock Size	Length of Stay	13.2

missing for the important paths involving behaviour and flock sizes on other prey areas. A full test of the new hypothesis would require a further experiment where these data were also measured. Whether or not the additional mechanism proposed in model II also operates in natural situations is of course unknown, though (theoretically at least) the necessary measures could also be taken from naturally-occurring flocks.

It has been argued that showing local enhancement differentially to different flock sizes when moving will be a more efficient way of locating the densest prey patches than choosing to land near any bird at random; and that giving up to move to an area where a larger flock than one's own is foraging, sooner than the giving-up-time decreed by optimal foraging criteria dictates, will in turn bring a further increase in the efficiency of dense prey patch location. Though intuitively reasonable, there is in fact no quantitative proof of this. A comparison of these different strategies by simulation is in preparation.

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APPENDICES

Appendix One

Summary of Invertebrate Densities and Dispersions from All Soil Core Samples Taken During the Study

Table 1 - Densities

Densities of invertebrates other than earthworms are expressed only as the mean number of individuals per core, since the sampling procedure was not standardized for these groups and thus population estimates calculated from these data may be unreliable.

Contents of the cores have been separated into earthworms (Lumbricidae) and any other invertebrate (see Methods and Prey sections for a summary of the main invertebrate groups represented in the cores). The latter has been split into those found above the soil surface of the core and those found below. The dispersion of 'all' invertebrates (excluding Lumbricidae) is also given - this can exceed the sum of 'above' and 'below' invertebrates since some individuals could not be categorized as occurring above or below the soil surface with certainty.

Table 2 - Dispersion

See Methods section for an explanation of the two techniques for testing the statistical significance of deviations of samples from a random distribution. The variance/mean ratio test was not computed for invertebrates other than earthworms, since the sampling procedure was not standardized on those groups and therefore population estimates based on the samples may be unreliable. However, the test for coherent clumping of dense cores was considered to be valid for these groups and was computed (see Methods section for justification).

Abbreviations

NAG	Non-agricultural Grass
TLU	Ungrazed Temporary Ley
TLG	Grazed Temporary Ley
PP	Permanent Pasture
DUNG	Samples from beneath cow pats
AG	Aggregated distribution
--	Not significantly different from random distribution
OV	Overdispersed
()	(Blanks indicate missing data)

Table A1.1: DENSITIES

						Mean N of Other Invertebrates per Core		
						Position Relative to Soil Surface:		
				Earthworm Density per Square Metre				
				Bio (g)				
Crop	Field	Date	N of Cores	Nos	Bio (g)	Above	Below	Either
WINTER								
NAG	56	20-11-79	42	49.3	31.8	0.33	0.19	0.71
	56	9- 2-80	42	181.3	85.5	0	0.20	0.20
	6	14-12-79	42	466.2	208.5	0	0.10	0.21
	6	9- 2-80	42	310.8	195.5	0	0.21	0.21
	57	21-11-79	42	61.7	32.1	0.12	0.48	1.05
	57	9- 2-80	42	129.5	94.5	0.03	0	0
	7	23-11-79	42	265.2	112.2	0.09	0.14	0.43
TLU	37	29-11-79	42	166.5	66.0	0.05	0.21	0.43
TLG	20	25-11-79	42	333.0	123.3	0.07	0.62	0.93
	22	27-11-79	42	240.3	93.4	0.05	0.24	0.29
	22	11- 2-80	42	233.1	82.9	0	0.02	0.02
PP	1a	6- 2-78	52	370.0	131.5	0.15	0.25	0.42
	1a	12-11-79	42	376.2	192.7	0.05	0.29	0.33
	1a	11-12-79	42	394.7	193.6	0	0.21	0.21
	1a	12- 1-80	42	252.8	86.9	0.02	0.40	0.50
	1a	11- 2-80	42	541.5	207.2	0	0.09	0.09
	1a	23-12-80	10	466.2	129.5	0	0.41	0.41
	1b	8-12-79	42	314.5	164.6	0.05	0.14	0.31
	1b	9- 2-80	42	235.4	120.1	0	0.45	0.45
	33a	11-12-79	42	271.3	101.7	0.17	0.24	0.43
	33b	14-12-79	42	492.1	165.8	0.10	0.30	0.47
	33b	9- 2-80	42	388.5	108.5	0	0	0
	35a	15-12-79	42	414.4	108.8	0	0	0
	35b	11-12-79	42	296.0	120.2	0	0.09	0.09
	30	15-12-79	10	310.8	121.7	-	-	-
DUNG	1a	14-11-79	10	854.7	624.2	-	0.70	0.70
	1a	23-12-80	10	543.9	274.5	-	0	0
Outside Study Area:								
PP	Mk.D1	2-12-79	42	191.2	125.8	0.02	0.07	0.19
	Mk.D2a	2-12-79	42	30.8	32.7	0.07	0.09	0.45
	Mk.D2a	27- 2-80	42	86.3	91.6	0.02	0.21	0.33
	Mk.D2b	2-12-79	42	154.2	69.7	0.02	0.05	0.19
	Mk.D2b	27- 2-80	42	178.7	109.5	0	0.09	0.12
	Oxon1	28-12-79	10	70.6	41.2	0.54	0.54	1.27
	Oxon2	28-12-79	10	129.5	35.6	0	0	0

Tab.A1.1(cont.): DENSITIES

						Mean N of Other Invertebrates per Core		
						Position Relative to Soil Surface:		
				Earthworm Density per Square Metre	Bio (g)			
Crop	Field	Date	N of Cores	Nos		Above	Below	Either
SPRING								
NAG	57	21- 5-80	10	25.9	15.5	0	0	0
TLG	20	20- 5-80	10	21.6	5.4	0.08	0.25	0.75
	18	8- 5-81	10	259.0	25.9	0.12	0.12	0.62
PP	1a	5- 3-80	10	410.1	152.2	0	0.08	0.08
	1a	14- 3-80	42	388.5	178.2	0.02	0.36	0.43
	1a	27- 3-80	10	466.2	161.9	0	0.10	0.10
	1a	15- 4-80	42	453.2	151.1	0.08	1.92	2.17
	1a	29- 4-80	42	74.0	23.1	0	0.64	0.98
	1a	13- 5-80	10	25.9	5.2	0	0.30	0.70
	1a	30- 3-81	10	518.0	132.1	0	0	0
	1a	21- 4-81	10	520.1	131.7	0.10	0.10	0.30
	1a	27- 4-81	42	388.5	84.1	0	0.12	0.21
	1a	3- 5-81	42	647.5	159.3	0	0.21	0.30
	1a	31- 5-81	10	595.7	108.8	0	0.30	0.30
	1b	3- 5-81	42	595.7	130.8	0	0.18	0.20
DUNG	1a	20- 5-80	10	77.7	46.6	-	0.70	1.20
SUMMER								
PP	1a	13- 6-80	10	155.4	40.1	0	0.10	0.20
DUNG	1a	13- 6-80	10	233.1	85.5	-	0.20	1.40
AUTUMN								
PP	1a	18- 9-79	42	252.8	111.3	-	-	-
	1a	4-10-79	42	413.2	170.2	0.06	0.43	0.79
	1a	3- 9-80	10	233.1	95.7	0	0.10	0.10
DUNG	1a	19- 9-79	10	725.2	347.1	-	1.30	2.10
Outside Study Area:								
PP	Oxon1	12-10-79	42	92.5	-	0.06	0.62	0.59
	Oxon3	11-10-79	42	30.8	-	0.12	0.40	1.12

Table A1.2: DISPERSION

Table A1.2: DISPERSION						Other		
						Invertebrates		
						Grid-Pattern		
						Method (Nos)		
						Position Relative		
						to Soil Surface:		
Crop	Field	Date	Earthworms V/M Ratio Method (Nos)	Grid-Pattern Method (Nos)	(Bio)	Above	Below	Either

WINTER								
NAG	56	20-11-79	AG	--	--	OV	--	--
	56	9- 2-80	AG					
	6	14-12-79	AG					
	6	9- 2-80	--					
	57	21-11-79	--	--	OV	AG	--	--
	57	9- 2-80	AG					
	7	23-11-79	--	--	--	--	--	--
TLU	37	29-11-79	AG	AG	--		--	--
TLG	20	25-11-79	p<.075	OV	OV		AG	--
	22	27-11-79	--	AG	AG		--	AG
	22	11- 2-80	--					
PP	1a	6- 2-78	AG					
	1a	12-11-79	--	AG	OV		OV	AG
	1a	11-12-79	AG	--	OV		--	--
	1a	12- 1-80	AG	AG	AG	AG	--	--
	1a	11- 2-80	p<.10					
	1a	23-12-80	--					
	1b	8-12-79	AG	AG	--		OV	OV
	1b	9- 2-80	--					
	33a	11-12-79	AG	AG	AG		AG	--
	33b	14-12-79	p<.10					
	33b	9- 2-80	--					
	35a	15-12-79	AG					
	35b	11-12-79	AG	OV	OV		--	--
	30	15-12-79	AG					
DUNG	1a	14-11-79	AG					
	1a	23-12-80	--					
Outside Study Area								
PP	Mk.D1	2-12-79	AG	AG	OV		AG	OV
	Mk.D2a	2-12-79	--	AG	AG	OV	AG	AG
	Mk.D2a	27- 2-80	AG	OV	OV		AG	--
	Mk.D2b	2-12-79	--	--	OV			OV
	Mk.D2b	27- 2-80	AG	AG	AG		AG	AG
	Oxon1	28-12-79	--					
	Oxon2	28-12-79	--					

Tab.A1.2(cont.): DISPERSION

Tab.A1.2(cont.): DISPERSION						Other		
						Invertebrates		
						Grid-Pattern		
						Method (Nos)		
						Position Relative		
						to Soil Surface:		
Crop	Field	Date	Earthworms	Grid-Pattern		Above	Below	Either
			V/M	Method	(Bio)			
			Ratio	(Nos)	(Nos)			
			Method					
			(Nos)					
SPRING								
NAG	57	21- 5-80	--					
TLG	20	20- 5-80	p<.075					
	18	8- 5-81	--					
PP	1a	5- 3-80	--					
	1a	14- 3-80	AG	AG	AG	--		OV
	1a	27- 3-80	--					
	1a	15- 4-80	--					
	1a	29- 4-80	AG	--	--	AG		AG
	1a	13- 5-80	--					
	1a	30- 3-81	--					
	1a	21- 4-81	--					
	1a	27- 4-81	--					
	1a	3- 5-81	--					
	1a	31- 5-81	--					
	1b	3- 5-81	--					
DUNG	1a	20- 5-80	--					
SUMMER								
PP	1a	13- 6-80	--					
DUNG	1a	13- 6-80	--					
AUTUMN								
PP	1a	18- 9-79	--	AG	--			
	1a	4-10-79	AG	AG	AG	OV	--	--
	1a	3- 9-80	AG					
DUNG	1a	19- 9-79	AG					
Outside Study Area								
PP	Oxon1	12-10-79	AG	AG		AG	OV	OV
	Oxon3	11-10-79	--	AG		AG	AG	AG

Appendix Two





Dispersion of Invertebrates from Samples of 42 Cores Taken as a Symmetrical 6 x 7m grid

See Methods section for an explanation of the two techniques for testing the statistical significance of deviations of samples from a random distribution. The variance/mean ratio test was not computed for invertebrates other than earthworms, since the sampling procedure was not standardized on those groups and therefore population estimates based on the samples may be unreliable. However, the test for coherent clumping of dense cores was considered to be valid for these groups and was computed (see Methods section for justification).

Contents of the cores have been separated into earthworms (Lumbricidae) and any other invertebrate (see Methods and Prey sections for a summary of the main invertebrate groups represented in the cores). The latter has been split into those found above the soil surface of the core and those found below, with Enchytraeidae treated separately. The dispersion of 'all' invertebrates (excluding Lumbricidae and Enchytraeidae) is also given - this can exceed the sum of 'above' and 'below' invertebrates since some individuals could not be categorized as occurring above or below the soil surface with certainty.

Keys

(a) Actual numbers/weight within each core

	Earthworms		Enchytraeidae	Other Invertebrates
	Nos	Biomass		
	0	0	Absent	0
	1-2	<0.5g	Present	1
	3-4	<1.5g	-	2-3
	>4	>1.5g	-	>3

(b) Deviation of each core from the sample mean




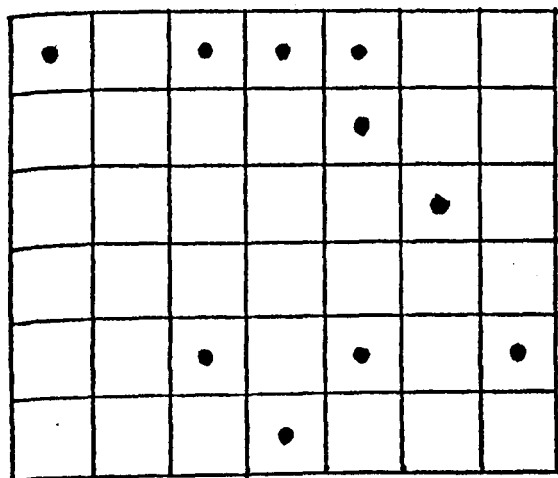
	Between -2 standard deviations and the mean
	Mean to +2 s.d.
	> +2 s.d.

Figure A2.1

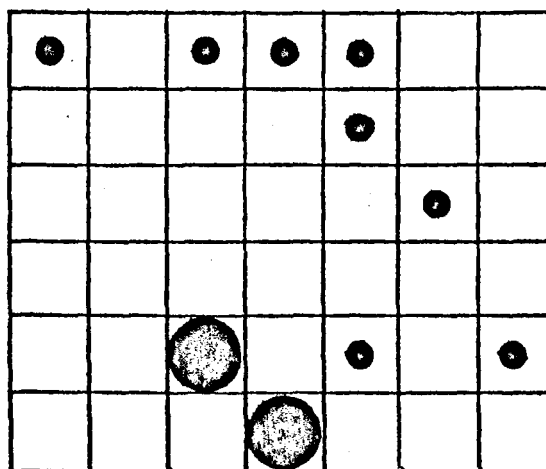
Date: 20-11-79
 Crop: Non-agricultural Grass
 Field: 56 (SJ 814452)

(a) Earthworm Numbers: Density per Square Metre = 49.3

Test for Dispersion ignoring spatial relationships between cores:
 Chi-square = 70.10 $p < 0.005 > 0.001$
 Conclusion: Aggregated

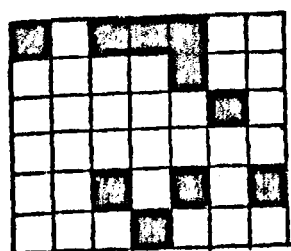


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

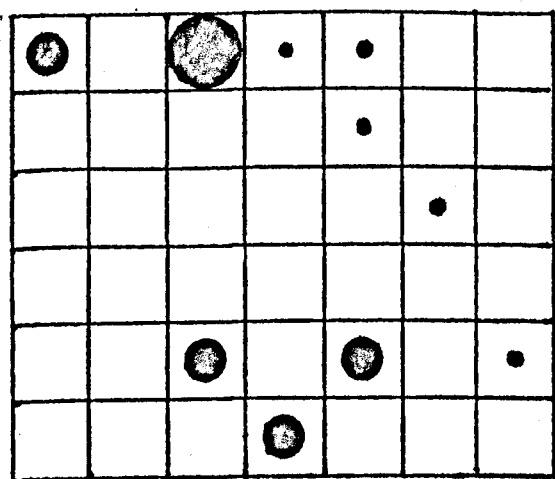


Dense = >0
 Sparse = 0

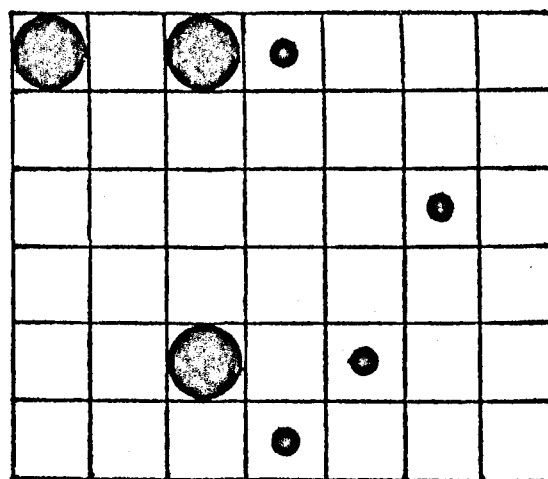
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 6.85 ± 0.67
 Observed dense-dense joins = 7
 Conclusion = Random

(b) Earthworm Biomass: Density per Square Metre = 31.8 gm

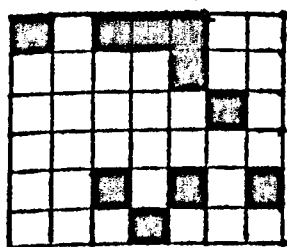


Actual biomass in each core



Standard deviation units

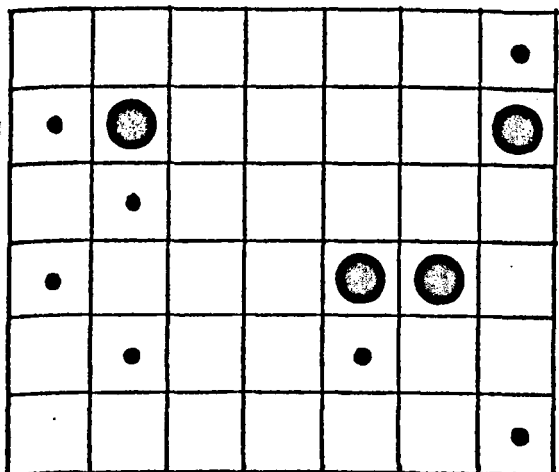
Test for Dispersion using spatial relationships between cores:



Dense = >0
Sparse = 0

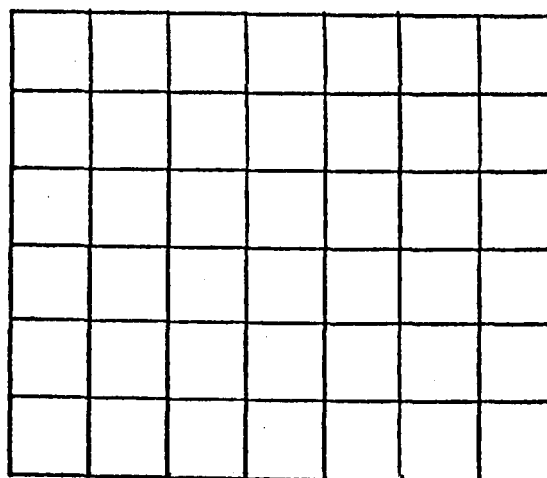
Expected dense-dense joins = 6.85 +/- 0.66
Observed dense-dense joins = 7
Conclusion = Random

(c) Invertebrates other than Earthworms (Numbers)



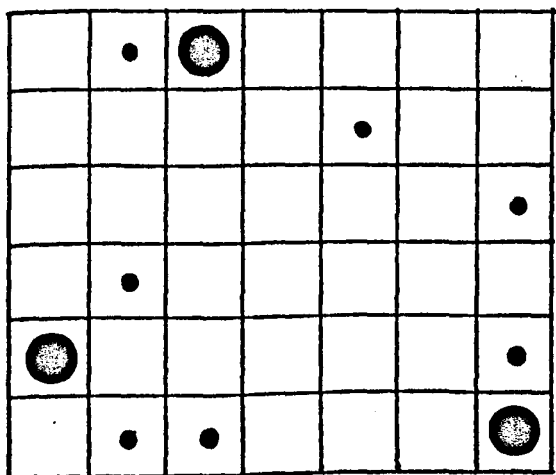
Below Soil Surface

Exp. D-D joins = 8.37 ± 0.72
 Obs. D-D joins = 9
 Conclusion = Random



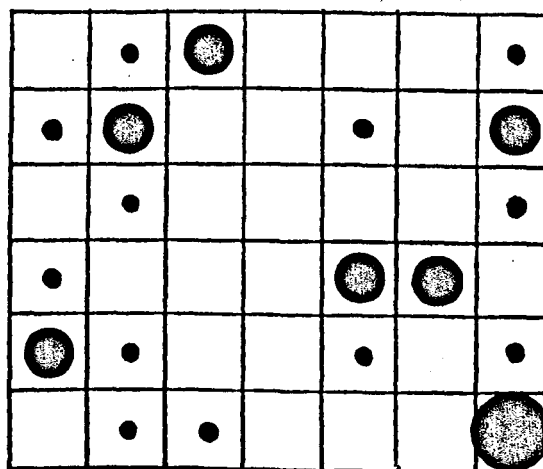
Enchytraeidae

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



Above Soil Surface

Exp. D-D joins = 6.85 ± 0.66
 Obs. D-D joins = 5
 Conclusion = Overdispersed



All (excluding Enchytraeidae)

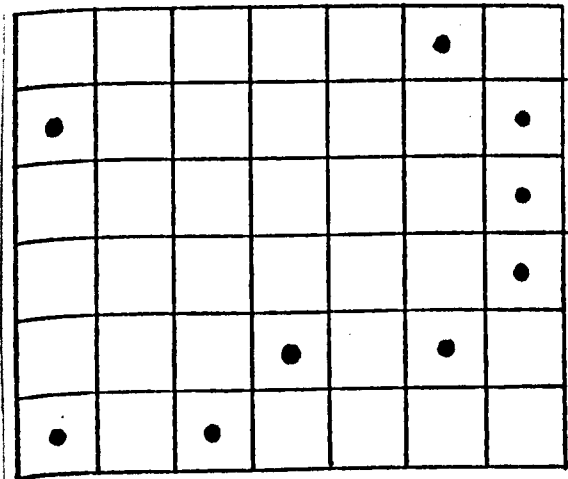
Exp. D-D joins = 28.91 ± 1.16
 Obs. D-D joins = 27
 Conclusion = Random

Figure A2.2

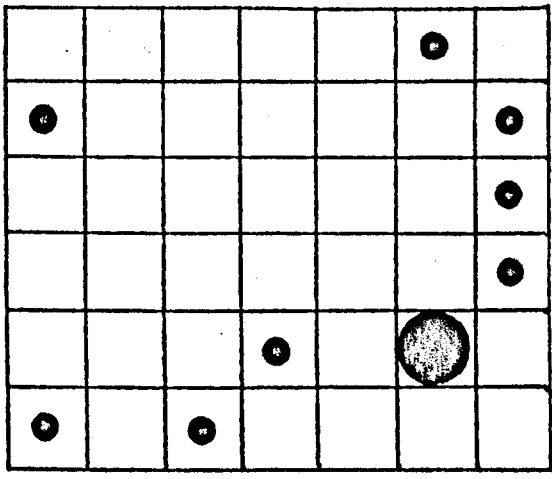
Date: 21-11-79
Crop: Non-agricultural Grass
Place: 57 (SJ 812449)

(a) Earthworm Numbers: Density per Square Metre = 61.7

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 40.48 $p < 0.5 > 0.4$
Conclusion: Random

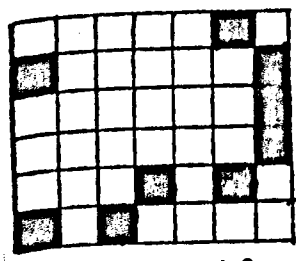


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

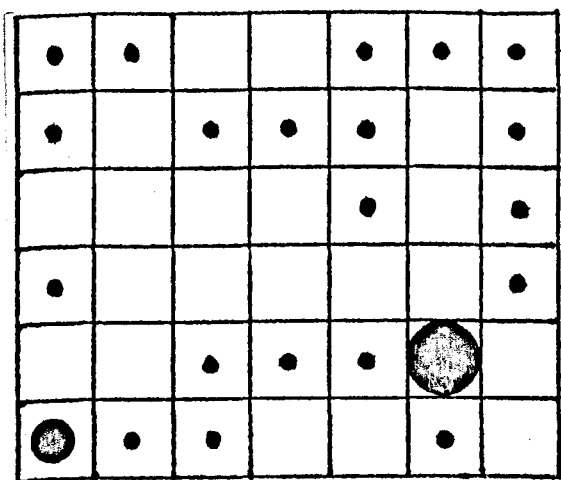


Dense = >0
Sparse = 0

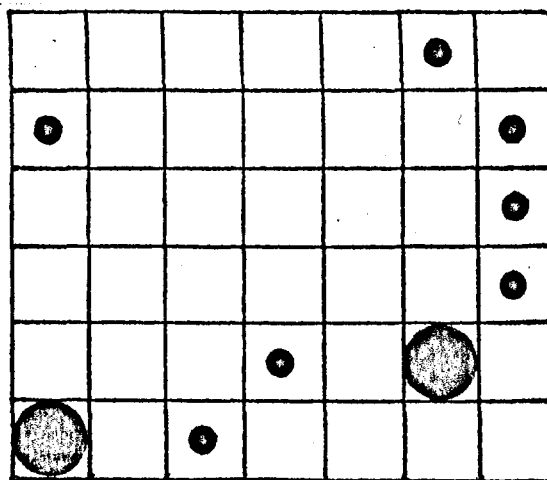
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 5.48 +/- 0.60
Observed dense-dense joins = 5
Conclusion = Random

(b) Earthworm Biomass: Density per Square Metre = 32.1 gm

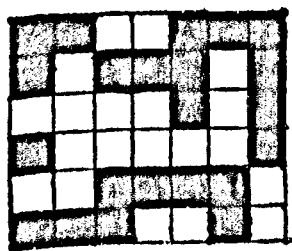


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



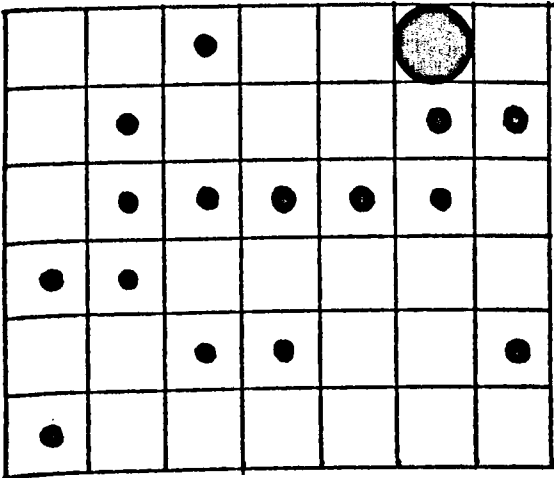
Dense = >0
Sparse = 0

Expected dense-dense joins = 35.15 +/- 1.22

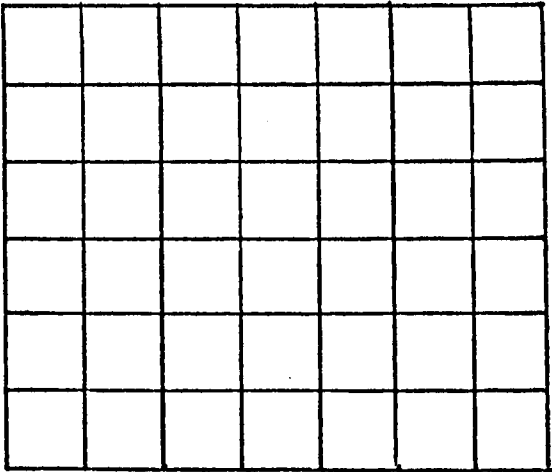
Observed dense-dense joins = 27

Conclusion = Overdispersed

(c) Invertebrates other than Earthworms (Numbers)



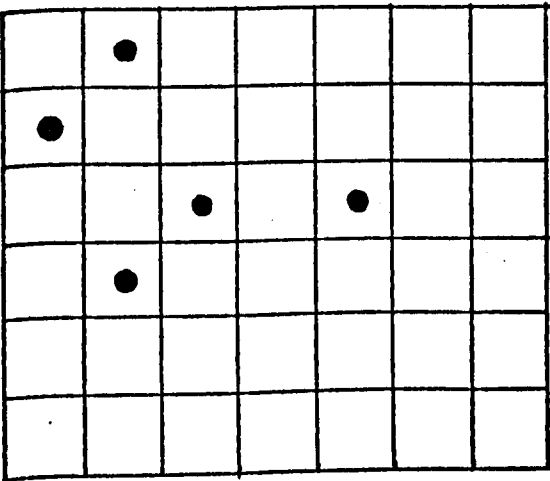
Below Soil Surface



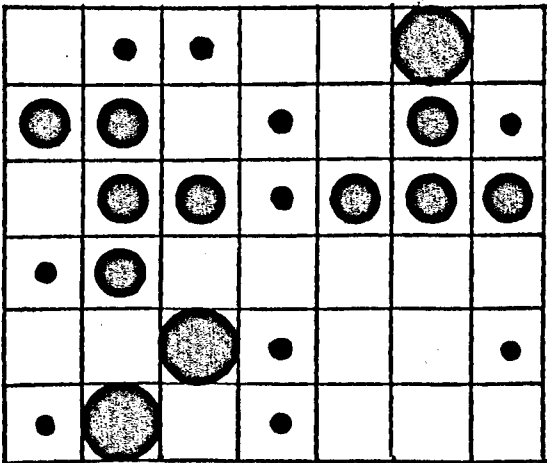
Enchytraeidae

Exp. D-D joins = 18.26 ± 0.99
Obs. D-D joins = 19
Conclusion = Random

Exp. D-D joins =
Obs. D-D joins =
Conclusion =



Above Soil Surface



All (excluding Enchytraeidae)

Exp. D-D joins = 1.52 ± 0.33
Obs. D-D joins = 2
Conclusion = Aggregated

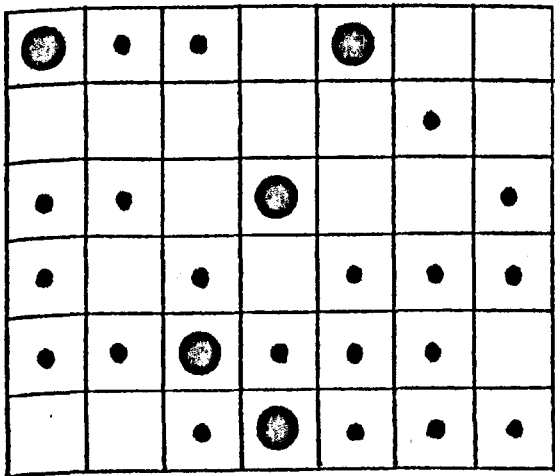
Exp. D-D joins = 35.15 ± 1.22
Obs. D-D joins = 35
Conclusion = Random

Figure A2.3

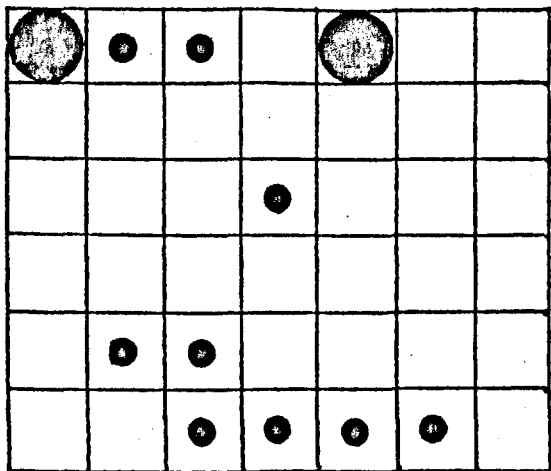
Date: 23-11-79
Crop: Non-agricultural Grass
Field: 7 (SJ 813455)

(a) Earthworm Numbers: Density per Square Metre = 265.2

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 51.73 $p < 0.15 > 0.1$
Conclusion: Random

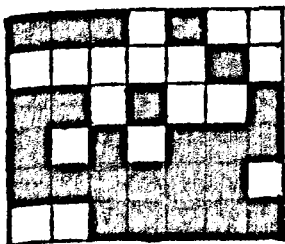


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

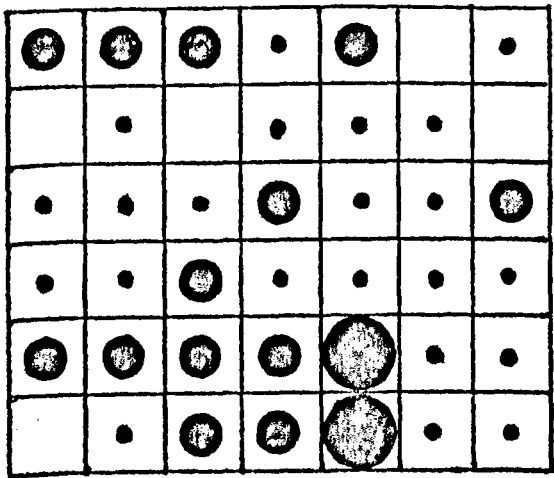


Dense = >0
Sparse = 0

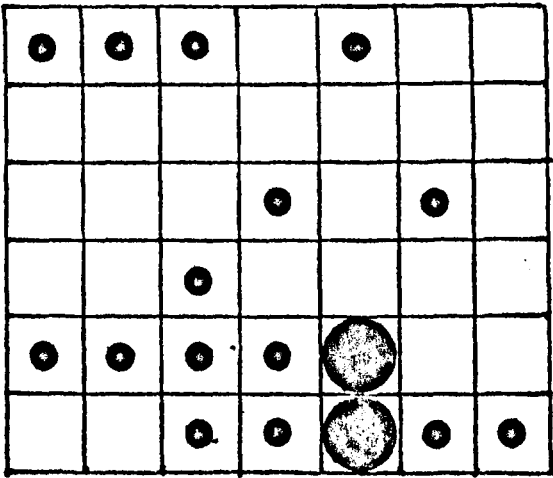
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 45.64 +/- 1.29
Observed dense-dense joins = 46
Conclusion = Random

(b) Earthworm Biomass: Density per Square Metre = 112.2 gm

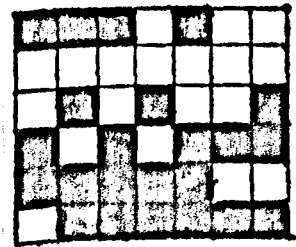


Actual biomass in each core



Standard deviation units

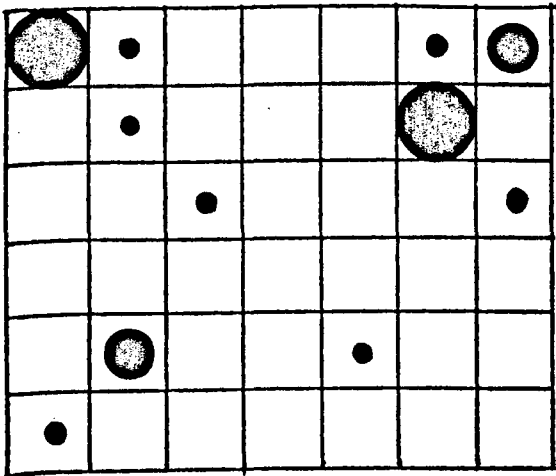
Test for Dispersion using spatial relationships between cores:



Dense = >0.2 g
Sparse = <0.2g

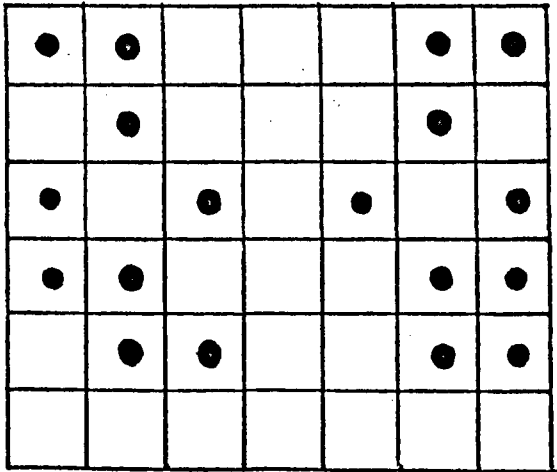
Expected dense-dense joins = 38.49 +/- 1.25
Observed dense-dense joins = 39
Conclusion = Random

(c) Invertebrates other than Earthworms (Numbers)



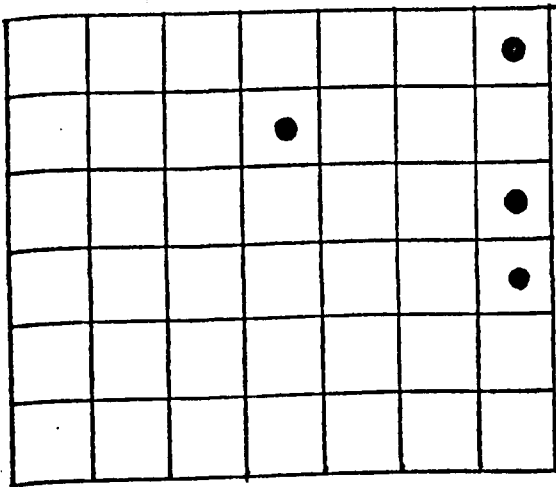
Below Soil Surface

Exp. D-D joins = 8.37 ± 0.72
Obs. D-D joins = 9
Conclusion = Random



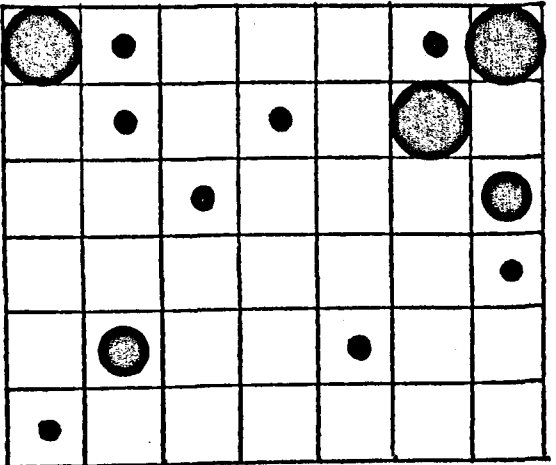
Enchytraeidae

Exp. D-D joins = 23.28 ± 1.08
Obs. D-D joins = 27
Conclusion = Aggregated



Above Soil Surface

Exp. D-D joins = 0.91 ± 0.26
Obs. D-D joins = 1
Conclusion = Random



All (excluding Enchytraeidae)

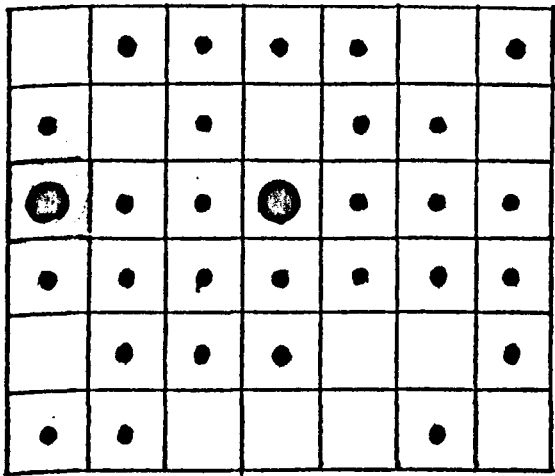
Exp. D-D joins = 11.87 ± 0.84
Obs. D-D joins = 11
Conclusion = Random

Figure A2.4

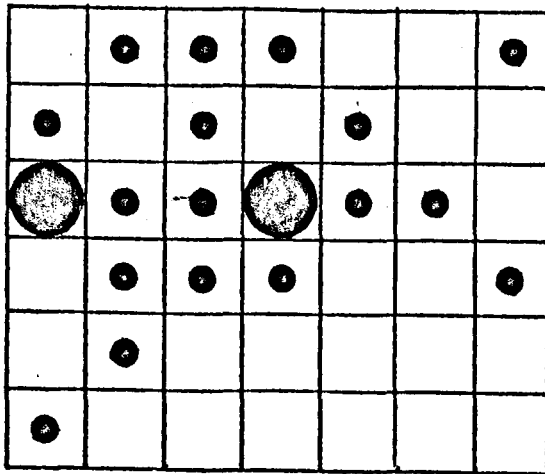
Date: 29-11-79
Crop: Temporary Ley Ungrazed
Field: 37 (SJ 807447)

(a) Earthworm Numbers: Density per Square Metre = 166.5

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 63.08 $p < 0.025 > 0.01$
Conclusion: Aggregated

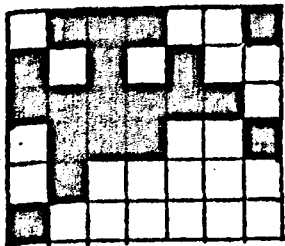


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

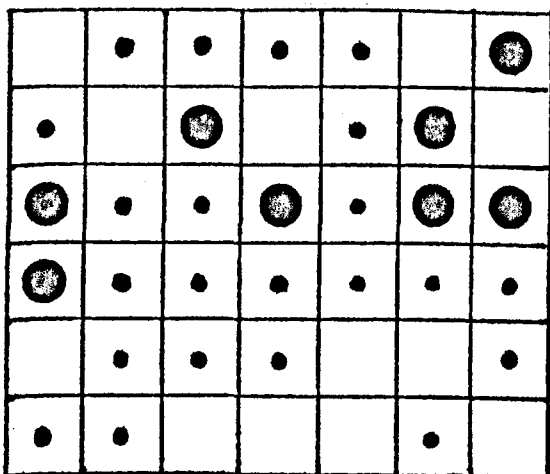


Expected dense-dense joins if sparse and dense cores were randomly mingled:

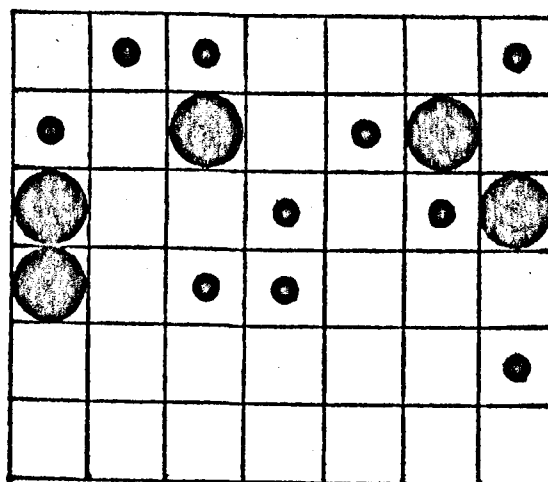
Mean with 95% confidence limits = 26.02 \pm 1.12
Observed dense-dense joins = 35
Conclusion = Aggregated

Dense = >1
Sparse = 0-1

(b) Earthworm Biomass: Density per Square Metre = 66.0 gm

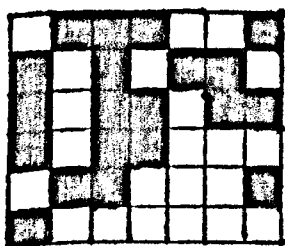


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



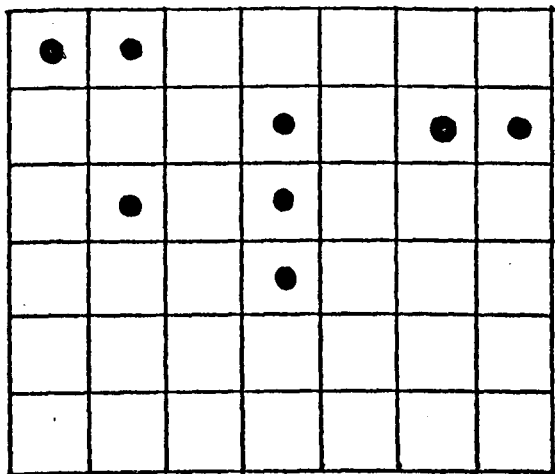
Dense = >0.1 g
Sparse = $0 - 0.1$ g

Expected dense-dense joins = 28.91 ± 1.16

Observed dense-dense joins = 30

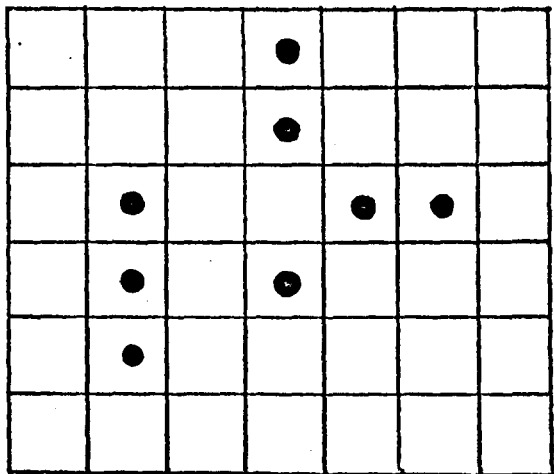
Conclusion = Random

(c) Invertebrates other than Earthworms (Numbers)



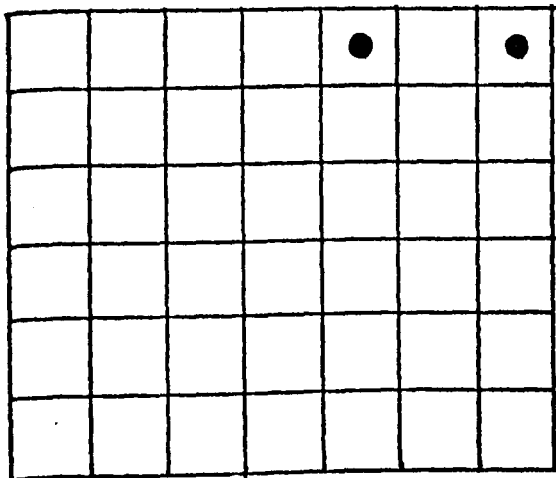
Below Soil Surface

Exp. D-D joins = 4.26 ± 0.54
Obs. D-D joins = 4
Conclusion = Random



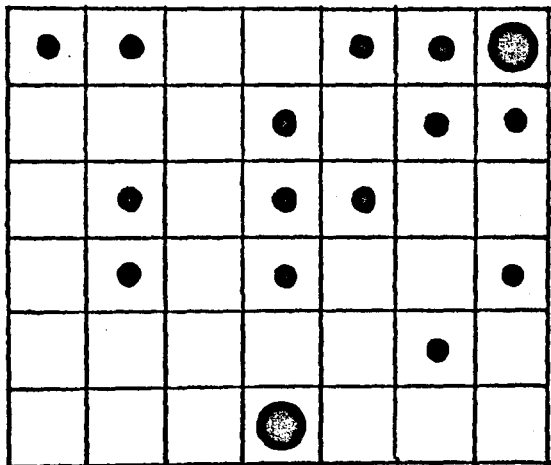
Enchytraeidae

Exp. D-D joins = 4.26 ± 0.54
Obs. D-D joins = 6
Conclusion = Aggregated



Above Soil Surface

Exp. D-D joins =
Obs. D-D joins =
Conclusion =



All (excluding Enchytraeidae)

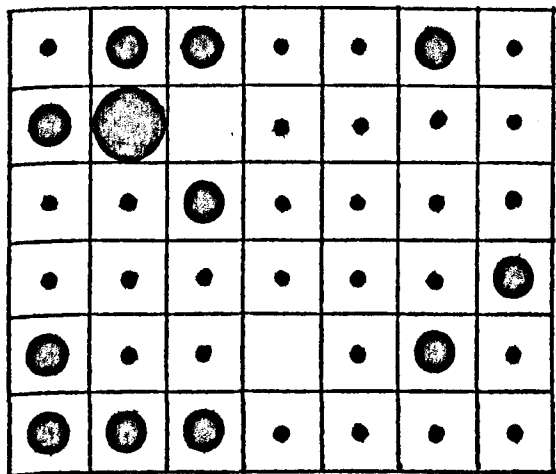
Exp. D-D joins = 18.26 ± 0.99
Obs. D-D joins = 17
Conclusion = Random

Figure A2.5

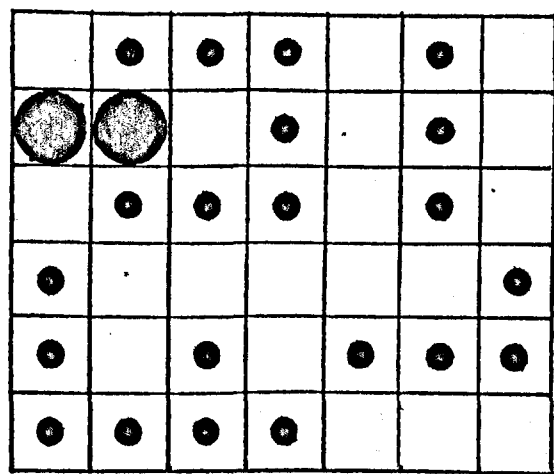
Date: 25-11-79
Crop: Temporary Ley Grazed
Field: 20 (SJ 823442)

(a) Earthworm Numbers: Density per Square Metre = 333.0

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 53.57 $p < 0.075 > 0.05$
Conclusion: (Random)

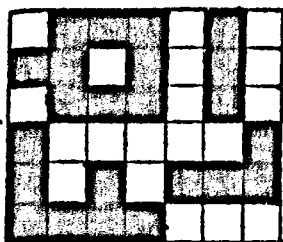


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

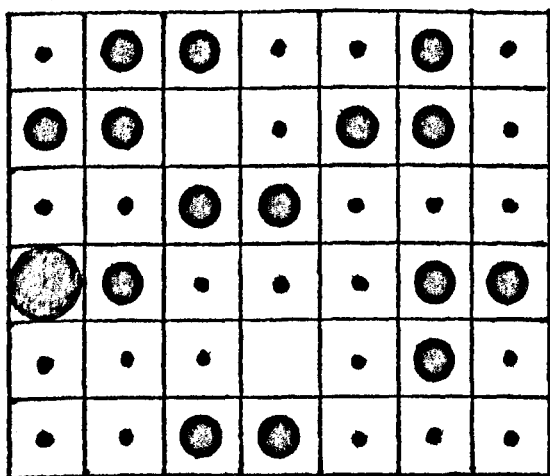


Dense = >3
Sparse = 0-3

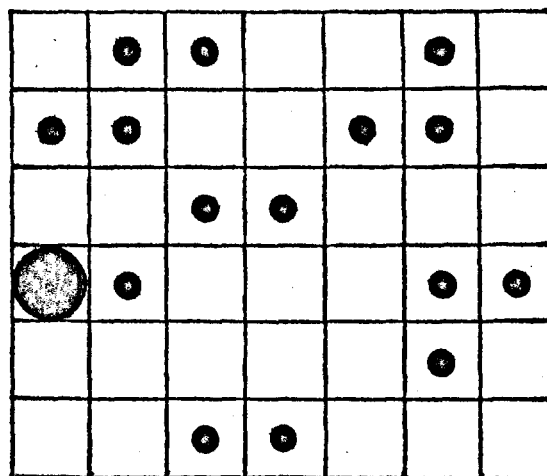
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 38.94 +/- 1.25
Observed dense-dense joins = 33
Conclusion = Overdispersed

(b) Earthworm Biomass: Density per Square Metre = 123.3 gm

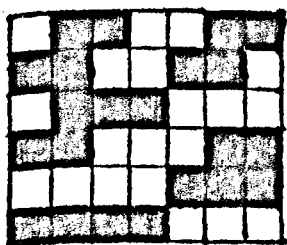


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



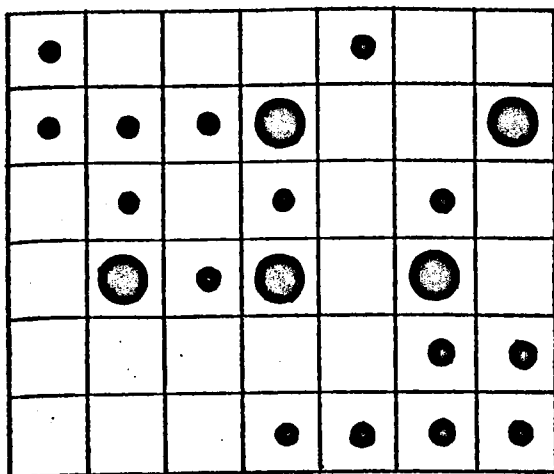
Dense = >0.35 g
Sparse = $0 - 0.35$ g

Expected dense-dense joins = 35.15 ± 1.22

Observed dense-dense joins = 31

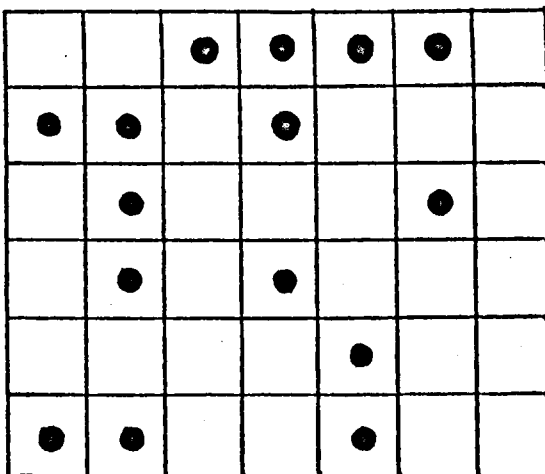
Conclusion = Overdispersed

(c) Invertebrates other than Earthworms (Numbers)



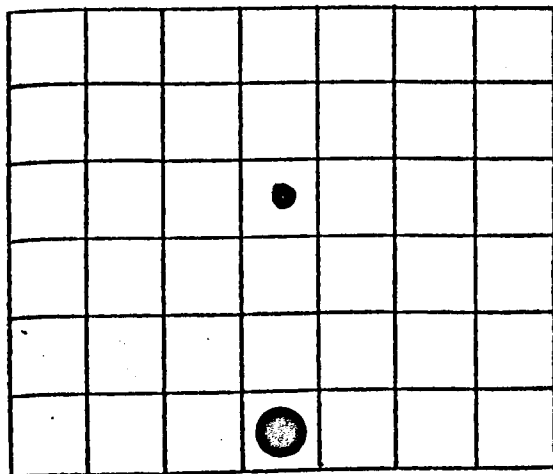
Below Soil Surface

Exp. D-D joins = 26.02 ± 1.12
 Obs. D-D joins = 31
 Conclusion = Aggregated



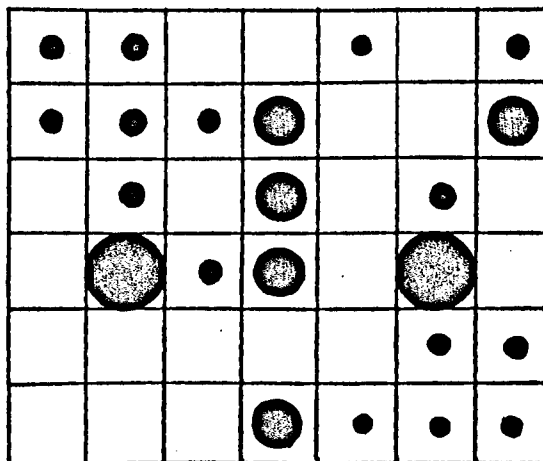
Enchytraeidae

Exp. D-D joins = 15.98 ± 0.94
 Obs. D-D joins = 13
 Conclusion = Overdispersed



Above Soil Surface

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



All (excluding Enchytraeidae)

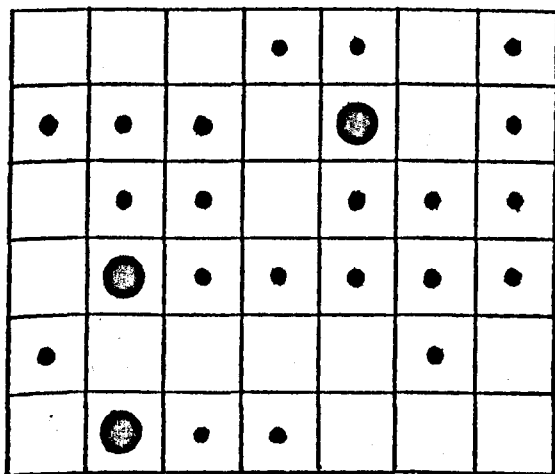
Exp. D-D joins = 35.15 ± 1.22
 Obs. D-D joins = 35
 Conclusion = Random

Figure A2.6

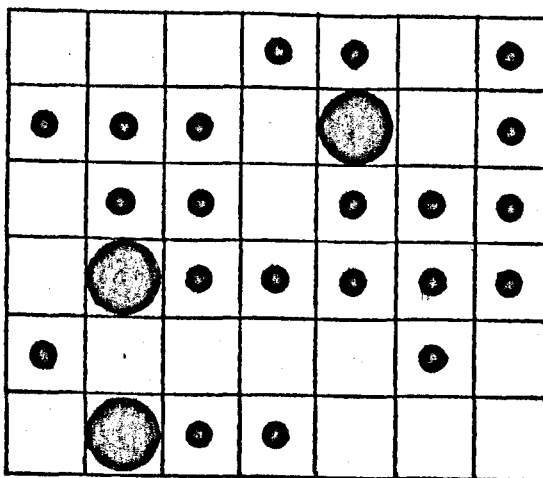
Date: 27-11-79
 Crop: Temporary Ley Grazed
 Field: 22 (SJ 821447)

(a) Earthworm Numbers: Density per Square Metre = 240.5

Test for Dispersion ignoring spatial relationships between cores:
 Chi-square = 46.07 $p < 0.3 > 0.2$
 Conclusion: Random

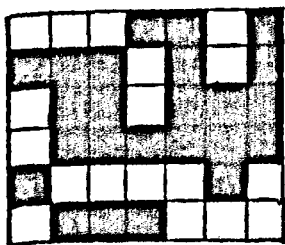


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

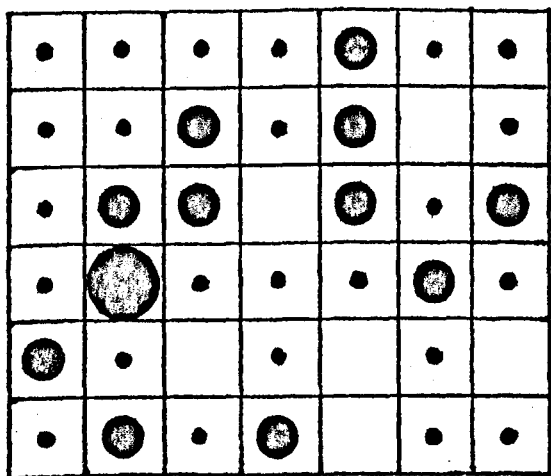


Expected dense-dense joins if sparse and dense cores were randomly mingled:

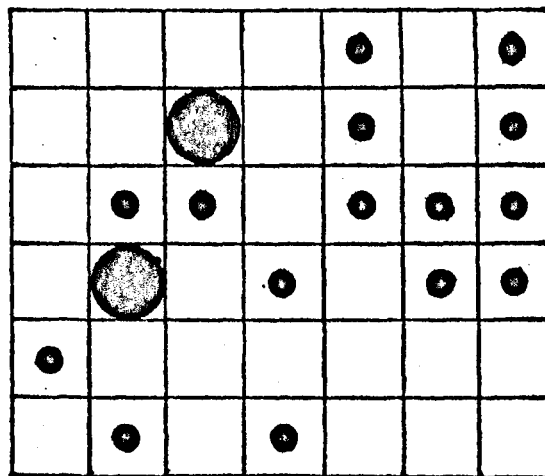
Mean with 95% confidence limits = 41.99 \pm 1.27
 Observed dense-dense joins = 44
 Conclusion = Aggregated

Dense = >0
 Sparse = 0

(b) Earthworm Biomass: Density, per Square Metre = 93.4 gm

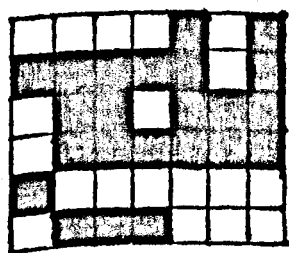


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



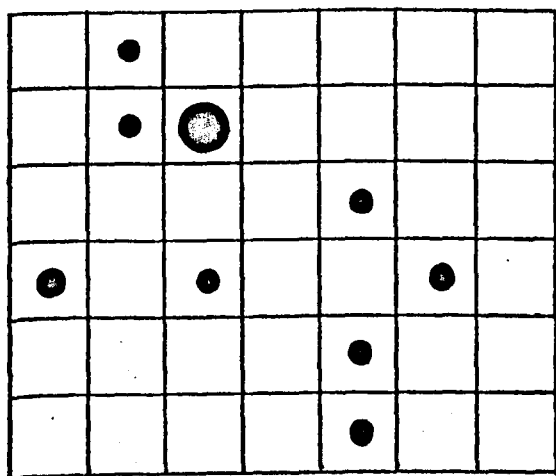
Dense = >0.15 g
Sparse = $0 - 0.15$ g

Expected dense-dense joins = 38.49 ± 1.25

Observed dense-dense joins = 42

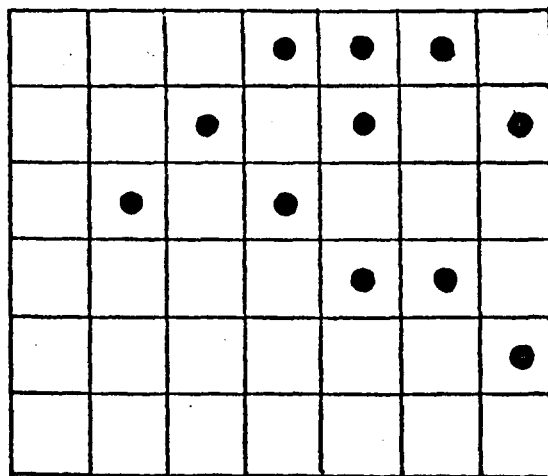
Conclusion = Aggregated

(c) Invertebrates other than Earthworms (Numbers)



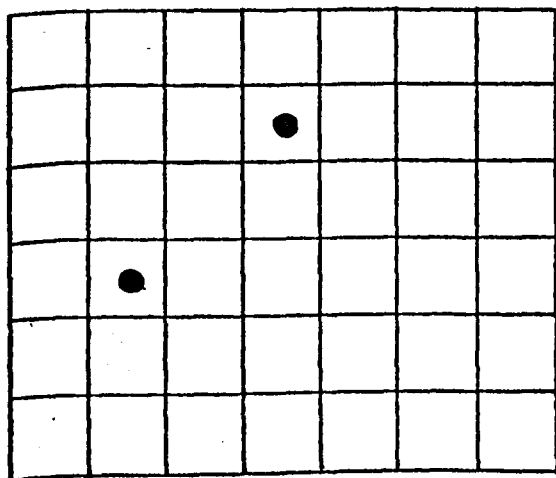
Below Soil Surface

Exp. D-D joins = 5.48 ± 0.60
 Obs. D-D joins = 6
 Conclusion = Random



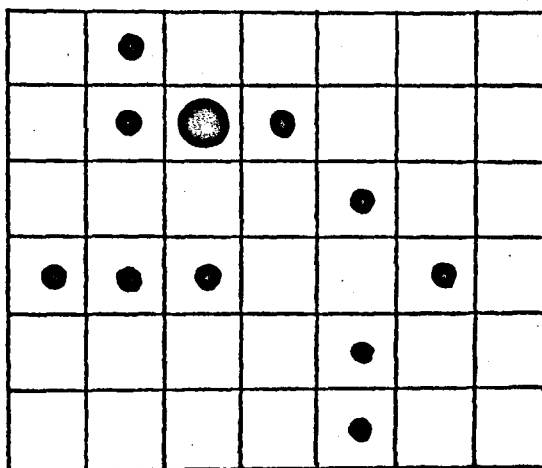
Enchytraeidae

Exp. D-D joins = 8.37 ± 0.72
 Obs. D-D joins = 11
 Conclusion = Aggregated



Above Soil Surface

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



All (excluding Enchytraeidae)

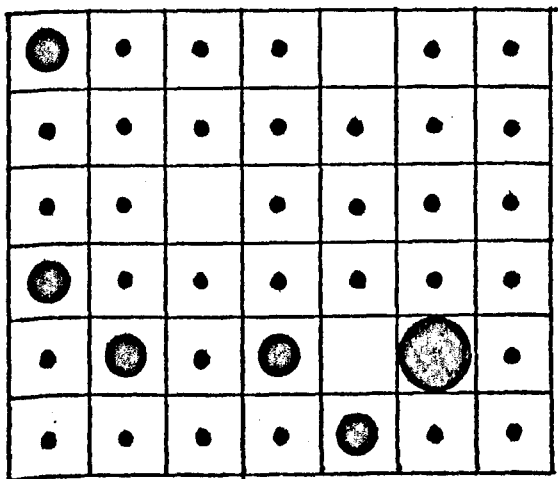
Exp. D-D joins = 8.37 ± 0.72
 Obs. D-D joins = 10
 Conclusion = Aggregated

Figure A2.7

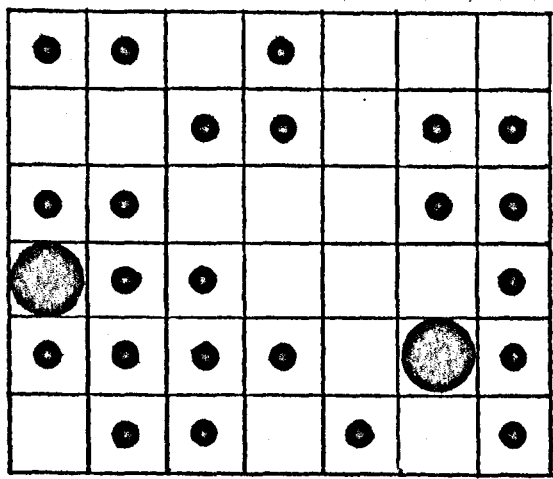
Date: 12-11-79
Crop: Permanent Pasture
Field: 1a (SJ 819452)

(a) Earthworm Numbers: Density per Square Metre = 376.2

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 48.75 $p < 0.2 > 0.15$
Conclusion: Random

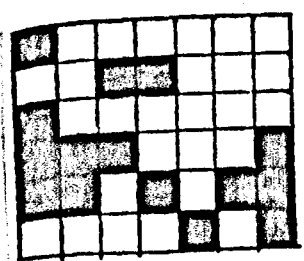


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

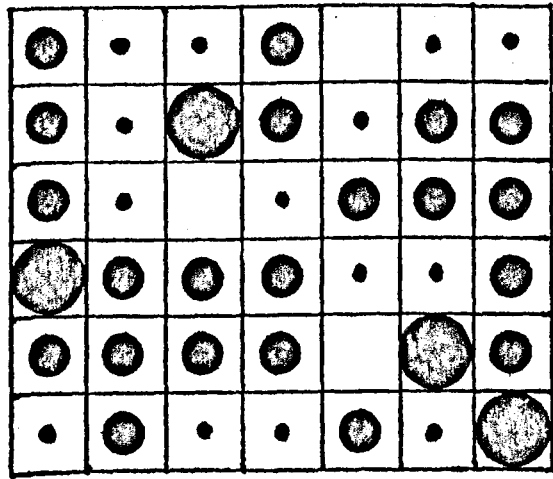


Dense = >3
Sparse = 0-3

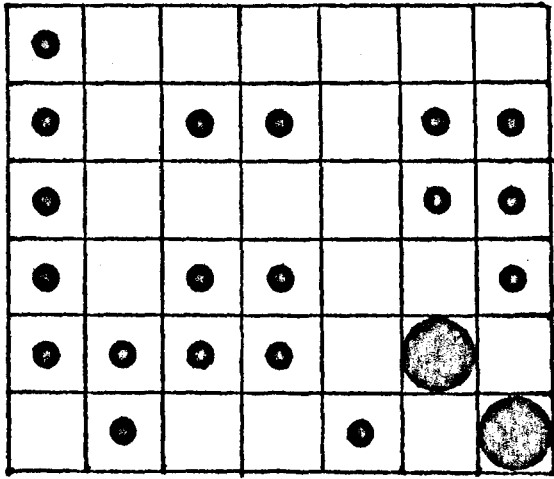
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 15.98 +/- 0.94
Observed dense-dense joins = 19
Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre = 192.7 gm

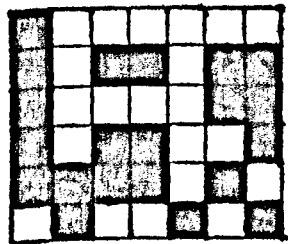


Actual biomass in each core



Standard deviation units

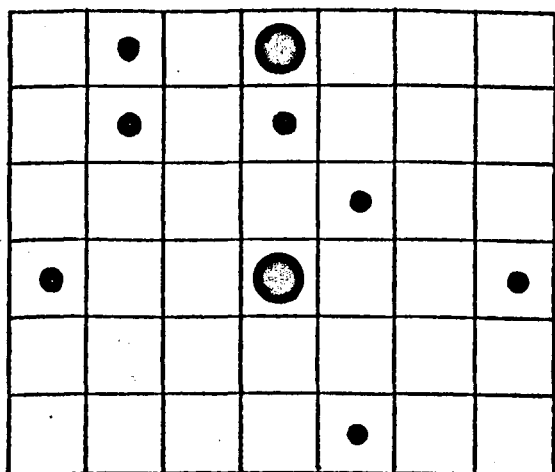
Test for Dispersion using spatial relationships between cores:



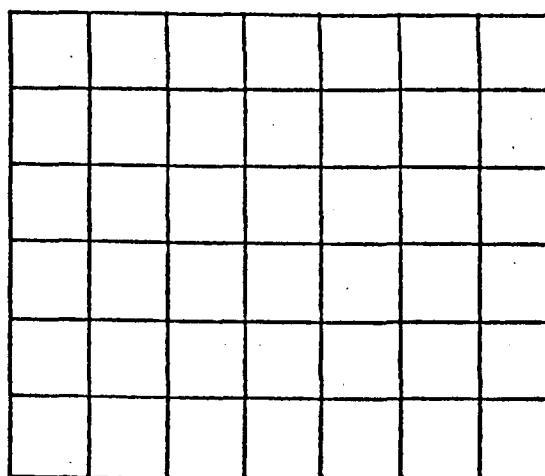
Expected dense-dense joins = 31.95 +/- 1.19
Observed dense-dense joins = 30
Conclusion = Overdispersed

Dense = >0.75 g
Sparse = 0 - 0.75 g

(c) Invertebrates other than Earthworms (Numbers)



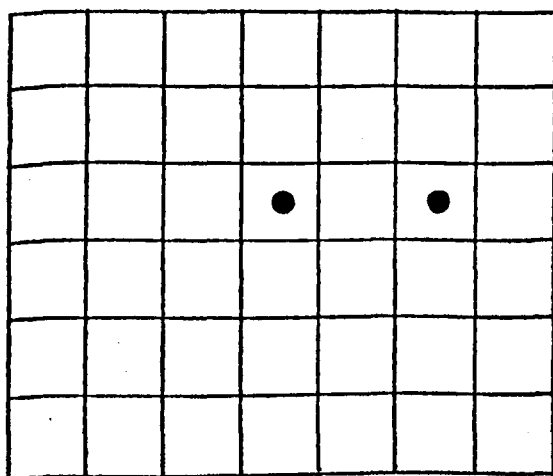
Below Soil Surface



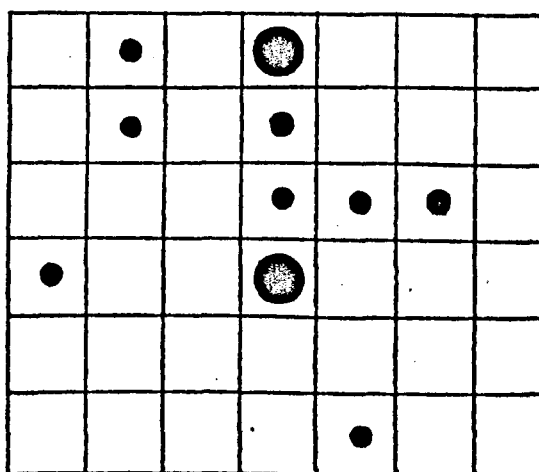
Enchytraeidae

Exp. D-D joins = 5.48 ± 0.60
 Obs. D-D joins = 3
 Conclusion = Overdispersed

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



Above Soil Surface



All (excluding Enchytraeidae)

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =

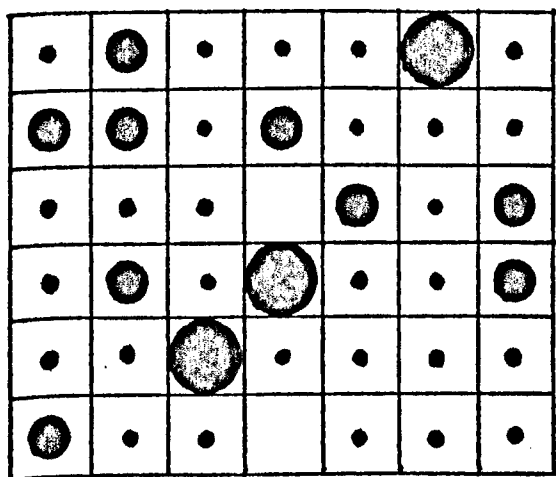
Exp. D-D joins = 6.85 ± 0.66
 Obs. D-D joins = 8
 Conclusion = Aggregated

Figure A2.8

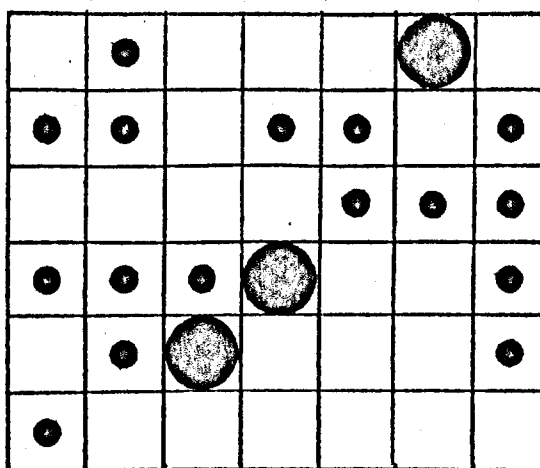
Date: 11-12-79
Crop: Permanent Pasture
Field: 1a (SJ 819452)

(a) Earthworm Numbers: Density per Square Metre = 394.7

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 74.47 $p < 0.001 > 0.0005$
Conclusion: Aggregated

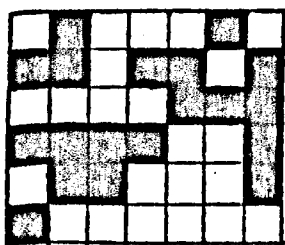


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

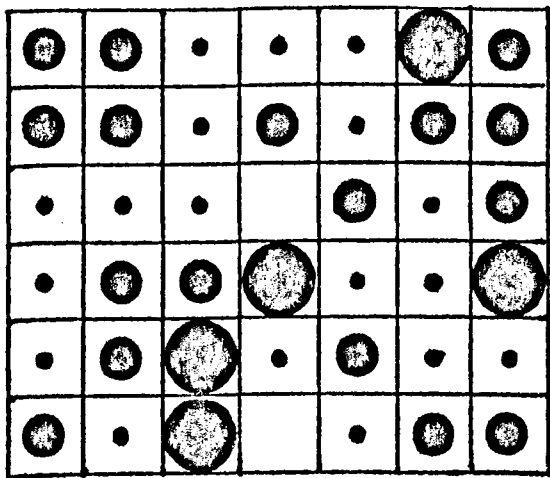


Expected dense-dense joins if sparse and dense cores were randomly mingled:

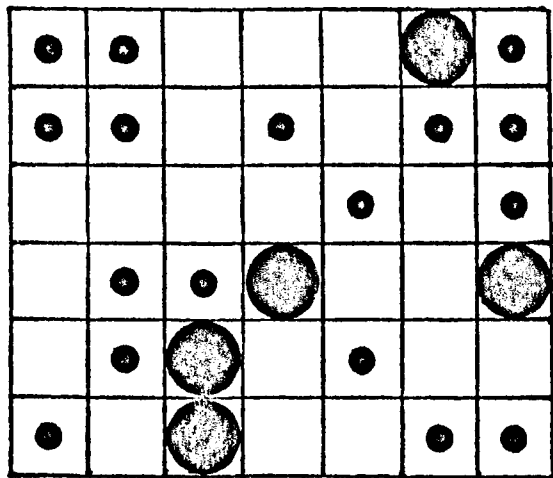
Mean with 95% confidence limits = 26.02 \pm 1.12
Observed dense-dense joins = 27
Conclusion = Random

Dense = >3
Sparse = 0-3

(b) Earthworm Biomass: Density per Square Metre = 193.6 gm

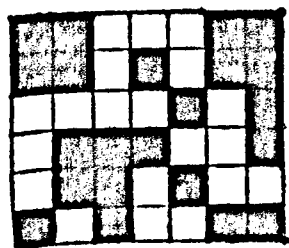


Actual biomass in each core



Standard deviation units

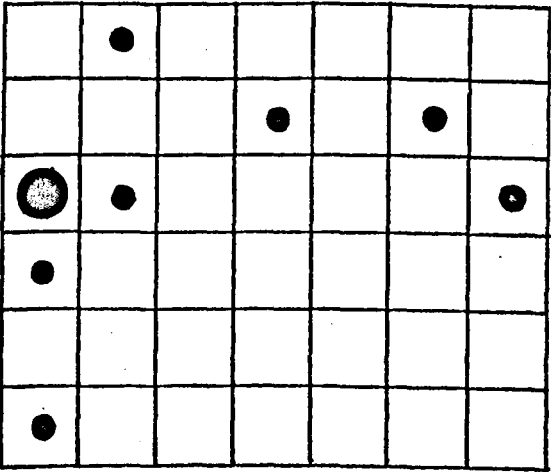
Test for Dispersion using spatial relationships between cores:



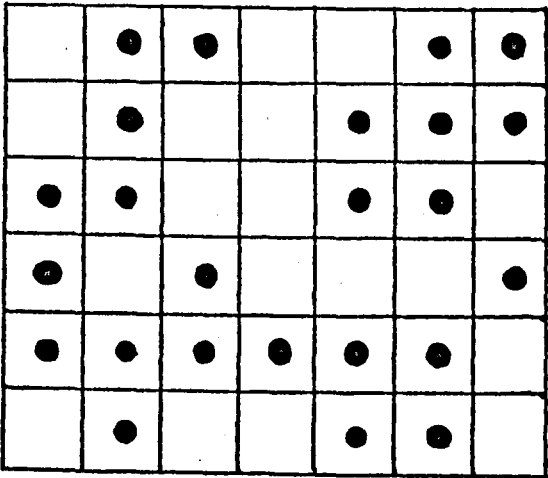
Dense = >0.45 g
Sparse = $0 - 0.45$ g

Expected dense-dense joins = 38.49 ± 1.25
Observed dense-dense joins = 32
Conclusion = Overdispersed

(c) Invertebrates other than Earthworms (Numbers)



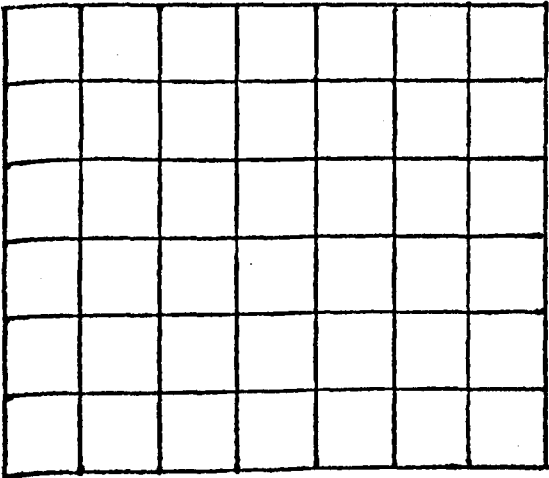
Below Soil Surface



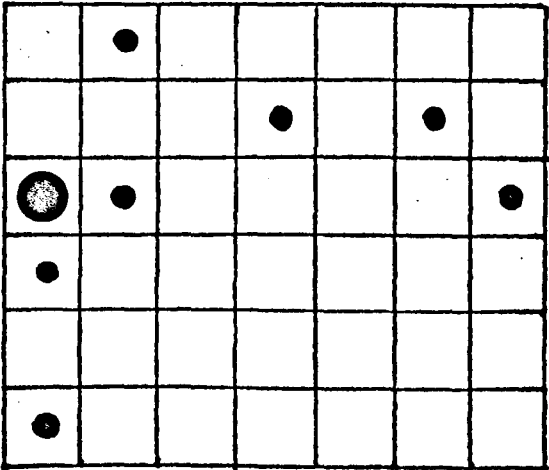
Enchytraeidae

Exp. D-D joins = 4.26 ± 0.54
Obs. D-D joins = 4
Conclusion = Random

Exp. D-D joins = 41.99 ± 1.27
Obs. D-D joins = 44
Conclusion = Aggregated



Above Soil Surface



All (excluding Enchytraeidae)

Exp. D-D joins =
Obs. D-D joins =
Conclusion =

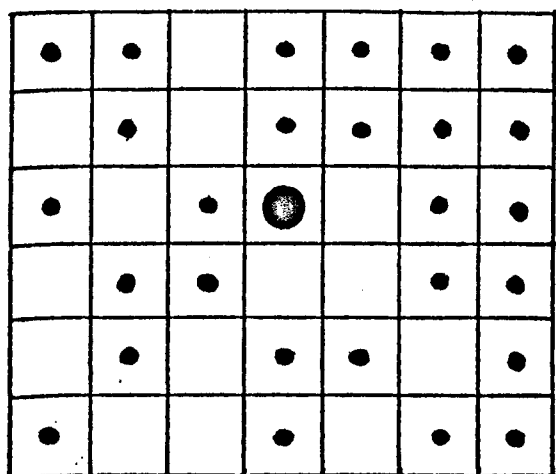
Exp. D-D joins = 4.26 ± 0.54
Obs. D-D joins = 4
Conclusion = Random

Figure A2.9

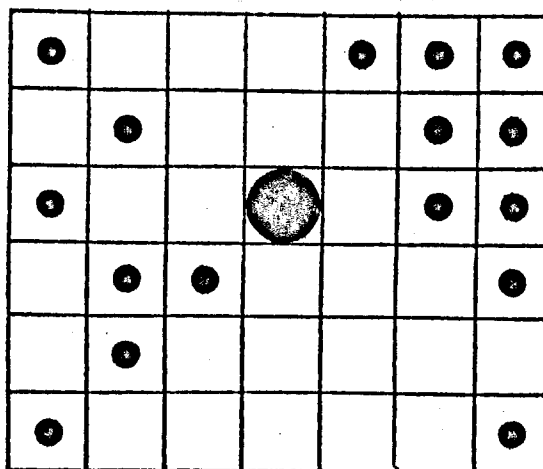
Date: 12-1-80
Crop: Permanent Pasture
Field: 1a (SJ 819452)

(a) Earthworm Numbers: Density per Square Metre = 252.8

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 55.95 $p < 0.05 > 0.025$
Conclusion: Aggregated

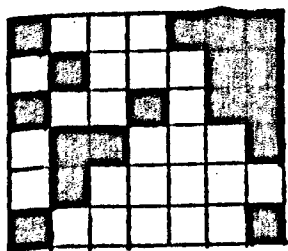


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

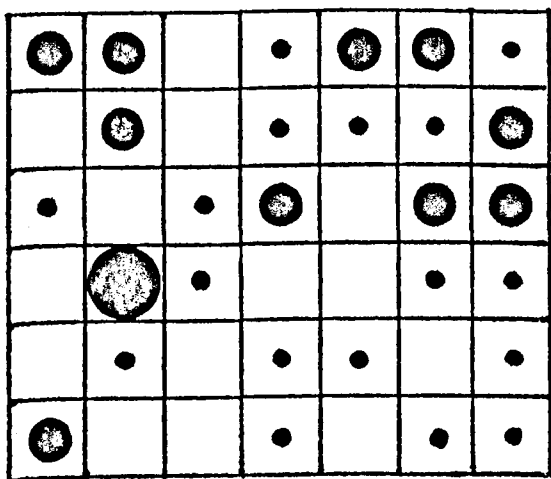


Dense = >1
Sparse = 0-1

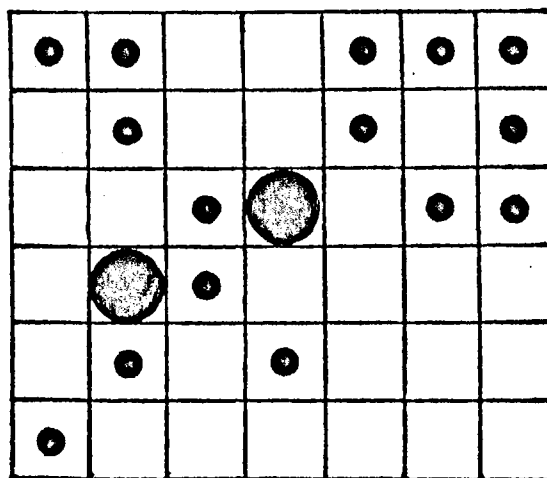
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 20.69 +/- 1.04
Observed dense-dense joins = 23
Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre = 86.9 gm

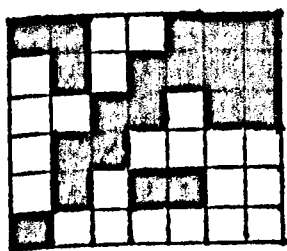


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



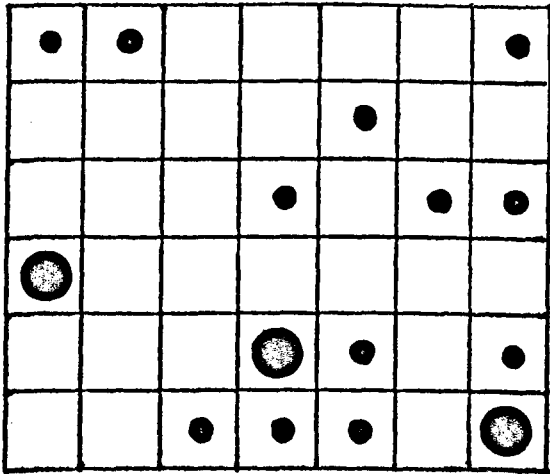
Dense = >0.25 g
Sparse = $0 - 0.25$ g

Expected dense-dense joins = 28.91 ± 1.16

Observed dense-dense joins = 36

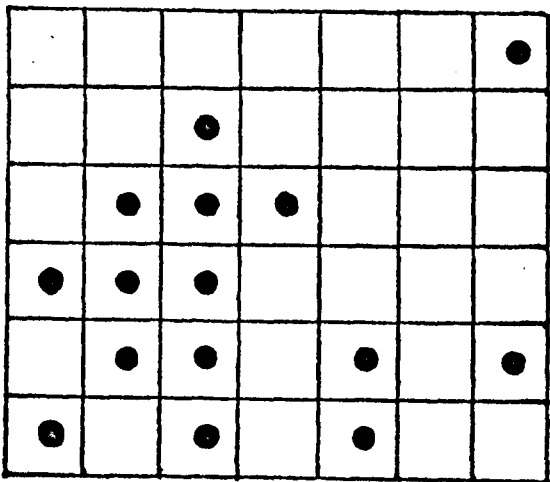
Conclusion = Aggregated

(c) Invertebrates other than Earthworms (Numbers)



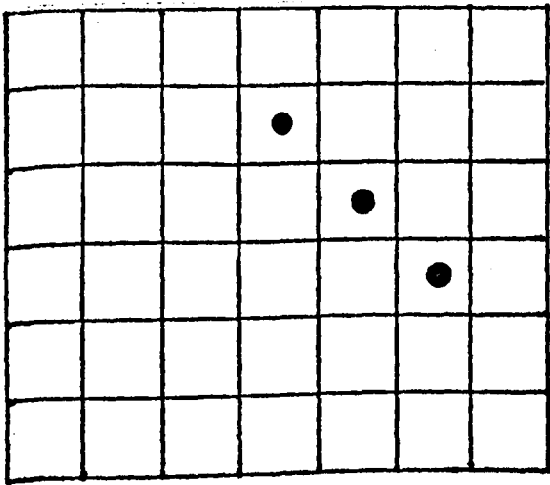
Below Soil Surface

Exp. D-D joins = 15.98 +/- 0.94
Obs. D-D joins = 13
Conclusion = Random



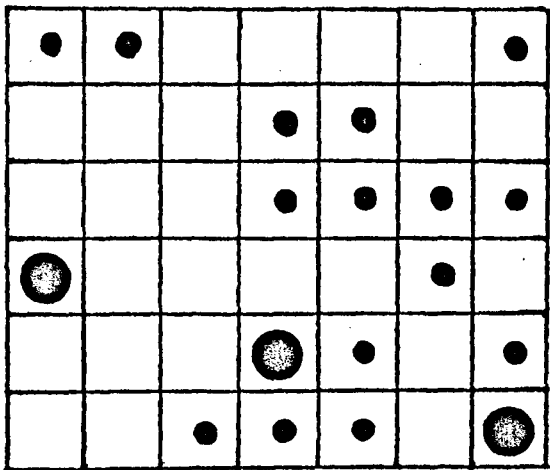
Enchytraeidae

Exp. D-D joins = 15.98 +/- 0.94
Obs. D-D joins = 23
Conclusion = Aggregated



Above Soil Surface

Exp. D-D joins = 0.46 +/- 0.19
Obs. D-D joins = 2
Conclusion = Aggregated



All (excluding Enchytraeidae)

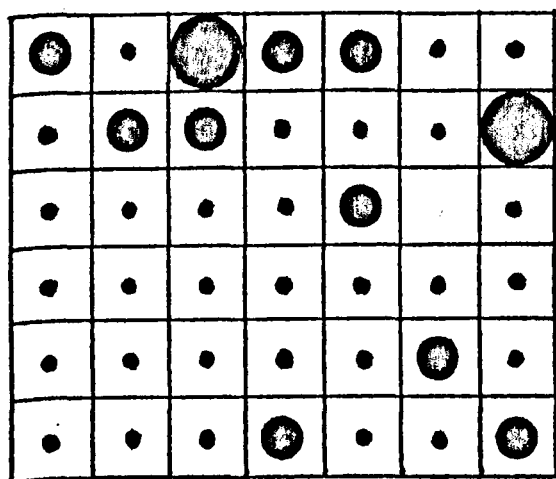
Exp. D-D joins = 23.28 +/- 1.08
Obs. D-D joins = 24
Conclusion = Random

Figure A2.10

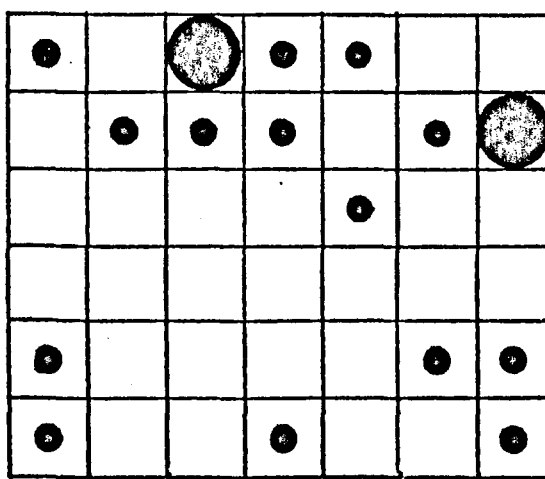
Date: 8-12-79
Crop: Permanent Pasture
Field: 1b (SJ 822453)

(a) Earthworm Numbers: Density per Square Metre = 314.5

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 74.63 $p < 0.001 > 0.0005$
Conclusion: Aggregated

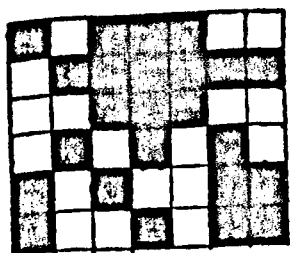


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

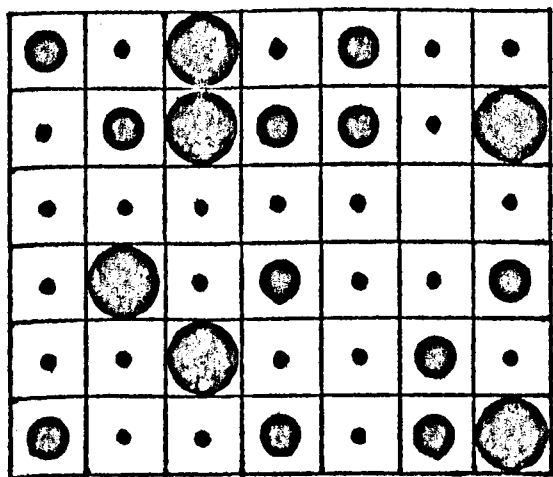


Dense = >2
Sparse = 0-2

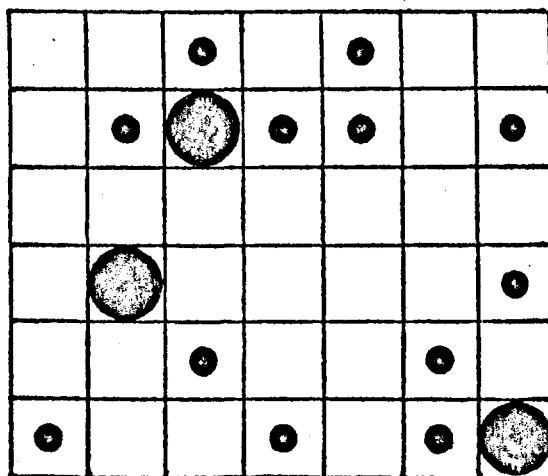
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 41.99 ± 1.27
Observed dense-dense joins = 46
Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre = 164.6 gm

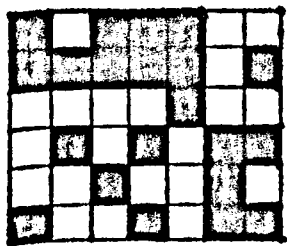


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



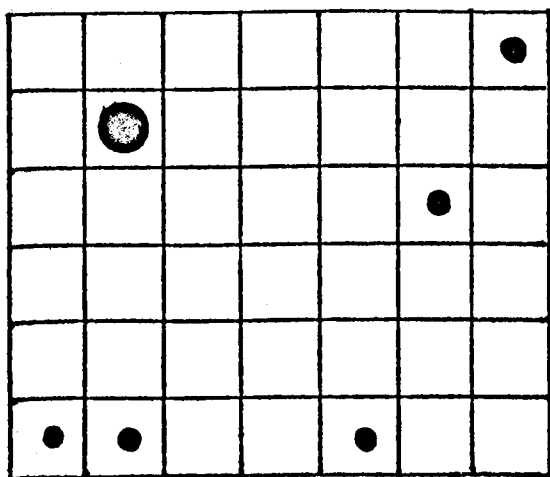
Dense = >0.3 g
Sparse = $0 - 0.3$ g

Expected dense-dense joins = 31.95 ± 1.19

Observed dense-dense joins = 29

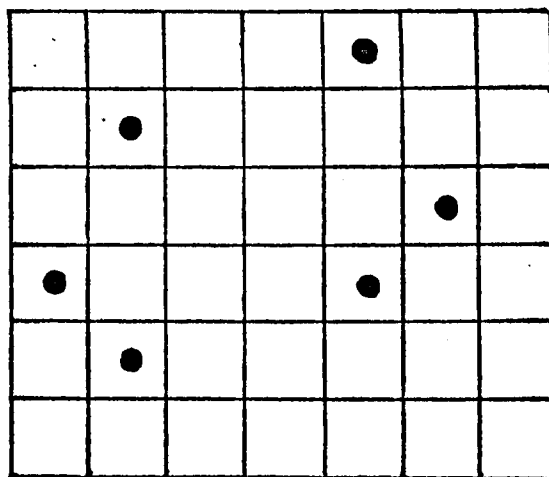
Conclusion = Random

(c) Invertebrates other than Earthworms (Numbers)



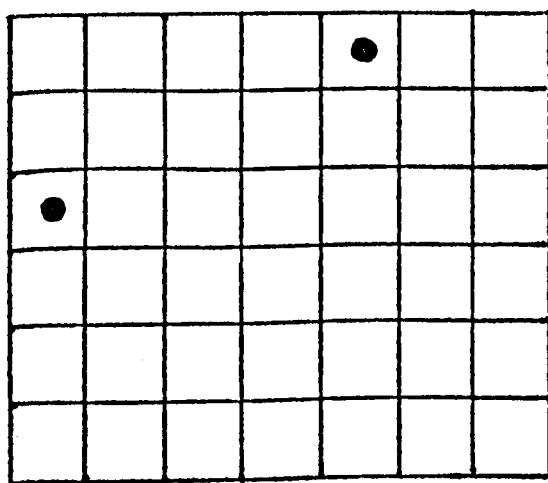
Below Soil Surface

Exp. D-D joins = 2.28 ± 0.40
 Obs. D-D joins = 1
 Conclusion = Overdispersed



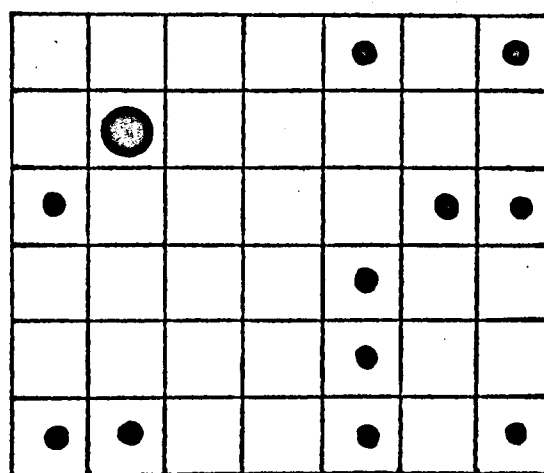
Enchytraeidae

Exp. D-D joins = 2.28 ± 0.40
 Obs. D-D joins = 2
 Conclusion = Random



Above Soil Surface

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



All (excluding Enchytraeidae)

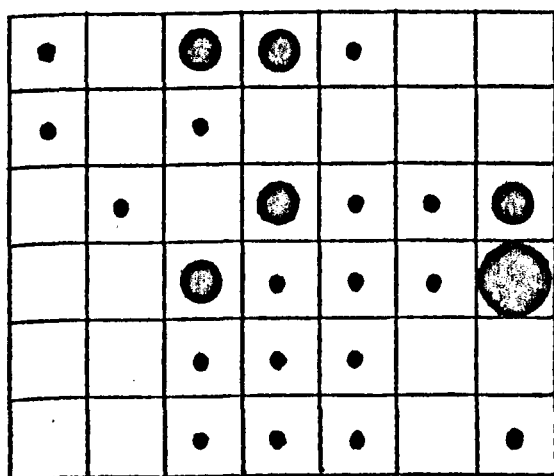
Exp. D-D joins = 10.04 ± 0.78
 Obs. D-D joins = 6
 Conclusion = Overdispersed

Figure A2.11

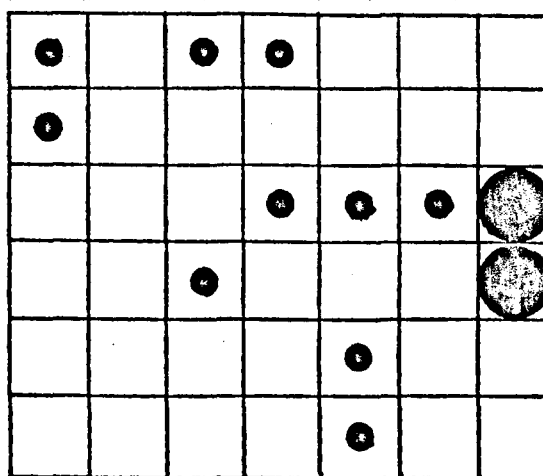
Date: 11-12-79
Crop: Permanent Pasture
Field: 33b (SJ 812445)

(a) Earthworm Numbers: Density per Square Metre = 271.3

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 62.87 $p < 0.025 > 0.01$
Conclusion: Aggregated

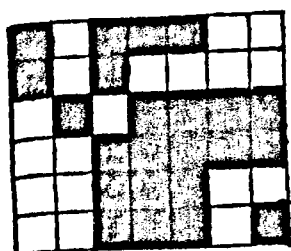


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

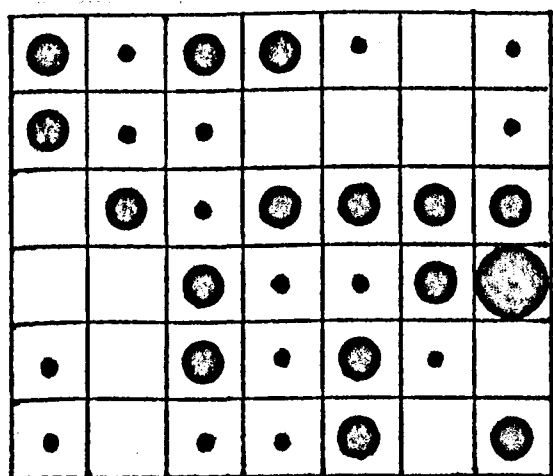


Dense = >0
Sparse = 0

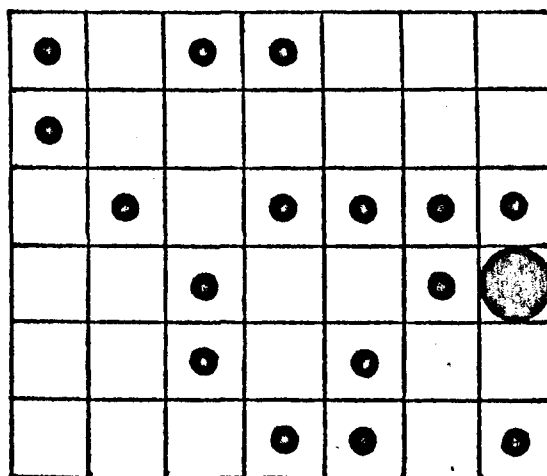
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 38.49 +/- 1.25
Observed dense-dense joins = 46
Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre = 101.7 gm

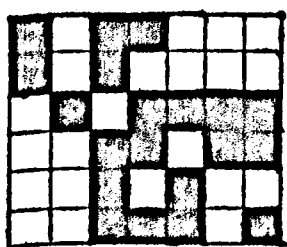


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



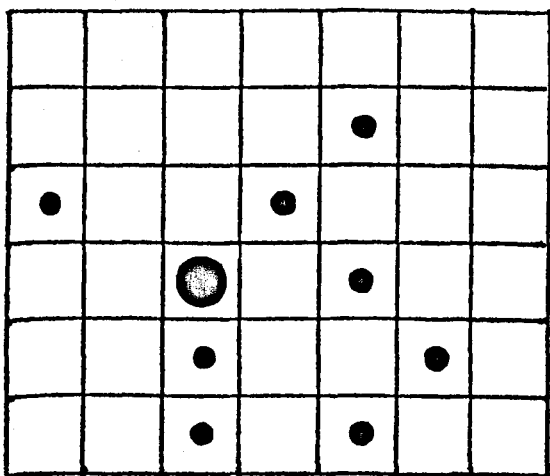
Dense = >0.2 g
Sparse = $0 - 0.2$ g

Expected dense-dense joins = 28.91 ± 1.16

Observed dense-dense joins = 31

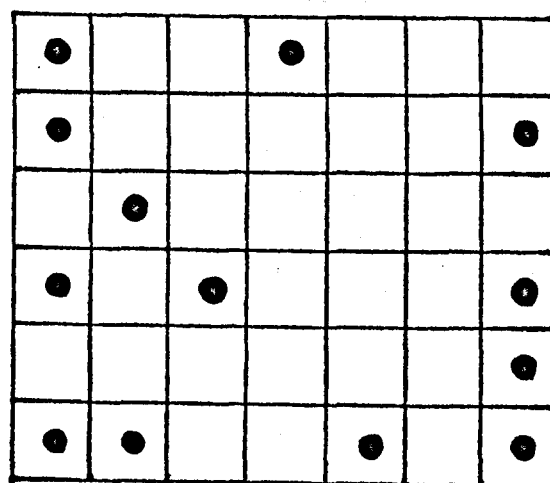
Conclusion = Aggregated

(c) Invertebrates other than Earthworms (Numbers)



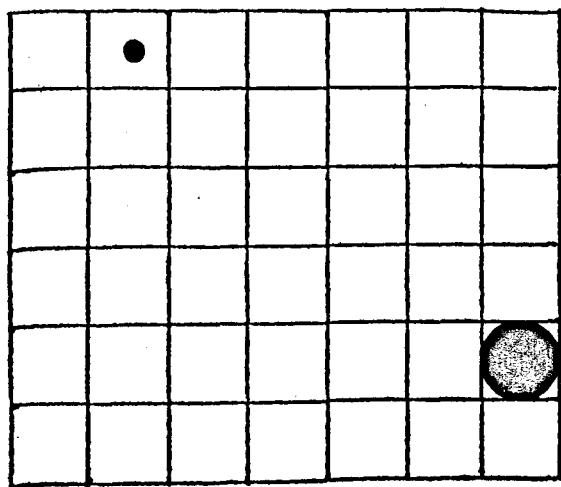
Below Soil Surface

Exp. D-D joins = 5.48 ± 0.60
 Obs. D-D joins = 7
 Conclusion = Aggregated



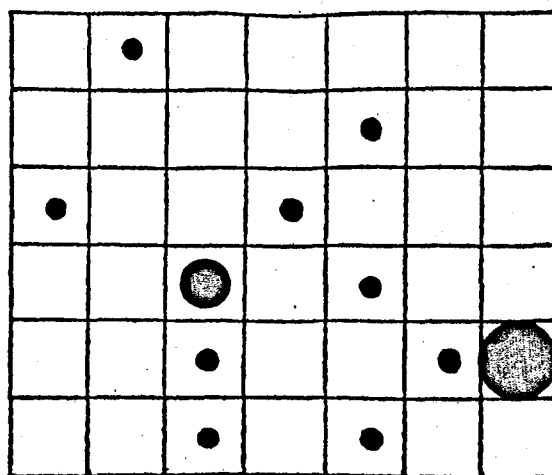
Enchytraeidae

Exp. D-D joins = 11.87 ± 0.84
 Obs. D-D joins = 7
 Conclusion = Overdispersed



Above Soil Surface

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



All (excluding Enchytraeidae)

Exp. D-D joins = 8.37 ± 0.72
 Obs. D-D joins = 8
 Conclusion = Random

Figure A2.12

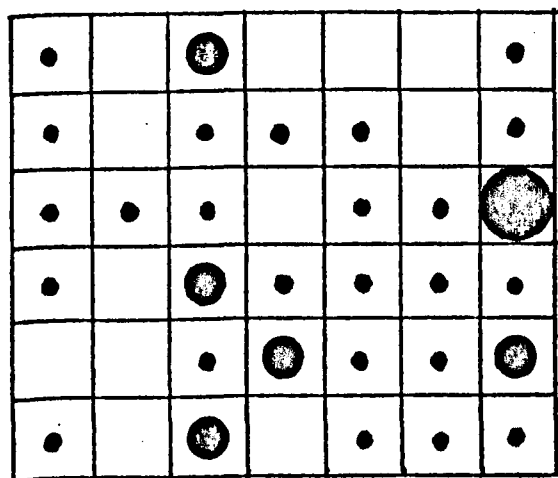
Date: 11-12-79
Crop: Permanent Pasture
Field: 35a (SJ 811443)

(a) Earthworm Numbers: Density per Square Metre = 296.0

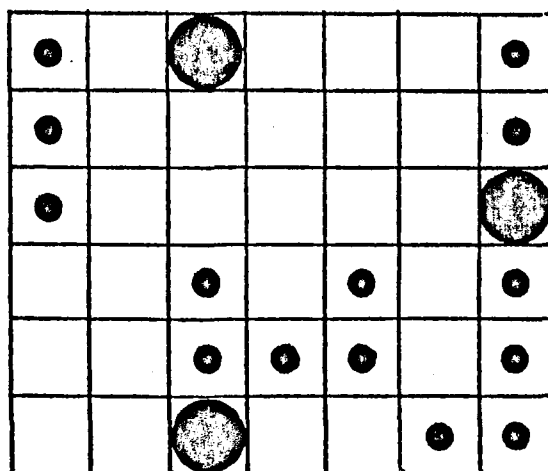
Test for Dispersion ignoring spatial relationships between cores:

Chi-square = 62.35 $p < 0.025 > 0.01$

Conclusion: Aggregated

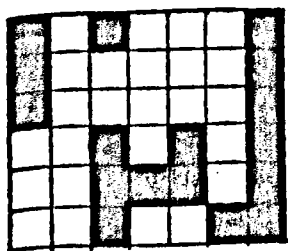


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



Expected dense-dense joins if sparse and dense cores were randomly mingled:

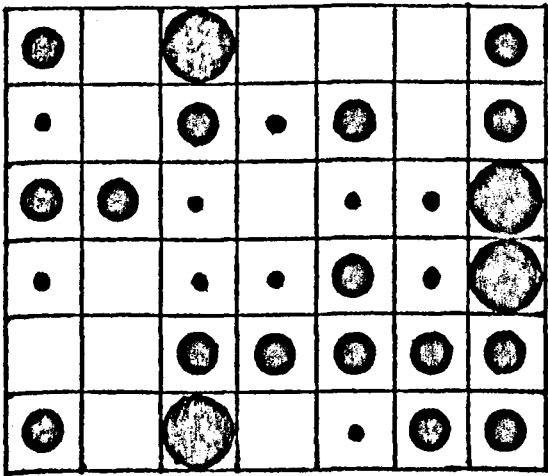
Mean with 95% confidence limits = 20.69 +/- 1.04

Observed dense-dense joins = 18

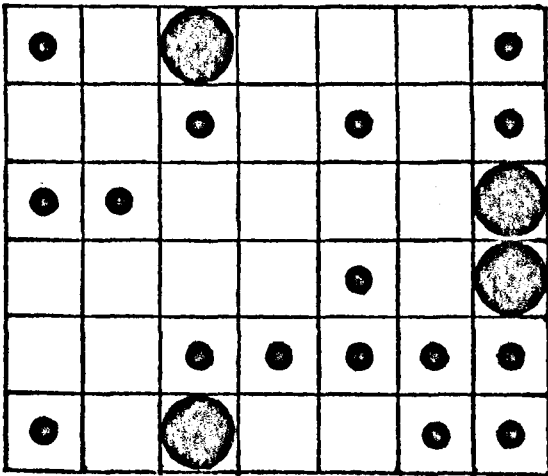
Conclusion = Overdispersed

Dense = >1
Sparse = 0-1

(b) Earthworm Biomass: Density per Square Metre = 120.2 gm

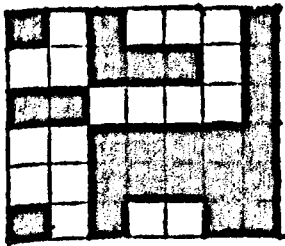


Actual biomass in each core



Standard deviation units

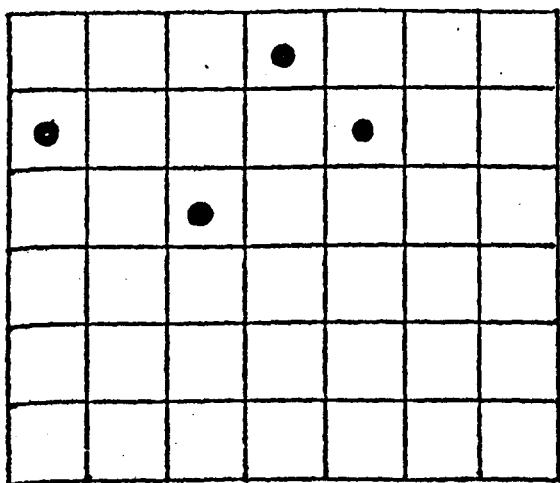
Test for Dispersion using spatial relationships between cores:



Dense = >0.15 g
Sparse = 0 - 0.15 g

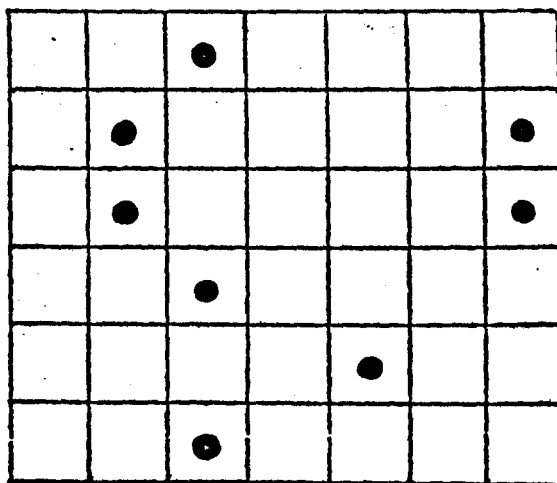
Expected dense-dense joins = 41.99 +/- 1.27
Observed dense-dense joins = 40
Conclusion = Overdispersed

(c) Invertebrates other than Earthworms (Numbers)



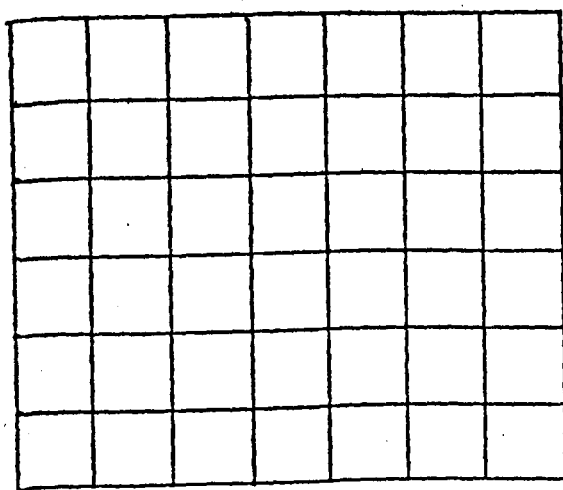
Below Soil Surface

Exp. D-D joins = 0.91 ± 0.26
Obs. D-D joins = 1
Conclusion = Random



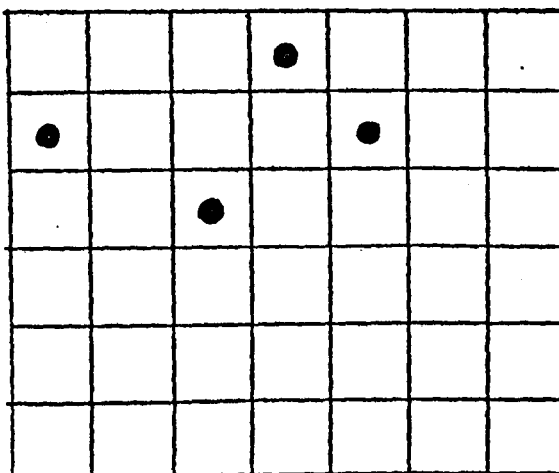
Enchytraeidae

Exp. D-D joins = 4.26 ± 0.54
Obs. D-D joins = 4
Conclusion = Random



Above Soil Surface

Exp. D-D joins =
Obs. D-D joins =
Conclusion =



All (excluding Enchytraeidae)

Exp. D-D joins = 0.91 ± 0.26
Obs. D-D joins = 1
Conclusion = Random

Figure A2.13

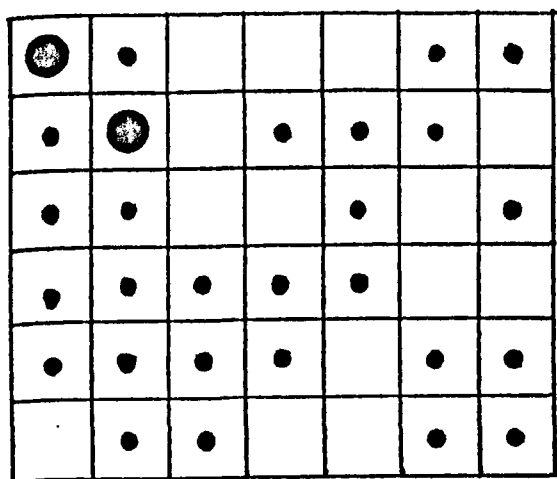
Date: 2-12-79
Crop: Permanent Pasture
Field: Market Drayton 1 (SJ 707351)

(a) Earthworm Numbers: Density per Square Metre = 191.2

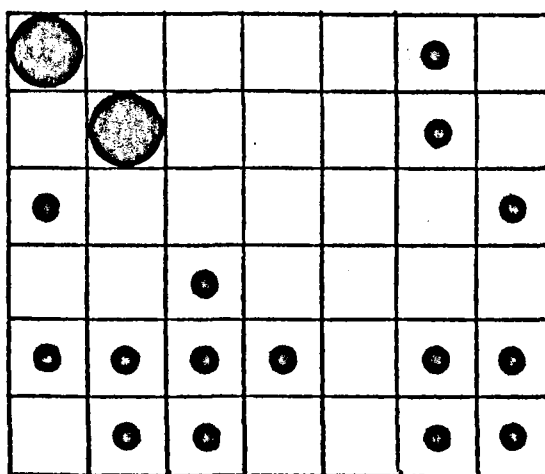
Test for Dispersion ignoring spatial relationships between cores:

Chi-square = 66.72 $p < 0.01 > 0.005$

Conclusion: Aggregated

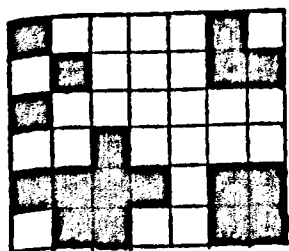


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



Dense = >1
Sparse = 0-1

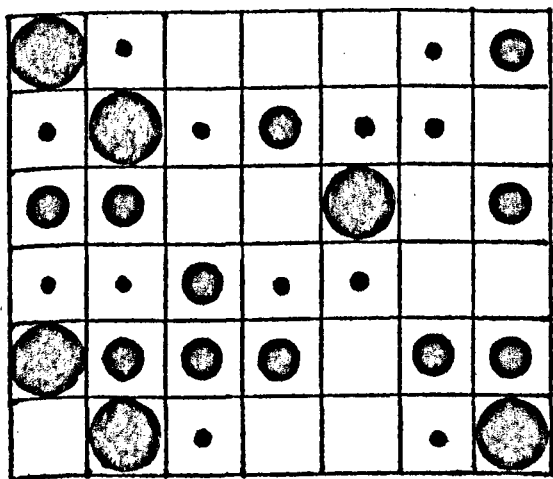
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 20.69 +/- 1.04

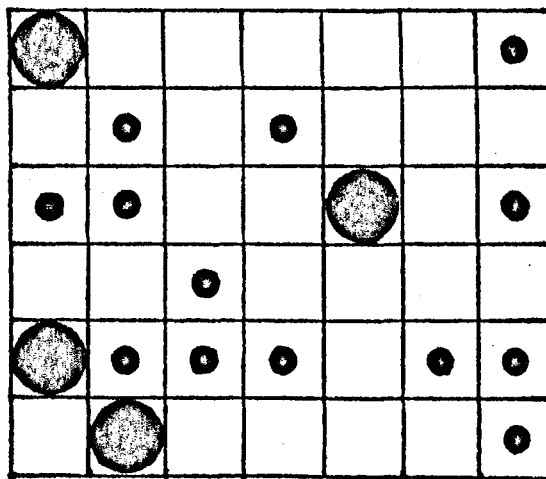
Observed dense-dense joins = 24

Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre = 125.9 gm

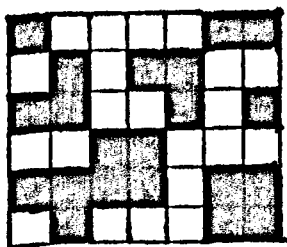


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



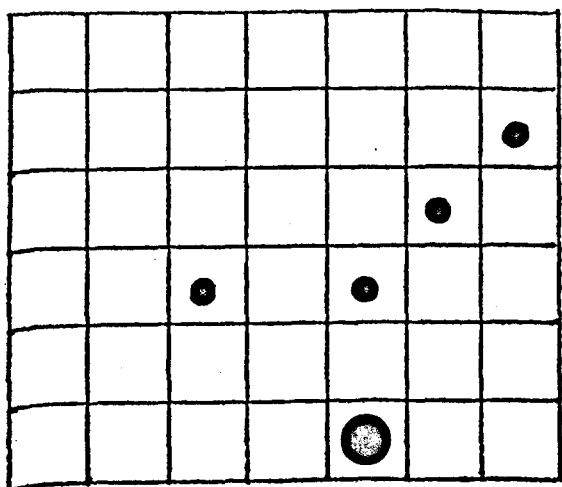
Dense = >0.2 g
Sparse = $0 - 0.2$ g

Expected dense-dense joins = 31.95 ± 1.19

Observed dense-dense joins = 28

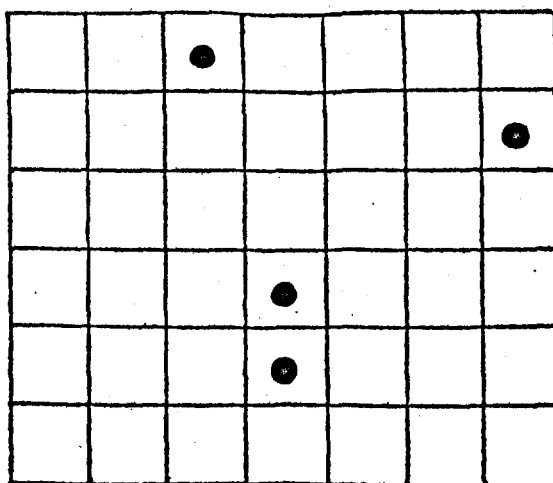
Conclusion = Overdispersed

(c) Invertebrates other than Earthworms (Numbers)



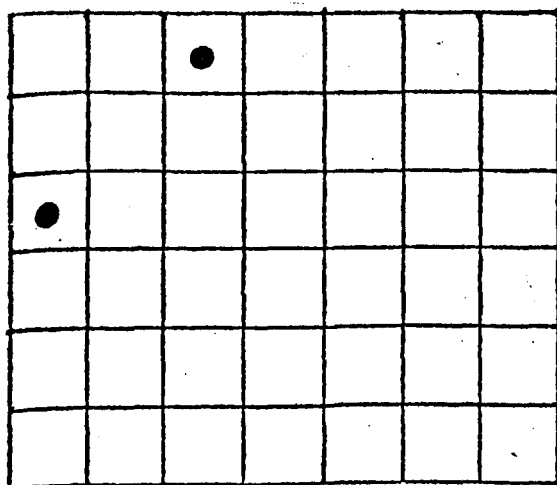
Below Soil Surface

Exp. D-D joins = 1.52 ± 0.33
 Obs. D-D joins = 2
 Conclusion = Aggregated



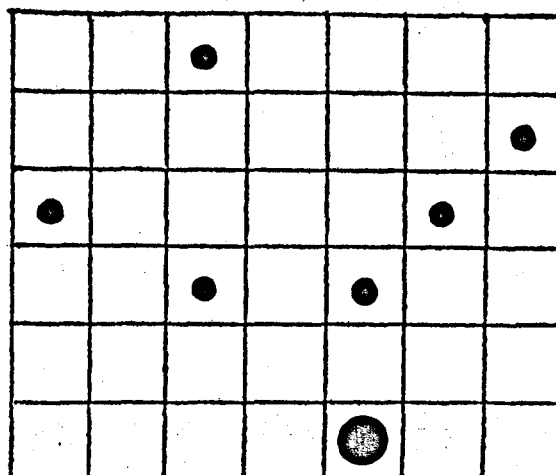
Enchytraeidae

Exp. D-D joins = 0.91 ± 0.26
 Obs. D-D joins = 1
 Conclusion = Random



Above Soil Surface

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



All (excluding Enchytraeidae)

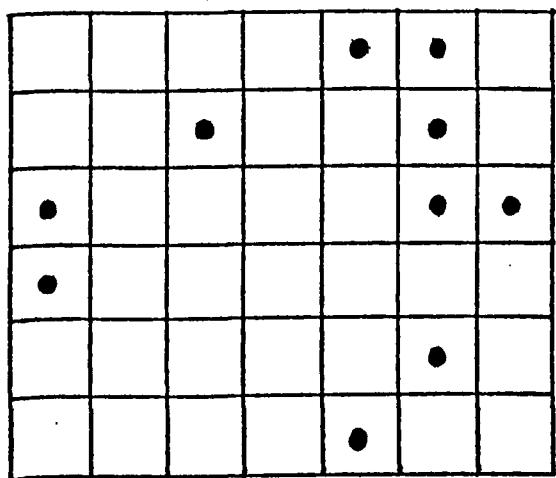
Exp. D-D joins = 3.19 ± 0.47
 Obs. D-D joins = 2
 Conclusion = Overdispersed

Figure A2.14

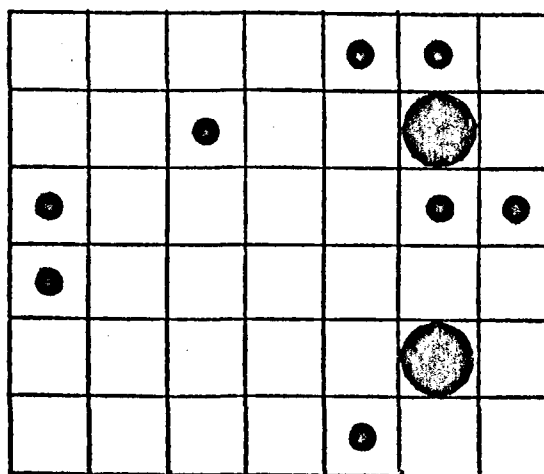
Date: 2-12-79
 Crop: Permanent Pasture
 Field: Market Drayton 2a (SJ 709355)

(a) Earthworm Numbers: Density per Square Metre = 30.8

Test for Dispersion ignoring spatial relationships between cores:
 Chi-square = 44.01 $p < 0.4 > 0.3$
 Conclusion: Random

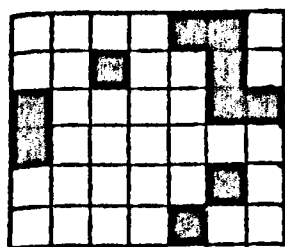


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



Expected dense-dense joins if sparse and dense cores were randomly mingled:

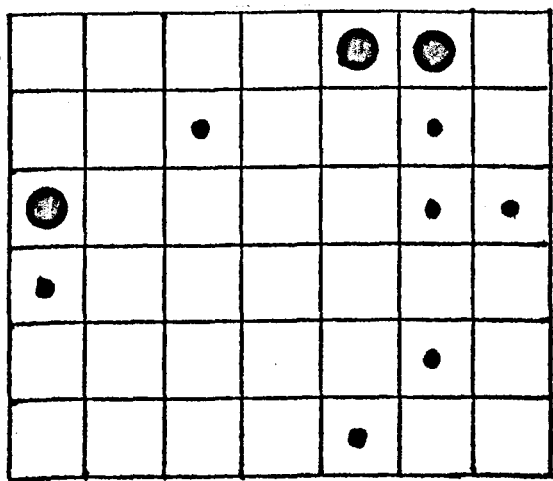
Mean with 95% confidence limits = 6.85 ± 0.66

Observed dense-dense joins = 8

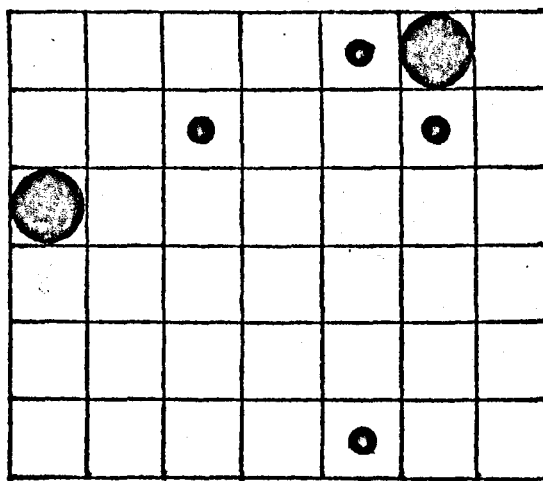
Conclusion = Aggregated

Dense = >0
 Sparse = 0

(b) Earthworm Biomass: Density per Square Metre = 32.7 gm

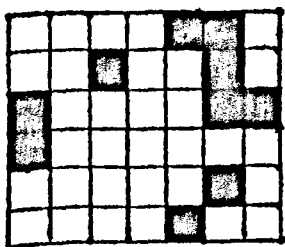


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



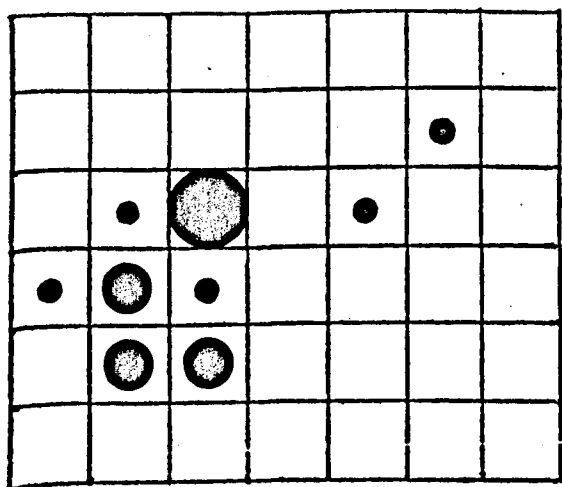
Dense = >0 g
Sparse = 0 g

Expected dense-dense joins = 6.85 ± 0.66

Observed dense-dense joins = 8

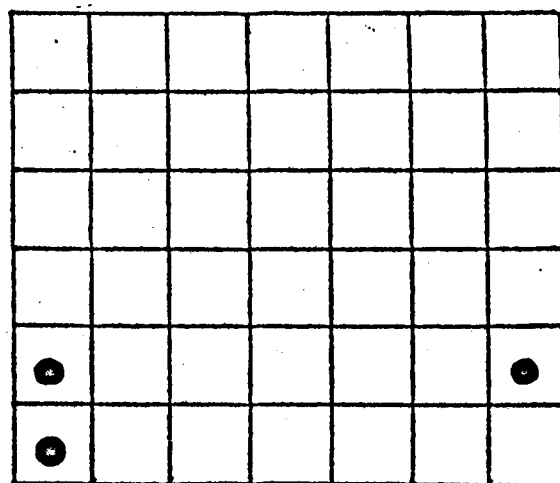
Conclusion = Aggregated

(c) Invertebrates other than Earthworms (Numbers)



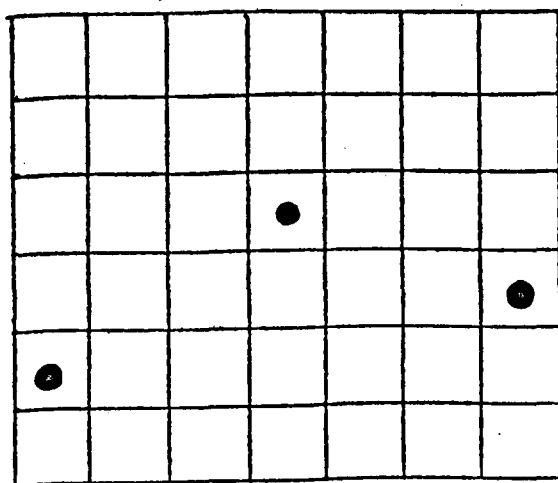
Below Soil Surface

Exp. D-D joins = 5.48 ± 0.60
 Obs. D-D joins = 16
 Conclusion = Aggregated



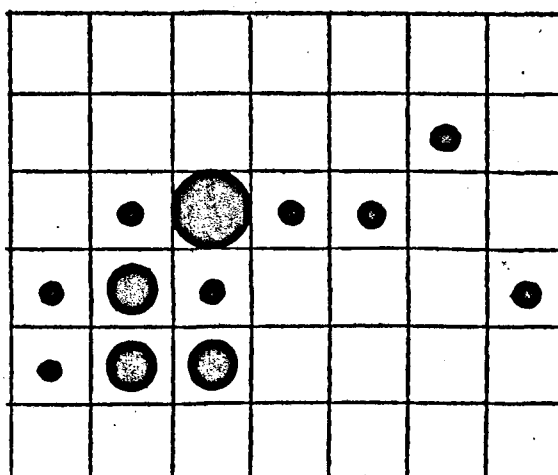
Enchytraeidae

Exp. D-D joins = 0.46 ± 0.19
 Obs. D-D joins = 1
 Conclusion = Aggregated



Above Soil Surface

Exp. D-D joins = 0.46 ± 0.19
 Obs. D-D joins = 0
 Conclusion = Overdispersed



All (excluding Enchytraeidae)

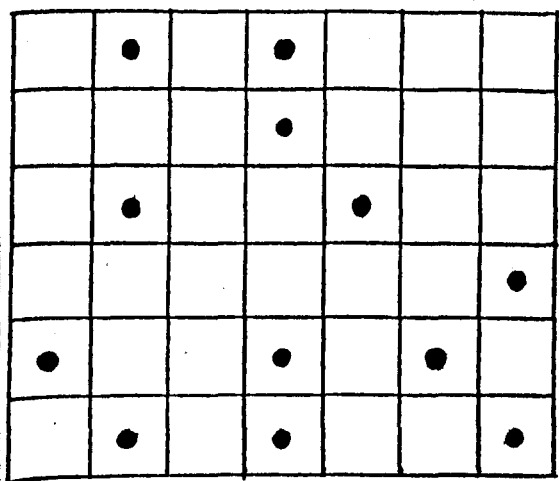
Exp. D-D joins = 10.04 ± 0.78
 Obs. D-D joins = 21
 Conclusion = Aggregated

Figure A2.15

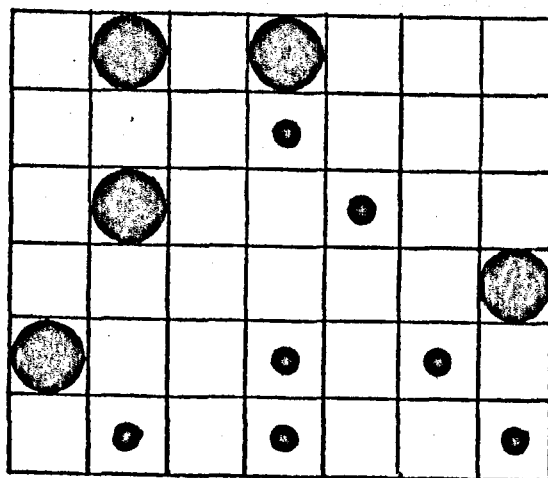
Date: 27-2-80
Crop: Permanent Pasture
Field: Market Drayton 2a (SJ 709355)

(a) Earthworm Numbers: Density per Square Metre = 86.3

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 56.58 $p < 0.05 > 0.025$
Conclusion: Aggregated

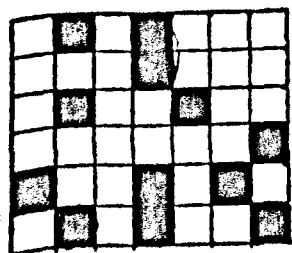


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



Dense = >0
Sparse = 0

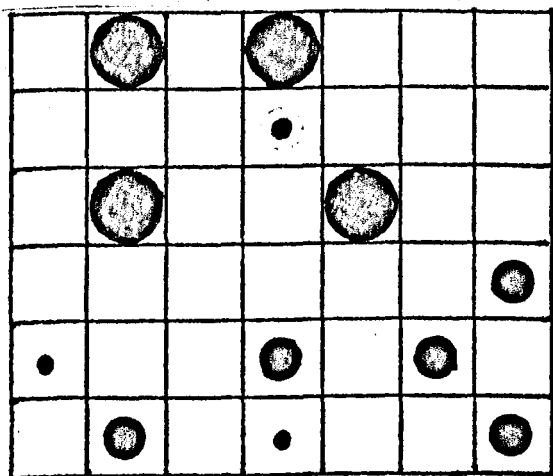
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 10.04 +/- 0.78

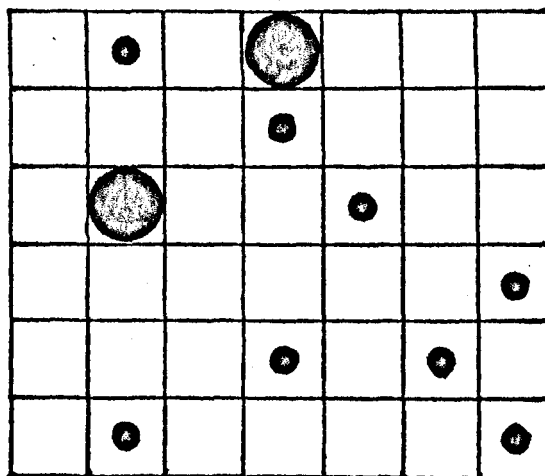
Observed dense-dense joins = 6

Conclusion = Overdispersed

(b) Earthworm Biomass: Density per Square Metre = 91.6 gm

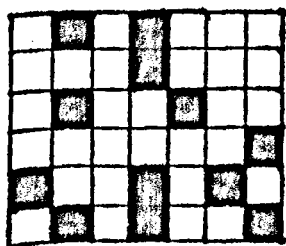


Actual biomass in each core



Standard deviation units

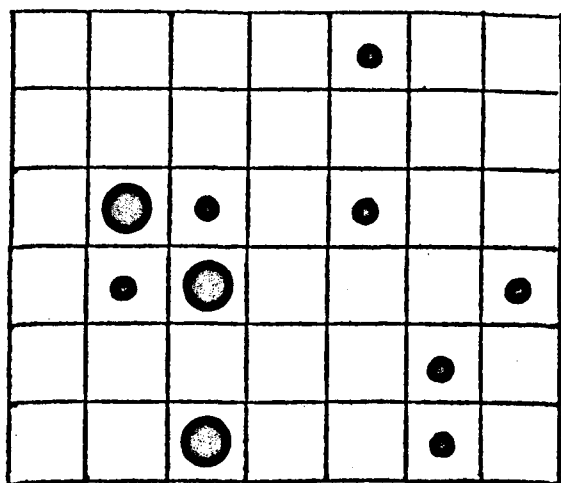
Test for Dispersion using spatial relationships between cores:



Dense = >0 g
Sparse = 0 g

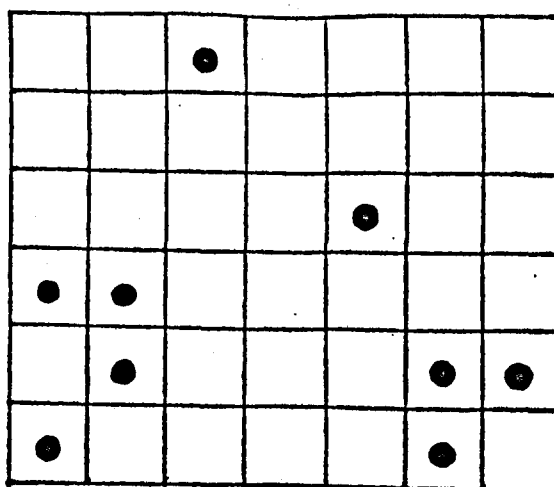
Expected dense-dense joins = 10.04 ± 0.78
Observed dense-dense joins = 6
Conclusion = Overdispersed

(c) Invertebrates other than Earthworms (Numbers)



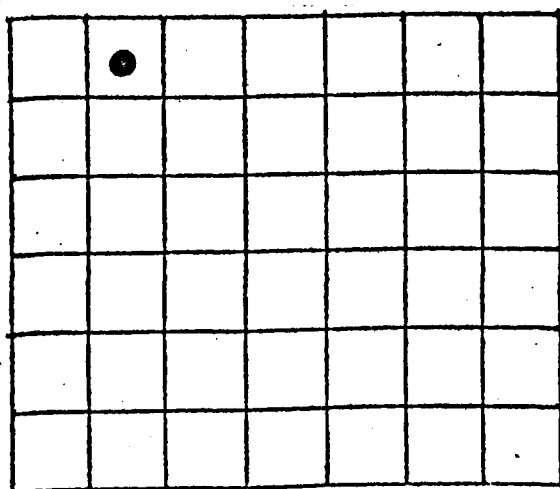
Below Soil Surface

Exp. D-D joins = 6.85 ± 0.66
 Obs. D-D joins = 8
 Conclusion = Aggregated



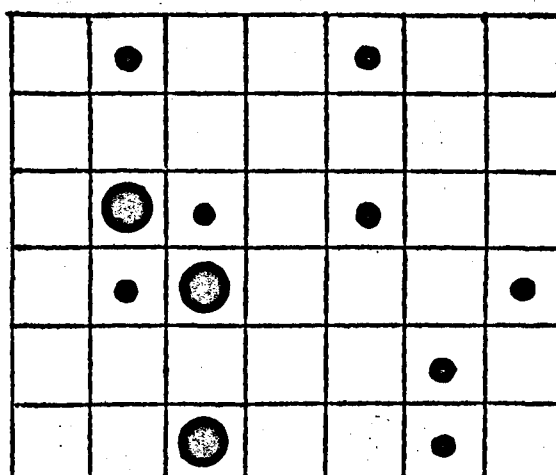
Enchytraeidae

Exp. D-D joins = 5.48 ± 0.60
 Obs. D-D joins = 7
 Conclusion = Aggregated



Above Soil Surface

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



All (excluding Enchytraeidae)

Exp. D-D joins = 8.37 ± 0.72
 Obs. D-D joins = 8
 Conclusion = Random

Figure A2.16

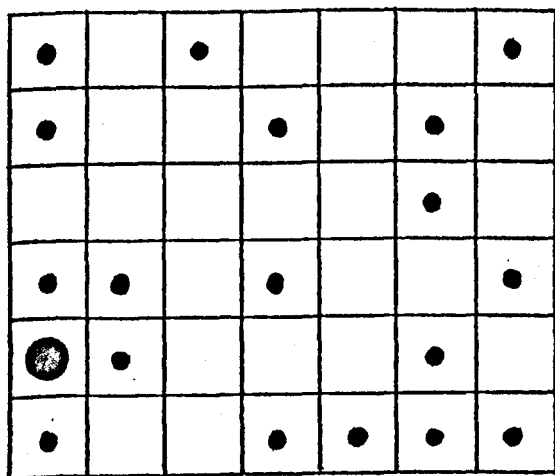
Date: 2-12-79
Crop: Permanent Pasture
Field: Market Drayton 2b (SJ 711355)

(a) Earthworm Numbers: Density per Square Metre = 154.2

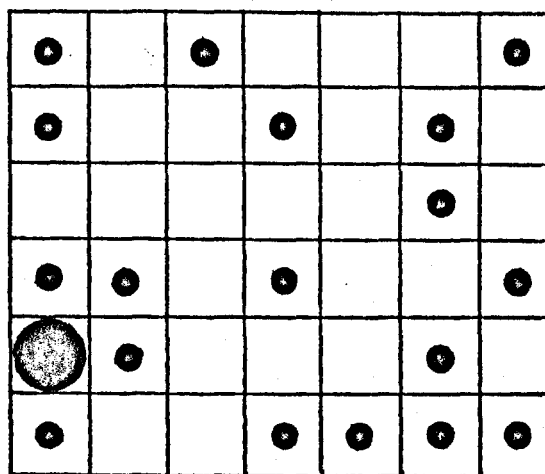
Test for Dispersion ignoring spatial relationships between cores:

Chi-square = 47.27 $p < 0.2 > 0.15$

Conclusion: Random

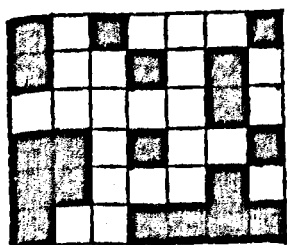


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



Expected dense-dense joins if sparse and dense cores were randomly mingled:

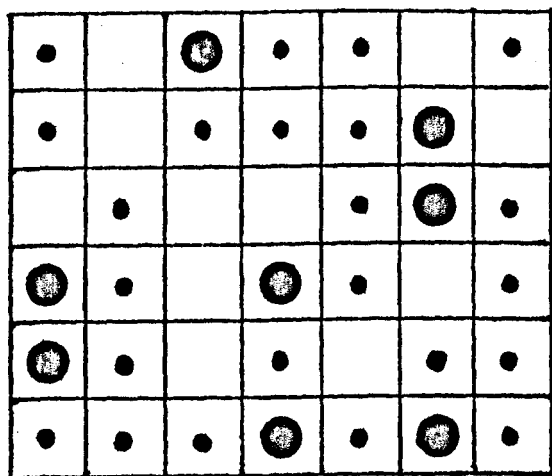
Mean with 95% confidence limits = 26.02 +/- 1.12

Observed dense-dense joins = 20

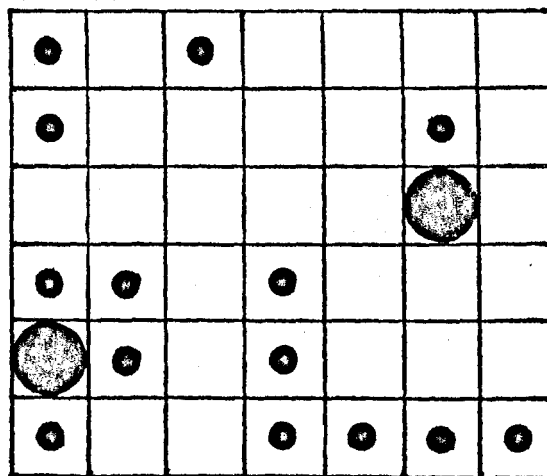
Conclusion = Overdispersed

Dense = >0
Sparse = 0

(b) Earthworm Biomass: Density per Square Metre = 69.7 gm

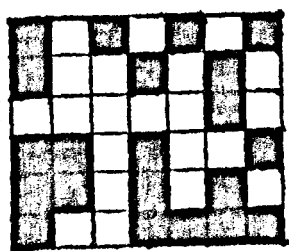


Actual biomass in each core



Standard deviation units

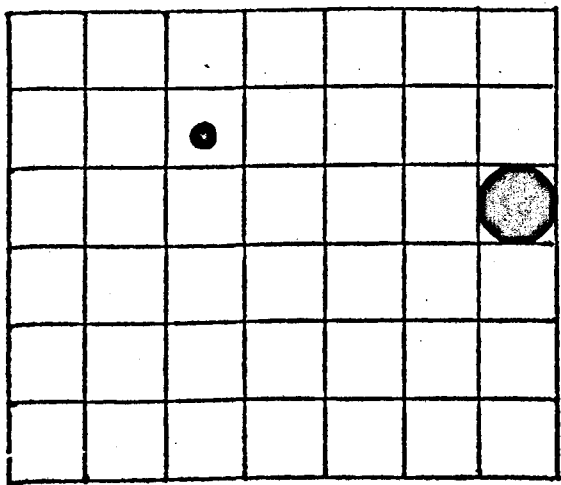
Test for Dispersion using spatial relationships between cores:



Dense = >0.15 g
Sparse = $0-0.15$ g

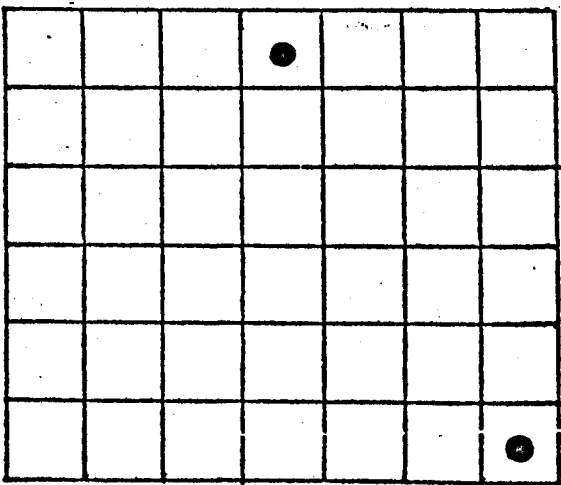
Expected dense-dense joins = 31.95 ± 1.19
Observed dense-dense joins = 25
Conclusion = Overdispersed

(c) Invertebrates other than Earthworms (Numbers)



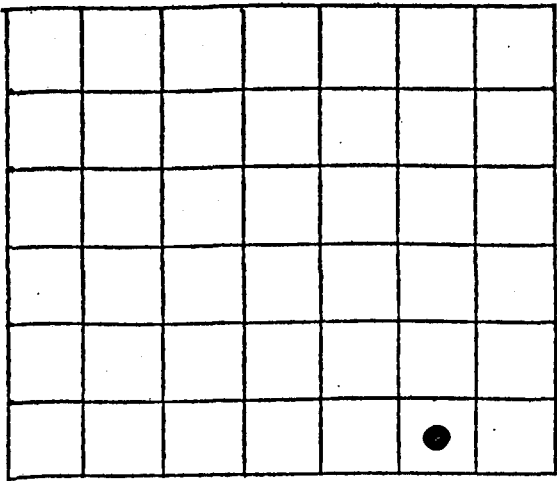
Below Soil Surface

Exp. D-D joins =
Obs. D-D joins =
Conclusion =



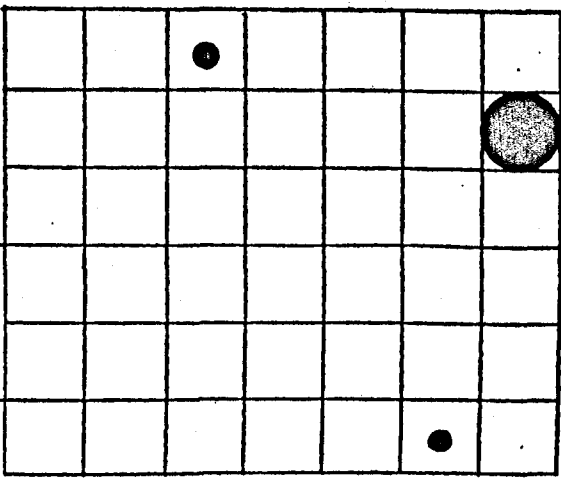
Enchytraeidae

Exp. D-D joins =
Obs. D-D joins =
Conclusion =



Above Soil Surface

Exp. D-D joins =
Obs. D-D joins =
Conclusion =



All (excluding Enchytraeidae)

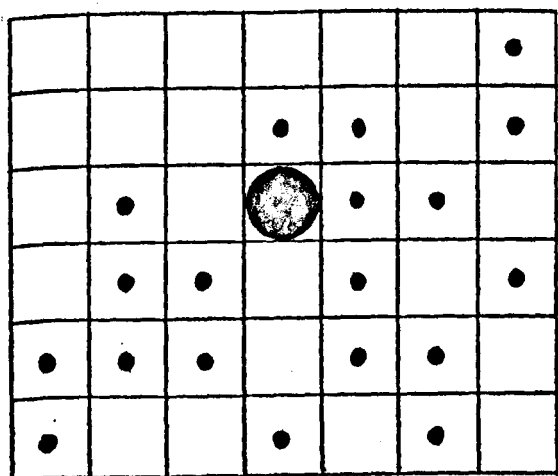
Exp. D-D joins = 0.46 +/- 0.19
Obs. D-D joins = 0
Conclusion = Overdispersed

Figure A2.17

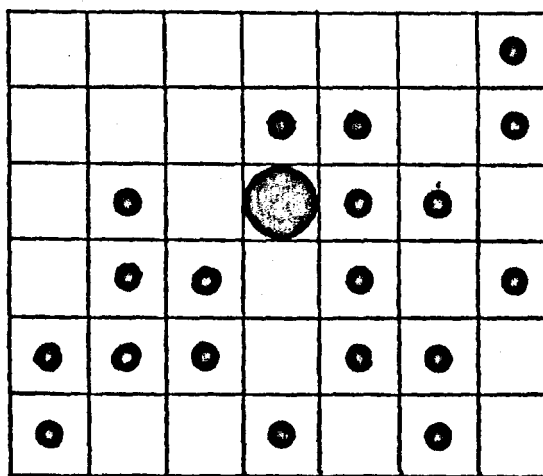
Date: 27-2-80
Crop: Permanent Pasture
Field: Market Drayton 2b (SJ 711355)

(a) Earthworm Numbers: Density per Square Metre = 178.8

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 56.51 $p < 0.05 > 0.025$
Conclusion: Aggregated

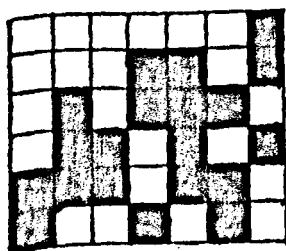


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



Dense = >0
Sparse = 0

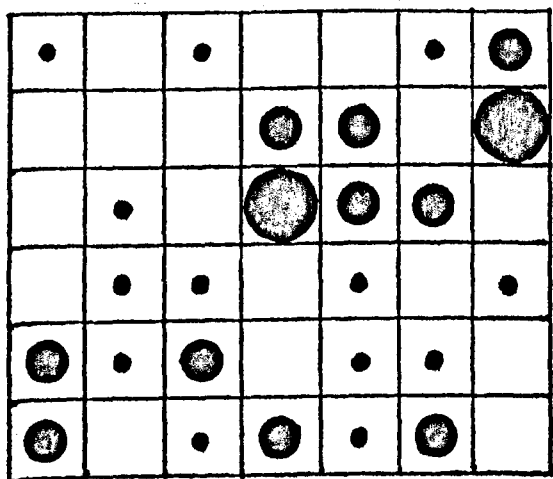
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 28.91 +/- 1.16

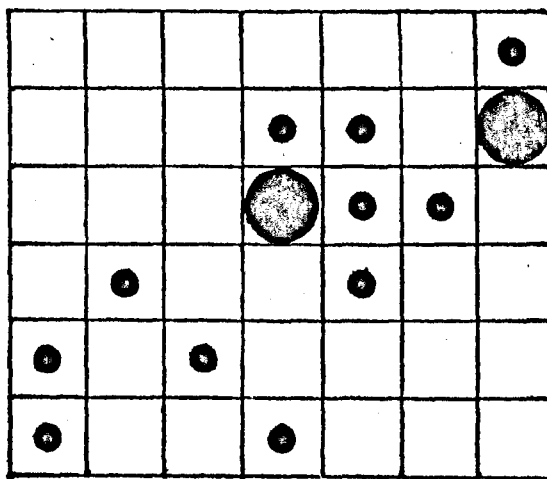
Observed dense-dense joins = 35

Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre = 109.5 gm

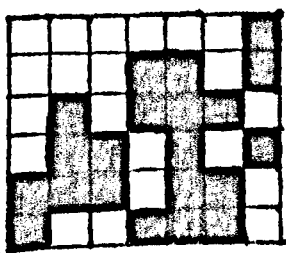


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



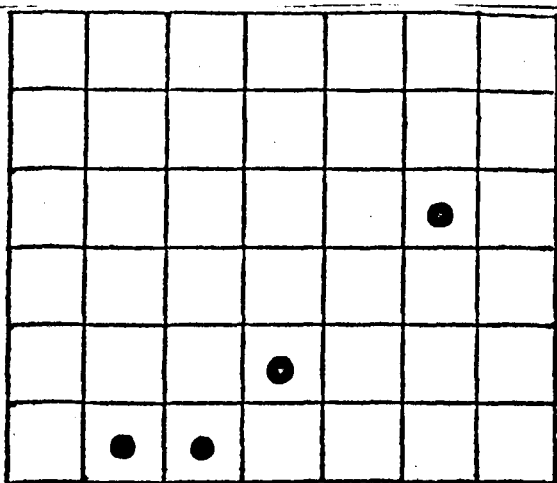
Dense = >0.05 g
Sparse = $0-0.05$ g

Expected dense-dense joins = 31.95 ± 1.19

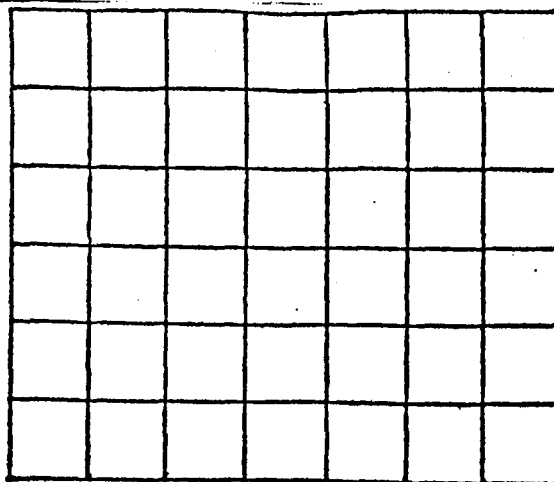
Observed dense-dense joins = 39

Conclusion = Aggregated

(c) Invertebrates other than Earthworms (Numbers)



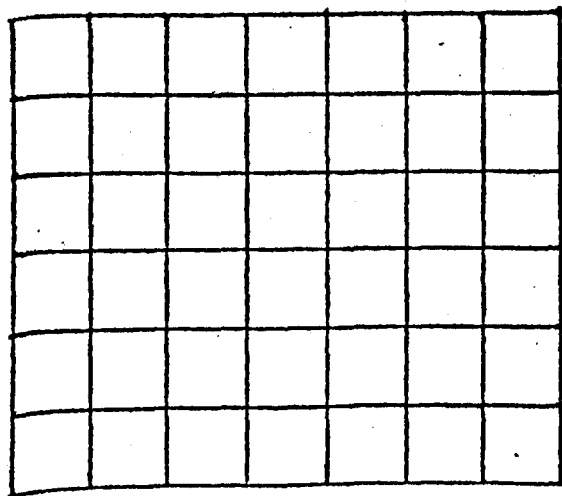
Below Soil Surface



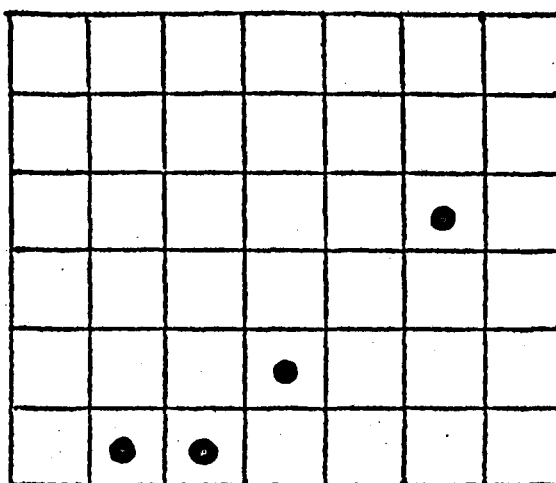
Enchytraeidae

Exp. D-D joins = 0.91 ± 0.26
Obs. D-D joins = 2
Conclusion = Aggregated

Exp. D-D joins =
Obs. D-D joins =
Conclusion =



Above Soil Surface



All (excluding Enchytraeidae)

Exp. D-D joins =
Obs. D-D joins =
Conclusion =

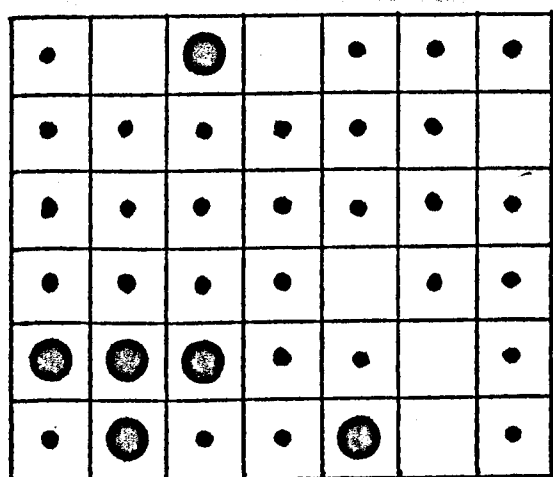
Exp. D-D joins = 0.91 ± 0.26
Obs. D-D joins = 2
Conclusion = Aggregated

Figure A2.18

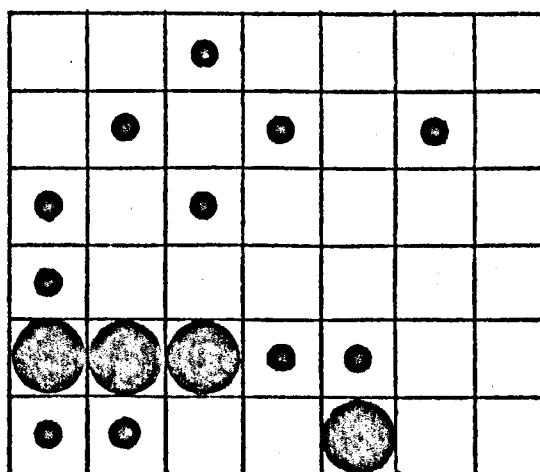
Date: 14-3-80
Crop: Permanent Pasture
Field: 1a (SJ 819452)

(a) Earthworm Numbers: Density per Square Metre = 388.5

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 77.84 $p < 0.0005$
Conclusion: Aggregated

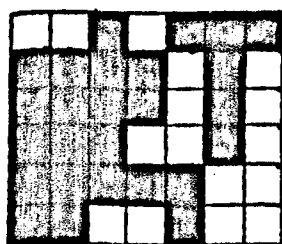


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

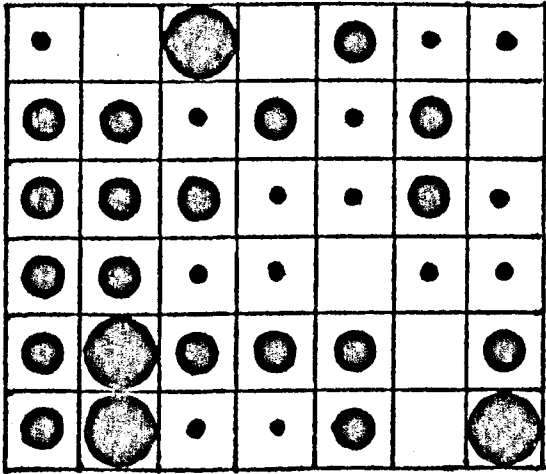


Dense = >1
Sparse = 0-1

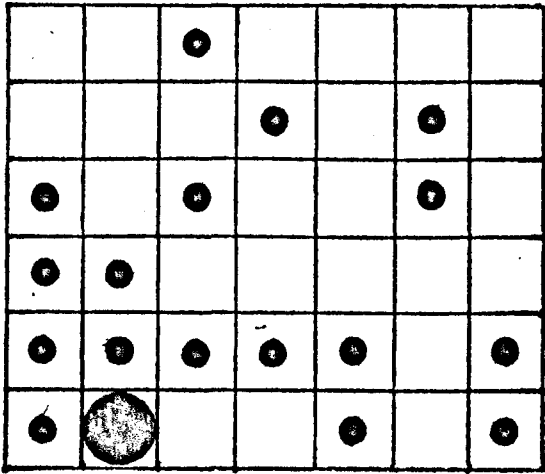
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 49.45 \pm 1.31
Observed dense-dense joins = 58
Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre = 178.2 gm

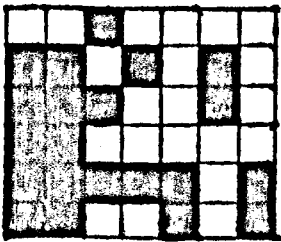


Actual biomass in each core



Standard deviation units

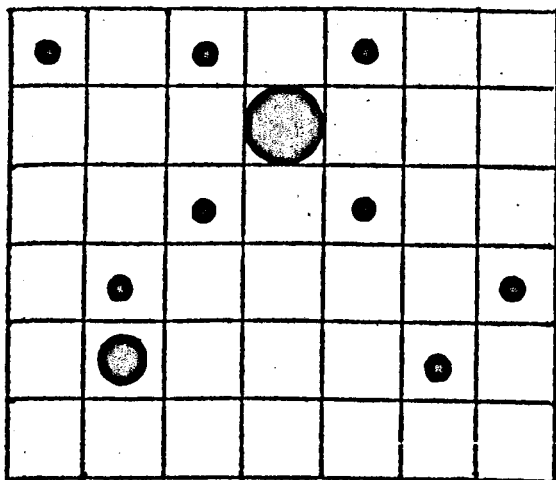
Test for Dispersion using spatial relationships between cores:



Dense = >0.5 g
Sparse = 0-0.5 g

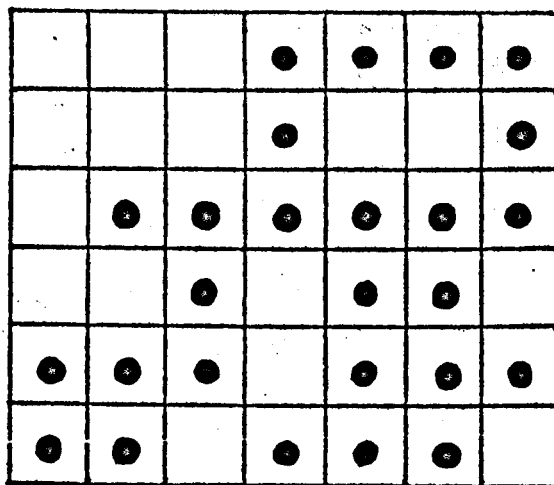
Expected dense-dense joins = 31.95 +/- 1.19
Observed dense-dense joins = 36
Conclusion = Aggregated

(c) Invertebrates other than Earthworms (Numbers)



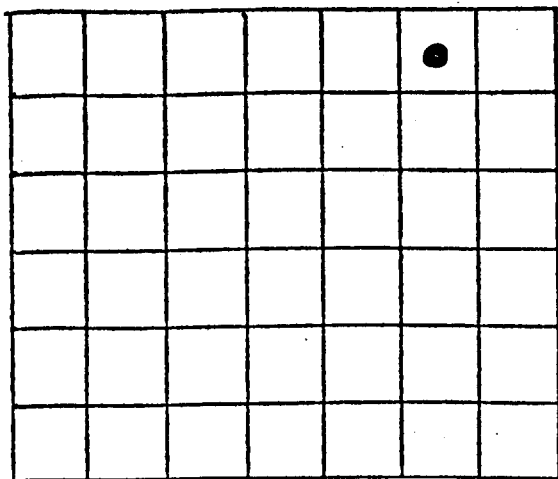
Below Soil Surface

Exp. D-D joins = 6.85 ± 0.66
 Obs. D-D joins = 7
 Conclusion = Random



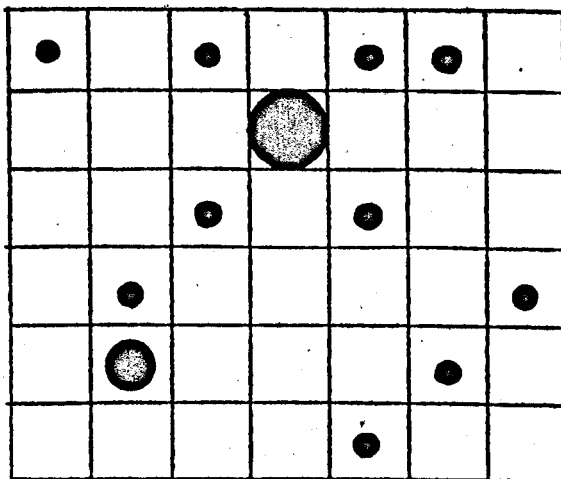
Enchytraeidae

Exp. D-D joins = 49.45 ± 1.31
 Obs. D-D joins = 53
 Conclusion = Aggregated



Above Soil Surface

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



All (excluding Enchytraeidae)

Exp. D-D joins = 10.04 ± 0.78
 Obs. D-D joins = 9
 Conclusion = Overdispersed

Figure A2.19

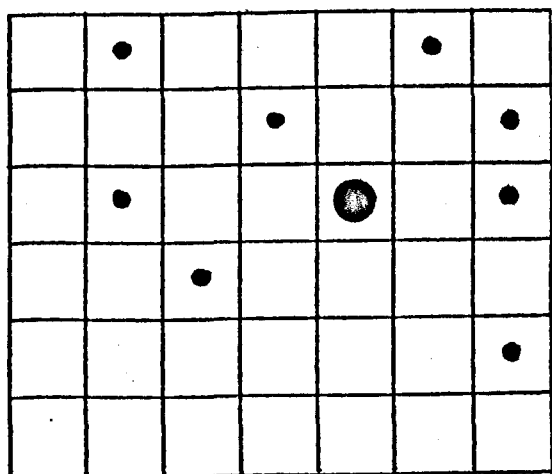
Date: 29-4-79
Crop: Permanent Pasture
Field: 1a (SJ 819452)

(a) Earthworm Numbers: Density per Square Metre = 74.0

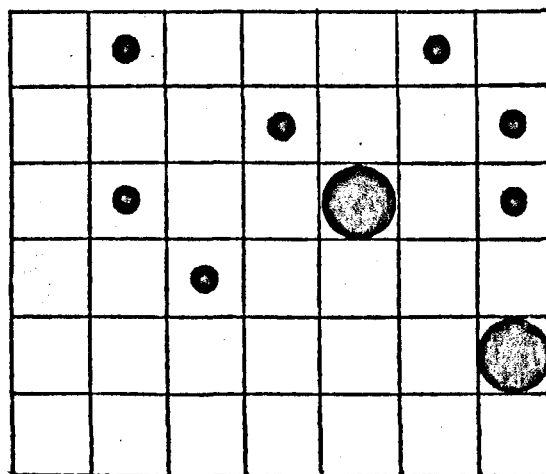
Test for Dispersion ignoring spatial relationships between cores:

Chi-square = 57.92 $p < 0.05 > 0.025$

Conclusion: Aggregated

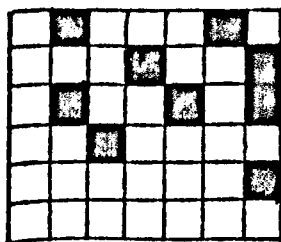


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



Dense = >0
Sparse = 0

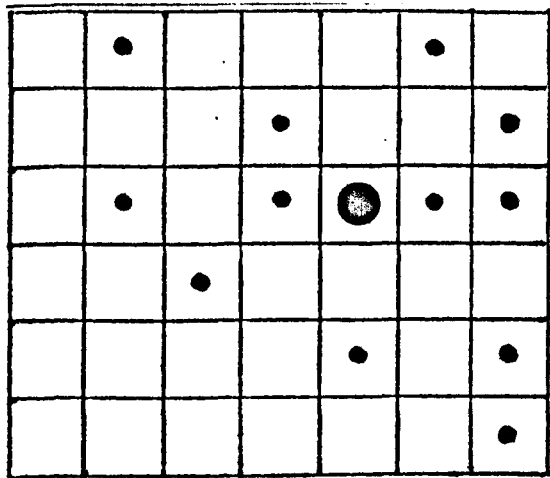
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 5.48 +/- 0.60

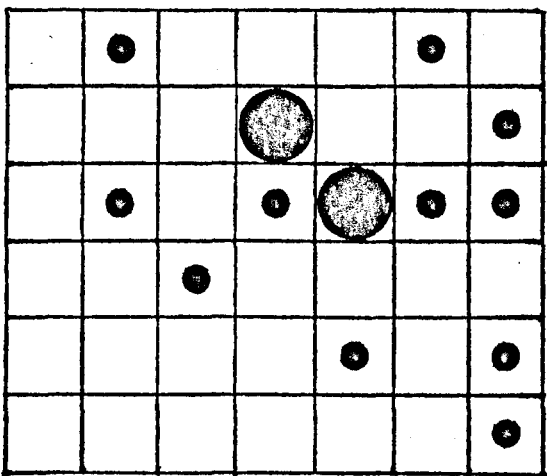
Observed dense-dense joins = 4

Conclusion = Random

(b) Earthworm Biomass: Density per Square Metre = 23.1 gm

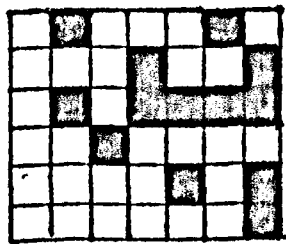


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

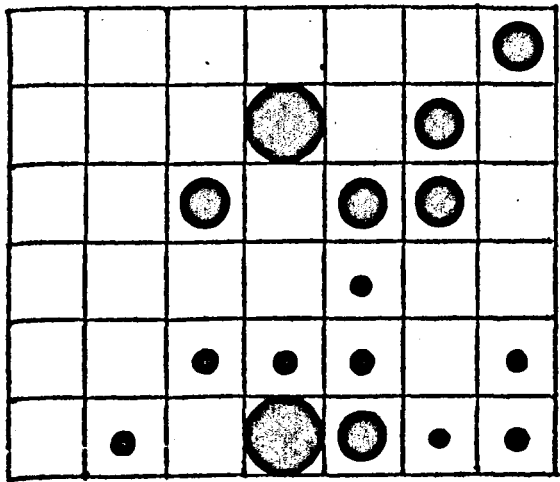


Dense = >0 g

Sparse = 0 g

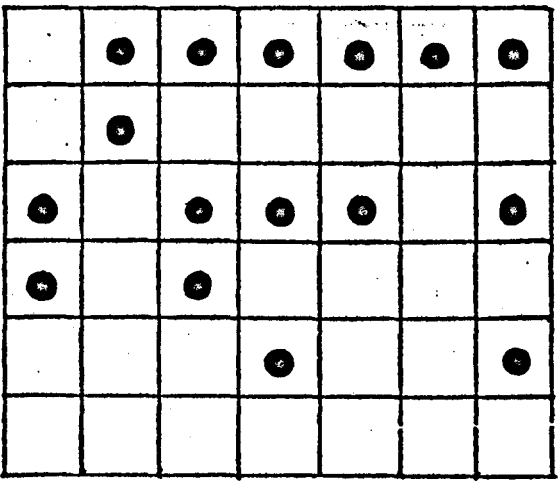
Expected dense-dense joins = 11.87 +/- 0.84
Observed dense-dense joins = 11
Conclusion = Random

(c) Invertebrates other than Earthworms (Numbers)



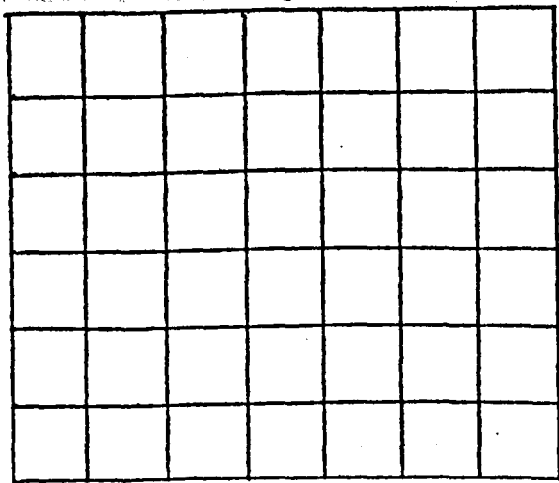
Below Soil Surface

Exp. D-D joins = 18.26 +/- 0.99
Obs. D-D joins = 24
Conclusion = Aggregated



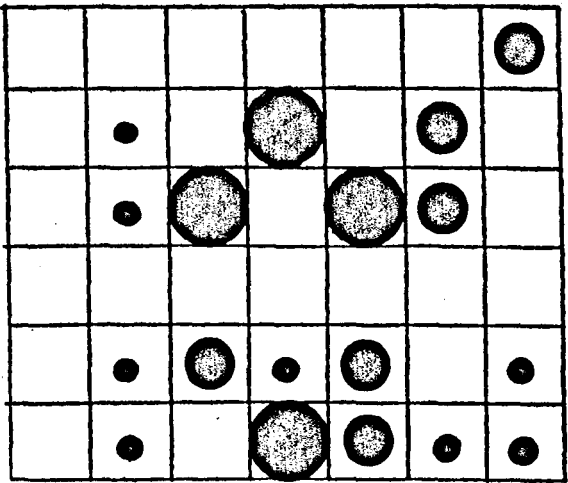
Enchytraeidae

Exp. D-D joins = 18.26 +/- 0.99
Obs. D-D joins = 14
Conclusion = Overdispersed



Above Soil Surface

Exp. D-D joins =
Obs. D-D joins =
Conclusion =



All (excluding Enchytraeidae)

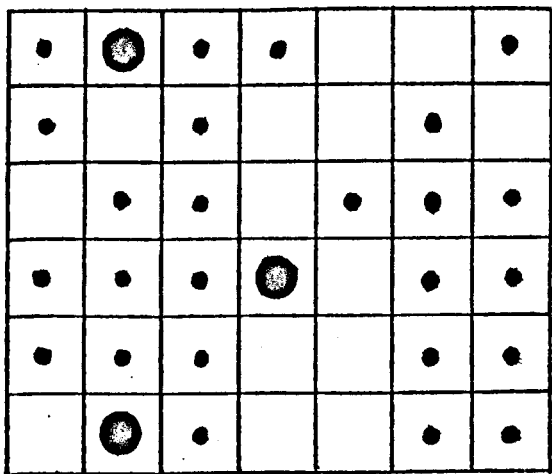
Exp. D-D joins = 28.91 +/- 1.16
Obs. D-D joins = 33
Conclusion = Aggregated

Figure A2.20

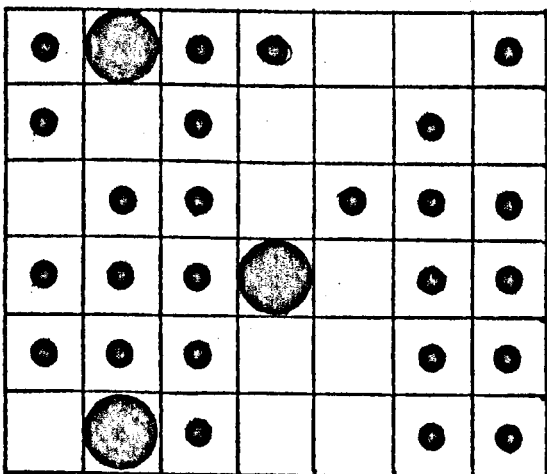
Date: 18-9-79
Crop: Permanent Pasture
Field: 1a (SJ 819452)

(a) Earthworm Numbers: Density per Square Metre = 252.8

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 35.62 $p < 0.7 > 0.6$
Conclusion: Random

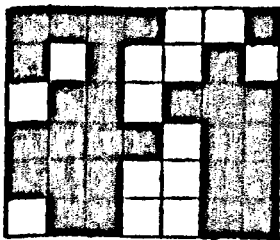


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

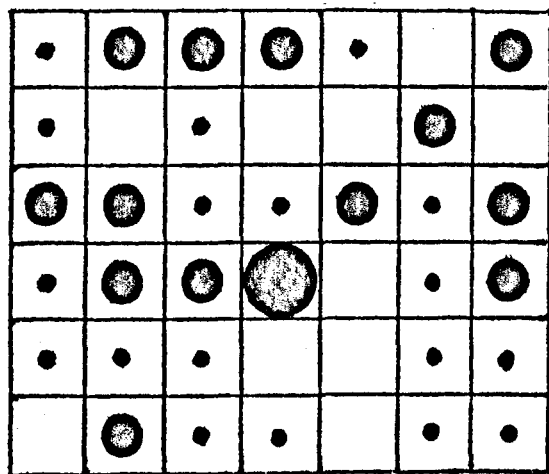


Dense = >0
Sparse = 0

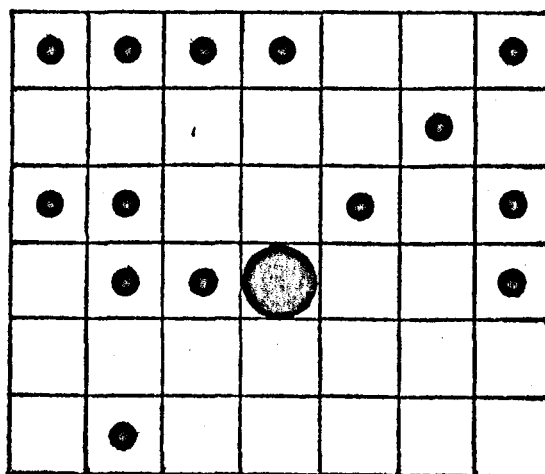
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 57.51 +/- 1.32
Observed dense-dense joins = 61
Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre = 111.3 gm

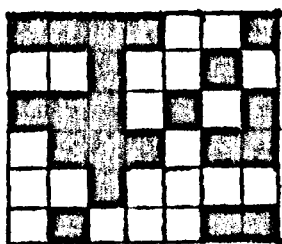


Actual biomass in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



Expected dense-dense joins = 31.95 ± 1.19

Observed dense-dense joins = 30

Conclusion = Random

Dense = >0.25 g

Sparse = $0-0.25$ g

(c) Invertebrates other than Earthworms (Numbers)

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Below Soil Surface

Exp. D-D joins =
Obs. D-D joins =
Conclusion =

Enchytraeidae

Exp. D-D joins =
Obs. D-D joins =
Conclusion =

Above Soil Surface

Exp. D-D joins =
Obs. D-D joins =
Conclusion =

All (excluding Enchytraeidae)

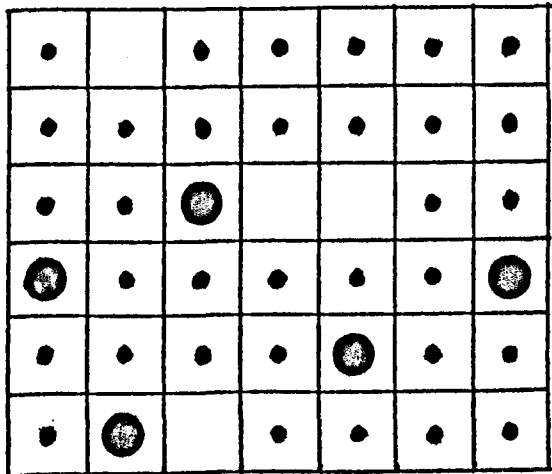
Exp. D-D joins =
Obs. D-D joins =
Conclusion =

Figure A2.21

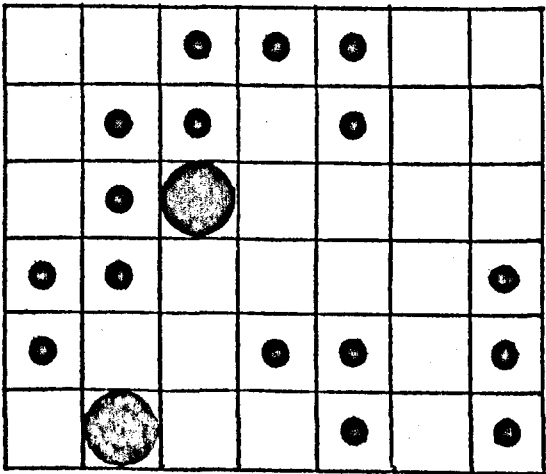
Date: 4-10-79
Crop: Permanent Pasture
Field: 1a (SJ 819452)

(a) Earthworm Numbers: Density per Square Metre = 413.2

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 57.68 $p < 0.05 > 0.025$
Conclusion: Aggregated

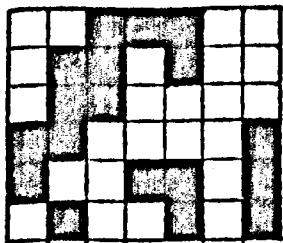


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:

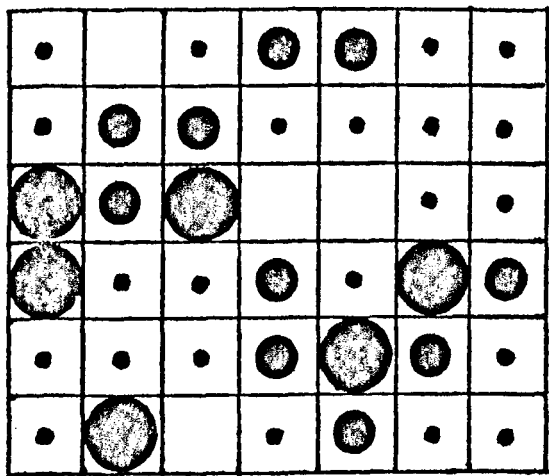


Dense = >2
Sparse = 0-2

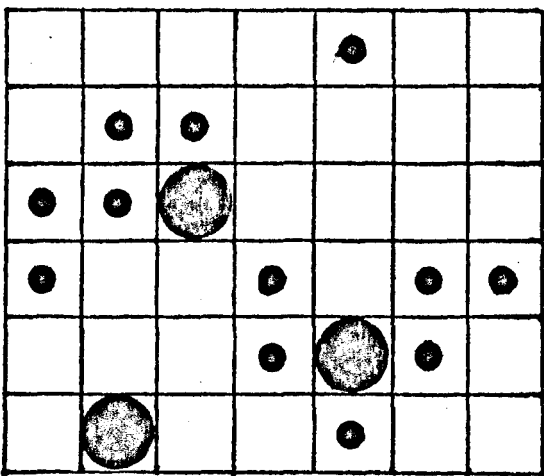
Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 23.28 +/- 1.08
Observed dense-dense joins = 25
Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre = 170.2 gm

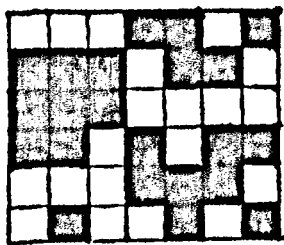


Actual biomass in each core



Standard deviation units

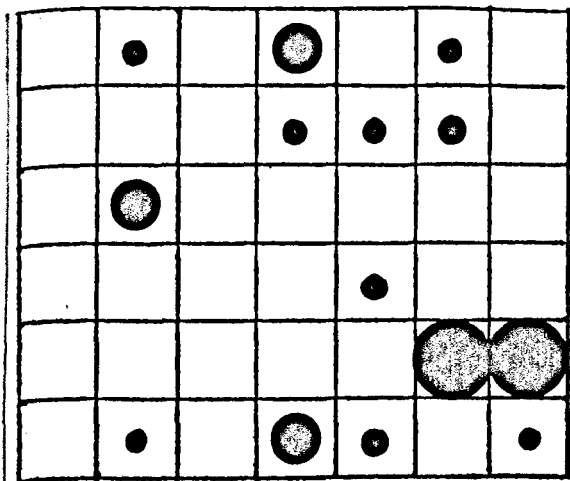
Test for Dispersion using spatial relationships between cores:



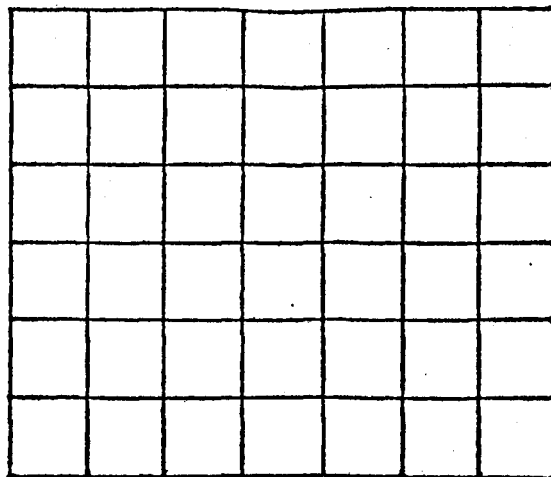
Dense = >0.3 g
Sparse = 0-0.3 g

Expected dense-dense joins = 35.15 +/- 1.22
Observed dense-dense joins = 37
Conclusion = Aggregated

(c) Invertebrates other than Earthworms (Numbers)



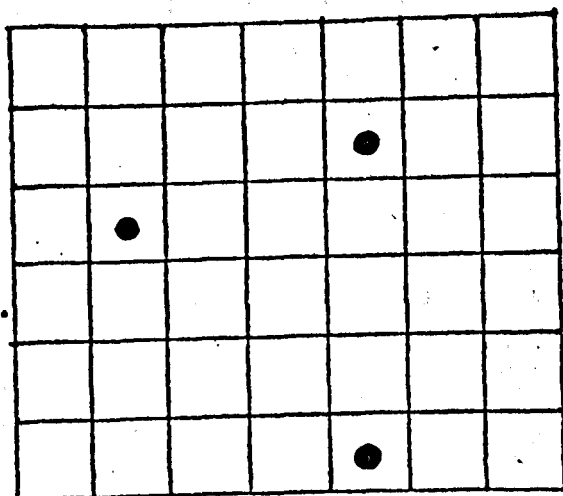
Below Soil Surface



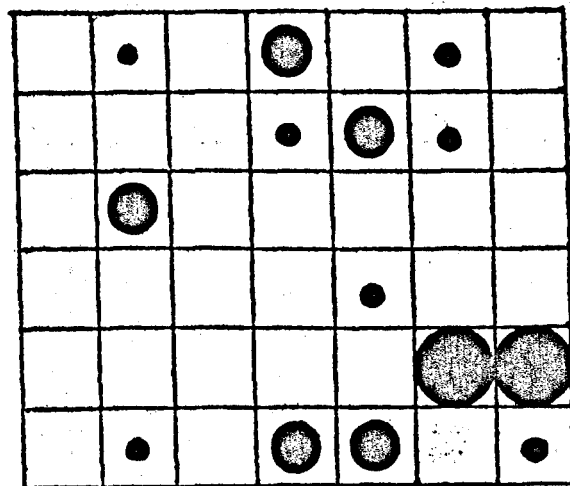
Enchytraeidae

Exp. D-D joins = 13.84 ± 0.89
 Obs. D-D joins = 12
 Conclusion = Random

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



Above Soil Surface



All (excluding Enchytraeidae)

Exp. D-D joins = 0.46 ± 0.19
 Obs. D-D joins = 0
 Conclusion = Overdispersed

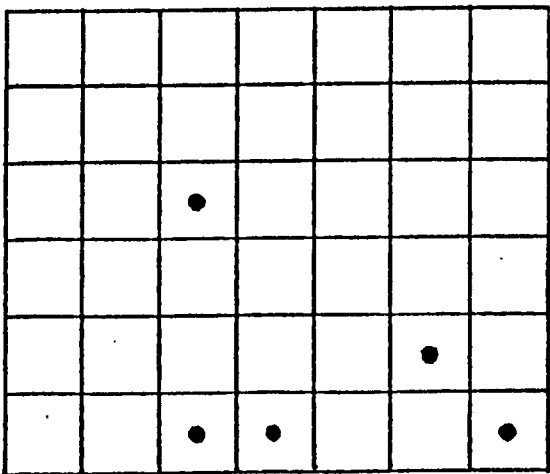
Exp. D-D joins = 13.84 ± 0.89
 Obs. D-D joins = 12
 Conclusion = Random

Figure A2.22

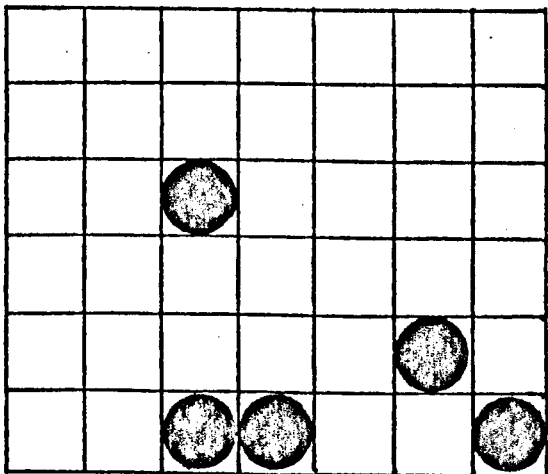
Date: 11-10-79
Crop: Permanent Pasture
Field: Oxon 3 (Port Meadow) (SP 488089)

(a) Earthworm Numbers: Density per Square Metre = 30.8

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 36.86 $p < 0.7 > 0.6$
Conclusion: Random

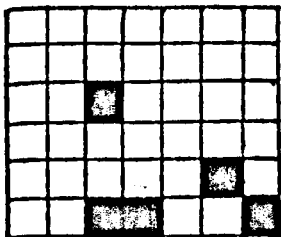


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



Dense = >0
Sparse = 0

Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 1.52 +/- 0.33
Observed dense-dense joins = 2
Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre =

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Actual biomass in each core

Standard deviation units

Test for Dispersion using spatial relationships between cores:

Expected dense-dense joins =

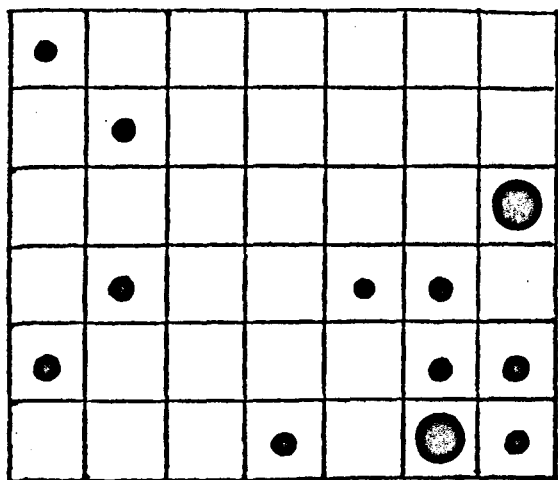
Observed dense-dense joins =

Conclusion =

Dense =

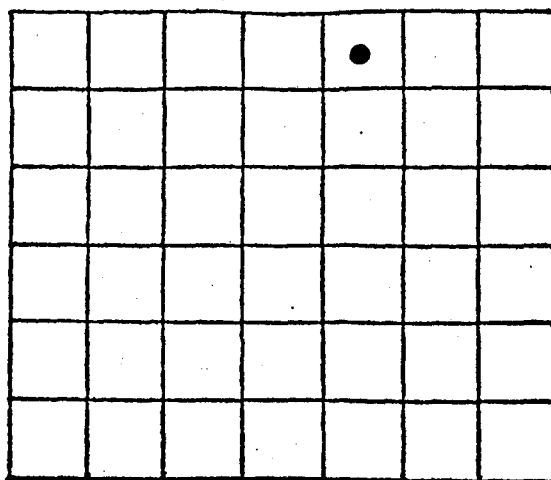
Sparse =

(c) Invertebrates other than Earthworms (Numbers)



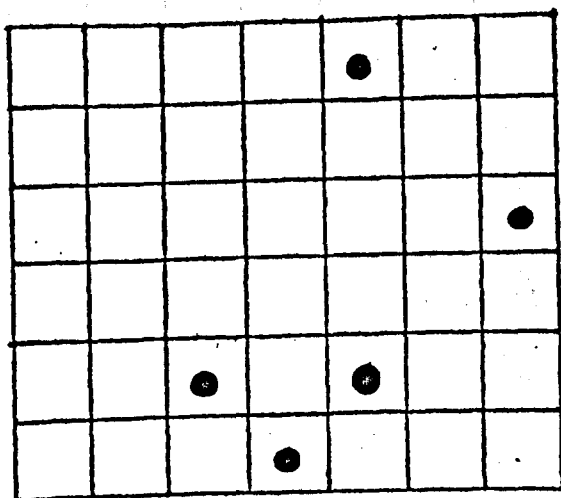
Below Soil Surface

Exp. D-D joins = 10.04 ± 0.78
 Obs. D-D joins = 13
 Conclusion = Aggregated



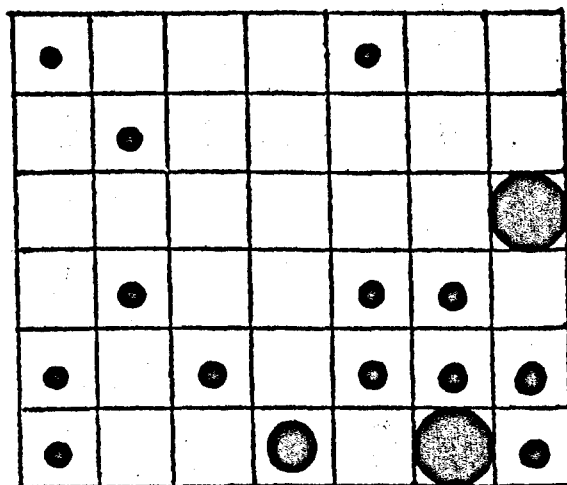
Enchytraeidae

Exp. D-D joins =
 Obs. D-D joins =
 Conclusion =



Above Soil Surface

Exp. D-D joins = 1.52 ± 0.33
 Obs. D-D joins = 2
 Conclusion = Aggregated



All (excluding Enchytraeidae)

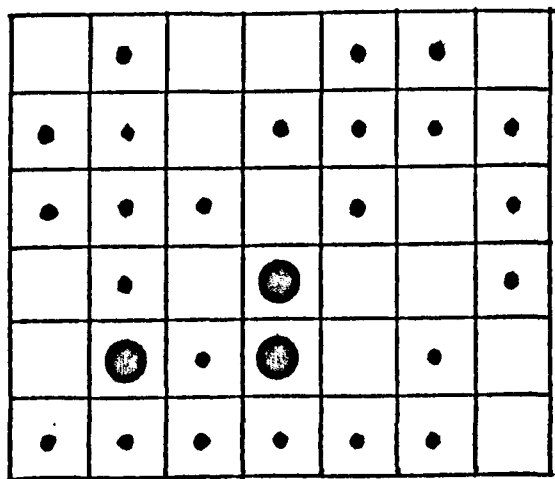
Exp. D-D joins = 18.26 ± 0.99
 Obs. D-D joins = 21
 Conclusion = Aggregated

Figure A2.23

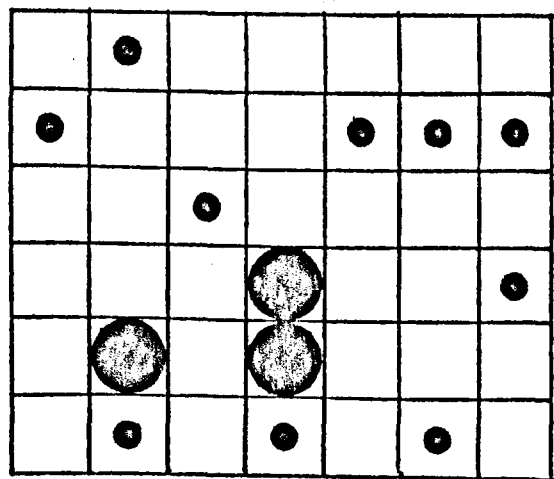
Date: 12-10-79
Crop: Permanent Pasture
Field: Oxon 2 (Farmoor) (SP 439068)

(a) Earthworm Numbers: Density per Square Metre = 92.5

Test for Dispersion ignoring spatial relationships between cores:
Chi-square = 67.92 $p < 0.005 > 0.001$
Conclusion: Aggregated

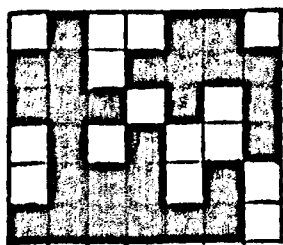


Actual numbers in each core



Standard deviation units

Test for Dispersion using spatial relationships between cores:



Dense = >0
Sparse = 0

Expected dense-dense joins if sparse and dense cores were randomly mingled:

Mean with 95% confidence limits = 53.40 +/- 1.32
Observed dense-dense joins = 55
Conclusion = Aggregated

(b) Earthworm Biomass: Density per Square Metre =

* DATA MISSING *
*

Actual biomass in each core

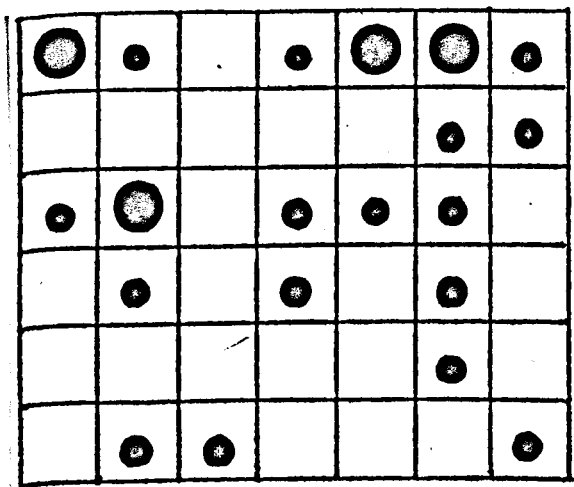
Standard deviation units

Test for Dispersion using spatial relationships between cores:

Expected dense-dense joins =
Observed dense-dense joins =
Conclusion =

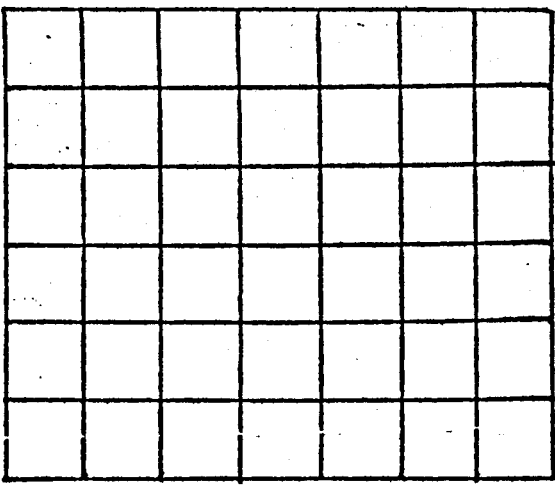
Dense =
Sparse =

(c) Invertebrates other than Earthworms (Numbers)



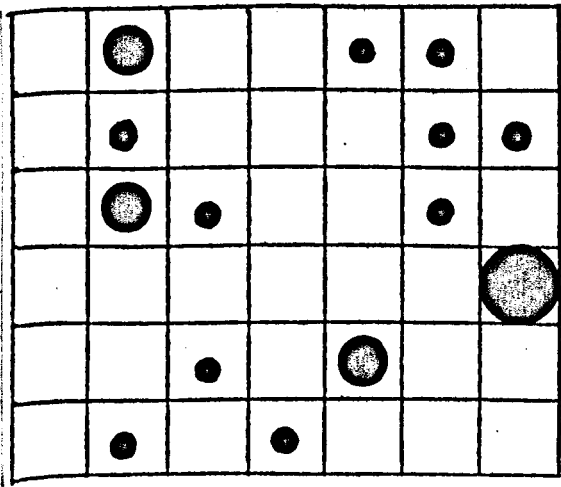
Below Soil Surface

Exp. D-D joins = 28.91 ± 1.16
Obs. D-D joins = 25
Conclusion = Overdispersed



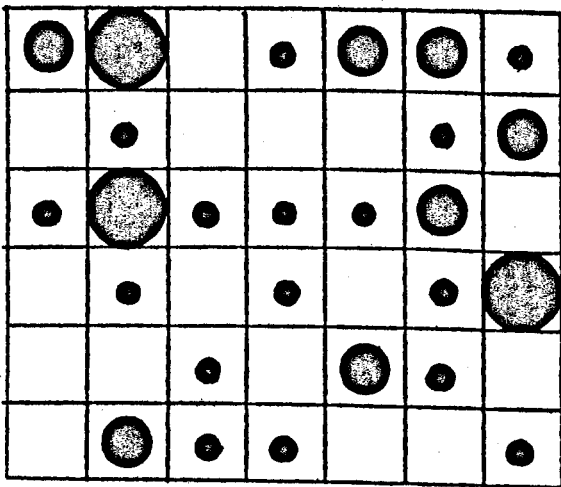
Enchytraeidae

Exp. D-D joins =
Obs. D-D joins =
Conclusion =



Above Soil Surface

Exp. D-D joins = 13.84 ± 0.89
Obs. D-D joins = 15
Conclusion = Aggregated



All (excluding Enchytraeidae)

Exp. D-D joins = 49.45 ± 1.31
Obs. D-D joins = 44
Conclusion = Overdispersed

Appendix Three

Analysis of variance summary tables

(a) Earthworm Numbers by Grass Field

Source	Sum of Squares	df	Variance Estimate	F	p
Field	175.93	13	13.53	9.766	***
Error	795.36	574	1.39		
Total	971.28	587			

Pairwise comparisons between fields (Scheffe test); homogeneous subsets, no pair of which differ at $p < 0.10$; fields may be identified by reference to figures 1.3.1 and 1.3.5:

Set 1: 56 57 38 22 30 7 33b 35a 1b 20
Set 2: 38 22 30 7 33b 35a 1b 20 1a 35b
Set 3: 22 30 7 33b 35a 1b 20 1a 35b 6
Set 4: 30 7 33b 35a 1b 20 1a 35b 6 33a

(b) Earthworm Biomass by Grass Field

Source	Sum of Squares	df	Variance Estimate	F	p
Field	23.95	13	1.80	7.309	***
Error	141.34	574	0.25		
Total	164.73	587			

Pairwise comparisons between fields (Scheffe test); homogeneous subsets, no pair of which differ at $p < 0.10$; fields may be identified by reference to figures 1.3.1 and 1.3.5:

Set 1: 56 57 38 22 33b 35b 7
Set 2: 38 22 33b 35b 7 35a 30 20
Set 3: 22 33b 35b 7 35a 30 20 1b 33a
Set 4: 35b 7 35a 30 20 1b 33a 1a
Set 5: 1b 33a 1a 6

(c) Earthworm Numbers by Crop

Source	Sum of Squares	df	Variance Estimate	F	p
Between	32.35	2	16.18	10.078	***
Linear	26.64	1	26.64	16.524	***
Non-Linear	5.71	1	5.71	3.561	n.s.
Error	938.93	585	1.60		
Total	971.28	587			

Pairwise comparisons between fields (Scheffe test); homogeneous subsets, no pair of which differ at $p < 0.10$; fields may be identified by reference to figures 1.3.1 and 1.3.5:

Set 1: Non-agricultural Grass, Ley
Set 2: Permanent Pasture

(d) Earthworm Biomass by Crop

Source	Sum of Squares	df	Variance Estimate	F	p
Between	4.21	2	2.10	7.670	***
Linear	2.91	1	2.91	10.534	***
Non-Linear	1.30	1	1.30	4.738	*
Error	160.52	585	0.27		
Total	164.73	587			

Pairwise comparisons between fields (Scheffe test); homogeneous subsets, no pair of which differ at $p < 0.10$; fields may be identified by reference to figures 1.3.1 and 1.3.5:

Set 1: Non-agricultural Grass, Ley
Set 2: Permanent Pasture

(e) Field by Date of Sampling -
earthworm numbers

Source	Sum of Squares	df	Variance Estimate	F	p
Field	177.13	6	29.52	24.31	***
Date	0.57	1	0.57	0.47	ns
F x D	49.81	6	8.30	6.83	***
Error	706.87	582	1.21		
Total	934.38	595			

(f) Field by Date of Sampling -
earthworm biomass

Source	Sum of Squares	df	Variance Estimate	F	p
Field	26.72	6	4.45	14.54	***
Date	0.02	1	0.02	0.07	ns
F x D	6.55	6	1.09	3.56	**
Error	178.31	582	0.31		
Total	211.60	595			

(g) Two Areas of Field 6 by Date of Sampling -
earthworm numbers

Source	Sum of Squares	df	Variance Estimate	F	p
Field	58.34	1	58.34	36.96	***
Date	2.15	1	2.15	1.36	ns
F x D	25.15	1	25.15	15.93	***
Error	258.88	164	1.58		
Total	344.52	167			

(h) Two Areas of Field 6 by Date of Sampling -
earthworm biomass

Source	Sum of Squares	df	Variance Estimate	F	p
Field	13.26	1	13.26	36.90	***
Date	0.05	1	0.05	0.14	ns
F x D	1.36	1	1.36	3.78	.056
Error	58.94	164	0.36		
Total	73.61	167			

(i) Two Areas of Field 1 by Date of Sampling -
earthworm numbers

Source	Sum of Squares	df	Variance Estimate	F	p
Field	28.59	1	28.59	20.89	***
Date	1.02	1	1.02	0.75	ns
F x D	10.86	1	10.86	7.94	**
Error	235.37	172	1.37		
Total	275.84	175			

(j) Two Areas of Field 1 by Date of Sampling -
earthworm biomass

Source	Sum of Squares	df	Variance Estimate	F	p
Field	2.60	1	2.60	6.44	*
Date	0.16	1	0.16	0.40	ns
F x D	0.77	1	0.77	1.92	.168
Error	69.36	172	0.40		
Total	72.89	175			

(k) Vigilance of four Corvid species at different flock sizes

Source	Sum of Squares	df	Variance Estimate	F	p
Main	24,023.0	4	6005.8	67.28	***
Error	12,407.6	139	89.3		
Total	36,430.6	143			

Summary of significant differences in prey intake rates between different crop types (for explanation of statistics, see appendix 7):

(a) carrion crow; nag, tlu, tlg and pp compared.

Microhab. or Feeding Action	Prey	F	p	Pairwise Differences (Scheffe p < 0.10)
S. Pick	Med.EW	3.78	*	nag: rest
S.Probe	Med.EW	4.41	**	nag: rest
Jab	Med.Inv.	3.40	*	tlu: rest
Dig	Med.Inv.	3.32	*	tlu: rest
Below Surface	All EW	2.82	*	tlu: rest

Summary of significant differences in prey intake rates between different crop types:

(b) magpie; nag, tlu, and pp compared.

Microhab. or Feeding Action	Prey	F	p	Pairwise Differences (Scheffe p < 0.10)
S. Pick	Sm. Inv.	5.44	**	pp,nag:nag,tlu
S-C Turn	Sm. Inv.	5.93	**	pp,nag:nag,tlu
S-C Turn	Med.Inv.	7.77	***	pp,nag:nag,tlu

Summary of significant differences in prey intake rates when other species were absent or present:

		Effect:		
		C = Carrion Crow		
		J = Jackdaw		
		M = Magpie		
		R = Rook		
Microhab. or Feeding Action	Prey		F	p

ROOK Intake Rate:				
S. Pick	Sm. Inv.	J	4.43	*
D. Probe	Sm. Inv.	C	5.52	*
D. Probe	Sm. Inv.	J	3.94	.052
D. Probe	Sm. EW	C x M	4.80	*
D. Probe	Lge. EW	C	4.26	*
Dig	Med. Inv.	M	5.33	*
Dig	Med. Inv.	C x M	8.36	**
Dig	Med. Inv.	J x M	17.24	***
Dig	Sm. EW	C x M	5.86	*
Dig	Sm. EW	J x M	5.69	*
Jab	Med. EW	C x J	4.36	*
			t	p

S. Pick	Med. Inv.	Any	2.09	*
D. Probe	Sm. Inv.	Any	2.92	**
Dig	Med. Inv.	Any	2.58	*
Jab	Sm. Inv.	Any	2.43	*
=====				

Appendix Five

Rook breeding biology and earthworm abundance; rook and carrion crow mortality.

Figure 1: From Hurton & Westwood (1977), based on various sources. Solid area at top of figure indicates the annual light cycle; solid line change in rook testis diameter; histogram indicates number of clutches laid in each month - dark bars Oxford, light bars Cambridgeshire; diagonal bar represents primary moult score; lower part of figure represents earthworm biomass (\pm s.e.).

Rooks time their breeding such that young are in the nest when earthworm availability is at a peak. Rooks moult when earthworm biomass is lowest.

Table 1: From Hurton & Westwood (1977): rooks breeding outside the time of maximum earthworm availability produced fewer fledglings.

Figure 2: From Hurton & Westwood (1974): significant relationship between the maximum number of rooks present in a Cambridgeshire study area during the breeding season and the minimum biomass of earthworms during the previous summer. Population size in the breeding season was related to the minimum earthworm availability in the previous summer, the period of lowest earthworm availability (fig.1) in the annual cycle. Population size was not related to earthworm availability during the current or previous breeding season, nor to the density of stubble grain available during the previous winter.

Figure 3: From Holyoak (1971): rook mortality, outside of the breeding season, peaks during the summer months, the period of moult (fig.1) and of lowest earthworm availability (fig.1).

FIGURE ONE

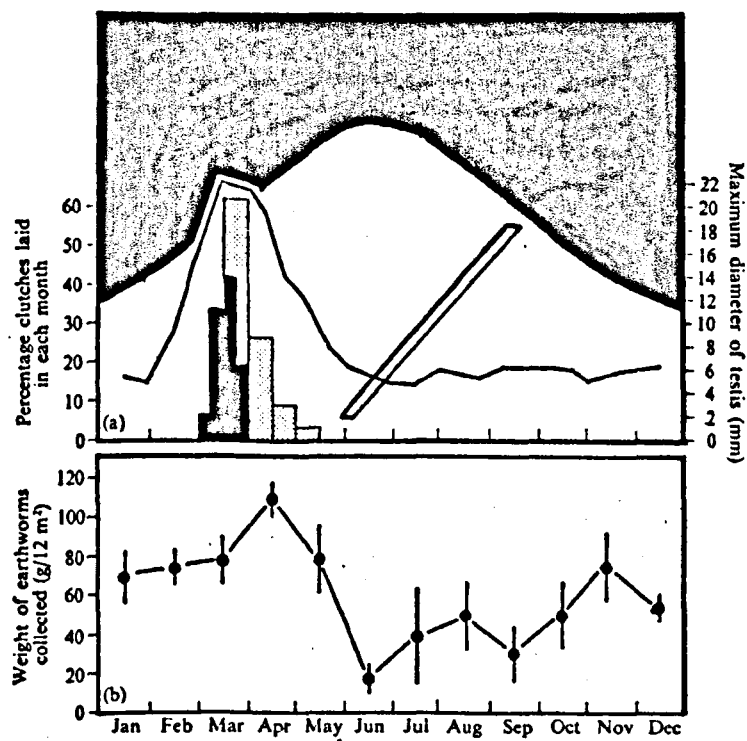


TABLE ONE

Breeding success and productivity of Rook in relation to clutch size and to season

	Number clutches laid (no. eggs)	Percentage of eggs laid which hatched	Percentage of eggs hatched which gave fledged young	Percentage of young fledged from eggs laid	Number chicks fledged per brood
<i>Total for season</i>					
March	138 (505)	66	84	56	2.0
1-15 April	58 (197)	73	85	62	2.1
16-30 April	20 (55)	51	93	47	1.3
May	7 (19)	(58)	(27)	(16)	0.4
<i>Clutch size in March</i>					
1	4 (4)	(25)	(100)	(25)	(0.3)
2	17 (34)	68	96	65	1.3
3	37 (111)	73	85	62	1.9
4	50 (200)	72	84	60	2.4
5-7	30 (156)	56	79	44	2.3

FIGURE TWO

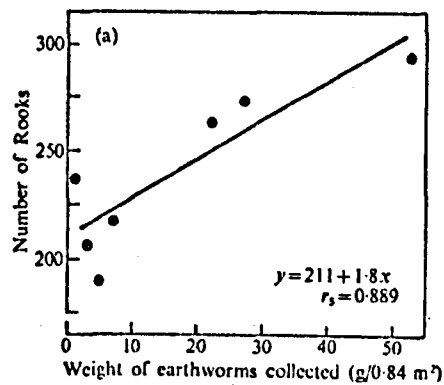
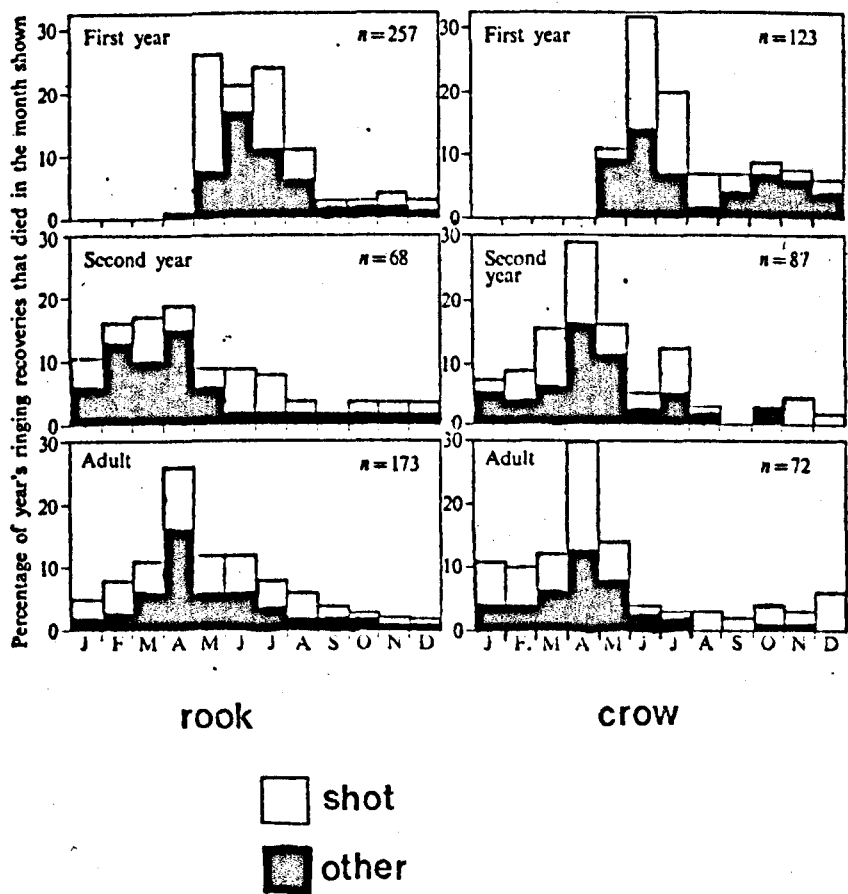


FIGURE THREE



Appendix Six

Morphological characteristics of four corvid species

(Actual measurements may be found in table 1.2.1)

(a) Ratios between species for various measures (the larger species is divided by the smaller in each case).

(b) Ratios between different measures within each species (the measure across the top has been divided by the measure down the side in each case).

(a) Ratios between species

WEIGHT	Average	Ratio with species:			
	with 3				
	Other				
Species	Species	C.Crow	Rook	Jackdaw	Magpie

Carrion Crow	1.97	-			
Rook	1.70	1.21	-		
Jackdaw	1.73	2.26	1.86	-	
Magpie	1.85	2.45	2.02	1.08	-

LENGTH	Average	Ratio with species:			
minus tail	with 3				
	Other				
Species	Species	C.Crow	Rook	Jackdaw	Magpie

Carrion Crow	2.35	-			
Rook	1.55	1.85	-		
Jackdaw	1.76	2.72	1.47	-	
Magpie	1.63	2.47	1.33	1.10	-

TAIL	Average	Ratio with species:			
	with 3				
	Other				
Species	Species	C.Crow	Rook	Jackdaw	Magpie

Carrion Crow	1.25	-			
Rook	1.25	1.11	-		
Jackdaw	1.47	1.40	1.26	-	
Magpie	1.45	1.24	1.38	1.10	-

WING	Average	Ratio with species:			
	with 3				
	Other				
Species	Species	C.Crow	Rook	Jackdaw	Magpie

Carrion Crow	1.39	-			
Rook	1.34	1.05	-		
Jackdaw	1.32	1.38	1.31	-	
Magpie	1.55	1.73	1.65	1.26	-

TARSUS	Average	Ratio with species:			
	with 3				
	Other				
Species	Species	C.Crow	Rook	Jackdaw	Magpie

Carrion Crow	1.23	-			
Rook	1.13	1.12	-		
Jackdaw	1.22	1.35	1.20	-	
Magpie	1.13	1.21	1.08	1.11	-

BILL LENGTH	Average	Ratio with species:			
	with 3				
	Other				
Species	Species	C.Crow	Rook	Jackdaw	Magpie

Carrion Crow	1.36	-			
Rook	1.45	1.08	-		
Jackdaw	1.48	1.59	1.72	-	
Magpie	1.36	1.42	1.54	1.12	-

BILL DEPTH	Average	Ratio with species:			
	with 3				
	Other				
Species	Species	C.Crow	Rook	Jackdaw	Magpie

Carrion Crow	1.29	-			
Rook	1.22	1.09	-		
Jackdaw	1.32	1.41	1.30	-	
Magpie	1.22	1.37	1.26	1.03	-

(b) Ratios within species

		Weight	Length	Tail	Wing	Tarsus	Bill Length	Bill Depth
Weight	C	-						
	R	-						
	J	-						
	M	-						
Length (minus Tail)	C	0.99	-					
	R	1.51	-					
	J	1.19	-					
	M	1.00	-					
Tail	C	3.00	3.03	-				
	R	2.76	1.82	-				
	J	1.86	1.56	-				
	M	0.99	0.99	-				
Wing	C	1.72	1.73	0.57	-			
	R	1.49	0.98	0.54	-			
	J	1.05	0.88	0.56	-			
	M	1.21	1.21	1.23	-			
Tarsus	C	9.42	9.51	3.13	5.49	-		
	R	8.64	5.72	3.13	5.81	-		
	J	5.59	4.68	3.00	5.34	-		
	M	4.63	4.63	4.69	3.82	-		
Bill Length	C	10.59	10.69	3.52	6.17	1.12	-	
	R	8.05	5.32	2.92	5.41	0.93	-	
	J	7.43	6.22	3.99	7.10	1.33	-	
	M	6.13	6.13	6.22	5.05	1.32	-	
Bill Depth	C	29.26	29.52	9.74	17.05	3.10	2.76	-
	R	26.17	17.31	9.49	17.60	3.03	3.25	-
	J	18.22	15.26	9.78	17.41	3.26	2.45	-
	M	16.33	16.33	16.55	13.45	2.66	2.66	-

Appendix 7

Foraging rates of four corvid species on grassland in winter

Summary tables of mean foraging rates (with standard deviation). See Methods section for how calorific and protein ingestion rates were estimated. The results of both parametric and non-parametric (Kruskal-Wallis) one-way analysis of variance are given for comparison. All variables were tested even though some groups had no non-zero scores, to allow inspection of where violation of assumptions began to cause differences in levels of significance between parametric and non-parametric tests (see Methods). The results of all possible pairwise comparisons amongst the four species are also given (Scheffe test); species separated by a colon differ significantly from one another.

Table 7.1

Total ingestion rates and rates for the different invertebrate types distinguished during direct observation of foraging birds.

Table 7.2

Peck rates (both successful and unsuccessful) for the different microhabitats.

Table 7.3

Peck rates for the different feeding actions.

Table 7.4

Ingestion rates, by microhabitat.

Table 7.5

Ingestion rates, by feeding action.

Table 7.6

Ingestion rates, by earthworm/other invertebrates, by microhabitat.

Table 7.7

Ingestion rates, by earthworm/other invertebrates, by feeding action.

Table 7.8

Ingestion rates, by invertebrates, by microhabitat.

Table 7.9

Ingestion rates, by invertebrates, by feeding action.

Table 7.1 - Ingestion rates for the different invertebrate types defined during direct observation in the field, and total ingestion rates, for four species

Mean (s.d.) rates per minute: N = Numbers ingested per min.
K = Kcal ingested per min.
P = g of protein-containing material ingested per min.

Prey Type	1 Rock	2 Carriacou Crow	3 Jackdaw	4 Hagpie	Pairwise	A-V		K-W	
					Differences (Scheffe) p<.10)	F	p	X2	p
Small	NI 0.41 I (0.57)	0.52 (0.72)	1.71 (1.36)	0.93 (0.90)	1,2:3,4 3:4	21.91	***	47.00	***
	KI 0.0028	0.0036	0.0115	0.0063					
	PI 0.0004	0.0005	0.0015	0.0008					
Medium	NI 0.26 I (0.38)	0.64 (0.79)	0.16 (0.25)	0.34 (0.40)	2:1,3,4	14.52	***	33.02	***
	KI 0.0468	0.1167	0.0287	0.0625					
	PI 0.0059	0.0148	0.0036	0.0079					
S.Worm	NI 0.51 I (0.73)	0.21 (0.58)	0.06 (0.25)	0.07 (0.13)	1:2,3,4	14.68	***	33.06	***
	KI 0.0926	0.0382	0.0105	0.0136					
	PI 0.0164	0.0068	0.0019	0.0024					
H.Worm	NI 0.88 I (0.23)	0.06 (0.13)	0	0	1,2:3,4	7.55	***	25.05	***
	KI 0.0346	0.0259	0	0					
	PI 0.0061	0.0046	0	0					
L.Worm	NI 0.06 I (0.28)	0.10 (0.64)	0	0	-	2.28	ns	13.90	**
	KI 0.0632	0.0942	0	0					
	PI 0.0112	0.0167	0	0					
Total Other Invertebrates	NI 0.67 KI 0.0496 PI 0.0063	1.16 0.1203 0.0153	1.87 0.0402 0.0051	1.27 0.0688 0.0087					
Total Worms	NI 0.65 KI 0.1904 PI 0.0337	0.37 0.1583 0.0281	0.06 0.0105 0.0019	0.07 0.0136 0.0024					
TOTAL	NI 1.32 KI 0.2400 PI 0.0400	1.53 0.2786 0.0434	1.93 0.0507 0.0070	1.34 0.0824 0.0111					

Table 7.2 - Peck rates for the different microhabitats

Feeding Actions/ Combined	Mean (s.d.) Rate per Min.				Pairwise Differ- ences (Scheffe p<.10)	A-V F p	K-W X2 p
All Feeding Attempts, Both Successful and Unsuccessful	1	2	3	4			
Micro Habitat	Rook	Crow	Jackdaw	Magpie			
Above Soil Surface	1.41 (1.22)	2.21 (2.08)	2.81 (2.32)	2.07 (1.40)	1:2,3	6.65 ***	16.94 ***
Beneath Clods/Stones	0.32 (0.61)	0.39 (0.73)	0.95 (1.56)	0.96 (1.06)	1,2:3,4	9.03 ***	25.36 ***
Within/ Beneath Dung	0.36 (0.73)	1.00 (2.24)	1.56 (2.29)	0.55 (1.36)	3:1,4	5.60 ***	18.37 ***
Beneath Soil Surface	3.69 (2.92)	0.37 (1.02)	0.07 (0.18)	0.07 (0.16)	1:2,3,4	202.21 ***	179.73 ***

Table 7.3 - Peck rates for the different feeding actions

All Feeding Attempts, Both Successful and Unsuccessful	Mean (s.d.) Rate per Min.				Pairwise Differences (Scheffe)	A-V		K-W		
	1	2	3	4						
	Carrion									
	Rook	Crow	Jackdaw	Magpie		F	p	X2	p	
Feeding Action										
Surface Pick	1.27 (1.13)	1.57 (1.81)	2.13 (1.85)	1.65 (1.13)	1:3	3.50	*	8.34	*	
Pounce	0.04 (0.27)	0.31 (0.77)	0.28 (0.90)	0.21 (0.35)	1:4,2	4.11	**	26.50	***	
Jump	0	0	0.26 (0.88)	0	3:1,2,4	9.02	***	35.32	***	
Surface Probe	0.10 (0.22)	0.33 (0.62)	0.13 (0.31)	0.21 (0.35)	2:1,3	4.93	**	14.59	**	
Clod/Stone Turn	0.32 (0.62)	0.39 (0.73)	0.95 (1.56)	0.96 (1.06)	1,2:3,4	9.03	***	25.36	***	
Dung Turn	0.36 (0.73)	0.98 (2.24)	1.56 (2.29)	0.85 (1.84)	3:1,4	5.55	***	18.22	***	
Dung Crumble	0	0.02 (0.15)	0	0	-	1.48	ns	6.68	ns	
Deep Probe	1.52 (1.61)	0.08 (0.37)	0.03 (0.12)	0.02 (0.07)	1:2,3,4	90.81	***	131.41	***	
Dig	0.39 (0.68)	0.09 (0.64)	0	0.02 (0.08)	1:2,3,4	18.25	***	57.03	***	
Jab	1.78 (2.73)	0.20 (0.63)	0.04 (0.14)	0.03 (0.13)	1:2,3,4	51.73	***	105.88	***	

Table 7.4 - Ingestion rates for the different microhabitats

Mean (s.d.) rates per minute: N = Numbers ingested per min.
 K = Kcal ingested per min.
 P = g of protein-containing material ingested per min.

Feeding Actions						Pairwise			
Combined						Differ-			
All						ences		A-V	
Invertebrate						(Scheffe		p	
Prey Types		1	2	3	4	p<.10)		K-W	
Micro Habitat		Rook	Crow	Jackdaw	Magpie	F		X2	
						p		p	
=====		=====				=====		=====	
Above Soil Surface	N	0.30	0.91	1.05	0.87	1:2,3,4		8.80 ***	
	(s.d.)	(0.51)	(1.08)	(1.21)	(0.74)			30.07 ***	
	K	0.0248	0.1877	0.0313	0.0498				
	P	0.0041	0.0305	0.0045	0.0070				
Beneath Clods/Stones	N	0.09	0.10	0.39	0.20	3:1,2		3.81 *	
	(s.d.)	(0.29)	(0.29)	(1.04)	(0.45)			7.01 *	
	K	0.0104	0.0109	0.0085	0.0092				
	P	0.0016	0.0015	0.0011	0.0012				
Within/ Beneath Dung	N	0.07	0.40	0.47	0.32	1:3		2.72 *	
	(s.d.)	(0.22)	(1.19)	(1.08)	(0.93)			9.68 *	
	K	0.0068	0.0558	0.0063	0.0216				
	P	0.0011	0.0077	0.0008	0.0027				
Beneath Soil Surface	N	0.39	0.15	0.02	0.02	1:2,3,4		56.45 ***	
	(s.d.)	(0.93)	(0.71)	(0.11)	(0.08)			121.17 ***	
	K	0.1980	0.0240	0.0045	0.0018				
	P	0.0332	0.0036	0.0006	0.0002				
=====		=====				=====		=====	

Table 7.5 - Ingestion rates for the different feeding actions

Mean (s.d.) rates per minute: N = Numbers ingested per min.

K = Kcal ingested per min.

P = g of protein-containing material
ingested per min.

All Invertebrate Prey Types		1	2	3	4	Pairwise Differences (Scheffe p<.10)	A-V F p	K-W K2 p
Feeding Action		Rook	Carrion Crow	Jackdaw	Magpie			
=====	=====	=====	=====	=====	=====	=====	=====	=====
Surface Pick	N	0.23	0.64	0.73	0.68	1:2,3,4	6.48 ***	24.16 ***
		(0.44)	(0.86)	(0.93)	(0.63)			
	K	0.0161	0.0691	0.0244	0.0361			
	P	0.0026	0.0104	0.0036	0.0050			
Pounce	N	0.03	0.17	0.01	0.10	2:1,3	4.58 **	23.06 ***
		(0.26)	(0.67)	(0.05)	(0.24)			
	K	0.0062	0.1028	0.0001	0.0071			
	P	0.0011	0.0180	0.00003	0.0011			
Jump	N	0	0	0.26	0	3:1,2,4	9.02 ***	35.32 ***
				(0.88)				
	K	0	0	0.0017	0			
	P	0	0	0.0002	0			
Surface Probe	N	0.03	0.11	0.06	0.08	-	2.09 ns	7.60 ns
		(0.22)	(0.62)	(0.31)	(0.35)			
	K	0.0024	0.0158	0.0052	0.0066			
	P	0.0004	0.0021	0.0007	0.0009			
=====	=====	=====	=====	=====	=====	=====	=====	=====
Clod/Stone Turn	N	0.09	0.10	0.39	0.20	-	2.52 ns	7.01 ns
		(0.29)	(0.29)	(1.04)	(0.45)			
	K	0.0104	0.0109	0.0085	0.0092			
	P	0.0016	0.0015	0.0011	0.0012			
=====	=====	=====	=====	=====	=====	=====	=====	=====
Dung Turn	N	0.07	0.39	0.47	0.32	1:3	2.67 *	9.47 *
		(0.22)	(1.19)	(1.08)	(0.93)			
	K	0.0068	0.0558	0.0063	0.0216			
	P	0.0011	0.0077	0.0008	0.0027			
Dung Crumble	N	0	0.01	0	0	-	0.73 ns	2.21 ns
			(0.05)					
	K	0	0.0001	0	0			
	P	0	0.00003	0	0			
=====	=====	=====	=====	=====	=====	=====	=====	=====
Deep Probe	N	0.47	0.04	0.01	0.01	1:2,3,4	30.02 ***	88.74 ***

Table 7.6 - Ingestion rates, by earthworm/other invertebrate, by micro-habitat

Mean (s.d.) rates per minute: N = Numbers ingested per min.
K = Kcal ingested per min.
P = g of protein-containing material ingested per min.

Feeding Actions						Pairwise				
Combined						Differ-				
						ences	A-V		K-W	
Combined Prey		1	2	3	4	(Scheffe				
Types: Earth-						p<.10)	F	p	X2	p
worms and Other										
Invertebrates										
Micro- Prey										
Habitat Type		Rook	Crow	Jackdaw	Magpie					
=====										
Above	Other	IN 0.19	0.63	0.99	0.79	1:2,3,4	12.93	***	36.02	***
Soil		(0.37)	(0.85)	(1.23)	(0.71)					
Surface		K 0.0061	0.0557	0.0208	0.0362					
		P 0.0008	0.0071	0.0027	0.0046					
	Worms	IN 0.10	0.25	0.06	0.07	2:3	4.03	**	19.73	***
		(0.39)	(0.72)	(0.25)	(0.13)					
		K 0.0187	0.1320	0.0105	0.0136					
		P 0.0033	0.0234	0.0019	0.0024					
=====										
Within/	Other	IN 0.04	0.34	0.47	0.32	1:3	3.41	*	13.58	**
Beneath		(0.19)	(0.89)	(1.08)	(0.93)					
Dung		K 0.0012	0.0429	0.0063	0.0216					
		P 0.0001	0.0054	0.0008	0.0027					
	Worms	IN 0.02	0.06	0	0	-	1.60	ns	5.85	ns
		(0.12)	(0.41)							
		K 0.0056	0.0130	0	0					
		P 0.0010	0.0023	0	0					
=====										
Beneath	Other	IN 0.06	0.08	0.39	0.14	3:1,2	3.26	*	4.39	ns
Clods/		(0.24)	(0.26)	(1.04)	(0.41)					
Stones		K 0.0047	0.0081	0.0085	0.0092					
		P 0.0006	0.0010	0.0011	0.0012					
	Worms	IN 0.03	0.01	0.01	0.01	-	2.57	ns	7.44	ns
		(0.13)	(0.08)	(0.06)	(0.05)					
		K 0.0057	0.0028	0.0008	0.0009					
		P 0.0010	0.0005	0.0001	0.0001					
=====										
Beneath	Other	IN 0.37	0.11	0.02	0.02	1:2,3,4	18.54	***	57.15	***
Soil		(0.56)	(0.64)	(0.11)	(0.08)					
Surface		K 0.0376	0.0136	0.0045	0.0018					
		P 0.0048	0.0017	0.0006	0.0002					
	Worms	IN 0.50	0.04	0.01	0.01	1:2,3,4	39.64	***	111.95	***
		(0.71)	(0.31)	(0.05)	(0.06)					
		K 0.1603	0.0106	0.0008	0.0008					
		P 0.0284	0.0019	0.0001	0.0001					
=====										

Table 7.7 - Ingestion rates, by earthworm/other invertebrate, by feeding action

Combined Prey					Pairwise			
Types: Earth-								
worms and Other								
Invertebrates		1	2	3	4	Differ-		
						ences	A-V	
						(Scheffe	K-W	
Feeding	Prey		Carrion			p<.10)	F p	
Action	Type		Rook	Crow	Jackdaw	Magpie	X2 p	
=====								
Surface Pick	Other	NI	0.17	0.50	0.67	0.64	1:2,3,4 7.05 *** 27.64 ***	
		I	(0.37)	(0.78)	(0.94)	(0.60)		
		K	0.0054	0.0375	0.0139	0.0274		
		P	0.0007	0.0048	0.0018	0.0035		
Worms	Other	NI	0.06	0.11	0.06	0.05	- 1.34 ns 4.49 ns	
		I	(0.27)	(0.32)	(0.25)	(0.11)		
		K	0.0107	0.0316	0.0105	0.0087		
		P	0.0019	0.0056	0.0019	0.0015		

Pounce	Other	NI	0.01	0.03	0.01	0.08	4:1,3 6.07 *** 16.05 ***	
		I	(0.03)	(0.09)	(0.05)	(0.22)		
		K	0.0006	0.0044	0.0001	0.0036		
		P	0.0001	0.0006	0.00003	0.0005		
Worms	Other	NI	0.03	0.13	0	0.02	2:3 3.26 * 15.18 **	
		I	(0.26)	(0.66)		(0.08)		
		K	0.0057	0.0984	0	0.0035		
		P	0.0010	0.0174	0	0.0006		

Jump	Other	NI	0	0	0.26	0	3:1,2,4 9.02 *** 35.32 ***	
		I			(0.88)			
		K	0	0	0.0017	0		
		P	0	0	0.0002	0		

Surface Probe	Other	NI	0.01	0.09	0.06	0.08	1:2 2.74 * 9.51 *	
		I	(0.06)	(0.28)	(0.15)	(0.17)		
		K	0.0001	0.0137	0.0052	0.0052		
		P	0.00003	0.0017	0.0007	0.0007		
Worms	Other	NI	0.01	0.01	0	0.01	- 0.61 ns 1.91 ns	
		I	(0.08)	(0.05)		(0.05)		
		K	0.0023	0.0021	0	0.0014		
		P	0.0004	0.0004	0	0.0003		
=====								
Clod/Stone Turn	Other	NI	0.06	0.08	0.39	0.14	3:1,2 3.26 * 4.39 ns	
		I	(0.24)	(0.26)	(1.04)	(0.41)		
		K	0.0047	0.0081	0.0085	0.0092		
		P	0.0006	0.0010	0.0011	0.0012		
Worms	Other	NI	0.03	0.01	0.01	0.01	- 2.57 ns 7.44 ns	
		I	(0.13)	(0.08)	(0.05)	(0.06)		
		K	0.0057	0.0028	0.0007	0.0008		
		P	0.0010	0.0005	0.0001	0.0001		
=====								
Dung Turn	Other	NI	0.04	0.33	0.47	0.32	1:3 3.36 * 13.31 **	
		I	(0.19)	(0.89)	(1.08)	(0.93)		
		K	0.0012	0.0428	0.0063	0.0216		
		P	0.0001	0.0054	0.0008	0.0027		
Worms	Other	NI	0.02	0.06	0.01	0.01	- 1.60 ns 5.85 ns	
		I	(0.12)	(0.41)	(0.04)	(0.05)		
		K	0.0056	0.0130	0.0013	0.0013		
		P	0.0010	0.0023	0.0003	0.0003		

Dung Crumble	Other	NI	0	0.01	0	0	- 0.73 ns 2.21 ns	
		I		(0.05)				
		K	0	0.0001	0	0		
		P	0	0.00003	0	0		
=====								
Deep Probe	Other	NI	0.18	0.01	0.01	0.01	1:2,3,4 17.06 *** 52.27 ***	
		I	(0.42)	(0.04)	(0.06)	(0.03)		
		K	0.0187	0.0008	0.0005	0.0009		
		P	0.0024	0.0001	0.00007	0.0001		
Worms	Other	NI	0.27	0.03	0.01	0.01	1:2,3,4 18.15 *** 66.25 ***	
		I	(0.51)	(0.31)	(0.05)	(0.06)		
		K	0.0984	0.0060	0.0008	0.0009		
		P	0.0174	0.0011	0.0001	0.0001		

Dig	Other	NI	0.11	0.07	0.01	0.01	1:3,4 3.39 * 16.89 ***	
		I	(0.32)	(0.63)	(0.05)	(0.06)		
		K	0.0134	0.0090	0.0009	0.0009		
		P	0.0017	0.0011	0.0001	0.0001		
Worms	Other	NI	0.03	0	0	0	1:2,4 3.22 * 9.63 *	
		I	(0.16)					
		K	0.0063	0	0	0		
		P	0.0011	0	0	0		

Jab	Other	NI	0.07	0.03	0.02	0.01	1:4 2.76 * 7.36 ns	
		I	(0.26)	(0.11)	(0.11)	(0.05)		
		K	0.0055	0.0038	0.0045	0.0009		
		P	0.0007	0.0005	0.0006	0.0001		
Worms	Other	NI	0.19	0.01	0.01	0.01	1:2,3,4 11.53 *** 38.29 ***	
		I	(0.53)	(0.06)	(0.07)	(0.05)		
		K	0.0557	0.0046	0.0008	0.0008		
		P	0.0099	0.0008	0.0001	0.0001		

Table 7.8 - Ingestion rates, by invertebrate, by micro-habitat

Mean (s.d.) rates per minute: N = Numbers ingested per min.
K = Kcal ingested per min.
P = g of protein-containing material ingested per min.



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Table 7.9 is very large, and has therefore been scanned as two images

Table 7.9 - Ingestion rates, by invertebrate, by feeding action

Mean (s.d.) rates per minute: N = Numbers ingested per min.
K = Kcal ingested per min.
P = g of protein-containing material ingested per min.

		Pairwise Differences (Scheffe)				A-V		K-W	
		1	2	3	4				
Feeding Action	Prey Type	Rook	Carrion Crow	Jackdaw	Magpie	p<.10)	F	p	X2 p
=====									
Surface Pick	Fail	N 1.04	0.93	1.40	0.97	-	2.24	ns	4.49 ns
		I (1.10)	(1.22)	(1.37)	(0.92)				
		I							
	Small	N 0.15	0.31	0.62	0.51	1:3,4	7.56	***	23.57 ***
		I (0.32)	(0.61)	(0.85)	(0.56)	2:3			
		I K 0.0010	0.0021	0.0042	0.0034				
	Medium	N 0.02	0.19	0.05	0.13	1:2,4	9.19	***	27.21 ***
		I (0.10)	(0.30)	(0.16)	(0.24)	2:3			
		I K 0.0044	0.0355	0.0097	0.0240				
	S.Worm	N 0.06	0.08	0.06	0.05	-	0.22	ns	5.96 ns
		I (0.27)	(0.30)	(0.25)	(0.11)				
		I K 0.0107	0.0143	0.0105	0.0087				
Pounce	Fail	N 0	0.02	0	0	2:1,3,4	5.15	**	15.80 ***
		I (0.09)							
		I K 0	0.0102	0	0				
	Small	N 0.01	0.01	0.01	0.06	4:1,3,2	7.83	***	21.98 ***
		I (0.03)	(0.05)	(0.02)	(0.16)				
		I K 0.0001	0.0001	0.0001	0.0004				
	Medium	N 0.01	0.02	0.01	0.02	-	2.77	*	8.62 *
		I (0.02)	(0.08)	(0.03)	(0.07)				
		I K 0.0006	0.0044	0.0006	0.0032				
	S.Worm	N 0.03	0.02	0	0.02	-	0.63	ns	5.13 ns
		I (0.26)	(0.11)		(0.08)				
		I K 0.0057	0.0044	0	0.0035				
Jump	Fail	N 0	0.02	0	0	-	5.15	**	15.80 ***
		I (0.08)							
		I K 0	0.0094	0	0				
	Small	N 0	0.09	0	0	-	2.15	ns	13.50 **
		I (0.64)							
		I K 0	0.0845	0	0				
	Medium	N 0.01	0.07	0.03	0.03	1:2	3.28	*	12.09 **
		I (0.05)	(0.26)	(0.12)	(0.09)				
		I K 0.0006	0.0136	0.0049	0.0049				
	S.Worm	N 0.01	0.01	0	0.01	-	0.77	ns	1.91 ns
		I (0.08)	(0.03)		(0.05)				
		I K 0.0023	0.0009	0	0.0014				
Clod/Stone Turn	Fail	N 0.23	0.29	0.57	0.76	1:3,4	8.81	***	28.37 ***
		I (0.43)	(0.58)	(0.91)	(0.84)	2:4			
		I							
	Small	N 0.04	0.04	0.35	0.09	3:1,2,4	5.20	**	7.22 ns
		I (0.20)	(0.16)	(0.97)	(0.28)				
		I K 0.0003	0.0003	0.0024	0.0006				
	Medium	N 0.02	0.04	0.03	0.05	-	0.34	ns	3.34 ns
		I (0.12)	(0.16)	(0.15)	(0.15)				
		I K 0.0044	0.0078	0.0062	0.0086				
	S.Worm	N 0.03	0.01	0.01	0.01	1:3,4	2.99	*	7.54 ns
		I (0.13)	(0.05)	(0.04)	(0.05)				
		I K 0.0057	0.0015	0.0013	0.0013				
Dung Turn	Fail	N 0	0.01	0	0	-	0.73	ns	2.21 ns
		I (0.04)							
		I K 0	0.0014	0	0				
	Small	N 0.04	0.10	0.45	0.21	3:1,2	5.81	***	16.19 ***
		I (0.16)	(0.37)	(1.02)	(0.62)				
		I K 0.0003	0.0007	0.0030	0.0014				
	Medium	N 0.01	0.23	0.02	0.11	2:1,3	6.17	***	16.58 ***
		I (0.04)	(0.66)	(0.08)	(0.37)				
		I K 0.0009	0.0421	0.0033	0.0201				
	S.Worm	N 0.02	0.06	0.01	0.01	-	1.38	ns	5.16 ns
		I (0.09)	(0.40)	(0.04)	(0.05)				
		I K 0.0033	0.0107	0.0015	0.0015				
Deep Probe	Fail	N 0.01	0.01	0	0	-	0.76	ns	2.68 ns
		I (0.05)	(0.04)						
		I K 0.0023	0.0022	0	0				
	Small	N 0.08	0	0	0	1:2,3,4	8.84	***	29.51 ***
		I (0.26)							
		I K 0.0006	0	0	0				
	Medium	N 0.10	0.01	0.01	0.01	1:2,3,4	10.73	***	31.63 ***
		I (0.27)	(0.04)	(0.05)	(0.03)				
		I K 0.0182	0.0008	0.0006	0.0009				
	S.Worm	N 0.19	0.03	0.01	0.01	1:2,3,4	11.62	***	48.48 ***
		I (0.51)	(0.10)	(0.03)	(0.03)				
		I K 0.0001	0.0001	0.00007	0.0001				

Appendix Eight

Data not included in this thesis

Other data than those described in this thesis were collected during the period funded by the studentship held by the author, but were not considered to fit the main "storyline" of the thesis. Publications are in press or preparation in the following areas, with the exception of (4) where insufficient data exist at present:

- (1) Seasonal trends in habitat use by four Corvid species.
- (2) Caching and recovery of food by rooks and carrion crows (see Waite, in press).
- (3) Seasonal trends in rook social and foraging behaviour and ecology.
- (4) Comparison of carrion crow and rook social organisation in the breeding season, in relation to food supply.
- (5) Long-term detailed census of the utilisation of a single permanent pasture by four Corvid species, in relation to seasonal and meteorological trends, grazing intensity, and invertebrate fauna.
- (6) The foraging behaviour of 'third birds' within carrion crow territories in winter, compared to the foraging behaviour of the resident pair.


```

10 randomize
12 open "tempop.dat" for output as file #2
34 print "Schoener (1968) niche overlap index (theta) - random generation"
36 print #2:"Schoener (1968) niche overlap index (theta) - random generation"
50 print " "
51 print #2: " "
52 print "version for matrix input of 4 species data"
53 print "(usually in order: rook,crow,jackdaw,magpie)"
54 print "(data must be stored in tempdata.dat for this version of program)"
55 print "(data must have an initial variable as well as the 4 species; it"
56 print " must number consecutively from 1 to n, where n = n of rows)"
57 print "(numbers must be separated by commas)" \ print \ print
58 print "name of the resource "; \ input n$
59 print #2:"name of the resource is "; n$
61 print "how many components to the resource (0 to finish) "; \ input n
62 print #2:"how many components to the resource (0 to finish) ";n
63 print " "
64 print #2: " "
65 print "output is stored in tempop.dat"
70 if n<1 then 3000
80 goto 1500
90 a1=0\ a2=0\ a3=0\ a4=0\ a5=0\ a6=0\ b1=0\ b2=0\ b3=0\ b4=0\ d1=0\ d2=0\ d3=0
91 e1=0\ e2=0\ e3=0\ e4=0\ f1=0\ f2=0\ f3=0\ f4=0\ f5=0\ f6=0
92 d4=0\ d5=0\ d6=0\ m1=0\ m2=0\ m3=0\ m4=0\ o1=0\ o2=0\ p1=0\ p2=0\ q1=0\ q2=0\ r1=0\ r2=0
94 s1=0\ s2=0\ s3=0\ s4=0\ t1=0\ t2=0\ t3=0\ t4=0\ t5=0\ t6=0
96 w1=0\ w2=0\ w3=0\ w4=0\ w5=0\ w6=0
100 for i=1 to n
120 t1=t1+v(i)*x(i)
121 t2=t2+v(i)*y(i)
122 t3=t3+v(i)*z(i)
123 t4=t4+x(i)*y(i)
124 t5=t5+x(i)*z(i)
125 t6=t6+y(i)*z(i)
130 o1=o1+v(i)
140 p1=p1+x(i)
142 q1=q1+y(i)
144 r1=r1+z(i)
150 o2=o2+v(i)*v(i)
160 p2=p2+x(i)*x(i)
162 q2=q2+y(i)*y(i)
164 r2=r2+z(i)*z(i)
170 next i
180 m1=m1+o1/n
190 m2=m2+p1/n
192 m3=m3+q1/n
194 m4=m4+r1/n
200 s1=s1+sqr(o2/n)
210 s2=s2+sqr(p2/n)
212 s3=s3+sqr(q2/n)
214 s4=s4+sqr(r2/n)
220 b1=b1+((1/(o2/(o1*o1)))-1)/(n-1)
230 b2=b2+((1/(p2/(p1*p1)))-1)/(n-1)
232 b3=b3+((1/(q2/(q1*q1)))-1)/(n-1)
234 b4=b4+((1/(r2/(r1*r1)))-1)/(n-1)
240 if m1<m2 then 260
250 d1=d1+m1-m2
255 if m2<=m1 then 270
260 d1=d1+m2-m1
270 w1=w1+sqr(((s1*s1)+(s2*s2))/2)
280 a1=a1+sqr(o2*p2)
340 if m1<m3 then 360
350 d2=d2+m1-m3
355 if m3<=m1 then 370
360 d2=d2+m3-m1
370 w2=w2+sqr(((s1*s1)+(s3*s3))/2)
380 a2=a2+sqr(o2*q2)
440 if m1<m4 then 460
450 d3=d3+m1-m4
455 if m4<=m1 then 470
460 d3=d3+m4-m1
470 w3=w3+sqr(((s1*s1)+(s4*s4))/2)
480 a3=a3+sqr(o2*r2)
540 if m2<m3 then 560
550 d4=d4+m2-m3
555 if m3<=m2 then 570
560 d4=d4+m3-m2
570 w4=w4+sqr(((s2*s2)+(s3*s3))/2)
580 a4=a4+sqr(p2*q2)
640 if m2<m4 then 660
650 d5=d5+m2-m4
655 if m4<=m2 then 670
660 d5=d5+m4-m2
670 w5=w5+sqr(((s2*s2)+(s4*s4))/2)
680 a5=a5+sqr(p2*r2)
740 if m3<m4 then 760
750 d6=d6+m3-m4
755 if m4<=m3 then 770
760 d6=d6+m4-m3
770 w6=w6+sqr(((s3*s3)+(s4*s4))/2)
780 a6=a6+sqr(q2*r2)
781 for i = 1 to n
784 e1=v(i)/o1
786 e2=x(i)/p1
788 e3=y(i)/q1
790 e4=z(i)/r1
800 if e1>e2 then 806
802 f1=f1+e2-e1
804 if e2>=e1 then 810
806 f1=f1+e1-e2
810 if e1>e3 then 816
812 f2=f2+e3-e1
814 if e3>=e1 then 820
816 f2=f2+e1-e3
820 if e1>e4 then 826
822 f3=f3+e4-e1
824 if e4>=e1 then 830
826 f3=f3+e1-e4
830 if e2>e3 then 836
832 f4=f4+e3-e2
834 if e3>=e2 then 840
836 f4=f4+e2-e3
840 if e2>e4 then 846
842 f5=f5+e4-e2
844 if e4>=e2 then 850
846 f5=f5+e2-e4
850 if e3>e4 then 856
852 f6=f6+e4-e3
854 if e4>=e3 then 860
856 f6=f6+e3-e4
860 next i
870 print #2:1-(0.5*f1),1-(0.5*f2),1-(0.5*f3),1-(0.5*f4),1-(0.5*f5),1-(0.5*f6)
1390 goto 2900
1500 open "tempdata.dat" for input as file #1
1510 dim v(200),x(200),y(200),z(200)
1520 for i=1 to n
1530 input #1:c,v(i),x(i),y(i),z(i)
1540 next i
1550 dim v2(200),x2(200),y2(200),z2(200)
1560 dim c(4,100)
1561 c9=1
1562 for i=1 to 4
1563 for j=1 to 100
1564 c(i,j)=0
1565 next j
1566 next i
1570 let x9=int(rnd*n)+1
1580 if c(1,x9)=1 then goto 1570
1590 let v2(c9)=v(x9)
1600 let c(1,x9)=1
1610 let c9=c9+1
1620 if c9 <= n then goto 1570
1621 c9=1
1630 let x9=int(rnd*n)+1
1640 if c(2,x9)=1 then goto 1630
1650 let x2(c9)=x(x9)
1660 let c(2,x9)=1
1670 let c9=c9+1
1680 if c9 <= n then goto 1630
1681 c9=1
1730 let x9=int(rnd*n)+1
1740 if c(3,x9)=1 then goto 1730
1750 let y2(c9)=y(x9)
1760 let c(3,x9)=1
1770 let c9=c9+1
1780 if c9 <= n then goto 1730
1781 c9=1
1830 let x9=int(rnd*n)+1
1840 if c(4,x9)=1 then goto 1830
1850 let z2(c9)=z(x9)
1860 let c(4,x9)=1
1870 let c9=c9+1
1880 if c9 <= n then goto 1830
1881 for i=1 to 200
1882 v(i) = v2(i)
1883 x(i) = x2(i)
1884 y(i) = y2(i)
1885 z(i) = z2(i)
1886 next i
1900 goto 90
2900 if h9=100 then end
2910 let h9=h9+1
2911 print "Iteration";h9
2920 goto 1561
3000 end

```

```

10 print "this calculates t for the difference between randomly"
20 print "generated mean theta (for N = 100 iterations) and the"
30 print "observed theta" \print
40 print "input observed overlap value";\input a
50 print "input calculated overlap value";\input b
60 print "input calculated s.d."; \input c
70 d=abs(b-a)
80 e=sqr(100/101)
90 print "t = ";(d*e)/c
100 if (d*e)/c >= 1.984 then 120
110 print "not significantly different from random" \print
115 goto 40
120 print "significantly different from random (p < 0.05 or less)" \print
130 goto 40
140 end

```