Determination of the proximate factors in nest site selection of three species of waders within a large, dry salt marsh

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Determination of the Proximate Factors in Nest Site Selection of Three Species of Waders within a Large, Dry Salt Marsh.

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1.0 Introduction

Natural selection has directed that animal species tend to become adapted to a specific habitat. For species whose members are capable of moving out of their selected habitat, the principle of natural selection indicates that a mechanism develops, which enables the species to recognise the habitat to which it is adapted. This mechanism is particularly notable in birds. Habitat selection in birds is most clear in nest site selection and it is this aspect which is the main concern of this study.

When considering the factors affecting the selection of nest sites it is necessary to differentiate between ultimate and proximate factors. The former are those which affect the survival rate (e.g. predation) and hence affect the nest site selection behaviour through evolution. The proximate factors are environmental stimuli which the bird selects. They may not have immediate survival value, e.g. Klomp (1953) found that Lapwings, *Vanellus vanellus*, avoided breeding in fields with trees in the vicinity (the proximate factor) as they were there less able to drive off crows (predators of eggs and chicks), than in open areas. Here again predation is the ultimate factor.

The proximate factors selected for are based on the ancestral habitat and are passed on genetically, although they can be modified to some extent by imprinting (Hilden 1965). Therefore if some individuals move into an area different from their ancestral habitat, either due to competition or some other pressure, they will select features of their new environment which are associated with the optimum nest sites of their previous habitat. These features may not be the optimum for the new habitat. For example Lack (1933) found Ringed Plovers only on the gravel areas of the Brecklands, although they appeared to be structurally suited to inhabiting areas of short grass. This selection of areas resembling their ancestral habitat of pebble shores restricted their distribution. Thus it can be seen that selection of a particular proximate factor does not automatically imply an associated advantageous ultimate factor, if the bird is not in the ancestral habitat of the species.

It is likely that there are two stages in the selection of the proximate factors:-

i) Selection of those factors which are characteristic of the general habitat, e.g. vegetation type.

ii) Selection of the exact nest site, e.g. distance from a creek.

This may imply that in ground nesting species, such as waders, the latter stage is less important than the former as the requirements for the exact nest site do not appear to be exacting. However in some species, for example hole-nesters, the latter requirement may outweigh the former.

The following model was developed to describe part of the selection mechanism for these proximate factors.

$$\sum_{ij} a_{ij} . y_{ij} \geqslant b_{jk} . K_j$$

where:-

y_{ij} is the ith proximate factor relevant to the nest site selection mechanism of the jth species;

a_{ij} is some measure of the relative importance of the ith proximate factor for the jth species;

K_j is the level of accumulated stimuli required for the settling reaction in the jth species

b_{jk} is a factor which modifies the threshold required for the settling reaction. It is dependent on the internal motivation of the kth individual of the jth species.

The derivation of the model is based on the following information:-

a) "birds are guided to their breeding stations by a primarily innate reaction released by certain environmental stimuli, on the principle of summation of heterogeneous stimuli, as in instinctive activities in general. The threshold for the release of the reaction is dependent on the internal motivation of the bird." (Hilden 1965).

This indicates that the appropriate model contains a summation, and that the settling reaction occurs when that summation exceeds some level of accumulated stimuli. This threshold is modified by the internal motivation of the individual bird.

b) "sometimes one key stimulus may outweigh others : in its absence other stimuli are never sufficient to induce the bird to settle in a territory" (Hilden 1965).

This implies some system of weighting for each factor.

c) As different species are adapted to different habitats, it would be expected that each species has a characteristic set of proximate factors to which they respond. Hence the suffix j in the equation.

Further characteristics of this model:-

Tinbergen (1948) pointed out that within summation of heterogeneous stimuli

"many reactions may occur even in the absence of one of the environmental stimuli provided the motivation, dependent on internal factors, is high enough".

Applying this to settling reactions, it can be seen that the settling reaction may occur in a bird even if one of the proximate factors, characteristic of the species, is absent. Tinbergen also noted that

"available evidence strongly suggests that innate releasing mechanisms are always responsive to a combination of only very few environmental stimuli".

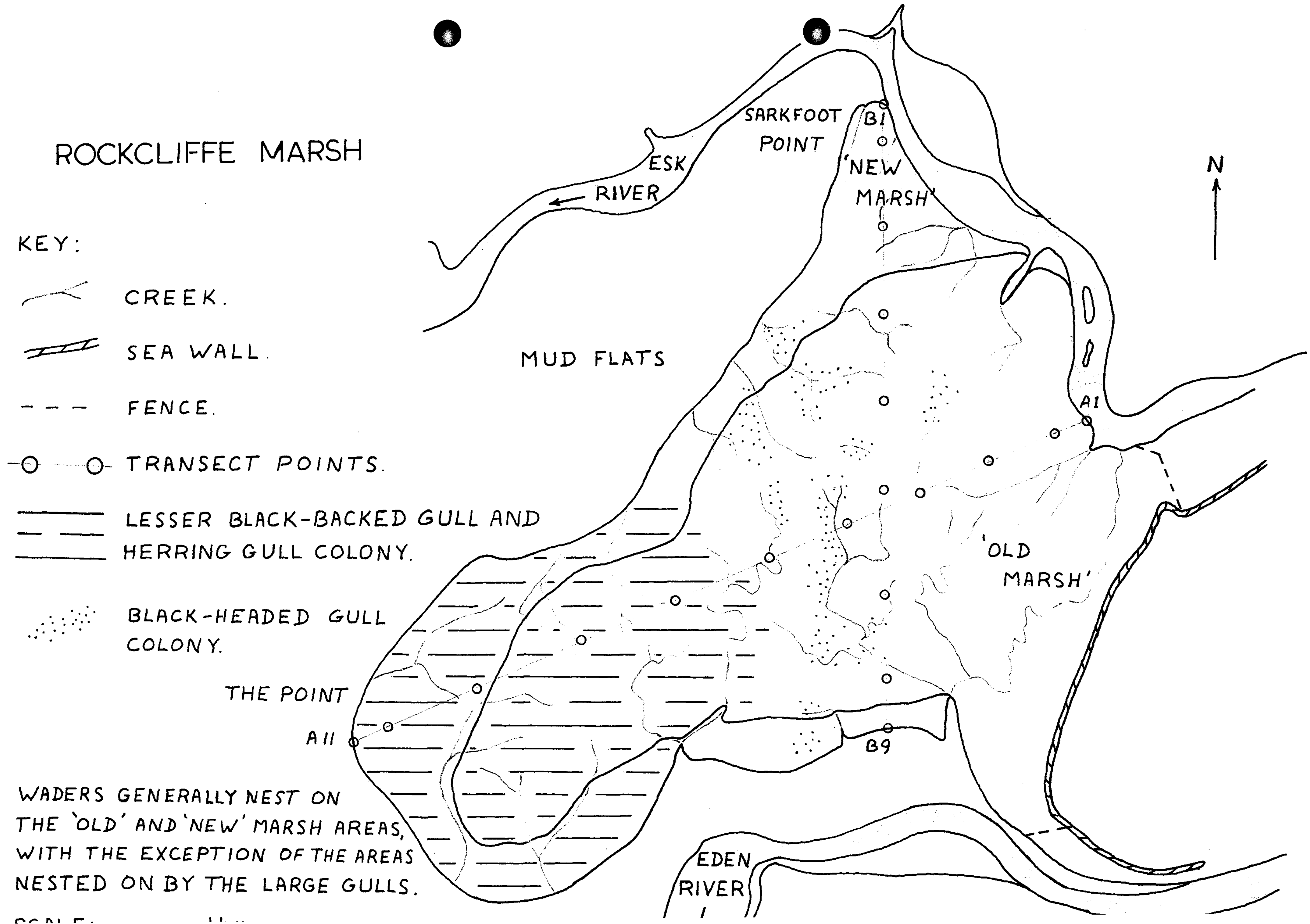
It would appear from this that for any individual selection, only a few proximate factors would be involved, and of these even fewer would be essential. This also implies, together with the information that the threshold for the settling reaction is dependent on the internal motivation of the bird, that different proximate factors could be selected by members of the same species.

The purpose of this study was to determine the proximate factors in nest site selection for each of three species of waders: Redshank (Tringa totanus Mathews), Oystercatcher (Haematopus ostralegus Neumann) and Lapwing (Vanellus vanellus L.). More particularly the purpose was to establish whether there were any differences between these three species. A secondary purpose was to establish the relative importance of the identified factors. The extent and scope of the study did not allow fulfillment of this secondary purpose, although in the discussion the factors of primary importance are indicated.

Rockcliffe Marsh, Cumbria, a large, dry salt marsh, is particularly suitable as the study area for the following reasons:-

i) The marsh is large and fairly uniform and possesses many areas which have different combinations of the various possible proximate factors under consideration. Also most of these factors do not appear to be correlated with each other, e.g. creeks occur over the whole marsh and are not more numerious in one vegetation type than in another. It is particularly advantageous that the possible proximate factors studied should not be correlated to each other as it would then be difficult to determine which of the correlated factors was being selected.

ii) The gradual gradation of some factors across the marsh, e.g. vegetation type, makes the differences selected for more clearly evident.


ROCKCLIFFE MARSH
KEY:
CREEK.
SEA WALL.
FENCE.
TRANSECT POINTS.
LESSER BLACK-BACKED GULL AND
HERRING GULL COLONY.
BLACK-HEADED GULL
COLONY.
THE POINT
A11
WADERS GENERALLY NEST ON
THE 'OLD' AND 'NEW' MARSH AREAS,
WITH THE EXCEPTION OF THE AREAS
NESTED ON BY THE LARGE GULLS.
ESK
RIVER
MUD FLATS
SARKFOOT
POINT
B1
'NEW
MARSH'
N
A1
'OLD
MARSH'
B9
EDEN
RIVER

ROCKCLIFFE MARSH

GENERAL VIEW OF THE MARSH
TAKEN FROM THE SEA WALL.

2.0 The Study Area

Rockcliffe Marsh is situated at the head of the Solway Firth between the rivers Esk and Eden (O.S. sheets 75 and 76, grid reference 325640) and lies approximately 10 km north-west of Carlisle. The land is owned by Castletown Estate and is used for summer grazing by cattle (approximately 1100 head of cattle were on the marsh this season). The owners have an agreement with the Cumbria Naturalists' Trust allowing wardening of the marsh from May till August each year to protect the breeding birds. The marsh is classified as a SSS1 by the Nature Conservancy and is considered to be one of the most important areas of its type in Britain.

The reserve is a dry salt marsh covering about 1130 ha. The area having increased by about 300 ha over the last 20 years due to deposition. The marsh is roughly triangular, about 4.3 km from east to west and 3.4 km from north to south and consists of firm turf interspersed with muddy drainage creeks which fill at high tide, (one creek is filled with run-off from agricultural land after heavy rainfall). The whole marsh is covered by the equinoctial spring tides; the presence and strength of a south-westerly wind and the amount of water in the Eden and Esk determining the extent of flooding.

The vegetation is very uniform and the average height is about 8 cm. The area and vegetation can be roughly divided into two basic types namely 'Old Marsh' and 'New Marsh' (further zones will be considered later on). The 'Old Marsh' type is a fescue grassland dominated by *Festuca rubra* L. with a tendency to a taller field type of vegetation towards the sea wall where *Lolium perenne* L. and *Bromus mollis* L. become important. The 'New Marsh' type is also dominated by *Festuca rubra* but is much sparser and possesses characteristic species such as *Armeria maritima* (Mill.) Willd., *Puccinellia maritima* (Huds.) Parl. and *Parapholis strigosa* (Dum.) C.E. Hubbard. This type covers large areas at Sarkfoot Point, The Point and towards the outer edges of the rest of the marsh. Only a small proportion is occasionally flooded. Areas which are frequently covered are in the process of being colonised by species such as *Plantago Maritima* L., *Aster tripolium* L., *Glaux maritima* L. and *Puccinellia maritima*.

A list of the main species of birds breeding on the marsh is given below together with the number of nests found in 1975.

Species	Number of nests found in 1975
Dunlin, *Calidris alpina* (Brehm).	5
Ringed Plover, *Charadrius hiaticula* L.	8
Reshank, *Tringa totanus* Mathews.	122
Lapwing, *Vanellus vanellus* L.	138
Oystercatcher, *Haematopus ostralegus* Neumann.	122
Common Tern, *Sterna hirundo* L.	244
Black-headed Gull, *Larus ridibundus* L.	1829
Lesser Black-backed Gull, *Larus fuscus* Brehm) Herring Gull, *Larus argentatus* Pontopp.)	1491
Skylark, *Alauda arvensis* L.	120

The Lesser Black-backed Gull and Herring Gull colonies cover a large area at The Point (see map). The ratio of Lesser Black-backed Gulls to Herring Gulls is approximately 4:1.

The Black-headed Gull colonies occur mainly along the edges of the drainage creeks and are distributed over most of the marsh.

Generally waders nested over most of the marsh with the exception of the area covered by the Lesser Black-backed Gull and Herring Gull colonies.

3.0 Methods

3.1 Field Methods

3.1.1 Data collection from an area surrounding each nest.

The four main alternative approaches to this study were:-

i) Selecting random areas and recording the characteristics of each area and the number of nests present, where each characteristic is a possible proximate factor. The characteristics could then be related to the presence or absence of nests, or to the density, of the different species and hence the proximate factors selected by each species could be calculated from their habitat preferences.

ii) Selecting areas at points along systematic transect lines.

iii) Selecting areas to include a sufficiently large sample from each vegetation zone.

iv) Recording the characteristics of an area around each nest found. The proportion of the nests of each species associated with a certain characteristic could then be compared with the random occurrence of this characteristic on the marsh to determine whether selection existed. Comparisons could also be made between species hence excluding the random samples.

The last method was chosen to enable as large a sample to be collected as possible. If any of the first three methods had been used a large number of known nests would have been ignored unless a large proportion of the area of the marsh was sampled by systematic searching, which was clearly impractical.

The data collected in this manner were supplemented by data collected from 2 transect lines set up across the marsh. The use of the transect data is based on the density of the adult waders in different areas and will be discussed later.

A total of 73 nests were recorded; 20 Redshank, 18 Lapwing, 26 Oystercatchers, 5 Ringed Plover and 4 Dunlin. Insufficient nests were found of the latter two species to obtain any significant results.

When recording the characteristics of a nest site an area of 10,000 m^2 around each nest was considered i.e. a radius of 56 m about the nest. This area was searched for the presence of any other nests and if present the number and distance between these and the first nest was recorded.

Long distances were measured by pacing. The error was not considered to be important as measurements referring to different species and to the random samples were equally affected.

The following information was recorded for each nest and will be discussed immediately after.

1. Date
2. Species
3. Marker number
4. Position ____Km N, ____Km E
5. Number of eggs
6. Number of chicks
7. Date 1st layed
8. Date of hatching
9. Abundance of nests:- Species. No. nests/ha

   i)
   ii)
   iii)
   etc.

   "for each nest"
10. Distance to nearest nest:- Species. Distance (m)

   i)
   ii)
   iii)
   etc.
11. Distance to sea wall or fence (m)
12. Distance to nearest creek or edge (m)
13. Abundance of driftwood, 0 to 5.
14. Distance of driftwood from nest (m)
15. Gravel or stone:- Yes/No
16. Abundance of tussocks, 0 to 5
17. Uneveness excluding tussocks, 1 to 4
18. Nest in tussock:- Yes/No
19. Height of tussock (cm)
20. Mean height of tussocks (cm)

21. Mean height of grass in between tussocks (cm)

22. Soil type (humus content), 1 to 3

23. Vegetation type of the area

24. Nearest transect type with similar vegetation

The abundance of driftwood was measured on a subjective scale of 0 to 5, 0 indicating none present and 5 a large amount. The abundance of grass tussocks was measured on a similar scale and the uneveness of the ground excluding the tussocks was measured on a 1 to 4 scale. For soil type a subjective measure of humus content was used on a 1 to 3 scale, 3 indicating a relatively high humus content and 1 a low content.

The various plant communities on the marsh were classified into a hierarchy of maturity. An area of 1 ha around each recorded nest was then classified into one of these types. The dominant plant species within 20 cm of each nest was also recorded.

The food availability at the nest sites was not sampled for the following reasons:- A number of core samples (10.2 cm x 7.6 cm) were taken from the marsh and less than 5 invertebrates greater than 2 mm in length were found in each sample. The samples were both hand sorted and put into Berlese Extraction Funnels. It was considered that invertebrates less than 2 mm long would not comprise an important part of the waders diet. Hence due to the low density of invertebrates it would have been necessary to use pitfall traps at each nest site in order to collect a sufficiently large sample. Due to the number of nests recorded and the area over which they were dispersed these could not have been collected under similar weather conditions. It would also have been impractical to sort the large number of samples collected.

The methods used in determining whether food is a proximate factor for the three waders will be discussed in the section on transect data.

The frequency of occurrences of various factors on the marsh were determined by walking over the marsh for 3 hours along a number of transect lines and stopping on the minute every 3 minutes to record the distance to the nearest creek, abundance of tussocks, soil type etc. This systematic selection of points seemed the simplest means of approximating to a random selection. It should be noted that the transects used here are separate from those used in 3.1.3. The area covered by the Lesser Black-backed Gull colony was not considered as few wading birds nested there.

3.1.2 Other data collection relating to the nest

3.1.2.1 Hatching success and predation

The number of eggs found in each nest were recorded and the nests were visited as often as possible on successive days so that the number of chicks hatching could be recorded. Chicks from about half the recorded nests were seen. Predated nests were also noted.

3.1.2.2 Distance that prefledgling birds move from the nest

a) Chicks were ringed and for those found again the distance from their nest was measured. Reshank chicks were very difficult to find and no ringed chick was found again.

b) A few adults were marked before their eggs hatched. Their presence, when exhibiting protective behaviour, indicates the presence of their chicks in the area. Hence a rough idea of the distance moved from the nest can be obtained.

One Redshank and three Oystercatcher adults were colour ringed. The birds were caught by placing funnel shaped traps over the nest towards the end of the incubation period when the birds were hard sitting, then leaving the area for a short time and approaching the nest from the entrance to the trap when the bird had returned to the nest. No Lapwings were caught as they were too suspicious to enter the traps.

Colour ringing was not effective as the bands were obscured by the grass when the birds were on the ground and could not be seen when the birds were in the air. Hence dyeing was tried. Picric Acid was used in a solution of 59% distilled water, 40% alcohol and 1% acetic acid, the latter two to increase the penetration of the dye, giving a dark yellow colour. This information was obtained from an unpublished report by the U.S. Department of the Interior, Fish and Wildlife Service. The solution was tried on a few old feathers to ensure that it did not damage the feather structure.

The marking was effective on the only Oystercatcher dyed, the dark yellow contrasting well with the white underwing. Two Redshanks were also dyed but were not seen again. They were either very wary of intruders after being handled and left the area when approached or otherwise the dye adversely affected them in some way. The eggs of all marked adults hatched and the chicks left the nests.

3.1.2.3 Faecal Pellets

Faeces evacuated by birds during handling were collected, preserved in 2% formalin and analysed for invertebrate remains at a later date.

3.1.3. Transect data and collection of invertebrates.

Two transect lines were established across the marsh, A and B (see map). A total of 16 points were marked out at approximately equal distances along the transect lines with wooden stakes. At these points pitfall traps were set and bird counts were recorded. Birds were also counted on the mud flats and river banks at the ends of the transect lines. Eight sets of bird counts were recorded in all and six sets of pitfall traps were collected.

The transect data were collected to provide data on further possible proximate factors. This was done by relating the number of birds at each point along the transects to the various characteristics of the area and determining which factors were being selected. This procedure was considered valid for the following reasons:-

i) Adults of the three wader species remain in the vicinity of the nest both before the eggs have hatched and also after the chicks have left the nest (this will be shown later).

ii) Of the three species studied it was noted that only the breeding waders occur on the marsh. This was concluded as alarmed and protective behaviour and was observed in nearly all individuals of the three species when approached on the marsh. The only exceptions were flocks of obvious non-breeders (Lapwings) which fed on the marsh and mud flats towards the end of the breeding season.

Hence it can be assumed that the number of nests in the area is proportional to the number of adults present. Therefore the number of adults indicate the attractiveness of the areas as nesting sites and this number can be correlated with the possible proximate factors.

It should be noted that this method only gives information on the selection of a general area suitable for a nest site and can not provide information on the finer selection of the precise point for a nest e.g. distance from a creek.

The possible proximate factors considered using this method were food availability and the effect of the presence of gulls on the waders.

The data were also used to study the distribution of invertebrates over the marsh and to determine whether this could be related to the vegetation types. This was done so that if vegetation was found to be a proximate factor then an association between vegetation and food supply would imply that food may have been the ultimate factor selected for rather than, say, cover.

With regard to food being an ultimate factor it should be noted that it is at the time when the young are in the prefledgling state that the abundance of food is important, rather than at the time when the nest is selected. Hence if food is an ultimate factor one proximate factor in the selection of the nest site must predict the food supply. This could be, say, vegetation type, or abundance of invertebrates if their distribution is not likely to change with time.

The bird counts were started and the initial traps were set on 19 June. More than half the waders had hatched by this time and hence the abundance of invertebrates can be related to the number of adults, and thereby the number of nests, to determine whether food supply was selected for.

3.1.3.1 <u>Bird counts</u>

The total number of birds of each species within a radius of approximately 250 m of the observer were counted. This was considered a reasonable maximum distance for the count not to be too biased in favour of conspicuous birds such as Oystercatchers compared to Redshanks. Densities cannot be directly based on this area as the birds move away from the centre. When the number of birds exceeded 30, e.g. in the gull colonies or waders on the mud flats, then a system of grouping in steps of 50 birds was used i.e. $x<50$, $50<x<100$ etc. Large flocks on the marsh were not counted as these were made up of non-breeding birds.

The time taken to complete both transects when counting birds and also collecting the samples from the pitfall traps was about 8 hours. Hence the counts were not done at either high or low tide alone. The transects were usually started between 10 and 11 a.m.

3.1.3.2 <u>Sampling for invertebrates</u>

One set of soil samples were collected from points along transect A using a 10.2 x 7.6 cm soil borer. Four samples were collected from each point and both sorted by hand and put into Berlese Extraction Funnels. Less than 5 invertebrates greater than 2 mm were found in each sample. Another set of soil samples were collected along transect B by digging up an area of 0.25 m^2 at each point and hand sorting it. No invertebrates were found in three of the seven samples although 8 tipulid larvae were found in one sample. Oystercatchers were often seen rooting about in the soil, however when these areas were searched by digging little could be found.

Hence the density of invertebrates on the marsh appears to be low and it was therefore decided to use pitfall traps as the main method of collection. Their use in the estimation of population density is questionable e.g. Greenslade (1964),

"pitfall trapping cannot properly be used for quantitative assessment of the Carabid fauna of any habitat, nor should it be employed to compare the numbers of one species in different habitats." Southwood (1968) considers that this can be applied to most species.

The quantity of animals collected in a pitfall trap is dependent on both the population density and also the activity of the animals. It is this last factor which complicates the interpretation of the results. This is because activity is a behavioural characteristic and varies between species. Activity is also dependent on temperature in invertebrates.

The temperature effect can be reduced by only comparing samples collected over the same period or under similar weather conditions. The behavioural effect means that the numbers of two different species collected may not be an indication of their relative population size. However theoretically it appears possible to compare the population densities of one species in different areas, provided the habitats of the two areas are similar. The last condition is necessary as the activity of an invertebrate is dependent on the physical structure of the habitat through which it is moving. As the variation in physical structure of the vegetation on Rockcliffe Marsh is not large it seems reasonable to use the data in this manner. The conclusions of Greenslade (1964) do not support this view however due to the low density of invertebrates no practical alternative method was available.

Three traps were initially set at each transect point and a fourth was added later. Plastic cups 69 mm in diameter were buried level to the surface and approximately 10 m apart. A small amount of water and a drop of detergent was added to each. The traps were initially left for one week before collection however it was found that the animals had started to decay and thereafter they were collected on the fifth day.

A number of traps were trodden on by cattle and other traps were pulled out of the ground by the larger gulls. Due to this a few sets of collections were discarded as some points had no intact samples. Thin wooden sticks had to be used to secure the traps in the ground in areas near the Lesser Black-backed Gull colonies. When collected the invertebrates were preserved in a 2% formalin solution.

Some larvae found in cow pats were collected as Oystercatchers were often observed breaking up the cow pats to obtain the larvae in them.

Invertebrates living in the creek muds were collected by sifting mud through graded meshes.

To determine whether cattle presence affected the invertebrate or bird life by means of their faeces, or some other factor, the number of cow pats in the area of each transect point were counted. This was done by counting the number of pats within 3 m of either side of ten 50 m transect lines.

3.2 Analytical Methods

3.2.1 Data collected from an area surrounding a nest

3.2.1.1 Comparison with the random samples

The purpose of the analyses was to determine whether the waders selected certain features of an area (the proximate factors) in which to build a nest. To do this the proportion of the total nests recorded of one species which occurred in an area possessing a particular characteristic, was calculated. This proportion was compared with the proportion of the random samples which also possessed this characteristic. The 'Null Hypothesis' for a χ^2 test was that the former proportion was obtained by random selection by the waders and hence could be combined with the latter. Therefore the expected values could be calculated from the pooled results, i.e. a homogeneity test was done on the two sets of data. If the probability of the 'Null Hypothesis' being valid was found to be less than .05 then it was assumed that the first set of data was not random. Hence the particular characteristic being studied was considered to be a proximate factor selected by the wader species under consideration.

A 2×2 χ^2 table was usually used however the method is also valid for a $2 \times c$ χ^2 table, where c is the number of columns For example; the distances of Oystercatcher's nests from the edges of creeks can be compared with what would be expected to occur randomly by counting the number of nests within distance groupings from the edge and comparing these with the random samples.

Null Hypothesis:- Both these sets of data occurred by chance

i.e. a test for homogeneity of data

	0 to 15 m	15 m to < 30 m	30 m and above	Total
Observed No. of Oystercatcher Nests	17	4	5	26
Random Samples	13	20	17	50
Total	30	24	22	76
Expected No. of Oystercatcher Nests	10.26*	8.21	7.53	26
Expected Random Samples	19.74	15.79	14.47	50
Total	30	24	22	76
Nests χ^2	4.43	2.16	0.85	
Random Samples χ^2	2.30	1.12	0.44	

*The expected value of 10.26 = $\frac{26}{76}$ X 30.

$$\sum \chi^2 = 11.30$$

Degrees of freedom = 1, because the expected values are based on the observed values and hence a further degree of freedom is lost.

The result is therefore highly significant ($P<.001$) and the 'Null Hypothesis' does not hold. Therefore the Oystercatchers exhibit a significant tendency to build nests less than 15 m away from the edge of a creek. Hence the distance from the edge of a creek is a proximate factor for the Oystercatchers during nest site selection. This method will be applied to the following factors recorded about the nest site areas. The numbers refer to the list given previously.

12. Distance to edge of creek.
13. Abundance of driftwood.
16. Abundance of tussocks.
17. Uneveness excluding tussocks.
22. Soil type (humus content).
23. Vegetation type.

3.2.1.2 Density of nests within the 1 ha area

To determine a hierarchy of importance of the proximate factors it would be necessary to know the density of nests in a number of different areas and to use the data in a regression analysis. However the sampling method used does not lend itself to the calculation of density for the following reasons:-

(i) An area of 1 ha around each nest found was searched for further nests and the total number of nests of each species was recorded. This resulted in:- (a) a minimum density of 1 for the species at the centre of the area; (b) a density of 0 for the other two species in more than half the cases recorded, and (c) a maximum density of 3 for each species due to the relatively small area considered. These data fit a Poisson distribution and not the normal distribution as required by regression analysis.

(ii) Each nest was considered to be the centre of an area and therefore when a few nests were close to each other these areas overlapped substantially. Therefore these nests contributed to two or more sets of density data. This could be overcome by only considering a nest once, however this would reduce the sample size drastically.

Because of these qualifications on the density data and also because of the shortage of time it was decided not to use the data in this form.

3.2.1.3 Presence or absence of waders nests in the 1 ha area

The data on the number of nests in each 1 ha area was used to draw up a table of the joint presence or absence of the three waders. From these data it could be determined whether the presence or absence of another wader of the same or another species increased the attractiveness of the area, i.e. whether they were a proximate factor.

Further information on whether the nests were clumped or evenly distributed could have been obtained by nearest neighbour analysis. However only the distances between nests less than 100 m apart were measured. It would therefore have been necessary to do the calculation on the basis of the proportion of nests which would be expected less than a certain distance apart and to compare this with the observed proportion. To find the expected value it is necessary to know the density of the nests on the marsh (Holme 1951). Qualifications regarding the density data have already been discussed. It was therefore decided not to do a nearest neighbour analysis.

3.2.2. Transect Data

3.2.2.1 Bird Counts

Eight sets of counts of all bird species were made along the transects between 19 June and 5 July, however the last two were discarded as the numbers of Redshanks and Lapwings on the marsh had started to decline. The Redshanks with fully fledged young left the marsh whereas the Lapwings formed large flocks, sometimes exceeding 500, and moved about the mud flats and marsh. The mean was taken of the 6 counts at each transect point. The counts of the birds feeding on the mud flats are not shown in the transect diagrams, as their numbers are not associated with the breeding areas. Flocks of non breeding waders on the marsh were not included in the counts for the same reason.

3.2.2.2 Invertebrate Data

The first nearly complete set of pitfall traps were collected on 16 July and traps collected between then and 31 July were used. The weather conditions during this time were fairly variable, however as the traps were out for 5 days at a time this evened out the variation to some extent.

The invertebrates from 6 traps at each transect point were counted, a total of 96 traps. They were divided into orders and then again into sizes e.g. Diptera >7 mm, 2 mm<Diptera <7 mm, Diptera <2 mm. Size classification rather than family or genus was chosed due to the limited time available for sorting. One transect point, A5, was covered in more detail to show the relative numbers of the different families which were collected. A specimen of each species found was taken out for identification at some later date.

About ten samples of each size group were weighed, the number of individuals in each sample depending on the size of animals considered. In some groups there were only a few individuals and in these cases only a few samples could be weighed. A number of individuals from each order in each size group were collected, dried and weighed. The mean weights per individual were calculated and these were used to convert the mean numbers of invertebrates counted into mean weights. The weights were expressed in mg per trap per day.

The weights were not used to determine the significance of differences of invertebrates between points on the transects as they represent a product of two means each with standard errors. Therefore when checking for significant differences the mean numbers of each size group in each trap were calculated together with their standard errors. These values were then used to calculate 'Students' t between all the points. Only those groups of invertebrates which contributed a sizeable proportion of the total weight of invertebrates collected at each point were compared. Tables were drawn up to show the weights of invertebrates collected at each point and also their mean weights in each vegetation type.

3.2.3. Classification of Vegetation

The vegetation was classified into different types for the following reasons:-

i) Plants can be considered to be sensitive indicators of their environment (Poore 1955). Therefore vegetation types may be indicative of areas of different food availability.

ii) The physical nature of the vegetation, e.g. density or height, is directly dependent on the species present and the birds or invertebrates may react to these differences.

Eight types of vegetation were identified. The classification used was based on a tabulation of the abundance of the species of plants against the various sampled points. Samples having a similar vegetation were grouped together.

The abundance of a species was based on its percentage cover of the area. The species and their abundances were recorded at each transect point, and also at various points having apparently different vegetation from areas already sampled. Each sample was a subjective mean of a whole area and more than simply a description of a single quadrat throw. In some cases the vegetation described by a single sample has been classified as a vegetation type.

The sociability of each species is not included as it is partly a characteristic of the species and also partly dependent on percentage cover. The latter was found to be more useful in determining differences.

The samples are tabulated in the next section.

4.0 Results and Analyses

4.1 Classification of Vegetation

The results of sampling the various vegetation areas are given in

Table 1. Each sample is a subjective mean of a whole area. The sample from each transect point is shown together with six others which were taken from areas of vegetation types not covered by the transect points. These are described below:-

C1 - Taken from the north west area of the marsh which is frequently covered by high tides.

C2 - Taken from an area a little higher than C1 at Sarkfoot Point.

C3 - This represents an area near the sea wall which is one of the maturist types of marsh vegetation.

C4 - Taken between transect points A5 and A6. This is a low area approximately 100 m wide on one side of a creek near the centre of the marsh. No other area of similar vegetation exists on the marsh. There are large Black-headed Gull colonies to the west of this area and it seems to form a border between the main Black-headed Gull colonies and the nesting areas of the waders although there are large overlaps further north.

C5 - This is an example of the vegetation occurring in a creek which is filled by high tides. It was taken from a creek near the Esk river.

F1 - An example of a field type of vegetation on the land side of the sea wall.

The physical characteristics of the vegetation were described on a 1 to 5 scale of increasing density. The bare ground present is given as percentage cover. The figures in the bulk of the table represent the percentage cover of each of the species, + indicates presence.

The first group of species* listed are the grasses, then the sedges and rushes and then the rest of the orders of plants are combined. The two groups besides the sedges and rushes are ordered such that the first species is characteristic of areas being colonised and this roughly grades down to species characteristic of mature grassland.

With the exception of the last two columns the samples were ordered such that the vegetation type increases in maturity from left to right. The result of both these groupings is a diagonal pattern from top left to bottom right.

Basis on which the vegetation types were differentiated:-

T1 - Plantago maritima is the dominant plant and this separates it from all other types.

T2 - Distinguished from T1 by a higher percentage of cover by grasses. And from the other types by its relatively low percentage of cover by grass, also its bareness and higher percentage cover by Puccinellia maritima and Parapholis strigosa.

T3 - Distinguished from T4 by the relatively high percentage of Festuca rubra, plus the presence of Puccinellia maritima and Parapholis strigosa, and also the relatively high percentage of Armeria maritima.

T4 - Distinguished from T5 and T6 by the absence or low percentage cover of the taller grasses such as Lolium perenne, Bromus mollis and Holcus lanatus, the usual presence of Glaux

VEGETATION TYPE T3 - 'NEW MARSH' AREA.
OYSTERCATCHER'S NEST IN FOREGROUND.

VEGETATION TYPE T6 - 'OLD MARSH' AREA

maritima and *Plantago maritima* and the absence of *Bellis perennis*.

T5 and T6 - T5 tended to occur in areas near the centre of the marsh surrounded by T4. The differences between T5 and T6 are not large, T6 having a higher percentage cover by the taller grasses such as *Holcus lanatus* and *Cynosurus Cristatus*, and less *Festuca rubra* and *Agrostis stolonifera* than T5.

The 'New Marsh' area is comprised of T1, T2 and T3. However as waders do not nest on T1 or T2 (because of frequent flooding) in discussion of nesting the term 'New Marsh' refers to T3, unless otherwise stated.

The 'Old Marsh' area is comprised of T4, T5 and T6. The latter two are referred to as 'mature grassland areas'.

The last three columns of the table represent very different types of vegetation and were included for descriptive purposes.

As can be seen the density of the vegetation is closely related to its classification.

*All specific names of plants used in the table and in this report generally are as used by Keble Martin (1969).

4.2 Results based on the area surrounding each recorded nest.

4.2.1 Determination of possible proximate factors

Taking note of work done on nest site selection and taking note of the characteristics of the area and of the species of study, seven factors emerged as possible proximate factors. These were:-

i) Distance to nearest creek.

ii) Abundance of driftwood.

iii) Abundance of tussocks.

(iv) Uneveness excluding tussocks.

(v) Soil type (humus content).

(vi) Vegetation type.

(vii) Presence of other waders of the same or other species.

The information presented in the form of graphs in this section would be more correctly represented in the form of histograms. However it is considered that this form aids presentation.

i) Distance to nearest creek

The distance of each nest from the nearest creek was described in 5 m units e.g. 0 to <5, 5 to <10 etc. The numbers of nests in each distance group were then expressed as a percentage of the total number of recorded nests of that species. The results are given on Graphs 1 and 2. All percentages used in this section were derived in this manner. The random samples taken from the marsh are also shown.

The proportion of Oystercatcher nests found less than 10 m away from a creek is significantly higher ($P < .001$) than the proportion of the randomly sampled points which fell within this distance. Redshanks and Lapwings do not deviate significantly * from the distributions given by the random samples.

Hence for Redshanks and Lapwings the distance from the edge of a creek does not appear to be a proximate factor, or if it is then its importance relative to the other proximate factors for these two species is low.

For Oystercatchers distance to the edge of a creek is therefore clearly a proximate factor. It is a fairly important factor though not essential as a number of nests were not placed near a creek.

ii) Abundance of driftwood

The abundance of driftwood was found to be significantly associated with the vegetation types on the marsh. This was because the majority of the driftwood is deposited on the higher areas of the marsh as the tide recedes. The higher areas are covered by denser and taller vegetation than the lower areas.

The data on driftwood collected indicated that Lapwings had a

*Unless otherwise stated the significance level used is $p<.05$.

significantly greater tendency to nest amongst driftwood than did Redshanks. Insufficient data were available to differentiate between selection for driftwood and selection for vegetation type. However it is considered more likely that Lapwings would select for vegetation as they have previously been recorded as selecting (Klomp 1955). Hence the possibility of the abundance of driftwood being a proximate factor was not considered further.

iii) Abundance of tussocks

Graph 3 shows the number of nests found in each grade of abundance of tussocks. The distribution of the random samples is also shown.

The graph suggests that Redshanks have a marked preference for grades 1 and 2. When these two grades are combined a significance of $P<.01$ is obtained. The graph also shows that the Redshank numbers are low in areas of no tussocks, relative to the random samples. Also that they do not deviate from the random sample distribution for abundance of tussocks greater than 2. This suggests that Redshanks generally select areas possessing at least a few tussocks (the proximate factor), so that one is available for nest building, and that areas possessing more than this minimum have no added attraction.

The Lapwings appear to show some preference for areas with many tussocks, however the results are not significant. This preference may be associated with their preference for a denser type of vegetation which will be discussed later. Oystercatchers show no significant trends away from the random samples. Hence for these two species the abundance or presence of tussocks is notaproximate factor or at least is not an important factor.

iv) Uneveness excluding tussocks

The information collected is shown on Graph 4. No large deviations from the random samples are shown which suggest that this is not a proximate factor or at least not an important factor for any of the three species.

(v) Soil type (humus content)

The numbers of nests found in each soil type are given on Graph 5. The variation of the Lapwings and Oystercatchers from the random samples taken is not significant, whereas the differences between the Lapwings and Oystercatchers is significant. The trends correlate with the Lapwings' preference for areas having a dense type of vegetation whereas a large number of Oystercatcher nests occurred on sparse areas near the river banks. From the evidence available it cannot be determined whether the humus content of the soil is a factor selected for or whether it is correlated to some other factor selected for such as vegetation type. Also as neither of these two species deviated significantly from the random samples distribution it must be concluded that soil type is not a proximate factor or at least not an important one.

The rather strange distribution shown by the Redshanks is significantly different from the random samples. No explanation for the distribution can be put forward.

(vi) Vegetation types

See Graph 6. The histogram indicates 0% coverage of the marsh by gravel areas. This is because less than 1% of the marsh is covered by gravel and no random points fell on these areas.

The graph shows that Redshanks and Oystercatchers tend to prefer T3, the 'New Marsh' area, to T4. None of their deviations from the random sample distribution are significant.

The proportion of Lapwing nests found in T5 and T6 is significantly greater than the proportion of random samples falling in these two areas ($P<.01$). (T5 and T6 had to be combined for the expected value in the χ^2 test to be above 5). Hence the mature grassland vegetation on the marsh appears to be a proximate factor involved in the nest site selection of the Lapwings.

(vii) Presence of other waders of the same or another species

The number of cases of joint presence or absence of waders, within an area of 1 ha surrounding the nests of the three species, are given in Table 2, part A.

The densities of the three waders on the marsh are approximately equal as the total number of nests found in 1975 for each species were nearly equal. Hence the data shown in part A are not distorted by one species having a greater density than another. The proportion of Redshanks nesting within 56 m of another member of the same species (9/20), were compared with the corresponding numbers for Lapwings (2/18), and Oystercatchers (6/26). The proportions were compared by means of a χ^2 test. It was found that Redshanks have a significantly greater tendency to nest near another nest of the same species than do Lapwings. The difference between Redshanks and Oystercatchers is not significant.

These results are supported by the data given in Table 2, part B, which show that the minimum distance found between two Lapwing nests was 55 m, compared with 15 m between two Redshank nests. The data also indicate that the interspecific tolerance of proximity is high in all three species.

Hence, as the densities of the three species are approximately equal, it appears that Redshanks often select to nest near another nest of the same species. This means that the presence of a Redshank in an area increases the attractiveness of that area for another Redshank.

(viii) Further factors considered

Two other factors were recorded about the nest site area; mean height of tussocks and the mean height of grass in between tussocks. Neither of these factors was found to vary significantly between the nest sites of the three species of birds.

4.2.2 Further information obtained from the nest area.

4.2.2.1 Distances moved by prefledgling chicks from their nests.

i) Redshanks

No information. None of the 17 chicks ringed and 3 adults marked were encountered again.

ii) Lapwing and Oystercatcher chicks

Table 3 gives the distances moved by 7 ringed chicks, (4 Lapwings, and 3 Oystercatchers), which were found again. One Lapwing chick was found twice.

iii) Oystercatcher adults

One ringed adult at Sarkfoot Point was seen less than 50 m away from the nest on three occasions during the first three weeks after the eggs had hatched. The dyed adult at Edenside was seen less than 50 m from the nest during the first two weeks and less than 100 m from the nest during the next two weeks. It was last seen in the area 5 weeks after the chicks had hatched.

The results indicate that Oystercatchers remain close to their original nest site whereas Lapwings tend to wander over a greater distance. It would therefore be expected that food availability would be a more important factor in nest site selection for the Oystercatchers than for the Lapwings.

Although no formal results are available for the Redshanks they did not appear to move far from their nests, the distance being similar to that of Oystercatchers. This statement is based on the observation of 3 Redshanks in sparsely populated areas which remained in these areas for more than two weeks and behaved as though they had chicks.

4.2.2.2 Faecal droppings

Table 4 shows the invertebrate remains found in the faeces of 6 Oystercatchers; 4 chicks and 2 adults.

The first two chicks were found within 50 m of each other and yet their food intake was markedly different. This may have been due to age or individual food preferences.

The results of the capture of invertebrates in the pitfall traps in the next section indicate that the 'New Marsh' area at Sarkfoot Point is characterised by its low Coleoptera and high Diptera populations compared with the 'Old Marsh'. The results in this section show that individuals do not necessarily select the invertebrates which are shown to be most common by the pitfall traps.

The results from the faecal droppings also show that the Oystercatcher as a species is not specialised in its diet with regard to Diptera or Coleoptera.

4.3 Results based on the Transect data

4.3.1 Invertebrate data

4.3.1.1 Hand sorted samples

The following were the only invertebrates found in the 0.25m^2 hand sorted samples taken along transect B:-

'New Marsh'	B2	- none
	B3	- none
'Old Marsh'	B4	- 1 *Tipula paludosa* Larva
	B5	- 2 " " Larvae
	B6	- 8 " " "
	B7	- none
	B8	- 1 Coleoptera Larvae

These samples agree with the pitfall captures which suggest that Diptera and Coleoptera are the only abundant invertebrate groups on the marsh besides the Araneae.

Very few earthworms occur on the marsh. The only ones found were under logs near the sea wall. None were found in dung or soil cores taken elsewhere on the marsh.

The invertebrates found in cattle dung were:-

a) Dung beetle larvae (Geotropes and Aphodius)

b) Tipulidae larvae

c) Other Diptera larvae

A high proportion of large cow pats were found broken up by birds. Oystercatchers were often observed probing them.

The sea creek muds contained species of Nereidae, Gammaridae, Talitridae and Carophium sp..

4.3.1.2 Pitfall traps

At each of the sixteen transect points three traps were set and a fourth was added later. The contents of intact traps were collected at five day intervals and the traps reset. This collection continued until six trap contents were available for analysis at each point. This was necessary because the traps were susceptible to damage by cattle and by the Lesser Black-backed Gulls. It was therefore necessary to combine data collected under different weather conditions. However as each trap was set for a five day period a variety of weather conditions were covered, thus reducing the possible error in the numbers of invertebrates collected due to weather differences.

The first few batches of samples collected from the pitfall traps were discarded as some complete sets at certain transect points were emptied by the large gulls. Hence there is a time lag between the period when the bird counts were made and when the invertebrates were collected. However no general trend of change in invertebrate numbers with time was found. Therefore correlations could be made between the bird counts and the numbers of invertebrates.

Table 5 is a list of the families of invertebrates found in the pitfall traps to show which families occur in the size divisions used. The numbers found in 3 pitfall traps at transect point A5 are also given and those species normally associated with cattle (Laurence 1954) are indicated.

The invertebrate orders were divided into size groups to increase the accuracy of the conversion from numbers to weight. The results are given as the weight of the whole order.

Table 6 gives the dry weights of the orders of invertebrates collected at each transect point expressed in terms of mg per trap per day. The occasional relatively high weights in the orders are mainly due to the capture of a large member of that order. It is evident that Diptera comprise the major portion of the invertebrates collected. Coleoptera and Araneae are the second most important. These three orders of invertebrates are plotted on Graphs 7 and 8, together with the mean number of cow pats counted. The weights of these three orders are also expressed as a percentage of the total dry weight collected, in Table 7.

i) Correlation of Diptera to the number of cow pats

Cow pats form the main food source on the marsh for Diptera and they also indicate the amount of time spent in the area by the cattle. It would therefore be expected that the number of Diptera would be closely correlated to the number of cow pats. From Graphs 7 and 8 this appears to be the case with the exception of points B2, B3 and A4.

Graph 9 is a scatter diagram of the total Diptera weight at each transect point, plotted against the number of cow pats. From Graphs 8 and 9 it appears that some other important factor is affecting the numbers of Diptera at points B2 and B3. This interfering factor may be the distribution of overwintering Diptera larvae. Their distribution will largely depend on the distribution of cow pats towards the end of autumn, when the cattle are removed from the marsh. Therefore the distribution of cattle the previous year may have a large influence on the distribution of the larvae emerging in the spring (Laurence (1954) points out that overwintering larvae may take between 90 and 200 days before emergence). This in turn will determine the distribution of adult Diptera in the spring. The cow pats in areas of initially high Diptera numbers will be better utilised for egg deposition than in other areas and this may distort the correlation of Diptera with cow pats for the rest of the season.

As points B2 and B3 deviate markedly from the general trend they were excluded from the correlation of Diptera with number of cow pats. A significant correlation ($P<.02$) was found for the remaining points. It was therefore concluded that cattle presence generally governs the distribution of Diptera across the marsh.

The weights of Araneae and Coleoptera are not correlated with the abundance of cow pats.

ii) Factors affecting cattle distribution and thereby the distribution of Diptera

The 10 counts of cow pats at each transect point (Section 3.1.3.2), were each assigned to one of the vegetation types. The mean number and standard error of these counts were then calculated for each vegetation type and are given below:-

	Vegetation type			
	T3	T4	T5	T6
Mean number of cow pats	24.5	56.3	78.6	72.3
Standard error	1.7	1.8	4.6	4.8

With the exception of T5 and T6 the mean numbers ± 2S.E. do not overlap and hence the differences between the mean numbers are significant. It is evident that the cattle have a preference for the mature grassland areas, (T5 and T6). From Table 7 it is evident that the percentage that Diptera comprise of the total weight of invertebrates collected, decreases from A2 to A10.

From Graph 7 it can also be seen that both the weights of Diptera and the number of cow pats tend to decrease from A2 to A10. The significance of this decrease can be determined by assuming a unit distance between each transect point, and correlating both weight of Diptera collected and the number of cow pats against this distance. For Diptera $m = 1.12$, $c = 17.88$, r = 0.78; and for number of cow pats m = -6.81, c = 83.57, r = 0.77; degrees of freedom = 7 for both. The results are significant (P<.02).

The vegetation is roughly graded from a mature grassland type at point A2 down to the sparse 'New Marsh' type at A10. From the information given on the type of vegetation preferred by cattle, it can be concluded that the gradation of vegetation across the marsh determines the cattle distribution and thereby the distribution of Diptera. This will be taken a step further in a later section when it will be shown that the numbers of Oystercatchers are correlated with the weight of Diptera collected.

iii) Invertebrate distribution with respect to vegetation type.

The weights of the invertebrates from each transect point were grouped according to the vegetational types to determine the pattern of distribution. Table 8 gives these mean values in terms of mg per trap per day. Table 9 gives the percentage contribution of the three main orders.

The mean and standard error of the numbers of individuals found in each vegetation type were calculated. 'Students' t was used to determine whether the differences between the main groups were significant. Only the Diptera, Coleoptera and Araneae were considered as they were the main contributors to the total biomass. And of these only the size groups in each which significantly contributed to the total weight of the order were compared across vegetation type.

The vegetation of The Point (transect points A9 and A10) and Sarkfoot Point (B2 and B3) were very similar and were classified in the 'New Marsh' type (T3) group, however these two areas exhibit large differences in the invertebrate densities found. Because of these differences the 'New Marsh' area in Table 4 has been divided into T3A and T3B, the latter being based on transect points B2 and B3.

The number of Diptera in T3B is significantly larger than that in T3A and the number of Coleoptera, Araneae and gamarids significantly lower. Therefore these two areas possessing the same vegetation, have a significantly different spectrum of invertebrates.

From Table 8 it can be seen that the weight of Diptera collected in T6 does not vary greatly from that collected in the other 'Old Marsh' types (T4 and T5), nor from that collected in a field (F1). It is also evident that this weight lies in between the weights collected from the two 'New Marsh' areas. As the vegetation types exhibit increasing maturity from T3 up to T6 it is evident that the densities of Diptera are not correlated with the vegetation types.

With regard to Table 8, the large weight of Coleoptera collected in a field (F1) was due to the large number of Coleoptera between 7 mm and 15 mm collected. The number collected was significantly greater than all the marsh collections. Two large carabid beetles (18 mm) were collected at transect point A2. This contributes 2.71 mg to the total of 3.99 mg for the mature grassland type T6. This leaves the weight of the remaining Coleoptera in the area not varying greatly from that over the rest of the marsh. Tables 8 and 9 suggest that there may be an increase in Coleoptera density with increasing maturity of vegetation type. However comparing the numbers collected indicates that this increase is not statistically significant. Therefore on the marsh there does not appear to be a close correlation between the density of Coleoptera and the vegetation types. This is also true of Araneae.

From Table 6 it is evident that the total weight of invertebrates collected at each transect point does not vary greatly; the mean weight collected was 19.6 mg/trap/day and the greatest deviation from this is 8.9 mg.

Invertebrate densities do not appear to be closely correlated with the vegetation types. Hence each vegetation type is not indicative of the invertebrate densities which occur in it. It is therefore concluded that vegetation is unlikely to be selected for as a proximate factor for food.

4.3.2 Bird counts and correlation to invertebrate data

The mean numbers of waders, gulls and terns, based on 6 counts at each transect point, are shown on Graphs 10 to 13. The number of birds within a radius of 250 m of each transect point were counted. The counts were made between 19 June and 30 June. Counts made on the mud flats, the end points of each transect, are not shown as they bear little relation to the territories of birds on the marsh.

4.3.2.1 The presence of gulls as a proximate factor for waders.

The transect data were collected before the gull colonies broke up. As these colonies were formed while the waders were selecting their nest sites, the presence or absence of a gull colony, (i.e. large numbers of gulls), in the transect data, can be considered as a possible proximate factor in the nest site selection of the waders.

i) Transect A

From a comparison of Graphs 10 and 11 it can be seen that there is a marked reduction in the numbers of waders, particularly Redshanks and Lapwings, in the vicinity of large gull colonies. The sharp reduction occurs between A5 and A6 where the Black-headed Gull colony starts. The Black-headed Gulls counted at A5 were on the periphery of the 250 m radius within which birds were counted, the main colony being around A6. The Common Terns arrived after the gulls and nested amongst them. The Lesser Black-backed Gull and Herring Gull colony starts at A8, A7 being a buffer zone in which no gulls nest. Aerial conflicts between the small gulls and terns and the large gulls appeared to be much more frequent over this area of the marsh than over other areas.

The bird counts along transect A give a good picture of the zonation of bird species across the marsh. Using transect A data, a correlation of the numbers of waders with the numbers of large gulls was made. Only the Oystercatchers showed a significant negative correlation. This is initially rather surprising as the Oystercatchers appear to be less affected by the large gulls than do the Redshanks or Lapwings. However this is due to the lower numbers of the latter two used in the correlation. Using a 2 x 2 Contingency table based on joint absence or joint presence gave a value of 3.65 for both Redshanks and Lapwings. However this value is not significant, the sample size being too small. Using the data from both transect lines shows that the three species of waders all have a significantly negative correlation with the presence of large numbers of Herring Gulls and Lesser Black-backed Gulls.

ii) Transect B

Transect B skirted the edge of 5 large Black-headed Gull colonies but did not go through any. From Graphs 12 and 13 it appears that waders are not adversely affected by the presence of small numbers (less than 15) of Black-headed Gulls. Several cases of Lapwings nesting near small colonies of Black-headed Gulls were found where the nesting sites had been selected after the gulls had laid.

The close relationship between the Common Terns and the Black-headed Gulls shown along transect A is not shown along transect B. Terns were found nesting near all the species of wading birds on the marsh.

Correlations were made between the numbers of Redshanks and Lapwings and Oystercatchers based on data from transects A and B but excluding points A7 to A10, as the Lesser Black-backed Gulls and Herring Gulls were the dominating influence in this area. There is a significant correlation between Redshanks and Lapwings. This may be because either both species find the same areas attractive, or because the presence of Lapwings offers some protection to the Redshanks. The correlation of the numbers of Oystercatchers with those of Redshanks and Lapwings was not significant, however their distribution was similar, (r = + 0.235, d.f. = 10 with Redshanks; and r = + 0.463, d.f. = 10 with Lapwings).

4.3.2.2 Correlations of bird counts with the weight of invertebrates collected.

The correlations in this section were also based on the data from both transect lines (again excluding A7 to A10).

Neither Redshanks nor Lapwings showed any significant correlation with any of the invertebrate orders considered, or with the total invertebrate weight collected at each transect point. None of the waders were correlated with the number of cow pats.

A scatter diagram of Oystercatchers against weight of Diptera collected is given on Graph 14. All points are statistically equally weighted. It is evident that B4 deviates from the general trend. B4 can be excluded on the assumption that an intervening factor was distorting the distribution of Oystercatchers in this area. This factor may have been the presence of about 15 carrion crows near the centre of the marsh towards the end of the breeding season. Excluding B4 a correlation coefficient of 0.773 is obtained which is significant to $P<.01$.

This information plus the evidence given previously that Oystercatchers do not wander far from their nest sites, suggests that food is one of the factors involved in the Oystercatchers' selection of its nest site.

Table 1

DESCRIPTION AND CLASSIFICATION OF VEGETATION

Vegetation Type	T1	T2	T3				T4										T5	T6		Field	Low wet area	Sea creek
Transect No. or Sample No.	C1	C2	A10	B2	A9	B3	A3	A4	A6	A7	A8	B4	B5	B6	B7	B8	A5	A2	C3	F1	C4	C5
Physical (1 to 5)	1	1	2	2	2	2	3	3	3	4	4	3	3	4	4	4	5	5	5	5	2	3
Bare ground (%)	25	25	10	10	5	5	1	2	1	1	1	1	1	1	1	1	0	0	0	5	5	25
Puccinellia maritima	+	10	5	+	5	5															20	20
Parapholis strigosa	+	10	+	5		5								+								
Festuca rubra	+	10	70	70	60	60	40	40	40	40	40	50	50	40	50	50	30	20	20			5
Agrostis stolonifera		10	+	+	+	+	20	20	20	20	20	20	20	20	10	10	10	5	5		40	10
Poa annua				+			5	5	10	5	10	5	5	10	+	+	5	5	5	40		
Agropyron repens				+						+			+	+					+			+
Lolium perenne																	10	10	5	5		+
Bromus mollis										+	+						+	10	+	+		
Holcus lanatus										+							+	+	20	5		
Cynosurus cristatus																			10	10		
Alopecurus geniculatus																					+	+
Agrostis tenuis																				10		

A. JOINT PRESENCE OR ABSENCE OF WADERS IN AN AREA OF 1 ha AROUND THE NESTS

Species within a radius of 56 m		Species at the centre of the 1 ha area		
		Redshank	Lapwing	Oystercatcher
Redshank	Present	9	6	6
	Absent	11	12	20
Lapwing	Present	6	2	4
	Absent	14	16	22
Oystercatcher	Present	6	4	6
	Absent	14	14	20
Any of the above three	Present	15	11	14
	Absent	5	7	12

B. MINIMUM DISTANCES FOUND BETWEEN NESTS

	Redshank	Lapwing	Oystercatcher
Redshank	15 m	4 m	4 m
Lapwing		55 m	6 m
Oystercatcher			20 m

Table 3

DISTANCES MOVED BY 7 PREFLEDGLING CHICKS

FROM THEIR NESTS

Species	Age when found (weeks)	Distance from nest (m)
Lapwing	1	50
	2	400
	3	200
	4	220
	4	500
Oystercatcher	1	20
	3	20
	4	10

Table 4

FAECAL ANALYSIS

	Position and nearest transect point	Faecal contents
1 Chick 3 weeks old	Border of 'Old' and 'New Marsh', 400 m from B3	Chitonous remains. Large number of elytra and legs of dung beetles (Aphodius sp.) and carabids.
1 Chick 1 week old	50 m from above position	No chitonous remains. A few wing membranes of Diptera and larval remains.
2 Chicks 2 weeks old	'Old Marsh' near A2	No chitonous remains.
1 Adult	'Old Marsh' near A3	A few chitonous remains of Coleoptera and Diptera.
1 Adult	'New Marsh' near B2	Chitonous remains, Coleoptera only.

Table 5

INVERTEBRATE FAMILIES IDENTIFIED

Order and size	Family	Pitfall traps at Transect Point A5			Associated with cattle
Diptera $\geqslant$ 7 mm	Calliphoridae, Lucilia			2	
	Muscidae, Fucellinae				
	Scatophagidae, Scopeuma	5	4	7	Yes
	Syrphidae				Yes
	<u>Tipula paludosa</u>	2		3	
	Tipulidae (others)				
2 mm < Diptera < 7 mm	Dolichopodidae	5	14	15	
	Ephydridae		3		
	Muscidae, Stomoxys	10	7	7	Yes
Diptera $\leqslant$ 2 mm	Not identified	20	45	15	
Hymenoptera	Not identified	5	3		
Hemiptera	Cercopidae				
Lepidoptera	Pterophoridae				
Coleoptera $\geqslant$ 15 mm	Carabidae				
7 mm $\leqslant$ Coleoptera < 15 mm	Carabidae	2			
2 mm < Coleoptera < 7	Carabidae	3	7	2	
	Cantharidae				
	Coccinellidae				
	Cureulionidae				
	Scarabaeidae	4	7	6	
Coleoptera $\leqslant$ 2 mm	Staphylinoidae				
Araneae	Not identified	18	54	20	
Acari (mites)	Not identified	5	5		

Table 6

DRY WEIGHTS OF INVERTEBRATES COLLECTED AT EACH TRANSECT POINT (mg/trap/day)

Transect point	Veget-ation type	Diptera	Hymen-optera	Hem-iptera	Lepid-optera	Cole-optera	Aran-eae	Acari (mites)	Larvae	Gama-rids	Collem-bola	Total
A2	T6	16.86	0.11	0.03	0.23	3.99	2.38	0.13	0.18	0	0.04	23.95
A3	T4	14.34	0.13	0.04	0.23	0.83	3.36	0.18	0	0	0	19.11
A4	T4	19.67	0.11	0.13	0.23	0.91	4.78	0.13	0	0	0	25.96
A5	T5	11.94	0.01	0.03	0	1.93	2.71	0.28	0	0.18	0.01	17.09
A6	T4	9.16	0.03	0	0.23	1.55	3.09	0.08	0.18	0	0.04	14.36
A7	T4	9.21	0.03	0.03	0	2.77	3.03	0.73	0	0.72	0.05	16.57
A8	T4	11.87	0.07	0.03	0.46	4.62	5.40	0.33	0.18	0.36	0.05	23.37
A9	T3	9.38	0.14	0.16	0.23	2.75	3.81	1.13	0.22	3.97	0.03	21.82
A10	T3	8.37	2.59	0.21	0	0.18	2.90	0	0.04	0	0	14.29
B2	T3	18.78	3.51	0.10	0.47	0.03	0.50	0.30	0	0	0	23.69
B3	T3	26.33	0.03	0.20	0.47	0.07	0.69	0.48	0.22	0	0	28.49
B4	T4	12.45	0.03	0.06	0.70	1.27	1.10	0.15	0	0	0.04	15.80
B5	T4	12.21	2.68	0.15	0.23	0.84	1.92	0.35	0	0	0.06	18.44
B6	T4	11.29	0.03	0.03	0	1.01	2.96	0.53	0	0	0	15.85
B7	T4	9.37	2.62	0.03	0	1.29	3.51	0.13	0	0.03	0.02	17.00
B8	T4	14.83	0.05	0.13	0.70	0.11	1.94	0	0.11	0	0.01	17.88
F1	Field	16.38	2.60	0	0	4.19	2.21	0.03	0.22	0	0.08	25.71

Each point is based on data collected from 6 traps.

Table 7

DRY WEIGHTS OF INVERTEBRATES COLLECTED AT EACH TRANSECT POINT

(PERCENTAGE OF TOTAL WEIGHT COLLECTED)

Transect Point	Vegetation Type	Diptera (%)	Coleoptera (%)	Araneae (%)
A2	T6	70	17	10
A3	T4	75	4	18
A4	T4	75	3	18
A5	T5	70	11	16
A6	T4	64	11	21
A7	T4	56	17	18
A8	T4	51	20	23
A9	T3	43	13	17
A10	T3	59	1	20
B2	T3	79	0.1	2
B3	T3	92	0.2	2
B4	T4	79	8	7
B5	T4	66	5	10
B6	T4	71	6	19
B7	T4	54	8	21
B8	T4	83	1	11

Table 8

MEAN DRY WEIGHTS OF INVERTEBRATES IN EACH VEGETATION TYPE (mg/trap/day)

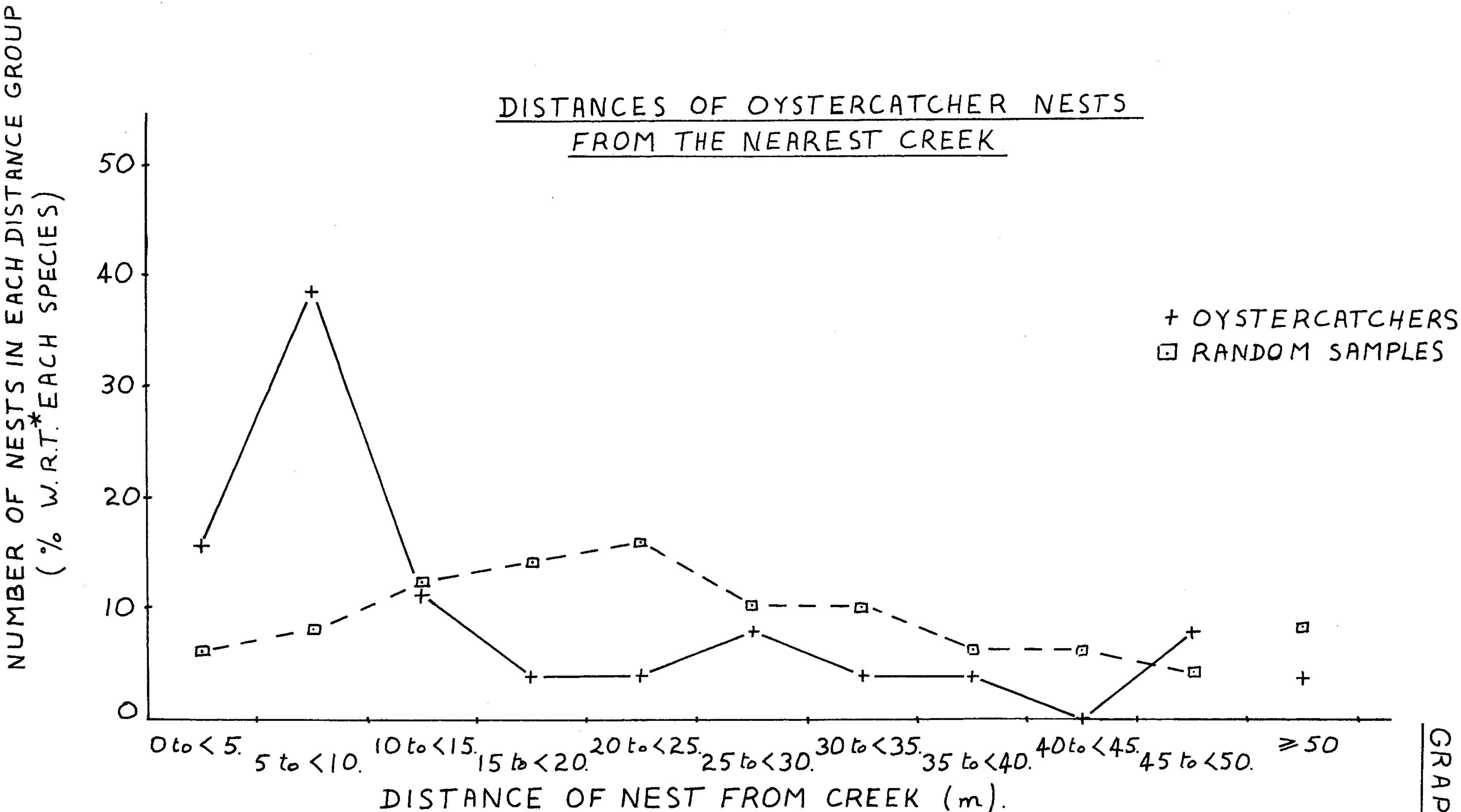
	T3A	T3B	T4	T5	T6	F1 (Field)
Diptera	8.87	22.55	12.44	11.94	16.86	16.38
Hymenoptera	1.36	1.81	0.58	0.01	0.11	2.60
Hemiptera	0.18	0.15	0.06	0.03	0.03	0
Lepidoptera	0.12	0.47	0.28	0	0.23	0
Coleoptera	1.46	0.05	1.52	1.93	3.99	4.19
Araneae	3.35	0.60	3.11	2.71	2.38	2.21
Acari	0.56	0.78	0.26	0.28	0.13	0.03
Larvae	0.13	0.11	0.04	0	0.18	0.22
Gamarids	1.98	0	0.13	0.18	0	0
Collembola	0.02	0	0.03	0.01	0.04	0.08
Total	18.05	26.09	18.43	17.09	23.95	25.71
Number of traps that each mean is based on	12	12	60	6	6	6

Table 9

MEAN DRY WEIGHTS OF INVERTEBRATES IN EACH VEGETATION TYPE (PERCENT)

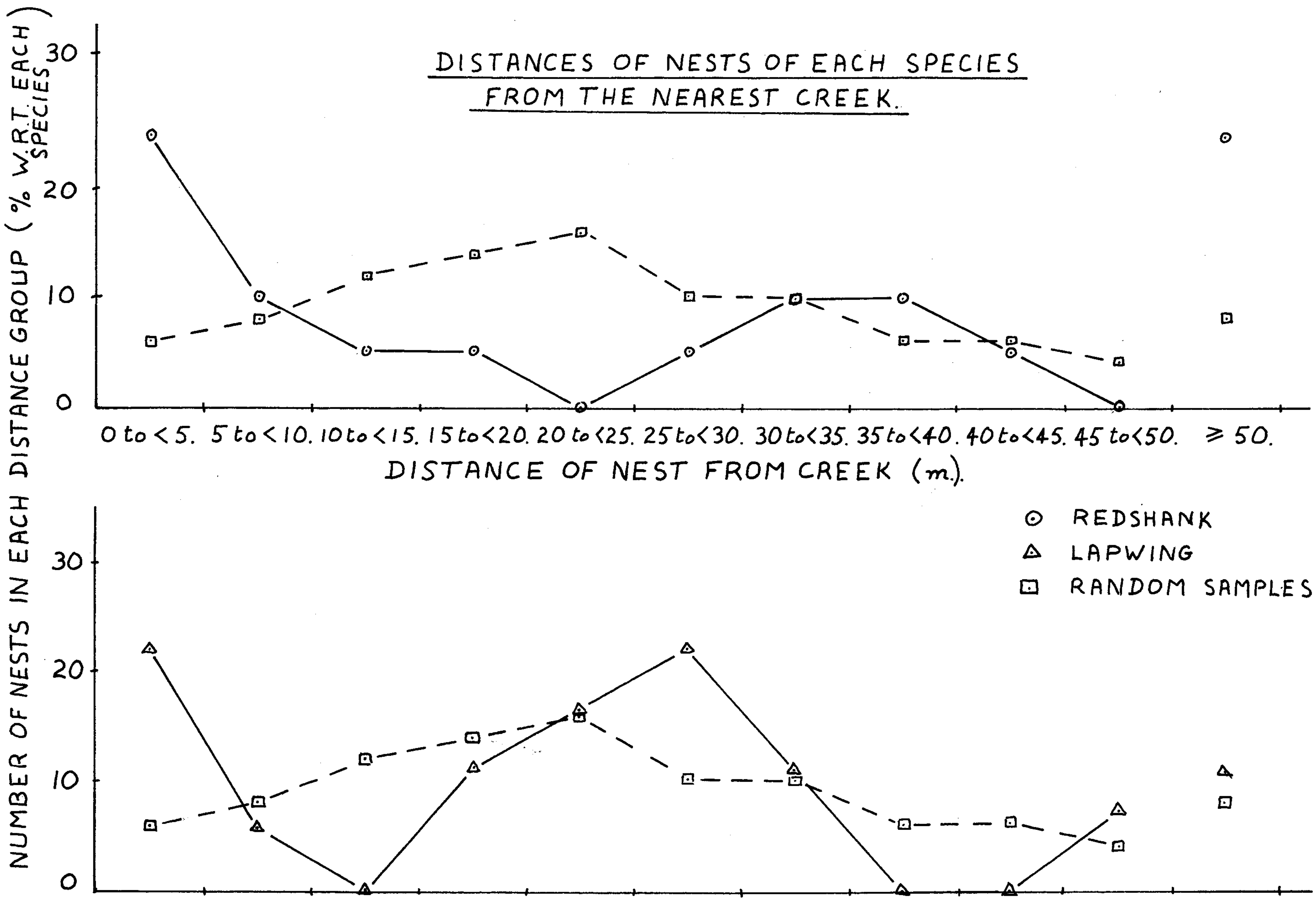
	Vegetation Type					
	T3A	T3B	T4	T5	T6	F1 (Field)
	(%)	(%)	(%)	(%)	(%)	(%)
Diptera	49	86	67	70	70	64
Coleoptera	8	0.2	8	11	17	16
Araneae	19	2	17	16	10	9

GRAPH 1



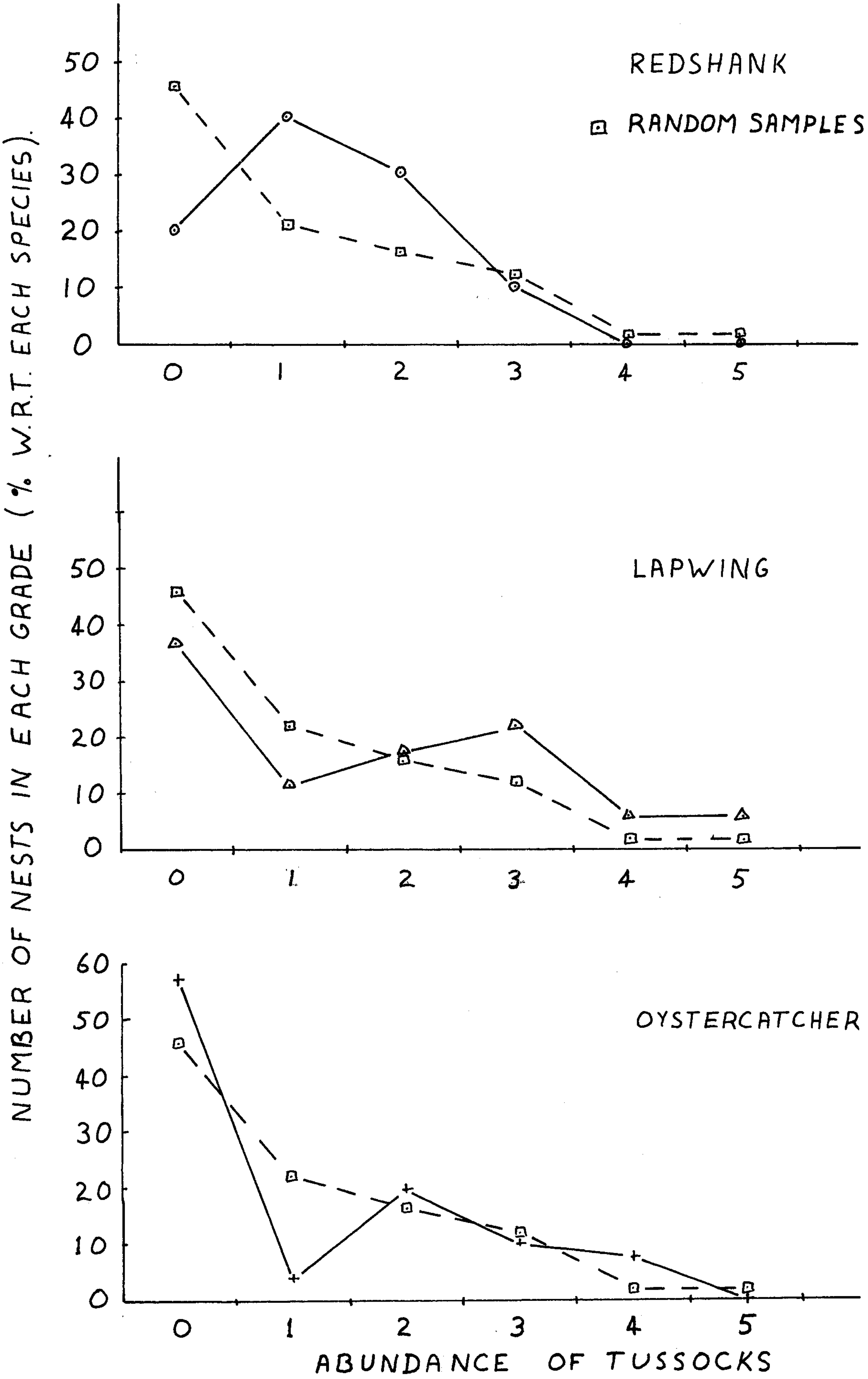
* W.R.T. ≡ WITH RESPECT TO

GRAPH 2

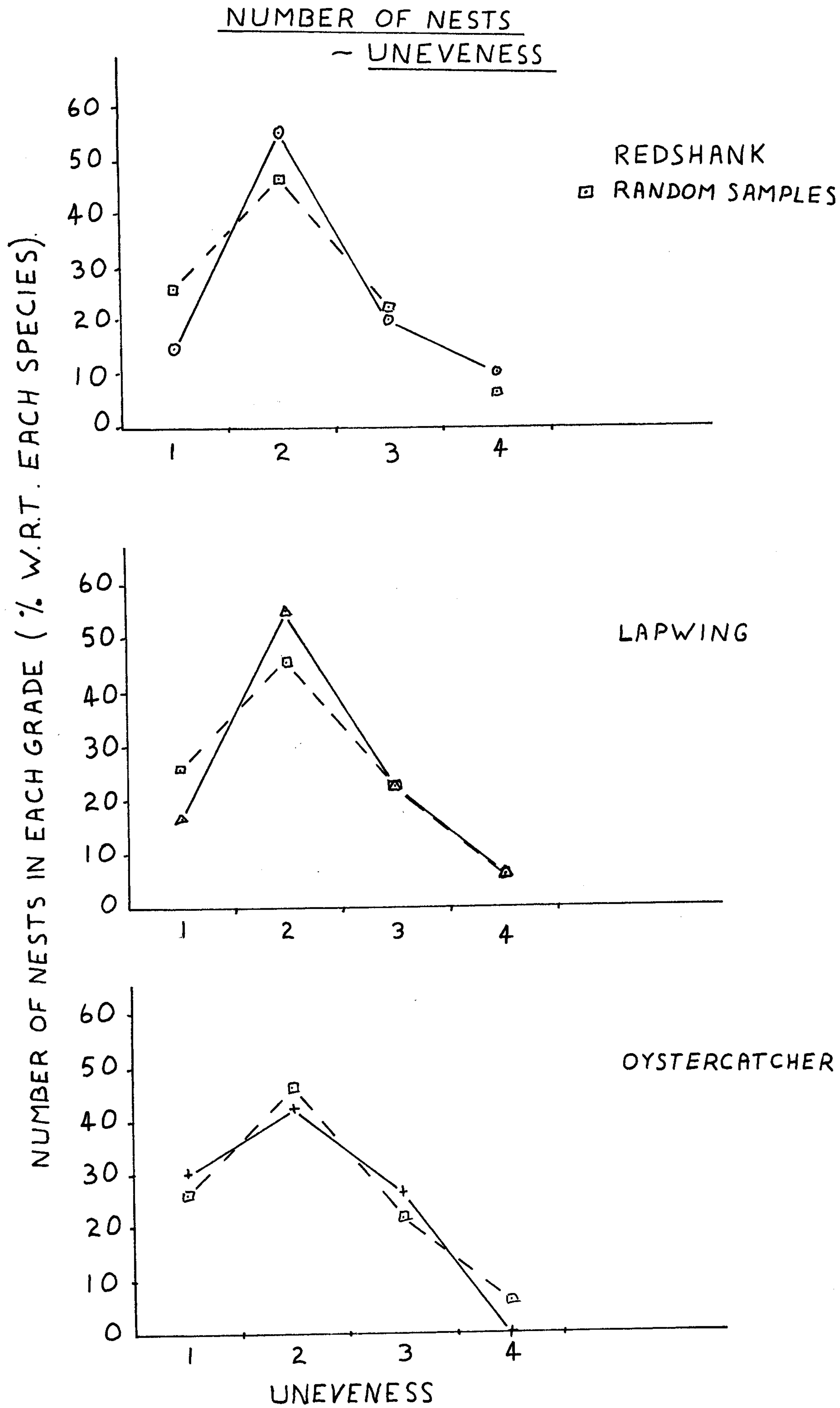

DISTANCES OF NESTS OF EACH SPECIES
FROM THE NEAREST CREEK.
NUMBER OF NESTS IN EACH DISTANCE GROUP (% W.R.T. EACH SPECIES)
30
20
10
0
0 to < 5. 5 to < 10. 10 to < 15. 15 to < 20. 20 to < 25. 25 to < 30. 30 to < 35. 35 to < 40. 40 to < 45. 45 to < 50. ≥ 50.
DISTANCE OF NEST FROM CREEK (m).
REDSHANK
LAPWING
RANDOM SAMPLES

GRAPH 3

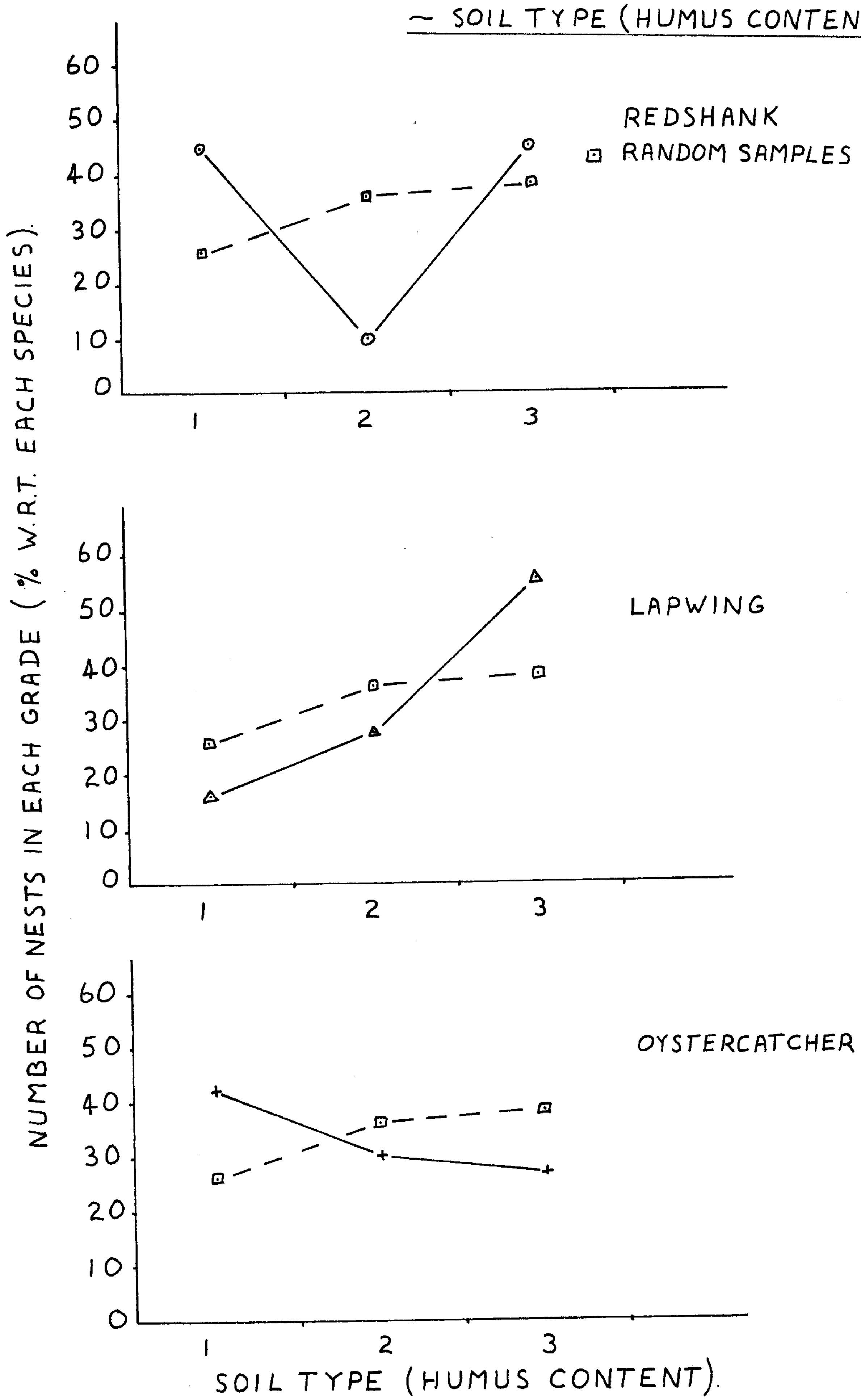
NUMBER OF NESTS ~ ABUNDANCE OF TUSSOCKS



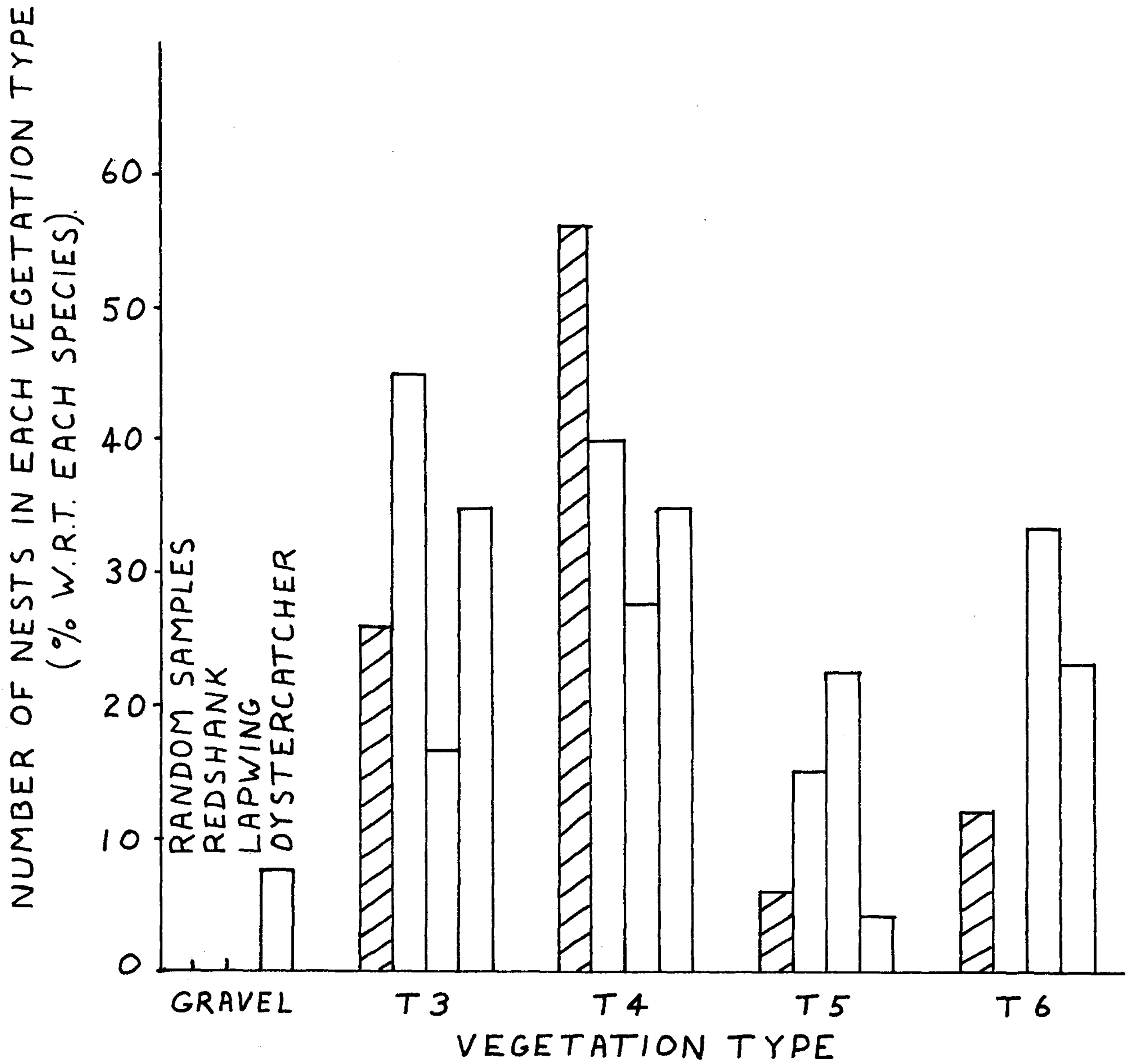
GRAPH 4


NUMBER OF NESTS
~ UNEVENESS
NUMBER OF NESTS IN EACH GRADE (% W.R.T. EACH SPECIES)
60
50
40
30
20
10
0
1
2
3
4
REDSHANK
RANDOM SAMPLES
LAPWING
OYSTERCATCHER
UNEVENESS

NUMBER OF NESTS ~ SOIL TYPE (HUMUS CONTENT).

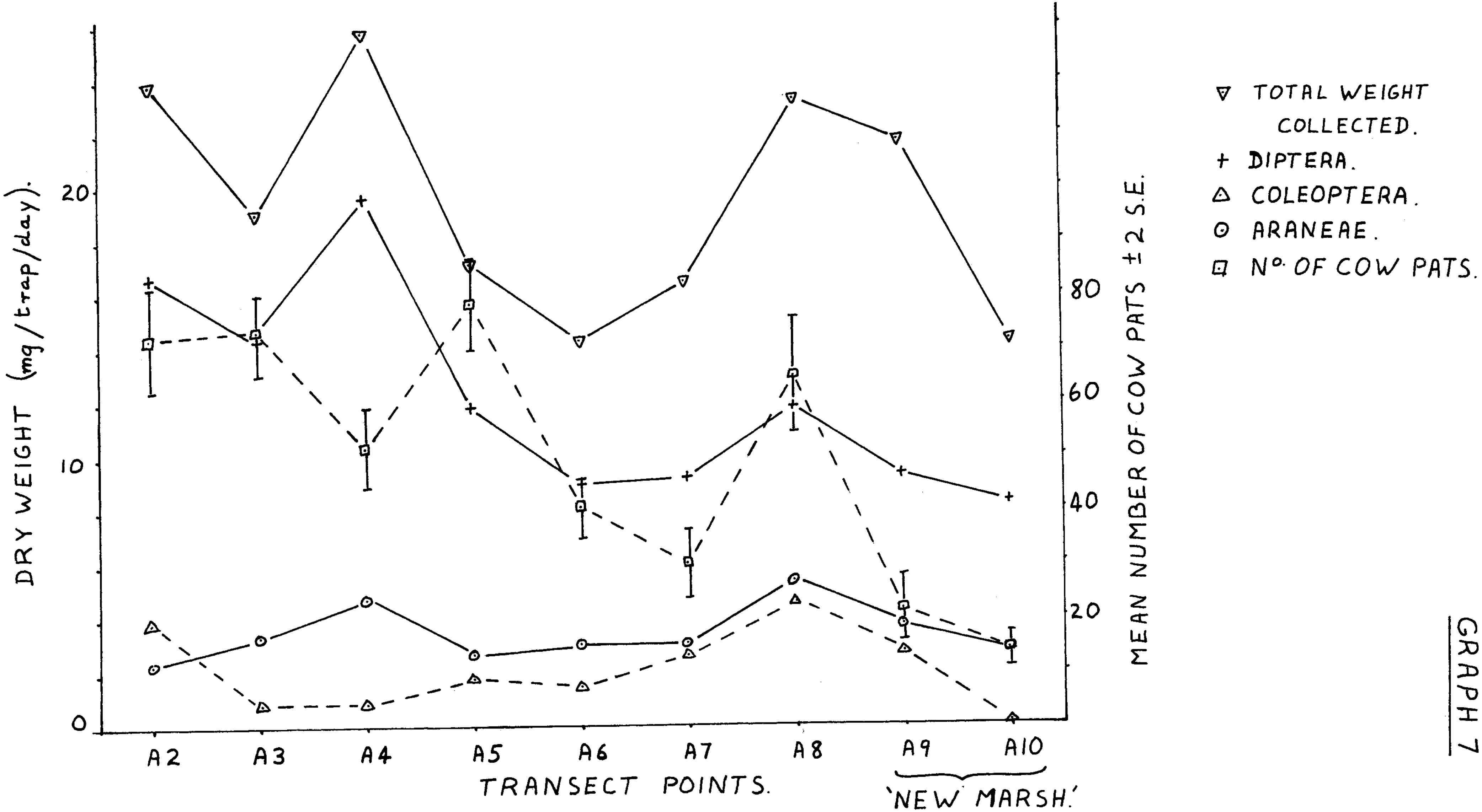


NUMBER OF NESTS
~ VEGETATION TYPE



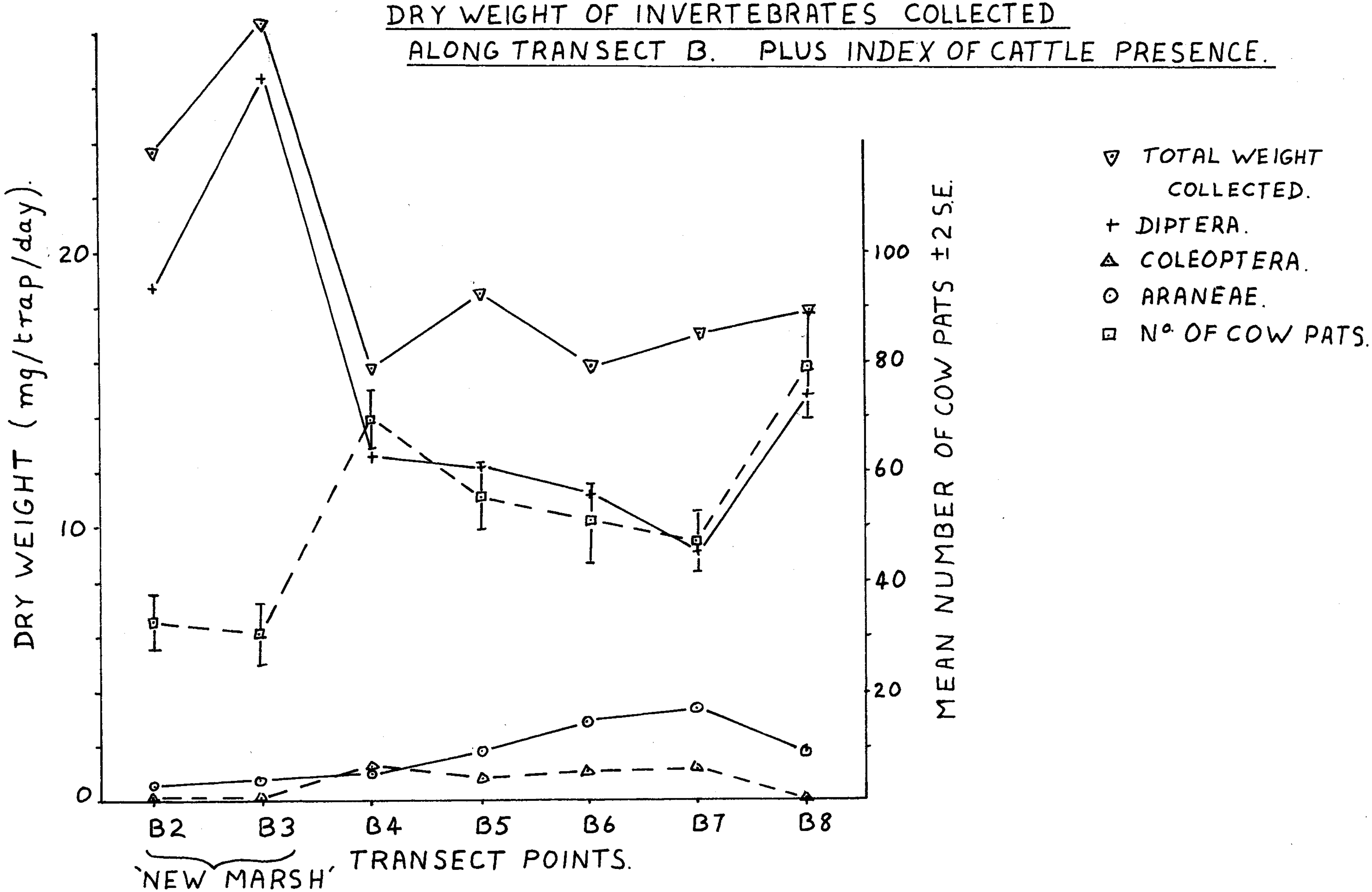
GRAPH 7

DRY WEIGHT OF INVERTEBRATES COLLECTED ALONG TRANSECT A. PLUS INDEX OF CATTLE PRESENCE.

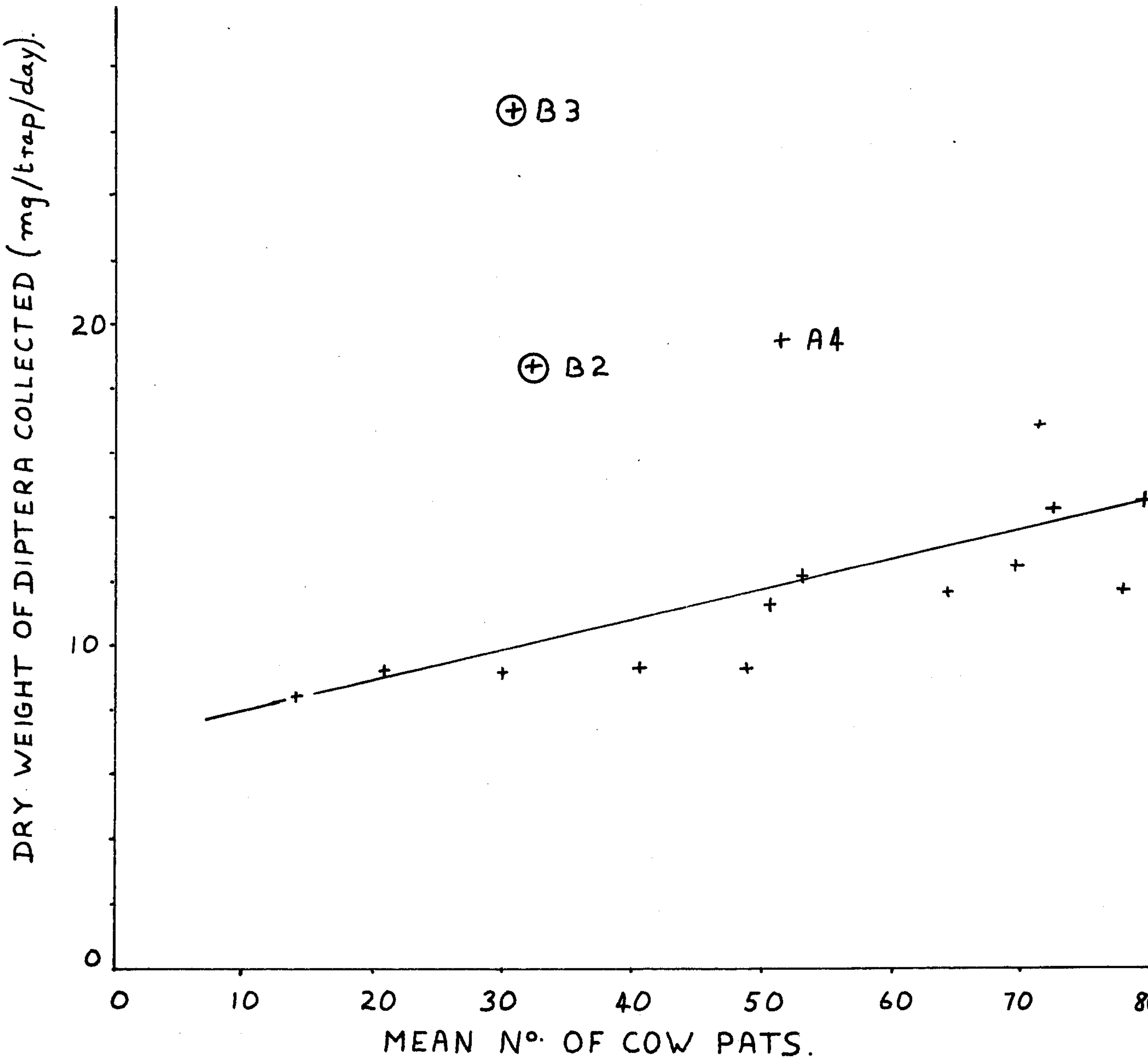


GRAPH 8

DRY WEIGHT OF INVERTEBRATES COLLECTED ALONG TRANSECT B. PLUS INDEX OF CATTLE PRESENCE.



WEIGHT OF DIPTERA COLLECTED ~ NUMBER OF COW PATS.



EXCLUDING B2 AND B3 :-

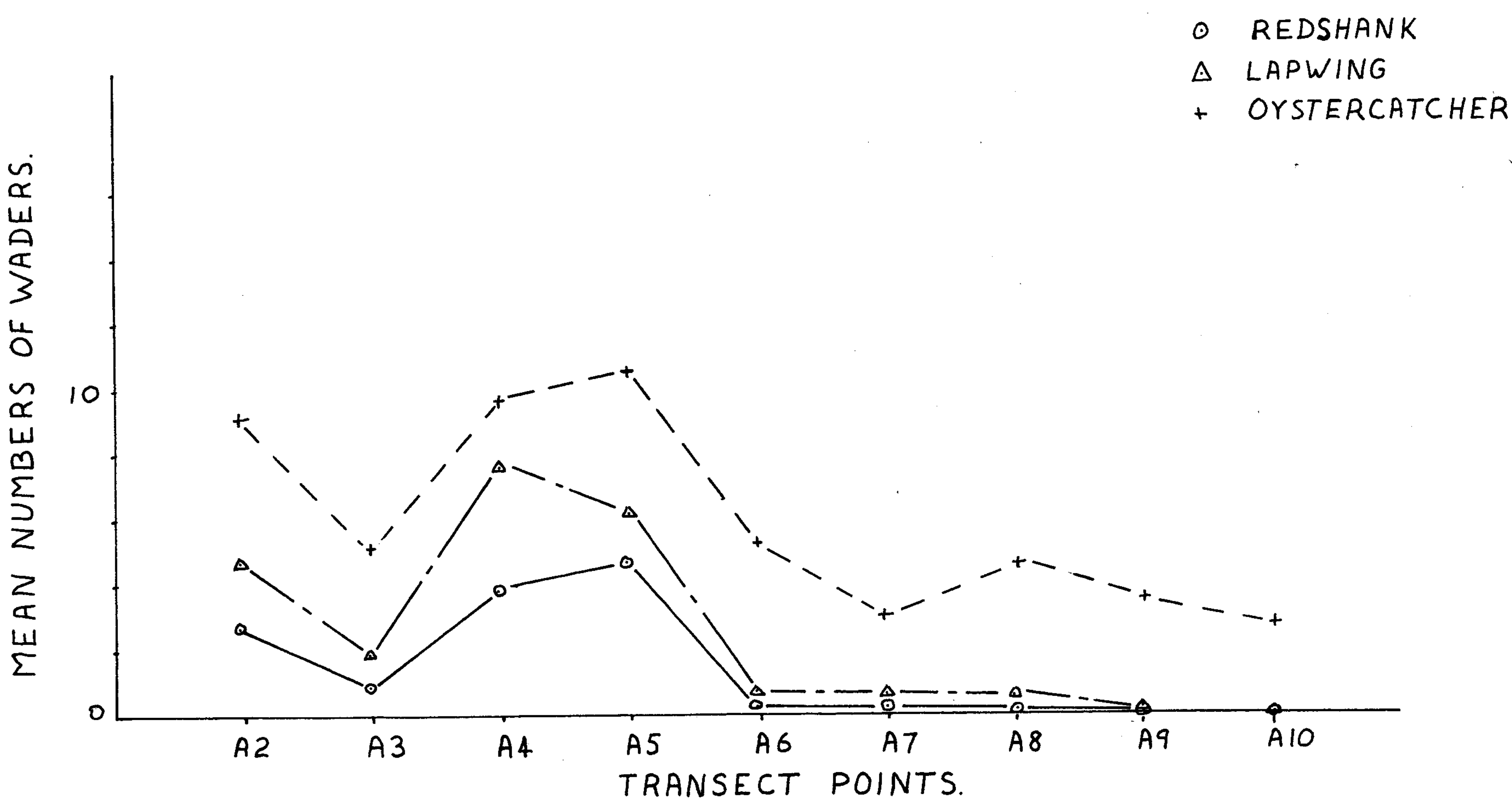
$m = 0.095$

$c = 7.142$

$r = 0.620$

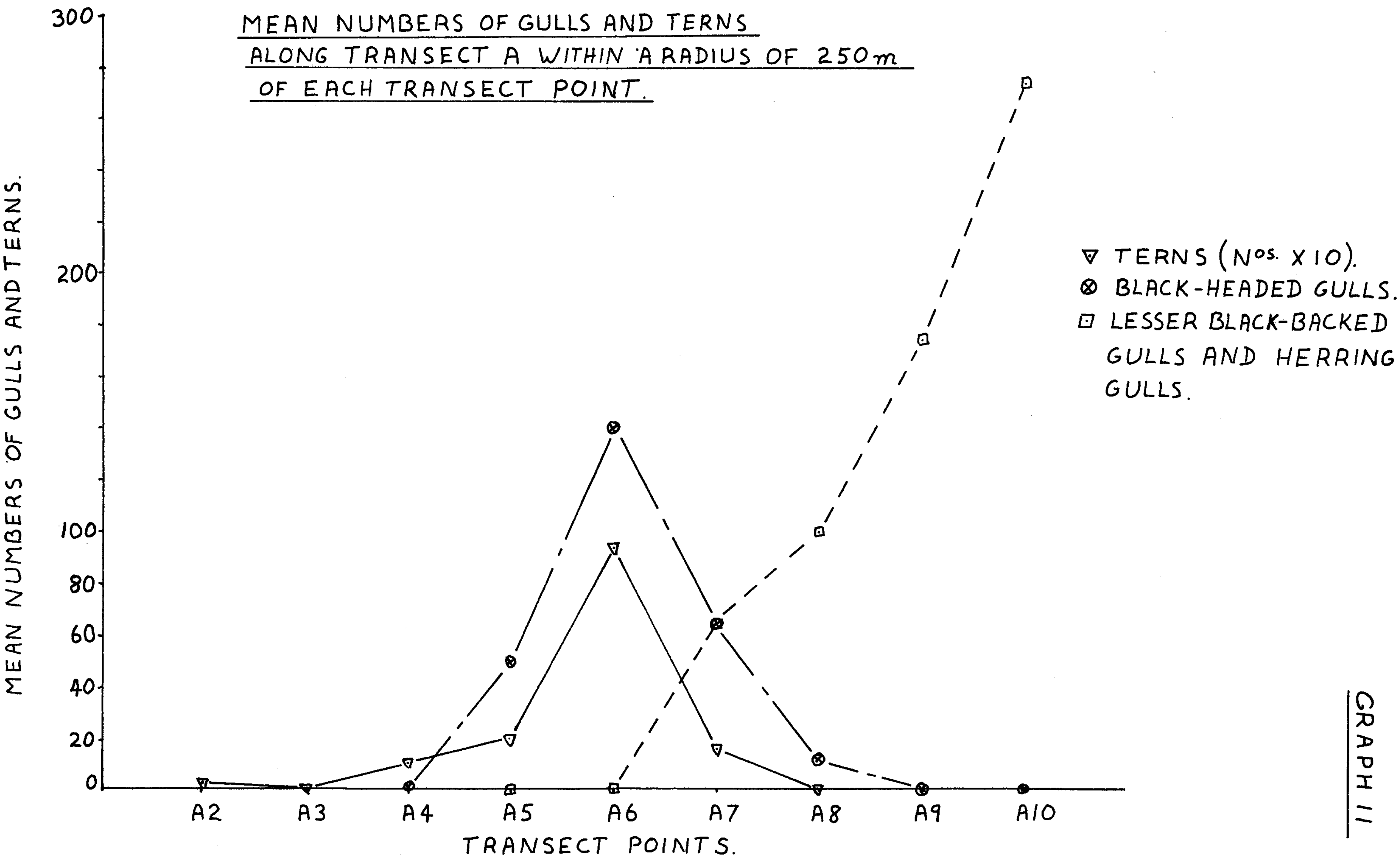
$d.f. = 12$

MEAN NUMBERS OF WADERS ALONG TRANSECT A WITHIN A RADIUS OF 250m OF EACH POINT.



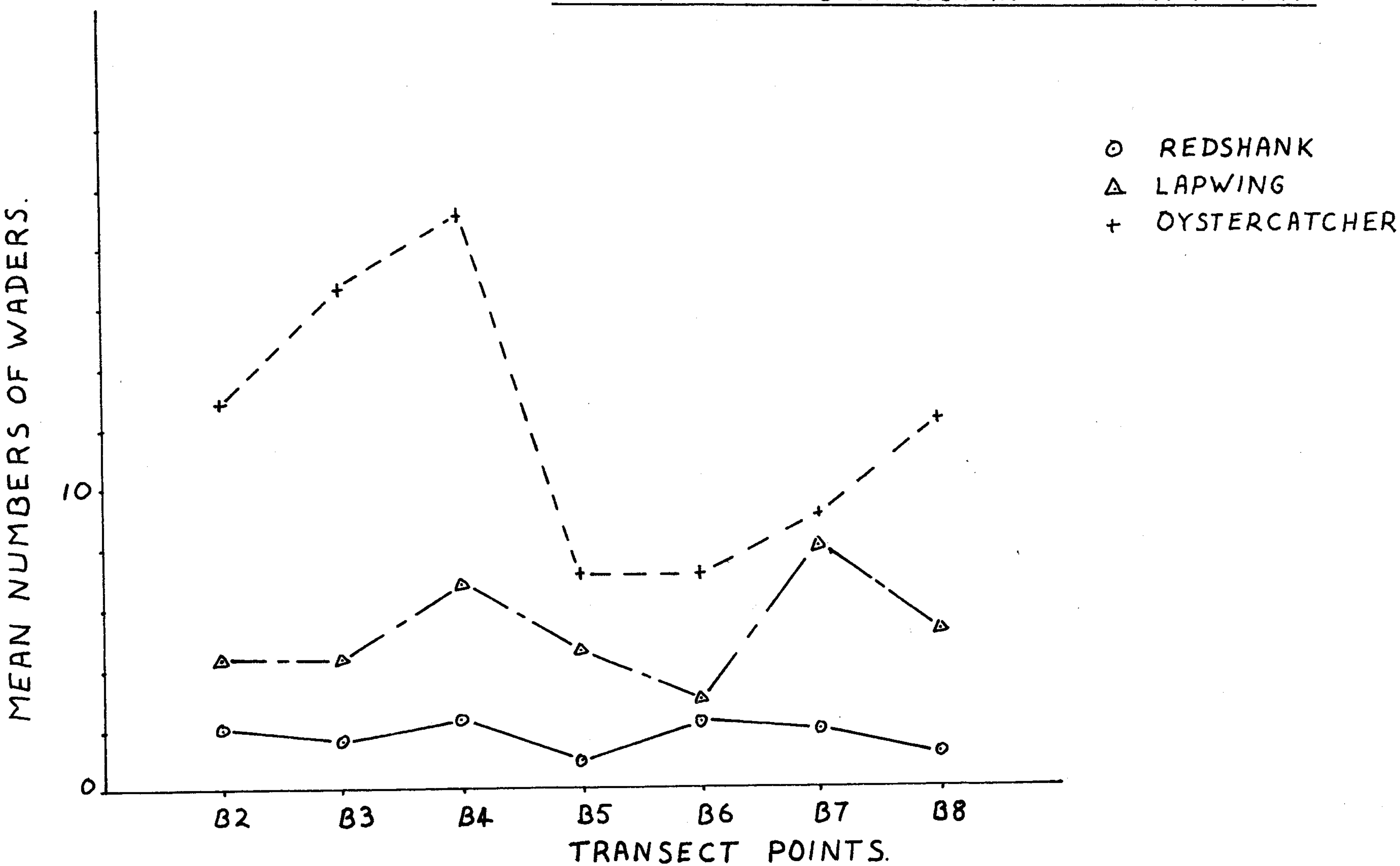
GRAPH II

MEAN NUMBERS OF GULLS AND TERNS ALONG TRANSECT A WITHIN A RADIUS OF 250m OF EACH TRANSECT POINT.



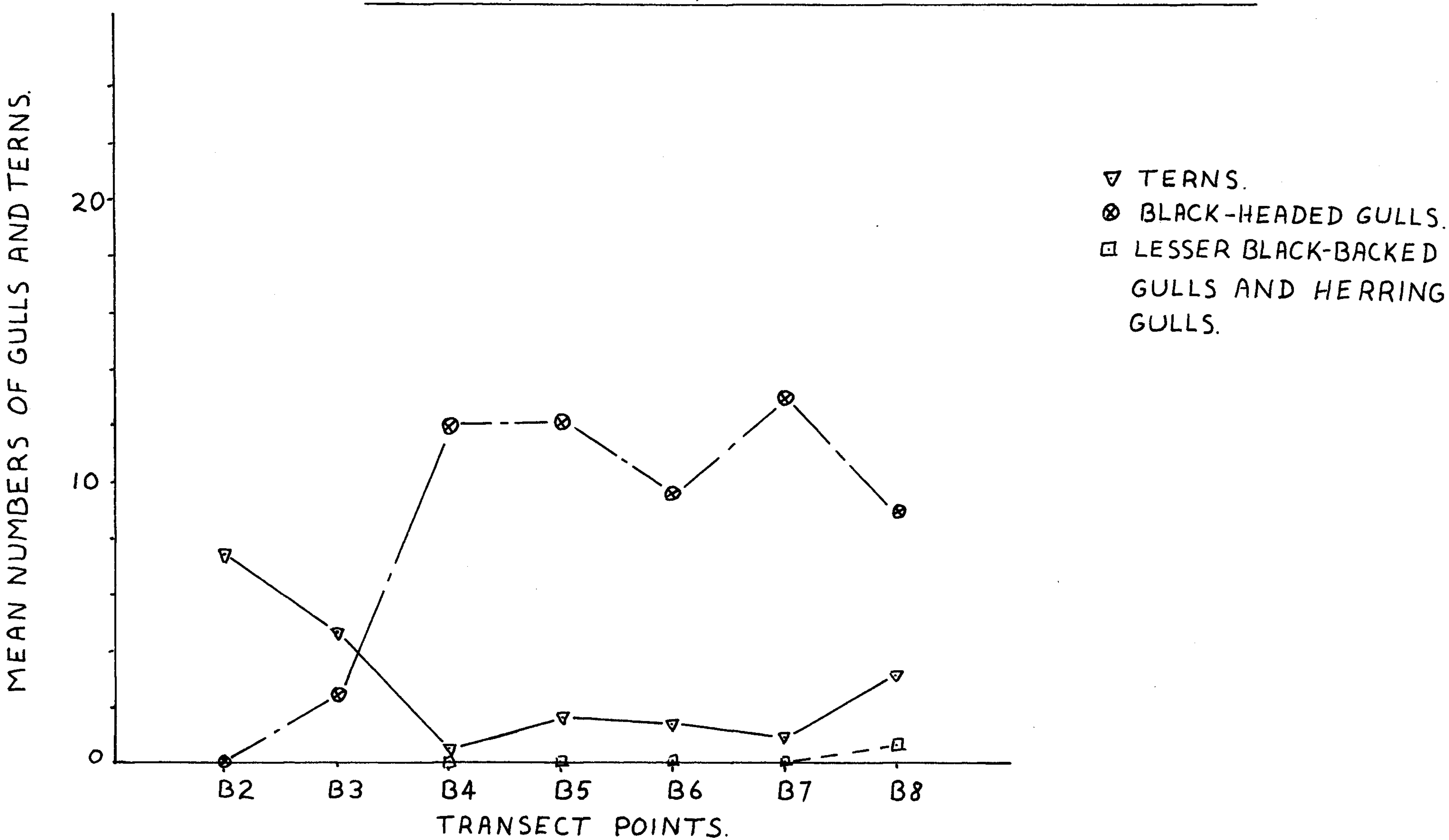
GRAPH 12

MEAN NUMBERS OF WADERS ALONG TRANSECT B WITHIN A RADIUS OF 250 m OF EACH POINT.

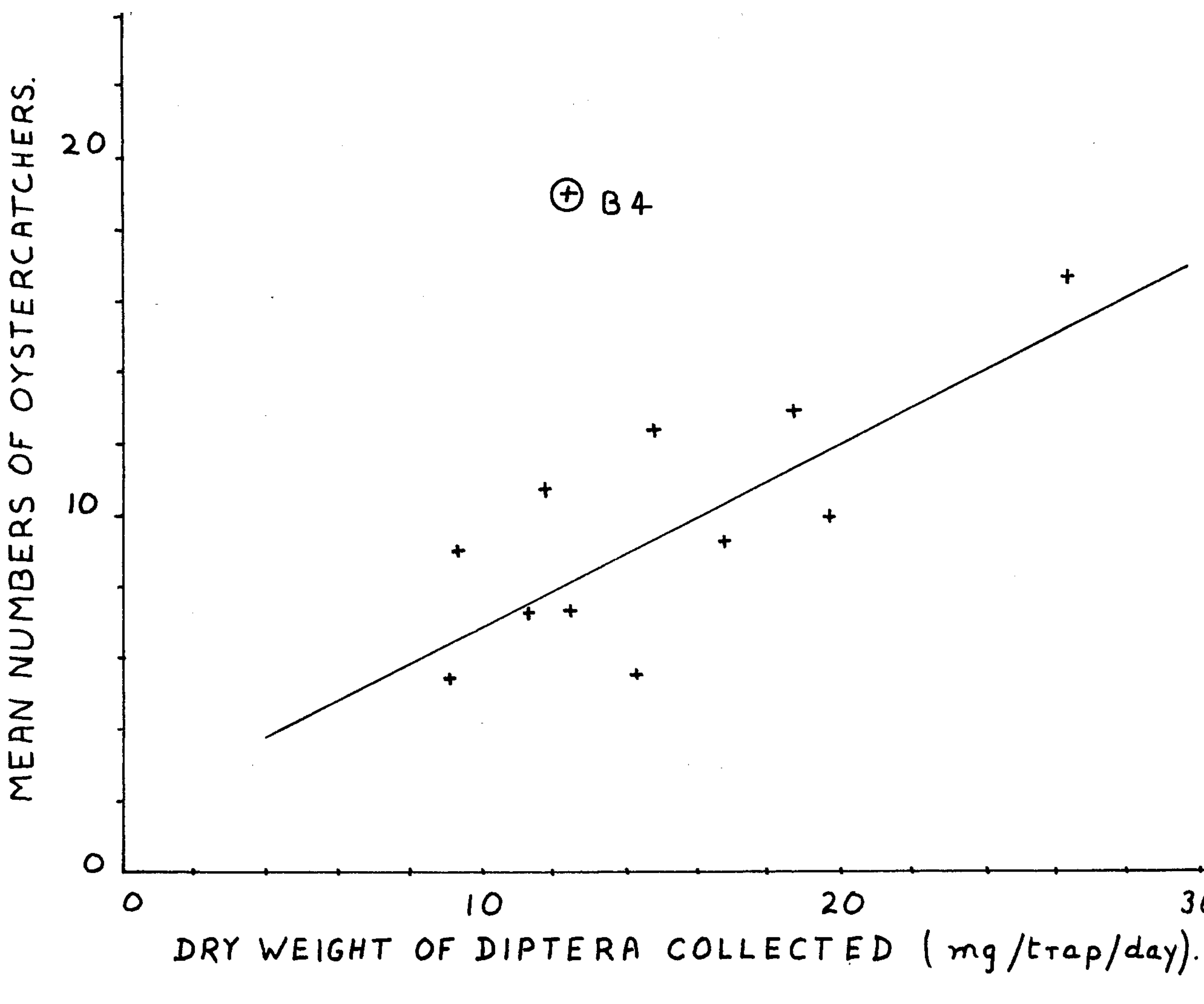


GRAPH 13

MEAN NUMBERS OF GULLS AND TERNS ALONG TRANSECT B WITHIN A RADIUS OF 250 m OF EACH TRANSECT POINT.



NUMBERS OF OYSTERCATCHERS ~ WEIGHT OF DIPTERA COLLECTED.



EXCLUDING B4:-

$m = 0.513$

$c = 1.899$

$r = 0.773$

d.f. = 9.

5.0 Discussion

Three main characteristics of the selection of proximate factors will be discussed before proceeding onto a discussion of those factors found:-

i) The mode of selection of a proximate factor.

ii) The order of selection of proximate factors.

iii) The relative importance of the proximate factors.

i) The mode of selection of a proximate factor.

Two basic modes of selection of proximate factors can be postulated from the model developed by the author in the introduction. The model is reproduced here for ease of reference.

$$\sum_{ij} a_{ij}.y_{ij} \geqslant b_{jk}.K_j$$

a) y_{ij} (the proximate factor) may take on the values of 0 or 1 only. This represents the selection of the proximate factor on the basis of presence or absence. In this case the weighting coefficient, a_{ij}, has a constant value.

b) y_{ij} may take on values from 0 upwards dependent on the quantity of the proximate factor in the area. This represents selection on the basis of abundance. In this case the weighting coefficient, a_{ij}, may either have a constant value or may be a function of the proximate factor. For example the product of the two may increase exponentially for a linear increase in abundance of the proximate factor.

ii) The order of selection of proximate factors.

In the introduction it was stated that there seemed likely to be two stages in the selection of proximate factors:-

a) Selection of those factors characteristic of the general habitat.

b) Selection of those factors which determine the exact siting of the nest.

In the discussion of the factors found, each factor will be classified into these two groups and will be graded in importance.

iii) The relative importance of the proximate factors.

The relative importance of the proximate factors selected by each species of wader will be graded as follows, beginning with the highest level of importance:-

Grade A - Those factors causing the absence of a species from an otherwise suitable habitat. In this case a single negative factor may outweigh the sum of all the positive factors.

Grade B - Those factors which influence the density of birds in a certain habitat.

Grade C - Those factors which determine the exact siting of the nest.

Using this system for waders implies that in the two stages of selection of proximate factors mentioned in (ii), factors in the first stage can be classified as grade A or B, and factors in the second stage as grade C only. This is considered to be reasonable as amongst waders the requirements for the exact nest site do not appear to be exacting.

Figure 1 is a schematic representation of the distribution of waders along a hypothetical transect covering all types of habitat found on the marsh and adjoining area. The data are based on the presence or absence of birds in the various areas. Areas in which birds do not occur may not be selected either because they lack positive proximate factors, or because of the presence of negative factors. This aspect will be discussed for the distributions shown:-

(i) No birds attempted to nest on frequently flooded areas, (flooded at least once a fortnight). These areas were sparsely vegetated but this factor would not deter Ringed Plovers and Oystercatchers. As they are low lying areas they retain a lot of surface water and this may act as the detering factor. Otherwise, if the period from when selection starts until the nest is built is longer than two weeks, then obviously the incoming tide would act as a negative proximate factor. From this it appears that Oystercatchers and Ringed Plovers do not nest in these areas because of a negative proximate factor of grade A, whereas the other three species do not select these areas due to a lack of positive proximate factors of grade B.

ii) Only Oystercatchers and Ringed Plovers nested on gravel areas. The other three species are likely to not select these areas due to a lack of positive proximate factors of grade C as the gravel areas were small and surrounded by the normal vegetation of the marsh.

iii) Ringed Plovers have never been recorded as breeding on the 'Old Marsh' areas. This could be due either to a lack of positive factors, such as bare ground, or otherwise the maturer vegetation could act as a negative factor. Ringed Plover nests were found on a gravel road going through the 'Old Marsh' area. The adults were often seen running through the vegetated areas and appeared structually suited to it. This bears out the findings of Lack (1933) on the Brecklands, where he pointed out that the distribution of Ringed Plovers in that area were restricted by their selection of their ancestral habitat.

iv) Lapwings were the only species of wader to nest in the adjoining fields. In other areas Redshanks and Oystercatchers are also known to nest in fields. Hence these latter species do not appear to select fields when other suitable areas are available. Therefore some proximate factor associated with fields, possibly trees, appears to be negative and of grade B importance for Redshanks and Oystercatchers. To classify them as grade A would imply that they never nested in fields.

v) No waders nested near the sea wall on the marsh side, the minimum distance being about 200m. Dunlin and Redshank nested farther from the sea wall than did Lapwing or Oystercatcher. It seems likely that the same factor as mentioned in (iv) was deterring the birds. As Lapwings were also deterred by this factor and yet nested in the adjoining fields, it seems likely that this factor has a lower importance for them than for the

Redshanks or Oystercatchers. Trees appear to be the most likely proximate factor in these two cases as Klomp (1953) found that Lapwings avoided breeding in fields with trees in the vicinity as they were there less able to drive off crows.

A summary of the results relating to further possible proximate factors is given for the three species of waders in Table 10. Referring to this table the factors selected by each species will be discussed:-

(i) Redshanks

From the transect data it is evident that the numbers of Redshanks and Lapwings are correlated with each other. However as the nest site data do not show this correlation, it may be that whereas Redshanks and Lapwings choose the same habitat, the presence of a member of the other species does not act as a proximate factor in the selection of the nest site.

From the nest site data it is apparent that the presence of a Redshank in an area acts as a positive proximate factor for another Redshank. This can only apply for the first two to three birds otherwise large colonies would exist. Therefore the mode of selection seems to be based on the abundance of nests with the weighting coefficient decreasing as the number of nests in the area increases. This factor would be selected for at the habitat stage of selection and have an importance level of grade B.

The tendency of Redshanks to select areas which possess at least a few tussocks was discussed earlier. It was also noted that they appeared to select on a basis of presence or absence rather than on abundance. This proximate factor can also be classified as being selected at the habitat stage of selection, with importance grade B.

When a nest was found in an area possessing tussocks it was almost invariably built within a tussock. It therefore appears that at the stage of selection of the exact nest site, a single tussock will act as a proximate factor. It is considered that the occurrence of tussocks as a proximate factor in both stages of selection is more likely than the alternative of a tussock being selected while the bird is still in the air.

Colonies of Lesser-black Gulls and Herring Gulls are negative proximate factors of grade A importance for both Redshanks and Lapwings. These latter species are almost totally excluded by this factor as only a couple of nests were found in the vicinity of the colonies. This factor would be selected at the habitat stage of selection and either mode of selection could apply.

ii) Lapwings

The significant correlation of Lapwings with Redshanks is not considered to indicate that the latter act as a proximate factor for the former, for reasons given in the previous section. The effects of colonies of the large gulls has also been discussed.

The mature type of vegetation, preferred by the Lapwings, would be selected at the habitat selection stage and have an importance of grade B.

iii) Oystercatchers

Colonies of the large gulls are also negative proximate factors for the Oystercatchers. However the Oystercatchers were not excluded from the area by the gulls and hence this factor is considered to have an importance of grade B, i.e. it affects density rather than presence or absence. The mode of selection cannot be determined from the evidence available.

The correlation of the total weight of invertebrates collected with the numbers of Oystercatchers is discounted. This is because the Diptera comprise the major portion of the weight collected and have a closer correlation with the numbers of Oystercatchers than does the total weight. The proximate factor selected to predict the density of Diptera is not known and will be discussed later. However it would be selected at the habitat stage of selection and have an importance of grade B.

The distance to the nearest creek is also a proximate factor for the

Oystercatcher and would be selected for when the exact positioning of the nest was being determined. It would have an importance of grade C and would be selected on a presence or absence basis.

Table 11 is a summary of the proximate factors found for each of the species. Redshanks, Lapwings and Oystercatchers all selected nest sites in both the 'New' and 'Old' marsh. Therefore the general terrain and vegetation of the marsh can be considered to be a positive proximate factor. However due to the vagueness of what is selected it has not been included in the summary.

From Table 11 it can be seen that two proximate factors were common to all three species, ie. the presence of colonies of Lesser Black-backed Gulls and Herring Gulls, and the presence of a deterring factor associated with fields, which is most likely to be the presence of trees. The rest of the proximate factors are unique to each species.

Taylor (1974) in her study on Lapwings breeding on marginal hill farmland found that Redshanks tended to avoid fields occupied by Lapwings. From observations on the marsh it appeared likely that Redshanks obtained some protection by nesting amongst Lapwings. However no significant association of nest sites was found in this study.

Redshanks showed a significant tendency to nest in the near vicinity of other members of the same species, whereas Lapwings did not. This conflicts with Klomp's (1953) findings of Lapwings breeding in fields where they showed distinct sociability.

Another finding of this study which was different from those of Taylor and Klomp, was that Lapwings show a preference for the mature type of vegetation. However this is a relative term as the tallest vegetation on the marsh was low compared to a field type of vegetation. It appears as though the birds were selecting a vegetation type approaching a field type.

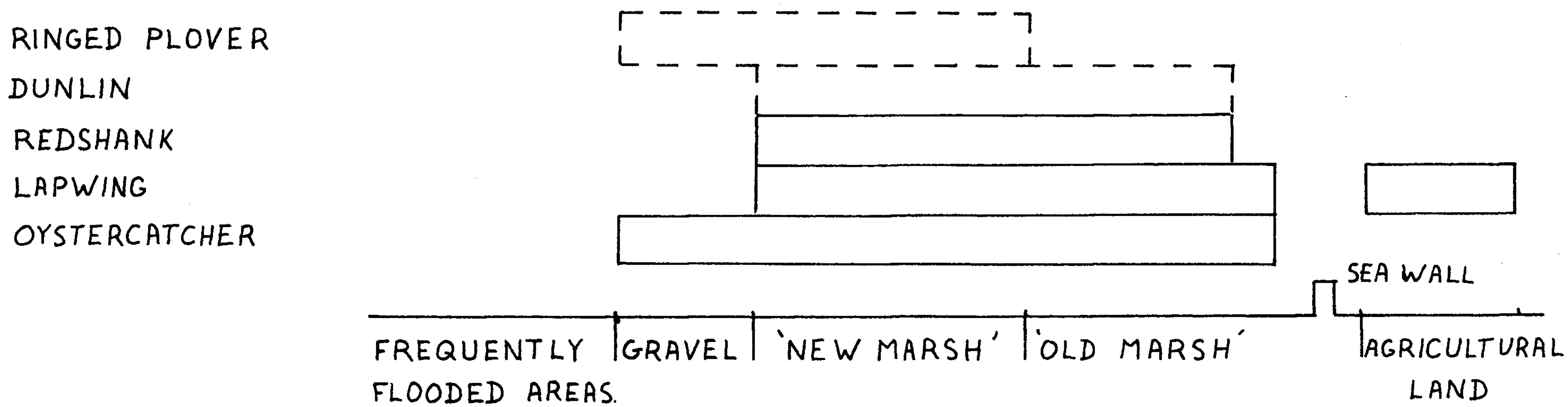
The ultimate factor associated with the Oystercatchers preference to nest near creeks (the proximate factor) is not clear. It appears most likely to be associated with protection of the young although as many chicks were found on the flat areas as in the creeks. Food does not appear to be a likely factor due to the proximity with which they nest near to the edge, 5m to 10m, a greater distance would make very little difference from this point of view.

The correlation of Oystercatchers to a food source, Diptera, is unusual as most workers have not found any association between food supply and the distribution of birds (Hilden 1965). However the correlation was highly significant ($P<.01$). Taylor (1974) found a correlation between soil fauna and Lapwing density in fields. The faecal samples from the Oystercatchers indicate that they do not have a specialised diet with regard to Diptera or Coleoptera. They also show that some Oystercatchers in areas having a high density of Diptera were predominantly feeding on Coleoptera. These results question the significance of the correlation, however only 6 faecal samples were obtained for analysis and this may not give a representative picture.

The proximate factor which is selected as an indicator of the likely abundance of Diptera for the period when the chicks leave the nest, is not known. It has previously been shown that the distribution of Diptera over the marsh is likely to remain fairly constant with time. Therefore the density of Diptera in a particular area at the time of nest site selection may act as the proximate factor.

FIGURE 1.

DISTRIBUTION OF WADERS
ON THE MARSH AND ADJOINING AREA



HYPOTHETICAL TRANSECT LINE.

RINGED PLOVER AND DUNLIN DISTRIBUTION SHOWN AS DASHED AS FEW NESTS WERE FOUND. (8 AND 5 RESPECTIVELY).

Table 10

A SUMMARY OF THE SIGNIFICANCE OF THE CORRELATIONS OF POSSIBLE PROXIMATE FACTORS WITH THE THREE SPECIES OF WADERS

	Redshank	Lapwing	Oystercatcher
i) Data from the 1 ha area surrounding each nest site			
Distance to nearest creek	O	O	+
Abundance of driftwood (excluded)			
Abundance of tussocks	+	O	O
Uneveness excluding tussocks	O	O	O
Soil type (humus content)	O	O	O
Vegetation type	O	+	O
Mean height of grass	O	O	O
Mean height of tussocks	O	O	O
Presence of other nests:			
Redshank	+	O	O
Lapwing	O	O	O
Oystercatcher	O	O	O
ii) Transect data			
Presence of other birds:			
Redshank		+	O
Lapwing	+		O
Oystercatcher	O	O	
Black-headed Gulls (Number < 15)	O	O	O
Lesser Black-backed Gulls, Herring Gulls	-	-	-
Food			
Diptera	O	O	+
Coleoptera	O	O	O
Araneae	O	O	O
Total of all invertebrates	O	O	+

Key:

O no significant correlation

\+ +ve correlation

\- -ve correlation

Table 11

SUMMARY OF PROXIMATE FACTORS FOUND

Species	Proximate factors	Stage of selection (cf 5.0 (ii))	Positive or negative	Grade of importance	Mode of selection
Redshank					
	Colonies of large gulls	General habitat	-	A	?
	Other Redshanks		+	B	abundance
	Trees		-	B	?
	Tussocks		+	B	p/a
	Tussock	Exact siting	+	C	p/a
Lapwing					
	Colonies of large gulls	General habitat	-	A	?
	Mature type of vegetation		+	B	p/a
	Trees		-	B	?
Oystercatcher					
	Colonies of large gulls	General habitat	-	A	?
	Frequently flooded areas		-	A	?
	Gravel areas		+	B	p/a
	Density of Diptera		+	B	?
	Trees		-	B	?
	Distance to nearest creek	Exact siting	+	C	p/a

Key:

p/a presence or absence

? the mode of selection cannot be determined from the evidence available

6.0 Conclusion

It has been shown that Redshanks, Lapwings and Oystercatchers each have a set of proximate factors which influence the selection of the nest sites. The following characteristics of these sets of factors were found:-

i) Some of the factors are common to all three species and some are unique to each species.

ii) No more than 6 factors were found for any one species.

iii) Only one factor was found to be invariably selected by all members of a species.

iv) Factors having both positive and negative effects were identified.

v) Factors were weighted differently in importance.

vi) Two modes of selection were identified.

vii) The majority of the proximate factors were associated with the general habitat stage of selection.

All these points conform with the model and its characteristics as discussed in the introduction and therefore support its validity.

Appendix

Clutch size and Hatching success.

The data collected are given in Table A.

i) Clutch size

If the number of eggs first found was below the normal clutch size then the area around the nest was searched for predated eggs. If one or more were found then they were included in the clutch size.

Four out of five Lapwing nests in which three eggs were recorded were found after 6 June, and are therefore most likely to be replaced sets.

ii) Hatching success

Predation of whole clutches were noted in 3 cases. See table for (a) and (b).

(a) The Redshank nest noted was predated within an hour of first recording the information about the nest. There were about 10 carrion crows in the area and they seem to be the most likely predators. Previous cases have been recorded of them following the movements of people searching for nests and then predating the nests afterwards.

(b) Of the two Oystercatchers nests destroyed one was trampled on by cattle and the other was destroyed by the gravel diggers.

Unhatched eggs left when the chicks left the nests were usually eaten within a few days.

The length of time that the eggs had been vulnerable before the nest was first found was not determined. Hence the hatching success values shown are the maximum values. Comparing these values between the species it can be seen that the differences are small.

The ratio of chicks to parents for the Oystercatchers is lower than for the other two. However as Oystercatchers generally have a longer lifespan than Redshanks or Lapwings (7 to 8 years as compared with 2 to 3 years (Lack 1954)), this does not indicate that as a species they are less successful on Rockcliffe Marsh than Redshanks or Lapwings.

Table A

CLUTCH SIZE

	Clutch size	Number of cases recorded		
		Redshank	Lapwing	Oystercatcher
	4	13	9	2
	3	3	5	12
	2	1	1	10
	1	0	0	0
Total cases		17	15	24
Mean clutch size		3.71	3.53	2.66

HATCHING SUCCESS

		Number of cases recorded		
No. Eggs	No. Chicks	Redshank	Lapwing	Oystercatcher
4	4	3	2	1
4	3	4	0	0
4	2	0	3	0
4	0	1 [a]	0	0
3	3	1	2	3
3	2	1	0	0
3	0	0	0	2 [b]
2	2	1	0	4
Total cases		11	7	10
Hatching success (%)		77.5	77.0	77.7
Chicks/Parents		1.41	1.43	1.05

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