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ASPECTS OF THE BREEDING BIOLOGY OF WADING BIRDS (CHARADRII) ON A SALTMARSH

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being a thesis presented in
candidature for the degree of
Doctor of Philosophy in the
University of Durham, 1979.

Plate I. Rockcliffe Marsh - a dry, cattle-grazed saltmarsh.

ABSTRACT

Aspects of the breeding biology of Lapwing, Oystercatcher and Redshank were studied on a dry, cattle-grazed saltmarsh, Rockcliffe Marsh, in Cumbria.

The vegetation of the marsh was predominantly graminoid, due to the influence of grazing and trampling by cattle. There was a halosere from the landward Lolio-cynosuretum to the seaward Puccinellietum.

Invertebrate abundance and biomass declined across the halosere, as did grazing intensity, which was indicated by cowpat density. Cowpat density was positively correlated with the abundance and biomass of Diptera and total invertebrates. The proportion of dung-associated invertebrates varied across the halosere, but over 80% of Diptera in each vegetation type were dung-associated.

The proportion of eggs plus chicks of each species which was trampled was positively correlated with cowpat density, indicating that cowpat density was a valid measure of grazing intensity.

Each wader species nested at a higher than average cowpat density where the mean cowpat density was low, to maximise food availability, and at a lower than average cowpat density where the mean cowpat density was high, to minimise the risk of trampling. Lapwing nest density was positively correlated with cowpat density (proximate factor) and total invertebrate biomass (ultimate factor). The main prey of adult and chick waders were dung-associated invertebrates.

The proximate factors involved in breeding area and nest-site selection by the fore-mentioned wader species and Dunlin and Ringed Plover were elucidated by a multivariate comparison of nest and non-nest samples. The proximate factors were typically related to those features associated with a grazed habitat, e.g. tussock abundance, cowpat density, and with the avoidance of inundation, e.g. distance to nearest creek and plateau edges. The proximate and ultimate factors were discussed with reference to their implications for breeding wader habitat management.

Acknowledgements

This study was carried out on Rockcliffe Marsh Local Nature Reserve while undertaking the duties of warden on behalf of Cumbria Naturalists' Trust. My sincere thanks are due to Mr. and Mrs. David Bailey, Mr. and Mrs. Ian Watson, Mr. and Mrs. T.J. Pattison and Miss E.H. Rhone who, in their various ways, gave me much assistance and showed me great kindness during my visits to Rockcliffe. I am also grateful to Castletown Estates for kindly permitting me to conduct my research on their land.

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Finally, I am indebted to my wife, Susan, for her undaunted patience, assistance and understanding during the past four years.

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SECTION 1

INTRODUCTION

The spatio-temporal distribution and abundance of organisms are the fundamentals of ecology. Typically, organisms are non-randomly distributed within their geographic range; this pattern is ultimately dependent on the differential survival of the individuals of a species, consequent on their adaptations to a limited range of habitats. Natural selection has determined that those species whose members are capable of self-directed locomotion have evolved a process by which they can recognise the habitats to which they are adapted. This process is called habitat selection.

Probably all vertebrates exhibit some degree of habitat selection; the process has been studied in fish (e.g. Brown & Green 1976, Casterlin & Reynolds 1977, Verwey 1949), amphibians (Beebee & Griffin 1977), reptiles (e.g. Heatwole 1978, Sexton & Claypole 1978), mammals (e.g. Funmilayo 1977, Lemen & Rosenzweig 1978) and reviewed in birds by Hilden (1965). Birds, being largely diurnal and relatively conspicuous, especially during the breeding season, are amenable to study. The laying of eggs in a nest provides an unequivocal indication of prolonged habitat utilization. Nest-site selection may be considered as a special form of habitat selection. For some species, e.g. hole-nesting birds, the nest-site requirements are so circumscribed that general habitat considerations are apparently of secondary importance; the presence or absence of potential nest-sites mainly determines the distribution of breeding birds (e.g. Campbell 1968, von Haartman 1957, 1971), although hole-nesting species may, nevertheless, have habitat preferences (Pulliainen 1977). In contrast, wading birds give pre-eminence to habitat selection and apparently choose their nest-sites "casually" (Landsborough-Thompson 1964). This implies that there are no major selective pressures influencing wader nest-site location. This ostensibly fortuitious process was examined with particular reference to nest-site selection by Lapwing, Oystercatcher, Redshank, Dunlin and Ringed Plover.* _A priori_, in the flat, exposed habitats preferred by these waders, any selection of nest-sites must be dependent on subtle, environmental cues.

It is necessary to distinguish between proximate and ultimate factors (Baker 1938) when considering habitat and nest-site selection. Ultimate factors are those which affect survival rate and thereby optimize selection. They are the prerequisites the environment must possess to maintain the species. Hilden (1965) considered that food; the requirements necessitated by the structural and functional characteristics of the species; and shelter from potential predators and adverse weather were the ultimate factors involved in avian habitat selection.

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* The scientific names of birds and mammals mentioned in the text are provided in Appendix 1.

Proximate factors do not necessarily have any intrinsic biological significance, but they do enable individuals of a species to recognise a suitable habitat, presumably similar to the ancestral one, by eliciting the settling reaction. Natural selection has usually determined the ancestral habitat to be an optimal one. A proximate factor may provide a consistent index of a biologically important, but less reliably sensed, environmental variable. For example, seasonal trends in temperature are more accurately reflected by photoperiod than by the fluctuating daily temperatures themselves. The specificity of the proximate factors may restrict a species' distribution, as Lack (1933) suggested for the Ringed Plover. Although the responsiveness to proximate factors is inherited, the nature of the response may be modified by imprinting (Klopfer 1963, Wecker 1963), enabling an extension of habitat range. However, Bendell & Elliott (1966) detected no influence of early experience of sub-optimal sites on the subsequent habitat selection of Blue Grouse, possibly because of the complexity of the habitats and their small sample of grouse. As Orians (1971) predicted, "there should exist a co-evolution between fitness (of the bird) in different environments and the capacity of those environments to evoke settling behaviour". A bird should, therefore, be stimulated by the relevant proximate factors to nest in the most appropriate habitat or site. Hilden's (1965) categories of proximate factors included:

a) landscape and terrain,
b) nest-, song-, feeding-, drinking-, and vantage-sites,
c) food
d) other animals of the same or a different species.

Klomp (1953) was the first to clearly distinguish between ultimate and proximate factors in the field. For example, he noted that the vicinity of trees (the proximate factor) was avoided by breeding Lapwings because they were less able to deter predacious crows (the ultimate factor) than in open areas. Similarly, Lemmetyinen (1971) experimentally demonstrated that losses of Common Tern broods to crows were higher near to trees and shrubs than at a distance from them.

The perceptual basis of habitat selection has been emphasized by Brock (1914, "mental bias"), Lack (1937, "psychological factors"), and Moreau (1935, "subjective factors"), who implicitly suggested that the proximate factors were perceived as a pattern or configuration (Gestalt perception, Kohler 1947). Each species has a perceptual environment or Umwelt (von Uexkull 1909), to the pattern of which it responds, according to a group of specific search images (Tinbergen 1951), which are genetically determined, but to some extent modifiable by experience.

Miller (1942) proposed that habitat selection was an instinctive, finely-balanced reaction to a few psychologically salient environmental variables or proximate factors. This innate response enables the consistent evaluation of alternative sites (McFarland 1977). Burger et al. (1976) regarded nest-site selection "as the product of a behavioural matrix for optimization of energy budgeting and breeding success". Their model delineated the inter-relationships between territory and nest-site characteristics, the energy requirements of the parents and egg and chick survival.

The only valid criteria of habitat or nest-site quality during the breeding season are breeding success, post-fledging mortality (only if the juveniles remain in the same habitat in which they were reared) and adult mortality. Of these, breeding success is the most amenable to study since estimates of adult and post-fledging mortalities require large numbers of marked individuals. The relative abundance of a species in different habitats may be a reliable preliminary index, but provides information on habitat preferences rather than habitat quality: the preferred habitat is not necessarily the optimum. By maximising breeding success and the survival of breeding adults, natural selection optimizes the process of habitat or nest-site selection (Caccamise 1977).

The role of interspecific competition has been emphasized in many studies of avian breeding communities (e.g. Bedard 1969, Fjeldsa 1973, Haila & Jarvinen 1977, Jenkins 1953, Svardson 1949), to determine the extent of niche segregation, especially between congeners. There have been few attempts to assess the optimal breeding habitat of a species in terms of breeding success.

Southwood & Cross (1969) elucidated the relationship between habitat and breeding success of the Partridge; insect abundance was correlated with the differential survival of young. Nettleship (1972) observed that the rate of predation of Puffin eggs (displaced to the burrow entrance) and chicks by gulls was a function of the time the adults were away from the nest. This, in turn, was related to the adults' greater susceptibility to kleptoparasitism on "level" rather than "sloped" breeding habitats. The incidence of predation was also related, in the Oystercatcher, to the duration that adults were away from their offspring whilst feeding (Safriel 1967). The choice of feeding area, rather than breeding habitat, indirectly affected Oystercatcher breeding success. Intertidal feeders were absent from their chicks for longer periods than were terrestrial feeders, and hence the chicks of the former suffered a higher predation rate. In colonial species, the social aspects of the biotic environment may influence breeding success. Breeding success was higher in the centre than the edge of the colony in the Kittiwake (Coulson 1968), the Shag (Coulson _et al_. 1968) and the Adelie Penguin (Oelke 1975), and higher in "dense" than "sparse" groups of the Guillemot (Birkhead 1977).

The genotypic selection mechanism may be influenced by early experience. The role of experience on the ontogeny of behaviour is usually one of reinforcement. Simple choice experiments indicate that whilst early habitat imprinting can decrease the preference for the optimal environment, it is not usually possible to reverse the affinity (Wecker 1963). Breeding-site tenacity is a form of habitat imprinting (Thorpe 1945), whereby birds faithfully return to their original breeding area each year. This tenacity may alter the process of habitat selection to the extent that a bird may return to a breeding area that has significantly deviated from the optimum determined by the innate releaser. This can result in the occupation of new habitats, but "the stimuli operating may be similar to those normally effective" (Hinde 1959). Once a change has occurred, that is not selectively disadvantageous, imprinting onto the habitat by newly-hatched chicks may perpetuate it, as Tast (1968) suggested to explain the change in the habitat requirements of the Linnet.

The differentiation between habitat and nest-site selection is one of degree, rather than an absolute distinction. The reaction to proximate factors probably occurs in at least two stages:

i) the selection of those factors, characteristic of the general habitat, to which the organism is morphologically and behaviourally adapted;
ii) the selection of the precise nest-site, particularly with regard to cover, camouflage and microhabitat.

Elliott (1975) developed a model to describe the selection of proximate factors. This model, with slight modifications, is reproduced here:

$$\sum_i a_i \cdot y_i \geq b_k \cdot K$$

where, for a given species:

y_i is the ith relevant proximate factor,

a_i is a measure of the relative importance of the ith proximate factor,

K is the level of accumulated stimuli required for the settling reaction,

b_k is a factor which modifies the threshold required for the settling reaction, and is dependent on the internal motivation of the kth individual.

The model contains a summation of heterogeneous stimuli (proximate factors) such that when a certain threshold of accumulated stimuli is exceeded, the settling reaction occurs (Hilden 1965). The threshold is subject to the motivation of the individual bird at a given time. The number of proximate factors necessary to evoke the settling response may be diminished if an individual's motivation is sufficiently high. Since some proximate factors will be more influential than others in precipitating the settling response there is a weighting system for each factor. The innate releaser is responsive to "a combination of only very few environmental stimuli" (Tinbergen 1948). The selection process is therefore dependent on a limited number of proximate factors, of which even fewer are essential. It follows that different proximate factors may be selected by members of the same species.

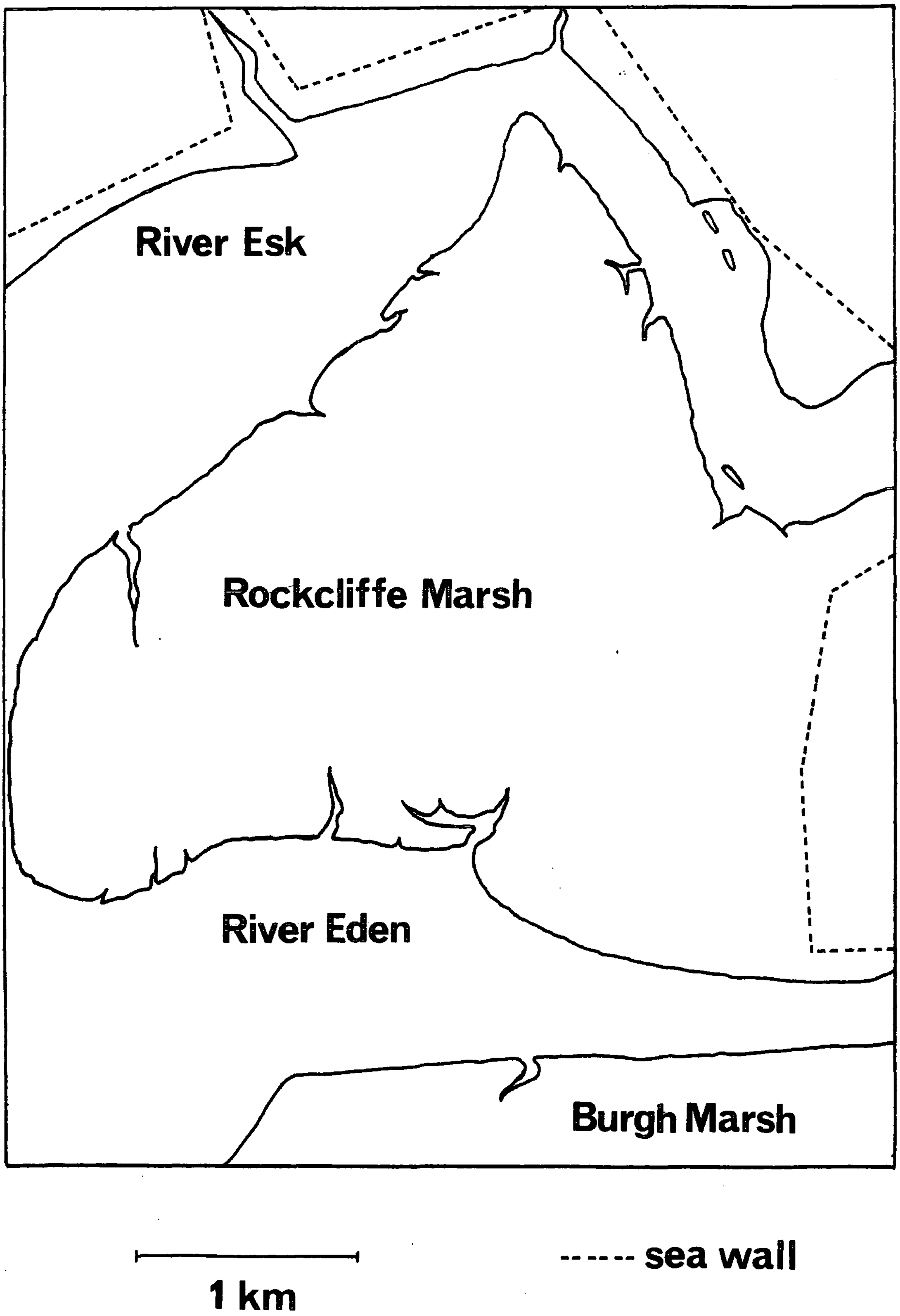
The principal aim of this study has been to determine the relative importance of the proximate factors involved in the processes of habitat and nest-site selection in wading birds. Except for Klomp's (1953) extensive study of Lapwing habitat selection and Heppleston's (1972) brief survey of Oystercatcher habitat preferences, there have been no detailed assessments of habitat or nest-site selection by wading birds. Surveys of breeding habitats have included those of Lapwing (Homes _et_ _al_. 1960, Imboden 1971a, b, Lister 1964, Williamson 1948), Oystercatcher (Heppleston 1971), Redshank (Thomas 1942), Dunlin (Soikkeli 1964) and Common Sandpiper (Cowper 1973). Only Klomp (1953) has attempted to determine the proximate and ultimate factors which are responsible for the observed distributions. It has been tacitly assumed that the preferred habitat is the optimum. However, Heppleston (1972) has demonstrated that the Oystercatcher in Scotland has a higher breeding success in recently-colonised, largely agricultural, inland habitats than in the ancestral coastal environment. These variations in breeding success may be related to breeding density rather than breeding site; at higher densities chicks and eggs were exposed to predation for longer periods because the adults were involved in more frequent territorial disputes than at lower densities (Heppleston 1972).

A study of the proximate and ultimate factors involved in nest-site and habitat selection is potentially of value in the management of breeding habitats. By manipulating the relevant proximate and ultimate factors, the abundance and breeding success of selected species could be increased. This may be particularly applicable to a species that is rare or on the edge of its breeding range. Sub-optimal habitats could be rendered more acceptable. Particular success has been achieved by the provision of suitable nest-boxes for hole-nesting birds (e.g. Bruns 1960, Valanne _et al_. 1968). However, a simple measure is unlikely to evince a similar success in the breeding habitats of waders.

The inter-relationships between waders and cattle were also examined. A relationship between Lapwing breeding density and cattle abundance was casually noted by Stubbs (1907). Williamson (1951) suggested that the droppings of Shetland ponies on Unst were of value to breeding Lapwings by increasing the abundance of available invertebrates. Grazing stock would also contribute to egg and chick mortality by trampling. It was therefore necessary to evaluate the beneficial and detrimental influences of the livestock on the breeding waders.

Multivariate analyses were performed by the IBM 370/168 computer at NUMAC using the Statistical Package for the Social Sciences (SPSS) (Nie _et al_. 1975).

Figure 1. Sketch map of Rockcliffe Marsh, Cumbria.


River Esk
Rockcliffe Marsh
River Eden
Burgh Marsh
1 km
sea wall

SECTION 2

THE STUDY AREA

Rockcliffe Marsh, part of Castletown Estates, is situated approximately 10km northwest of Carlisle, at the head of the Solway Firth where the rivers Esk and Eden converge (O.S. sheets 75 and 76, grid reference 325 640). The marsh is roughly triangular, being about 4km from east to west and 3km from north to south at its broadest points (figure 1). Its area is approximately 1100ha.

As a region of outstanding botanical and ornithological interest, of international importance, Rockcliffe Marsh is designated a Grade A Site of Special Scientific Interest (S.S.S.I.) by the Nature Conservancy Council (Ratcliffe 1977). Cumbria Naturalists' Trust manages the area as a nature reserve from March to August, and employs a warden between April and July to protect the avifauna from undue human disturbance during the breeding season.

Chapman (1960) categorised the Solway saltmarshes as Group 1 North European maritime marshes, sub-group (a), comprised of sandy mud dominated by grasses. Adam (1978) essentially retained this classification. The reserve is a dry saltmarsh of firm turf intersected by a dendritic pattern of muddy drainage creeks which fill at high tide. One creek drains the meadows behind the sea wall after heavy rainfall. Because of the fall in sea level relative to the land, the whole marsh is rarely inundated, and then only by unusually high, equinoctial spring tides. The presence and strength of a southwesterly wind and the water levels of the Esk and Eden determine the extent of flooding at these times.

The soil is a yellow-brown sandy loam or coastal gley which drains rapidly. The upper Solway sandflats and marshes have a remarkably homogeneous substratum comprised of more than 90% fine sand, i.e. particles of diameter 0.2-0.02mm (Marshall 1962). This fine sand is of marine rather than fluvial origin and has originated since the Pleistocene (Perkins 1968).

The area is subject to considerable accretion although some erosion also occurs (Steers 1964). Erosion is primarily due to periodic changes in the channels of the Solway; those of the Esk and Eden are known to move in very short periods of time (Chapman 1960). Using information derived from recent aerial photographs, Ordnance Survey maps (1853-1954), and late 18th century court cases (the briefs of which are deposited at Cumbria County Record Office, Carlisle) it was possible to estimate the nett annual accretion, in terms of area, on the marsh during the last two centuries (table 1). Blake (1955) suggested that there was no marsh prior to 1500, and its inception may not have occurred until the 17th century. During the past 200 years there has been a relatively constant rate of increase in area of 3.7ha per annum. This is the balance of accretion over erosion.

The rate of deposition is very rapid on the Puccinellietum (30mm p.a. at 4.5m O.D.), but markedly decreases as the height increases (12mm p.a. at 4.8m O.D.); very little deposition occurs above 4.8m O.D. (Marshall 1962).

Table 1. Estimated area of Rockcliffe Marsh at intervals during 1762 to 1978

YEAR	AREA (ha)
1762	200
1772	250
1853	600
1926	800
1955	850
1978	1100

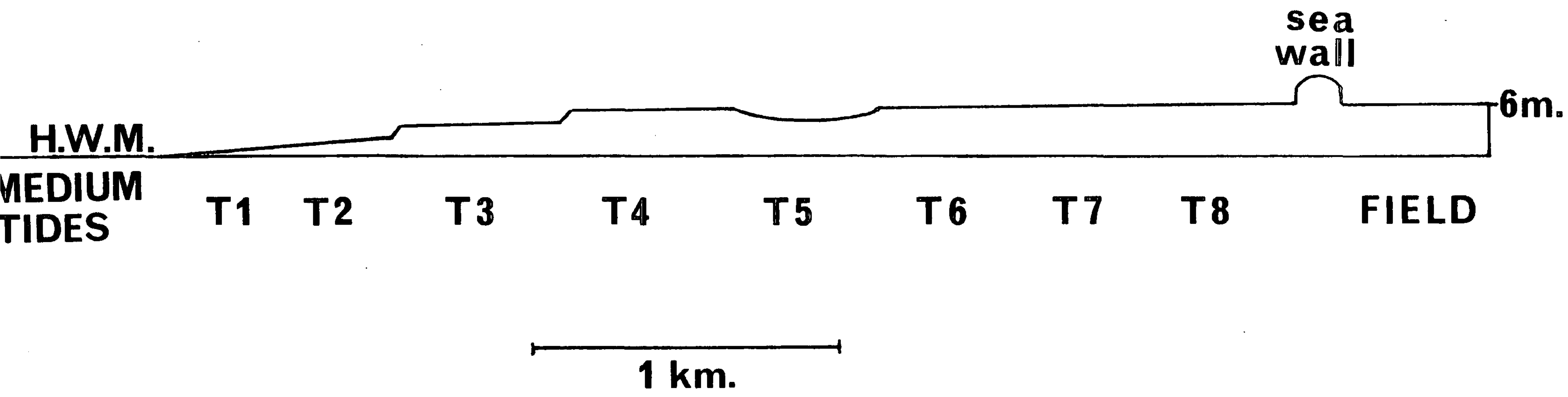
The marsh comprises three terraces (figure 2). The scarps between the plateaux are 30-60cm high, and may be vestigial erosion edges produced by haphazard changes in the courses of the river channels. Their persistence may have been due to a slight rise of the land relative to the sea (Marshall 1962). The terraces are generally saucer-shaped, with a depression in the middle caused by the preferential accretion of silts at the top of the scarps, in the same way that levees are formed on creek edges (Gray 1972). There are major discontinuities in the plant communities of different terraces, between, for example, vegetation types T_2 and T_3, and T_3 and T_4 (Section 3). Saltpans, apparently of creek origin (Chapman 1960), are fairly numerous.

These pans retain rainwater, at least temporarily, and provide loafing areas for gulls, in addition to drinking and bathing sites for waders.

The marsh is grazed by approximately 1000 cattle between May and October, and up to 7000 Barnacle and 5000 Pink-footed Geese between January and April. Grazing results in a close-cropped graminoid vegetation, which is cut to provide the famous "sea-washed" turf of Cumbria. Marshall (1962) stated that the grazing density of cattle on the Solway was among the highest on British saltmarshes, at 1 stock-unit to 2.0-2.5 acres (0.8-1.2ha). This stocking rate is still maintained. There is, however, little evidence of overgrazing. Although some areas are denuded of vegetation ("poached"), this damage is very localized, usually near favoured watering places and scratching posts.

Details of the vegetation, avifauna and invertebrate fauna are subsequently provided.

Figure 2. Profile of transect across Rockcliffe Marsh, indicating relative positions of vegetation types, T_1-T_8, and Field


sea
wall
6m.
H.W.M.
MEDIUM
TIDES
T1
T2
T3
T4
T5
T6
T7
T8
FIELD
1 km.

SECTION 3

PHYTOSOCIOLOGY

Plants are sensitive indicators of their environment (Poore 1955). The seral zonation of vegetation on maritime saltmarshes may be considered as the spatial expression of succession, and is related to the gradient in marsh height and hence tidal submergence (Adams 1963, Hinde 1954). On Rockcliffe Marsh this gradient is interrupted by three terraces which tend to support dissimilar plant communities, although these communities also exhibit trends in species composition and abundance with changes in elevation on each saucer-shaped terrace. However, altitude changes across the marsh are not marked, except at the edges of terraces which are steps approximately 0.5m high. Altitude only increases by 6m over a distance of 2-3km.

The frequency of inundation has a profound effect on the vegetation, so that the lower terraces sustain a predominantly halophytic community, whilst the upper terrace has glycophytic vegetation. Some ecoclinal species may occur on both the lower and upper terraces, e.g. Plantago maritima (Gregor 1946), Festuca rubra and Agrostis stolonifera (Hannon & Bradshaw 1968). The distribution of halophytes may be restricted because they are poor competitors with glycophytes on less saline soils (Barbour 1978).

The other main phytosociological influence, discussed later, is the grazing intensity of cattle between May and October, and to a lesser extent that of overwintering Barnacle and Pink-footed Geese. The geese, in contrast to the cattle, prefer the vegetation of the lower terrace (Reynolds & Owen 1977). Grazing results in a close-cropped, graminoid vegetation. In Britain, the majority of grasslands are "biotic plagio-climaxes", i.e. communities stabilized by grazing at a sub-climactic stage (Tansley 1939).

Phytosociological terminology is still not fully standardised, despite attempts by, for example, Chapman (1959) to establish a concensus, especially with regard to saltmarsh vegetation. The ecological classification of the "continental school" (e.g. Braun-Blanquet 1932), which is based on the classical taxonomic principles favoured by Chapman (1959), was used as the basis for the distinction of the vegetation types described below.

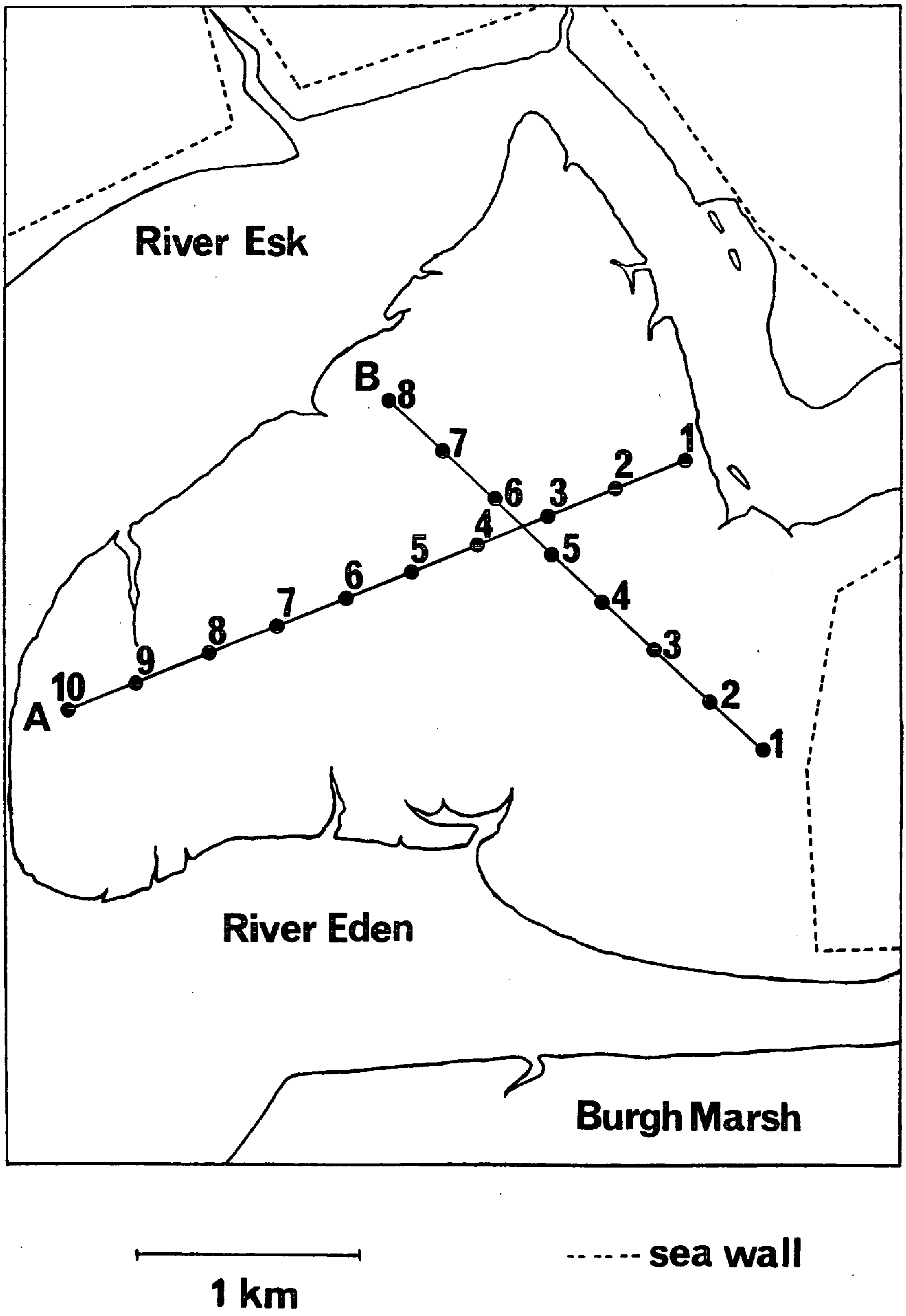
Methods

A simplified Braun-Blanquet (1932) method was used in the phytosociological survey. It is a proven method for providing an "understanding of the structural complexity of vegetation and of its relationship to environmental factors for a minimum of time input" (Moore *et al*. 1970). The classification was based on a simple tabulation of the percentage cover of each

Table 2. Plant species composition and percentage cover at transect points A1-10, B1-8, F1, GR and SC on Rockcliffe Marsh, 1976-78

VEGETATION TYPE	T1	T2	T3				T5	T4						T6		T7		T8	F1	GR	SC
TRANSECT NUMBER	A10	B8	A9	A8	B7	B6	A4	A7	A6	A5	B5	B4	A3	B3	B2	A2	A1	B1	F1	GR	SC
PHYSICAL (0-5)	1	1	2	2	2	2	4	3	3	3	4	3	4	3	4	4	4	5	5	0	2
% BARE GROUND	35	25	15	10	10	5	2	3	2	2	1	3	1	2	1	1	1	0	0	85	20
SPECIES:																					
Sagina maritima																				+	
Atriplex laciniata																				+	+
Oenanthe lachenalii																					+
Halimione portulacoides																					+
Juncus articulatus																					+
Spergularia marina	+	+																			+
S. media	+	+																			+
Aster tripolium	5	+																			5
Cochlearia danica	+	+	+																		+
Sagina nodosa	+	+		+																+	+
Agropyron junceiforme	+	+	+		+																+
Scirpus maritimus	+	5					+														15
Puccinellia maritima	5	15	5	5	+	5	20	+													25
Parapholis strigosa	+	10	+		5	5	+	5	+												+
Armeria maritima	+	5	5	5	5	10		+	+											+	+
Triglochin maritima	+	+			+					+										+	+
Glaux maritima	5	5	+	5	+	+	+		+		+									+	5
Plantago maritima	40	15	5	5	5	5	5	+			+										+
Festuca rubra		10	65	60	70	60	+	40	45	40	50	45	45	30	30	25	20	15		+	5
Agrostis stolonifera		5	+	+	+	+	30	25	20	20	15	20	25	15	10	5	5	5	5		10
Juncus gerardii			+	+			25	5	5	10	15	10	5	+							+
Carex distans				+	+		5	+		+	+										
Trifolium repens				5		+			+	5	+	+	+	10	5	10	5	5	5	+	
Plantago coronopus					+	+			+											+	
Agropyron repens						+						+									
Lotus corniculatus						+		+	+		+	+	+	+	+	+	5	+		+	
Cochlearia officinalis							+														10
Alopecurus geniculatus							+														+
Carex extensa							+														
C. flacca							+	+	5												
C. nigra							+			5											
C. panicea							+			+											
Eriophorum vaginatum							5														
Juncus effusus							5		+			+		+					5		
Potentilla anserina								5	5	5	5	10	+	+	5	+	5	+	5	+	
Leontodon autumnalis								5	5	5	10	5	5	15	15	10	5	5	5	+	
Poa annua								5	5	5	+	+	+	5	5	10	5	10	40	+	
Phleum pratense										+	+		+	5	+				5		
Holcus lanatus												+	+	5	10	5	5	5	5		
Bromus mollis													+	+	5	10	10	5	+		
Bellis perennis														+	+	5	5	10		+	
Stellaria media															+	+	5	+		+	
Cirsium vulgare															+	5	+	5			
Lolium perenne															+	+	10	15	5		
Geranium pratense																+	+				
Ononis spinosa																10	10				
Ranunculus acris																+	5	+			
Taraxacum officinale																	+	+	+	+	
Plantago major																	+	+			
Ranunculus repens																	+	+	+		
Agrostis tenuis																		5	10	+	
Cynosurus cristatus																		10	10		
Cirsium arvense																		+	+		
Crepis capillaris																		+	+		
Rumex obtusifolius																			+	+	
Achillea millefolium																			+		
Urtica dioica																			+		
Primula veris																			+		
Trifolium pratense																			+		
Dactylorhiza purpurella																			+		
Prunella vulgaris																				+	

Figure 3. The position of transect points along transects A and B, on Rockcliffe Marsh

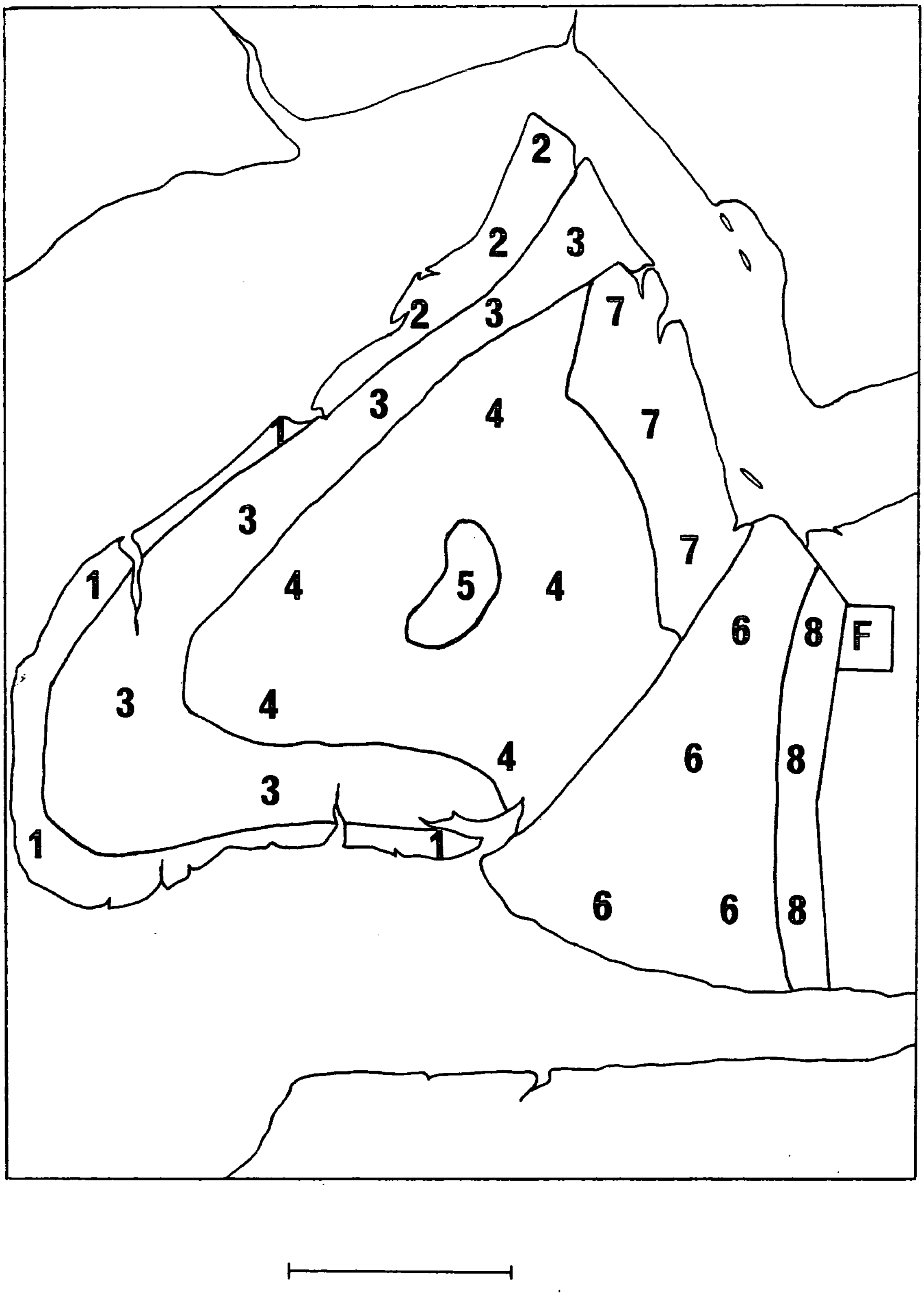

River Esk
B
8
7
6
5
4
3
2
1
A
10
9
8
7
6
5
4
3
2
1
River Eden
Burgh Marsh
1 km
sea wall

species at each sampling point. Samples having a similar vegetation were grouped and subsequently arranged to exemplify the succession across the marsh. Eleven vegetation types were distinguished (table 2). Samples were collected along two transects, A and B, across the length and breadth of the marsh (figure 3). A pasture behind the sea wall (F1), a gravel area (GR), and a sea creek (SC) were also sampled for comparative purposes since their vegetation differed notably from those communities already sampled. The same transect points were surveyed in 1976, 1977 and 1978 but there were no detectable changes in the percentage cover of each species.

Each sample was based on a $1m^2$ quadrat at each transect point. This sample size was consistent with that adopted by others studying herbaceous vegetation (Frenkel & Harrison 1974). The transect points were approximately 250m apart. Their location was selected in relatively homogeneous "typical" areas with regard to vegetation and topography to minimise the influence of any edge effects on the floristic composition (and the invertebrate fauna, which was also sampled).

The physical characteristics of the vegetation were coded on a 0-5 scale of increasing density. The proportion of unvegetated ground at each transect point was noted and reflects this scale. The percentage cover of each species was estimated to the nearest 5%. The presence of a species occupying less than 1% of the cover

Figure 4. Vegetation map of Rockcliffe Marsh. Numerals indicate vegetation types T_1 to T_8, and F indicates pasture behind sea wall


2
2
3
2
3
7
3
4
7
1
3
7
1
4
5
4
6
8
F
3
4
4
6
8
3
1
1
6
6
8
1 km

was denoted by +. With the exception of the final two columns of table 2, the vegetation types were ordered along a scale of increasing maturity from left to right. In general, the species were arranged along a continuum from those halophytes typical of scantily vegetated soils to the glycophytes characteristic of mature pastures. This arrangement of both transect data and species order was designed to enhance the graded nature of the sere. The epilittoral meadow ecosystem can be considered as a continuum (Wallentinus 1967).

The sociability of each species was not included since it is partly a characteristic of the species and is also related to percentage cover. Estimation of the latter property was economical of time and effort and proved adequate to distinguish vegetation types.

The scientific names of plants are those used by Clapham *et al*. (1968). The identifications were based on Hubbard (1968) and Keble-Martin (1969).

The vegetation

The vegetation types distinguished (figures 2 & 4, table 2) are described below in order of increasing maturity along the sere-climax:

VEGETATION TYPE

T1 *Plantago maritima* was the predominant species. This community therefore constituted a Plantaginetum maritimae. It was the only association dominated by a herbaceous species.

T2 *Plantago maritima* and *Puccinellia maritima* were co-dominant in this Puccinellietum maritimae.

T1 and T2 were associations in the alliance Puccinellion maritimae, a pioneer saltmarsh community which occurred below the high water mark of mean tides and was frequently inundated. No birds nested on the Pucinellion maritimae.

T3 The predominant species was *Festuca rubra*, whilst *Armeria maritima* was at its highest percentage cover. This association occurred at a slightly higher elevation than the Puccinellietum and was conveniently classified as a Juncetum gerardii, although the character species, *Juncus gerardii*, may be absent. *Festuca rubra* and *Armeria maritima* were constant species in this association which is subsumed under the alliance Armerion maritimae, and constitutes the General Saltmarsh Community of Chapman (1960).

T4	This vegetation type was also dominated by *Festuca rubra*, with *Agrostis stolonifera* as a sub-dominant. This Festucetosum rubrae (Wallentinus 1973) occurred on the higher levels of the marsh and may be considered as a degenerate form of the Juncetum gerardii.
T5	The low-lying basin on the first terrace remained water-logged for longer periods than any other area. Its anomalous vegetation was more reminiscent of sea creek vegetation or T3 than that of T4 by which it was surrounded. It was therefore tabulated between T3 and T4. *Puccinellia maritima*, *Agrostis stolonifera* and *Juncus gerardii* were the co-dominants in this Juncetum gerardii.
T6	T6 was very similar to T4 but had a higher percentage cover of grasses such as *Holcus lanatus* and forbs such as *Trifolium repens* and *Leontodon autumnalis*.
T7	The presence of *Ononis spinosa* was characteristic, although the predominant species was again *Festuca rubra*.
T8	*Festuca rubra* and *Lolium perenne* were co-dominants. *Cynosurus cristatus*, *Poa annua* and *Bellis perennis* were the other main components of this Lolio-Cynosuretum.

This community was described by Tansley (1939) as Agrostis-Festuca Grassland. It is the widespread pasture association of western Europe.

FIELD	*Poa annua* predominated in this Lolio-Cynosuretum.

The sea creek and gravel vegetation could not readily be placed in this continuum. The sea creeks were dominated by *Puccinellia maritima* and were largely inaccessible to cattle. This was confirmed by the presence of such grazing-intolerant species as *Aster tripolium* and *Cochlearia officinalis* (Gray & Scott 1977). The gravel area supported a diverse flora, including many ruderals, e.g. *Sagina maritima*, *Stellaria media* and *Achillea millefolium*, which had a low percentage cover.

The influence of the cattle

The grazing and trampling activities of the cattle have to a large extent, determined the species composition of the plant community. Although those species which are tolerant of trampling are often also grazing resistant, this does not necessarily obtain for all species (e.g. *Armeria maritima* which may be grazing resistant but is not very tolerant of trampling - Gillham 1956). Some species have a variable tolerance of grazing and trampling according to habitat and grazing intensity (Crawford & Liddle 1977, Dale & Weaver 1974). The communities of grazed and trampled areas are, however, remarkably similar, whatever the agent (e.g. Kydd 1964, Liddle 1975, Streeter 1971, Weaver & Dale 1978).

Bakker (1978), Beeftink (1977), Gray (1972) and Ranwell (1961) have emphasised the importance of grazing as a factor influencing saltmarsh vegetation. However, Chapman (1941) considered that the presence of Puccinellia maritima on west coast saltmarshes was consequent on their sandy sediment, rather than the influence of grazing. It is not possible to assess the relative importance of substrate and grazing on the vegetation of an area which has a long history of grazing (Adam 1978). Grazing reduces the halophytic element of the saltmarsh flora, but the species-richness may be increased (Westhoff 1971); these two tendencies were apparent on Rockcliffe Marsh.

Grazing and trampling affect not only species composition, but also the habits or growth forms of species. This latter influence was of direct importance to the breeding waders. The majority of grassland species are hemicryptophytes (Wells 1973), whose normally erect habits have become prostrate under a grazing regime. These prostrate species include Agrostis stolonifera, Trifolium repens, Potentilla anserina, Ranunculus repens and Carex flacca. Some species adopt a rosette growth form, with overlapping spirals of leaves, to minimise the impact of trampling, e.g. Bellis perennis and Plantago major. Gillham (1955) noted that dwarfing occurred in

Plantago coronopus, *Festuca rubra*, *Agrostis tenuis* and *Holcus lanatus* in grazed habitats. These adaptations of the growth form result in a very low vegetation height, regardless of the actual defoliation by grazing animals. This short vegetation is particularly suitable for breeding Lapwings and Oystercatchers. In contrast, grazing can also promote tussock formation in some species, e.g. *Eriophorum vaginatum* and *Festuca rubra*, thereby affording protection to the otherwise vulnerable growing points, (Wein 1973). Tussocks are the predominant nest-sites of Redshanks and Dunlins.

Grazing and trampling also prevent the formation of a deep litter layer (Welch & Rawes 1964). When litter is trampled its structure is fragmented and disintegrates. The removal of tall herbage by grazing exposes it to the drying action of the sun and wind, and subsequent dispersal (Duffey 1975). The loss of the litter layer permits the persistence of plants with a dwarfed growth form.

By modifying vegetation topography, grazing and trampling render the habitat more attractive to wading birds which prefer exposed habitats with short vegetation.

SECTION 4

THE AVIFAUNA

History

There was little detailed information on the status of the avifauna prior to 1970, although Brown (1974) summarized general trends for the period 1920-1970 on Cumbrian saltmarshes. It was, therefore, possible to obtain a qualitative impression of the trends during the last century. Recent data are tabulated (table 3), but earlier references are summarized below for each species.

LAPWING	The Lapwing was an abundant breeding bird on the Solway saltmarshes at the end of the 19th century (e.g. Armistead 1886, Service 1905); no major changes in status have been noted, although Brown (1974) suggested that a decline had occurred since 1920.
OYSTERCATCHER	Few pairs of Oystercatchers bred along the Solway at the end of the 19th century (e.g. MacPherson 1892). There has probably been a real increase in the Solway breeding population. This tendency reflects the national increase, and may be related to decreased predation by man (Sharrock 1976).

REDSHANK Heysham (1797, quoted in MacPherson 1892) considered the Redshank a scarce winter visitor to Cumberland. During the 19th century breeding became regular (Thomas 1942), until by the latter half of the century it was viewed as an abundant resident (Service 1905). Many pairs bred on Rockcliffe Marsh (MacPherson & Duckworth 1886), and saltmarshes remain the "strongest haunts" of the Redshank in Cumbria (Stokoe 1962).

DUNLIN There has been a marked decrease in the numbers of saltmarsh breeding Dunlin (Brown 1974, Stokoe 1962) since Service (1905) recorded "many pairs" on the Solway and MacPherson & Duckworth (1886) considered that the Cumberland "stronghold" of the Dunlin was Rockcliffe Marsh, where it nested in "considerable numbers"!

RINGED PLOVER Breeding was intermittent during the 19th century (MacPherson 1892) and the present small population is probably attracted by the gravel road which was constructed in the early 1960's and which is the main breeding site for Ringed Plovers on Rockcliffe Marsh.

COMMON TERN "Considerable numbers" were noted on Rockcliffe Marsh by MacPherson & Duckworth (1886). Between 1930 and 1950 the colony fluctuated between 100 and 170 pairs, but from 1950 to 1967 only 50 to 70 pairs occurred annually (Brown 1974). During the 1970's, there has been a slight, but fluctuating (95-240 pairs), resurgence in common with other major breeding sites (Lloyd *et al*. 1975).

BLACK-HEADED GULL The vicissitudes of the Black-headed Gullery have been well documented. A sporadic colony of a few pairs was present in 1859-63, 1870, and 1890-91 (MacPherson 1892). The inception of the present colony can be traced to 1908 (Harrison 1908). By the 1950's there were only about 40 pairs (Gribble 1962), but the colony growth rate has since notably increased, and there are now approximately 2000 pairs.

LESSER BLACK-BACKED AND HERRING GULLS Brown (1974) documented the growth of the mixed colony in which Lesser Black-backed Gulls predominate:

YEAR	NO. OF PAIRS
1925	1
1926	16
1933	250
1967	600 (including 20 pairs of Herring Gulls)

In 1928, the colony of Lesser Black-backed Gulls from Bowness Moss moved to Rockcliffe Marsh (Davis 1958). Since 1933 the annual growth rate has been approximately 15%, in common with many other colonies (Harris 1970).

GREAT BLACK-BACKED GULL None were recorded by MacPherson & Duckworth (1886), nor by Harrison & Hurrell (1933), although Brown (1974) noted occasional breeding between 1920 and 1950. Single nests were found in 1956 and 1957 (Davis 1958). Breeding is now regular.

The species composition of the breeding avifauna of Rockcliffe Marsh was similar to that of other grazed saltmarshes in Britain (e.g. Boorman & Ranwell 1977, Ferns 1977, Glue 1971, Greenhalgh 1971, Harrison 1974), and Europe (e.g. Hulscher 1970, Moller 1975, Soikkeli 1965, Turcek 1976).

Census methods

The number of nests found annually, between April and July, provided an index to monitor population fluctuations. This index was subject to potential errors:

1. The reserve warden differed in most years, so that individual ability and experience of nest-finding contributed to the annual variation, especially when the warden's research was not primarily concerned with the

wader populations, e.g. in 1973, and some areas may not have been adequately surveyed.

2. The time spent searching for nests varied annually according to the time available and weather conditions.
3. More effort was expended in the location of the nests of Dunlin, Ringed Plover and Redshank than of those of Lapwing or Oystercatcher.
4. Since 1976 the numbers of gull nests have been estimated.

Since sea-birds and waders cannot be adequately censused by the "mapping method" (International Bird Census Committee 1969), nest-marking represents the least ambivalent technique for censusing a relatively homogeneous area each year to obtain indices of population changes and community structure. Comparing six census techniques, Furness (1977) considered that nest marking was the most accurate method in large colonies of the Great Skua. For less colonial species, the technique probably underestimated the total numbers, although this would, to some extent, be compensated by the laying of replacement clutches.

The index was based, for all species, on the same procedure, that of nest counts. Each newly-discovered nest was marked by an inconspicuous cane placed 2-3m from the nest to ensure that the same nest would not be counted twice. Predators may have used the nest markers as a search image (Croze 1970, Hammond & Forward 1956), thereby resulting in the increased predation of marked nests (Picozzi 1975). This process would increase the proportion of replacement nests.

It was not possible to comply with all the assumptions of the census technique. A similar proportion of the nests of each species ~~were~~ was not marked; a higher percentage of the less common species, and those whose nests were difficult to locate, were probably marked because more time and effort were expended on them, e.g. Dunlin, Arguably, this was necessary to counteract their potential underestimation due to their rarity or concealment. The potential bias was further counterbalanced because during searches for the nests of rarer species those of more common ones were usually encountered. It was assumed that a similar proportion of nests were found each year for a given species.

Community structure

The community structure was examined to assess if any change had occurred during the period 1970-1978 (table 3). Margalef (1951) proposed a simple index of diversity:

$$\alpha = \frac{S - 1}{\log_e N}$$

where: α is an index of diversity
S is the number of species
N is the number of individuals

Table 3. Avian community structure of Rockcliffe Marsh, based on annual nest totals 1970-1978. Data obtained from Cumbria Naturalists' Trust, Warden's Annual Reports. C is constancy.

SPECIES	1970	1971	1972	1973	1974	1975	1976	1977	1978	C %
Shelduck				1	1	3	1	1	3	67
Mallard	5	8	9	4	7	8	8	17	10	100
Teal						2	1	1		33
Shoveler	1	1	1					1	2	56
Red-breasted Merganser		1	2	1	3	3	1	3	4	89
Moorhen	9	11	9	5	3	2	5	3	2	100
Oystercatcher	44	67	78	58	84	122	176	107	138	100
Ringed Plover	6	9	12	3	3	8	11	6	13	100
Lapwing	34	65	55	40	74	138	187	137	121	100
Dunlin	4	5	5	2	5	5	5	6	7	100
Redshank	38	79	39	67	68	122	182	85	97	100
Black-headed Gull	820	764	528	642	1369	1829	2657	2000*	2000*	100
Lesser Black-backed Gull	636	812	1518	953	1249	1491	1500*	1500*	1600*	100
and Herring Gull										100
Great Black-backed Gull	1	2	2	1	5	5	5	5	6	100
Common Gull			1							11
Common Tern and Arctic Tern	226	202	123	95	237	244	240	204	175	100
Skylark	44	64	47	45	76	120	72	72	49	100
Sand Martin	54	42	33	30*	34	21	29	38	41	100
Swallow	1		1						1	33
Meadow Pipit	3	6	7	11	13	9	9	12	26	100
Yellow Wagtail	1									11
Pied Wagtail			1							11
Carrion Crow			1	1						22
TOTAL NO.	1927	2138	2472	1959	3231	4132	5089	4198	4295	
TOTAL SPECIES	19	18	22	19	18	19	19	20	20	
MARGALEF'S ALPHA	2.38	2.22	2.69	2.37	2.10	2.16	2.11	2.28	2.27	

* indicates estimated values

Table 4. Sorensen's Quotient of Similarity of avian species composition on Rockcliffe Marsh for paired years (1970-1978).

YEAR	1970	1971	1972	1973	1974	1975	1976	1977
1971	0.92							
1972	0.88	0.90						
1973	0.84	0.92	0.88					
1974	0.86	0.94	0.85	0.97				
1975	0.84	0.92	0.83	0.95	0.97			
1976	0.84	0.92	0.83	0.95	0.97	1.00		
1977	0.87	0.95	0.86	0.92	0.95	0.97	0.97	
1978	0.92	0.95	0.90	0.92	0.95	0.92	0.92	0.95

The calculation of this index is greatly dependent on an accurate value of S. Although it was possible that rare breeding species were unnoticed, it was unlikely since birds are very conspicuous, visually and audibly, especially waders, which have very distinctive song-flights (Dabelsteen 1978). The number of individuals was underestimated; every nest of each species was not found. It was assumed that a similar proportion of the nests of each species was found each year and that a consistent estimate of the number of breeding pairs was obtained. There was little annual variation in Margalef's alpha (2.10-2.69) indicating that community structure was relatively stable during 1970 to 1978. This lack of variation was primarily due to the similar number (18-22) of species nesting each year.

To examine the similarity of the species composition over successive years, rather than the diversity, Sorensen's (1948) Quotient of Similarity (QS) was used:

$$QS = \frac{2j}{a + b}$$

where: a is the number of species in year A
b is the number of species in year B
j is the number of species recorded in both years

This quotient, by emphasizing the joint occurrence of species, measures the relative similarity of two habitats, or the same habitat in different years, with regard to species composition, but gives equal weighting to both rare and common species (Whittaker & Fairbanks 1958). The closer QS approximates to unity, the greater is the degree of similarity of species composition between paired years. The quotient is affected by sample size (Southwood 1966), but as the same area was censused in each year, and species number was fairly constant, this potential bias was minimised. The range of values of QS was 0.83-1.00 (table 4), which indicated that the species composition of the avifauna had not markedly altered during the period 1970-1978.

Constancy (C) was used to measure the regularity of breeding by each species. The constancy of breeding was the percentage of years in which a given species nested; if a species bred every year on Rockcliffe Marsh it had a constancy of 100%. Of the 25 recorded breeding species, 16 (64%) have bred each year. If an arbitrary constancy of at least 50% is taken to indicate regular breeding, then 19 (76%) of the 25 species were regular breeders. Of the remaining irregular breeders, the Teal, Yellow Wagtail and Common Gull nest only sporadically in Cumbria (Parslow 1973), and there were few suitable nest sites available for the Carrion Crow (e.g. trees) and Pied Wagtail (e.g. walls).

SECTION 5

THE INVERTEBRATE FAUNA

Marine saltmarshes sustain a varied and abundant invertebrate fauna (e.g. Davis & Gray 1966, Healy 1975, Paviour-Smith 1956). On Rockcliffe Marsh, the invertebrate fauna was largely comprised of dung-associated and euryhaline species. There were, therefore, affinities with the fauna of other saltmarshes (e.g. Appleton _et al_. n.d., Brough _et al_. 1964, Crossley 1977, Meijer 1977, Nicol 1935, Sutcliffe 1961) and with those of inland pastures (e.g. Curry 1976a, b, Edwards 1929, Southwood & van Emden 1967). Previous surveys of Solway saltmarsh invertebrates have included Hemiptera-Homoptera (Kenward 1973), Crustacea (Brady 1869-70), and a recent faunistic survey of Caerlaverock NNR (M. Nelson, pers. comm.).

Methods

(a) Pitfall trapping

The pitfall trap has been extensively used to sample such surface active arthropods as Araneida, Collembola and Coleoptera, especially Carabidae (e.g. Duffey 1962, Joosse & Kapteijn 1968, Workman 1978). The expediency and convenience of the technique commend pitfall trapping as a "potentially valuable means of monitoring certain animal populations" (Luff 1975). Pitfall trapping must be used with discretion, especially for comparative purposes. It is of little value for the direct estimation of populations, of the sex-ratio of a species, or for the comparison of communities (e.g. Briggs 1961, Ericson 1978), but it is adequate to assess the relative numbers of a species in different vegetation types (Greenslade 1964).

The sampling programme was primarily designed to determine the presence and relative abundance of epigeic invertebrates along two gradients across the halosere (transects A and B, see figure 3). Plastic cups (internal diameter 70mm) were used as traps, despite their low catching efficiency compared to glass traps (Luff 1975), because if damaged they would not be hazardous to stock. They were easy to remove, empty, clean (a clean, smooth surface was necessary to maintain retaining efficiency - Luff 1975), and reset. Since some of the traps were removed by cattle and gulls, small pliant canes were inserted into the soil on either side of the traps to prevent further losses.

To minimise predation, escape and deterioration of trapped specimens, 10% "Hospital Teepol L" was used as a preservative. Houston (1970) found no evidence that it acted either as an attractant, as formalin does (Luff 1968), or as a repellant to Coleoptera. Specimens were rapidly killed, preventing their escape and mutual predation, and adequately preserved for up to two weeks.

Four traps were arranged at the corners of a 10m square quadrat at each transect point. Captures are known to be reduced if the traps in a grid are closely spaced relative to the distance moved by the animals (Luff 1975). A quadrat of 10m square probably reduced the potential catch, but it was necessary to ensure that the areas sampled by the traps were equable with regard to vegetation cover and topography, which are known to influence trap efficiency (Mitchell 1963). The trap rims were set flush with the ground surface to ensure maximum catches (Greenslade 1964).

The contents of each trap were collected on every fifth day. Twelve collections were made in both 1976 and 1977 between April and June. Each trap was emptied into a phial containing 10% formalin, to preserve the contents for later examination and identification. Because of the high frequency of tidal inundation on the lower terrace, it was only possible to consistently sample transect points A1-8 and B1-6. A pasture behind the sea wall was also sampled.

The number of animals caught in pitfall traps is dependent on both activity, which is influenced by local climatic conditions (Greenslade 1961), and population size (e.g. Boyd 1960, Mitchell 1963). There may be a differential susceptibility of species to trapping according to behaviour (e.g. Luff 1978, Williams 1959), and larvae may not be caught unless they search for pupation or hibernation sites (Houston 1970). The phenology of individual species, notably the times of eclosion of eggs and pupae, affects the size of the effective trappable population.

The only feasible alternative for sampling the epigeic fauna was vacuum suction trapping. This technique has a high extraction efficiency for some Hemiptera, adult Diptera and Hymenoptera, but is less adequate for large invertebrates and larval Diptera and Coleoptera (Johnson _et_ _al_. 1957). This limited technique samples only a small area at one point in time so that numerous samples are ideally required over a series of 24 hour periods to accommodate the diurnal rhythmicity of different species. Invertebrates temporarily taking refuge in the soil or in grass roots are not sampled. The patchy distribution of many animals (Southwood 1966) and the relatively low overall density of organisms may result in large sampling errors. In contrast, pitfall trapping samples the epigeic fauna over a comparatively long period (5 days in this instance) during which the trapping areas are subject to similar climatic conditions. It was only necessary to obtain a relative, rather than an absolute, measure of wader prey availability, so pitfall trapping was used in preference to vacuum suction methods.

(b) Soil sampling

Soil samples were taken with a soil corer of internal diameter 3.6cm to a depth of 15cm. The samples were sieved and hand-sorted in the field. The maximum diameter of the sieve mesh was 3mm. All the animals retrieved were in the top 5-10cm of the soil. In each year, 30 samples were taken from the vicinity of transect points B2 (vegetation type T6) and B6 (T3), on the "old" and "new" marsh respectively. Transect B was selected because its whole length traversed areas where wader breeding density was high, in contrast to transect A which passed through the gulleries where wader nest density was reduced. In both years, half the samples were taken in the first week of May and half during the first week of June. The 15 samples were arranged in three equidistant rows on a 10m x 20m grid. Because of the paucity of invertebrates collected, the data for May and June were combined.

Table 5. Density (m^{-2}) of soil invertebrates recovered from 120 soil core samples, each of 10.2 cm^2, taken in 1976 and 1977, 30 on the "old" and 30 on the "new" marsh in each year.

		1976		1977	
		Mean	S.E.	Mean	S.E.
"Old" marsh (B2):	*Tipula paludosa* larvae	2.3	1.4	1.3	0.9
	Coleoptera larvae	1.0	0.7	0.7	0.5
	Total invertebrates	3.3	1.6	2.0	1.2
"New" marsh (B6):	*T. paludosa* larvae	0.3	0.3	0.3	0.3
	Coleoptera larvae	0.7	0.7	0.0	0.0
	Total invertebrates	1.0	0.7	0.3	0.3

In both years, the "old" marsh supported between 3 and 6 times more soil invertebrates than the "new" marsh (table 5). Further, approximately twice as many invertebrates were collected in 1976 than in 1977. It was not possible to assess the statistical significance of these tendencies, due to the sparse data.

Those areas where waders were previously observed feeding were also sampled in 1976. Of four 0.25m^2 samples, taken to a depth of 10cm, only one of the two on the "old" marsh contained any invertebrates. The 5 *Tipula paludosa* larvae obtained were thus at a mean density of 10 larvae m^{-2} on the "old" marsh. Final instar *T. paludosa* larvae have a density of 30-100 m^{-2} on moorland mineral soils (Coulson & Whittaker 1978) and up to 116 m^{-2} on inland pastures (Milne *et al.* 1965). The low densities of final instar larvae encountered on Rockcliffe Marsh may be due to the well-drained or saline substrate; tipulid larvae require moist conditions because they are susceptible to desiccation. The densities on Rockcliffe Marsh corresponded to those occurring on inland pastures during or subsequent to a drought (Milne *et al.* 1965).

Personal observations indicated that Diptera and Coleoptera larvae were aggregated under or in the immediate vicinity of cowpats. The few lumbricid worms found on the marsh were under old cowpats on the upper terrace near the sea wall. Lumbricids are rarely found where soil salinity exceeds 0.07M for long periods (Barley 1961), hence their exclusion from most of the salt-marsh. The scarcity of lumbricids was particularly noteworthy, since Hogstedt (1974) considered earthworms to be the main component of the diet of Lapwings in southern Sweden.

As the density of the soil fauna was apparently low, and soil samples provided little information for the time and labour expended, it was decided to utilize pitfall trapping as the main relative index of food availability to the waders.

Species composition

The invertebrates recovered from pitfall traps were usually identified to family, and where possible to species level (Appendix 2). The main keys used for the identification of invertebrates are listed in Appendix 3. Particular attention was devoted to those invertebrates greater than 3mm long, since these were more likely to feature in the waders' diet than smaller organisms; for example, Lapwing chicks prefer Coleoptera of a modal length greater than 5mm (Potts 1970).

(a) Dung-associated invertebrates

Dung-associated invertebrates (marked * in Appendix 2) were defined as those recorded or bred from bovine dung. The authorities are cited in Appendix 4. Personal observations supplemented this information. Species of Syrphidae, Sepsidae, Sphaeroceridae, Calliphoridae, Scathophagidae, Hydrophilidae, Staphylinidae and Scarabaeidae were frequently observed on cowpats.

Olechowicz (1974) proposed a functional classification of the colonising mesofauna of sheep dung which is also applicable to bovine dung. She recognised three major trophic groups which comprised the dung-associated fauna: primary coprophagans (obligatory species), largely confined to dung (e.g. Sepsidae, Sphaeroceridae, Scathophagidae, Scarabaeidae); secondary coprophagans, which were not obligatory coprophages (e.g. Chironomidae, Cecidomyiidae, Sciaridae, Psychodidae, some Staphylinidae); predators of both primary and secondary coprophagans (e.g. some Araneae, some Staphylinidae, Empididae, Dolichopodidae, some Muscidae); and parasitoids of coprophagans and predators (e.g. Ichneumonidae).

The classification of the dung fauna adopted in this study differed from that of Olechowicz (1974) in that predators and hymenopterous parasitoids which have frequently been recorded from dung were grouped with secondary coprophagans, for convenience, as facultative dung-associated species. The proportion of facultative dung-associated invertebrates was probably underestimated, because such predators as Carabidae were not included, although they were observed in the vicinity of cowpats, presumably in search of prey.

The only alternative habitat to cowdung for secondary coprophagans on the marsh was tidal debris, but much of this was unsuitable (glass, plastic, wood) and was concentrated along the sea wall, an area in which no wading birds were observed to feed.

(b) *Maritime invertebrates*

Apart from the estuarine molluscs and crustaceans, there were also species which frequently occur on salt-marshes, brackish ponds and sandy coasts. These included:

Araneae
Pardosa purbeckensis

Hemiptera
Salda spp.

Trichoptera
Limnephilus affinis

Diptera
Hilara lundbecki
Stratiomyidae
Dolichopus clavipes
Scathophaga litorea

Coleoptera
Dyschirius spp.
Broscus cephalotes
Bembidion spp.
Dicheirotrichus spp.
Agabus spp.
Bledius spp.

(c) *Marshland invertebrates*

Species characteristic of marshy areas included *Tipula nigra*, Ptychopteridae (Diptera), *Agonum* spp., *Badister bipustulatus*, *Pterostichus vernalis* and *P. nigrita* (Coleoptera). These species were largely restricted to the water-logged area, T5.

Tipula nigra was particularly of note. It is a local, uncommon species recorded no further north than Southport, Lancashire, by Coe *et al*. (1950). Robinson (1956) noted its occurrence near Morpeth, Northumberland, but it has not previously been reported from the Solway (Brown & Duncan 1949).

Invertebrate abundance and biomass

The invertebrates were counted and stored in 70% ethanol whilst each sample was being sorted and identified. They were subsequently dried and weighed on consecutive days until a steady dry weight was obtained. The specimens were weighed on a Mettler H51 AR Electronic Balance with a sensitivity of 0.01mg. Lipids can account for up to 45% of the total dry weight of some larvae (Wigglesworth 1972). A proportion of the lipid fraction will be soluble in organic solvents, such as ethanol, in which the invertebrates were stored for up to one week. A large loss of soluble lipids was only likely to occur if the invertebrates were macerated, but as most of them were intact, the loss of alcohol-soluble lipids was not considered a significant influence on the subsequently measured dry weights. Measurements indicated that the biomass was underestimated by 2-7%.

Arachnida, Diptera and Coleoptera were the major components of the fauna in terms of both abundance and biomass; the remaining orders (Collembola, Hymenoptera, Hemiptera and Lepidoptera predominated) were combined as "others".

Numbers and weights were expressed as mean values per trap per 5 day period, since at each transect point there were 4 traps which were emptied every fifth day. This standardization was necessary because traps were occasionally removed by cattle or gulls. When this occurred the sample sizes were accordingly rectified.

(a) Numbers

The mean numbers of invertebrates captured at each transect point in 1976 and 1977 are tabulated in Appendix 5. The transect data were grouped into the relevant vegetation types - Field, T8 (B1), T7 (A1, A2), T6 (B2, B3), T5 (A4), T4 (A3, A5, A6, A7, B4, B5) and T3 (A8, B6) - to indicate the relative abundance of each invertebrate group along the halosers (figures 5 and 6). In both years, the upper marsh (T8 and T7) had approximately twice the number of invertebrates that were on the lower marsh (T6-T3). This pattern was mainly determined by the abundance of Diptera.

The seasonal abundance of invertebrates between April and July (Appendix 6, figures 7 & 8) was similar in both years. There was a marked peak of abundance which was reflected by all groups, but especially by the Diptera. This peak shortly followed the introduction of cattle to the marsh on 3-4 May, 1976 and 4-5 May, 1977. The delay of the peak in 1977 by 5-10 days was associated with the lower mean temperatures in April and May 1977 than in 1976 (Appendix 8). There was evidence of smaller peaks of invertebrate abundance in June and July in both years, presumably due to the seasonal emergence of different species.

(b) Biomass

The mean invertebrate dry weights at each transect point (Appendix 7) were grouped according to vegetation type (figures 9 & 10). Fluctuations in biomass reflected those in abundance, with the upper marsh maintaining the greatest biomass, especially in T7. This pattern was similar in both 1976 and 1977.

Both biomass and numbers of total invertebrates were usually slightly higher in 1976 than 1977 at each transect point. It was not known whether this represented a real difference in the availability of prey to the wading birds, or a variability of trapping efficiency related to annual differences in temperature and rainfall.

Figure 5. Mean numbers of invertebrates (Arachnida, Diptera, Coleoptera, "others" and total) caught per pitfall trap per 5 days in each vegetation type, on Rockcliffe Marsh in 1976.

Error bars indicate one S.E. of mean. Numerals on abscissa indicate vegetation types 3 to 8. F is Field vegetation type.

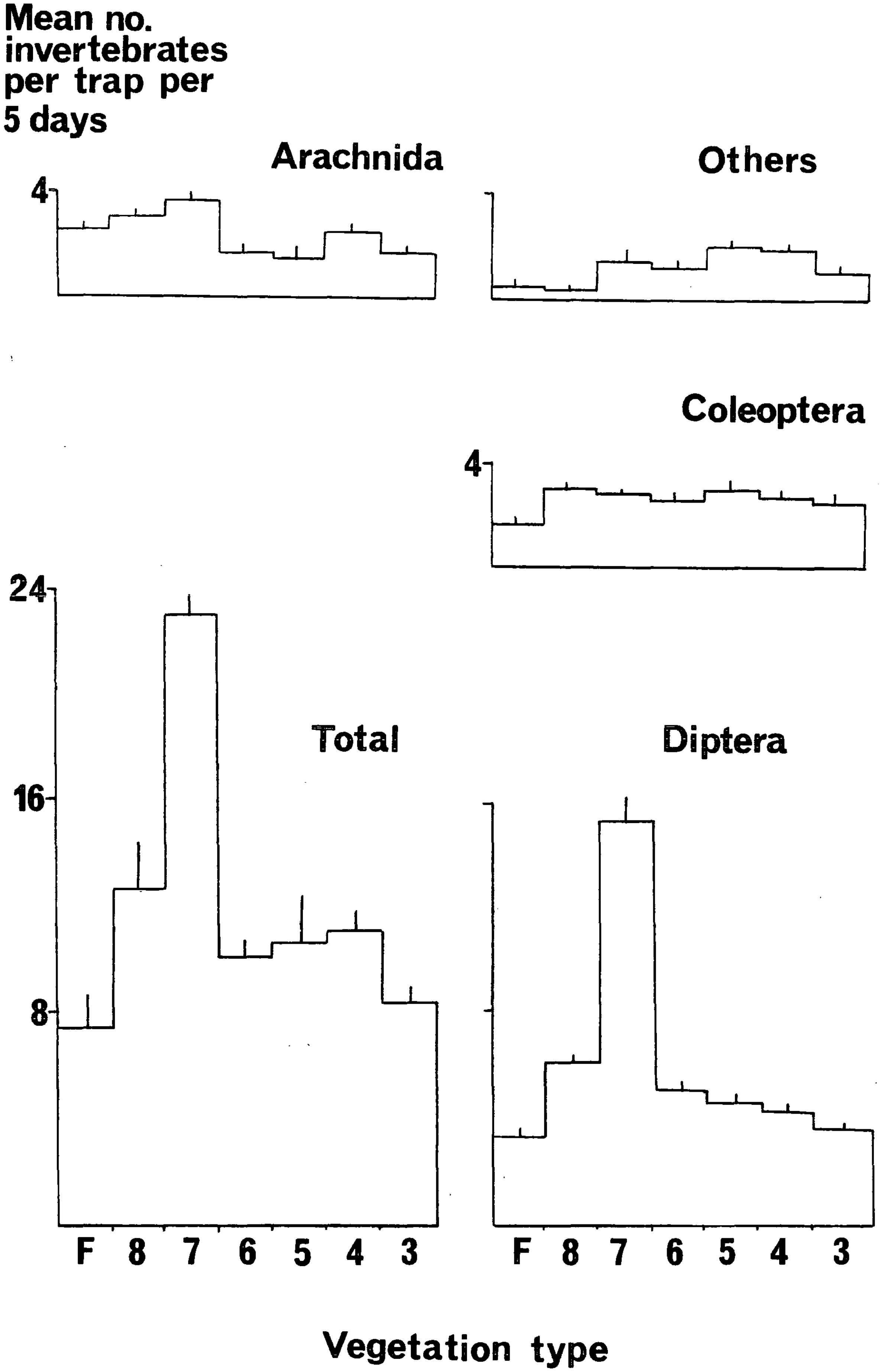

Mean no. invertebrates per trap per 5 days
Arachnida
Others
Coleoptera
Total
Diptera
4
4
24
16
8
F
8
7
6
5
4
3
F
8
7
6
5
4
3
Vegetation type

Figure 6. Mean numbers of invertebrates (Arachnida, Diptera, Coleoptera, "others" and total) caught per pitfall trap per 5 days in each vegetation type, on Rockcliffe Marsh in 1977.

Error bars indicate one S.E. of mean. Numerals on abscissa indicate vegetation types 3 to 8. F is Field vegetation type.

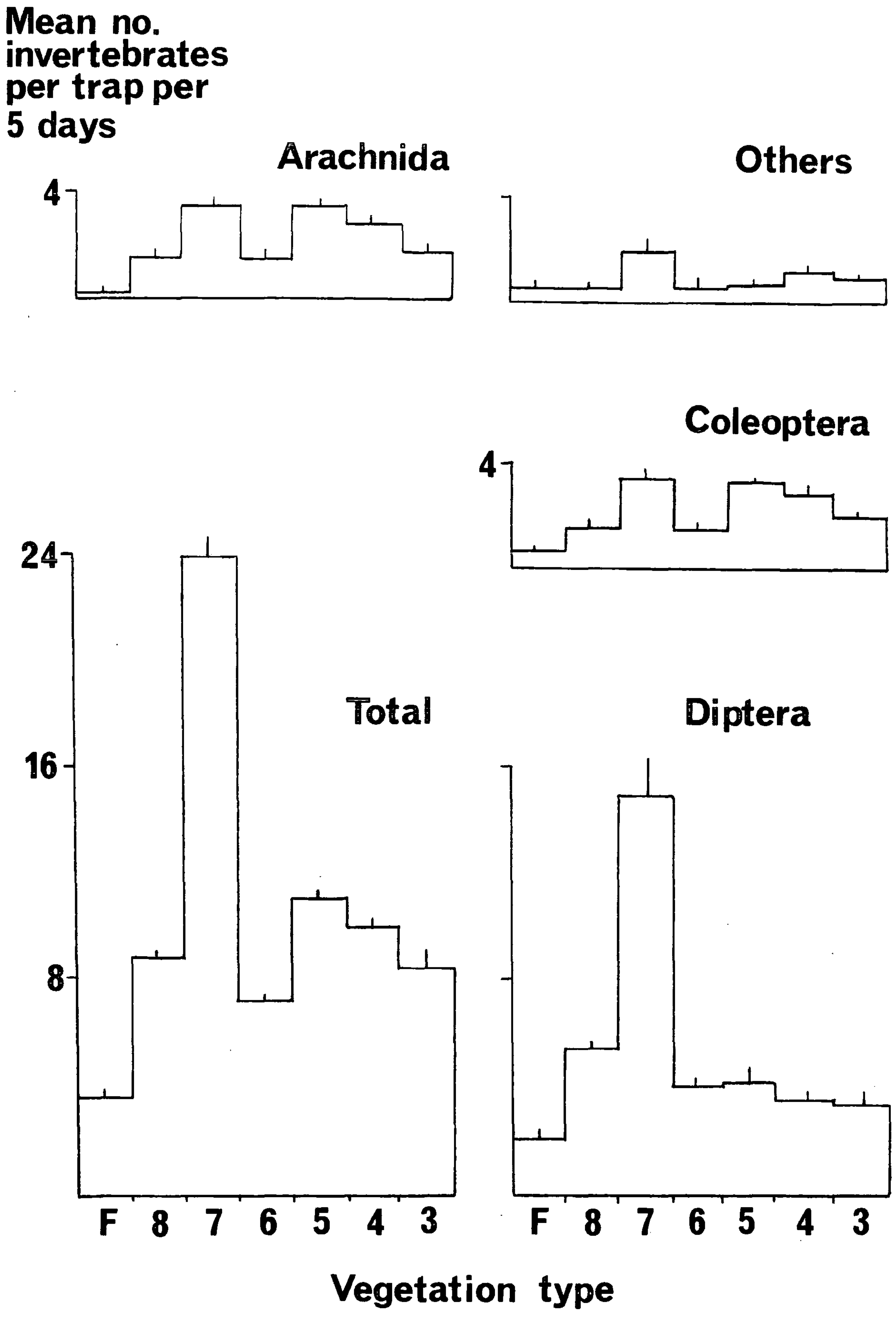

Mean no. invertebrates per trap per 5 days
Arachnida
Others
Coleoptera
Total
Diptera
4
4
24
16
8
F
8
7
6
5
4
3
F
8
7
6
5
4
3
Vegetation type

Figure 7. Mean numbers of invertebrates (Arachnida, Diptera, Coleoptera, "others" and total) caught per pitfall trap per trapping site (transect point) in each 5 day period, collected between 30 April and 24 June 1976, on Rockcliffe Marsh.

Error bars indicate one S.E. of mean.

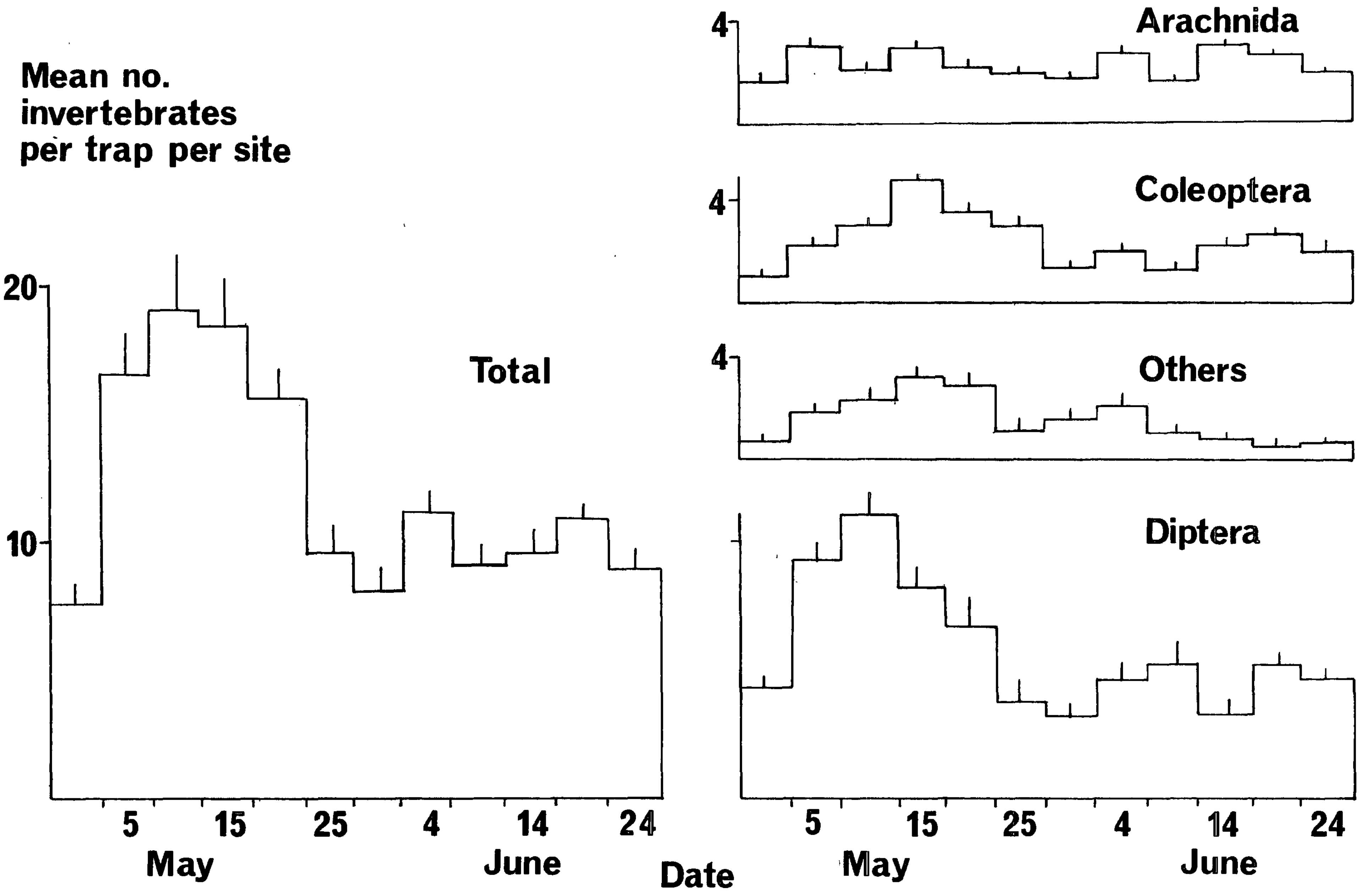

Mean no.
invertebrates
per trap per site
20
10
Total
5
15
25
4
14
24
May
June
Date
Arachnida
4
Coleoptera
4
Others
4
Diptera
5
15
25
4
14
24
May
June

Figure 8. Mean number of invertebrates (Arachnida, Diptera, Coleoptera, "others" and total) caught per pitfall trap per trapping site (transect point) in each 5 day period, collected between 30 April and 24 June 1977, on Rockcliffe Marsh.

Error bars indicate one S.E. of mean.

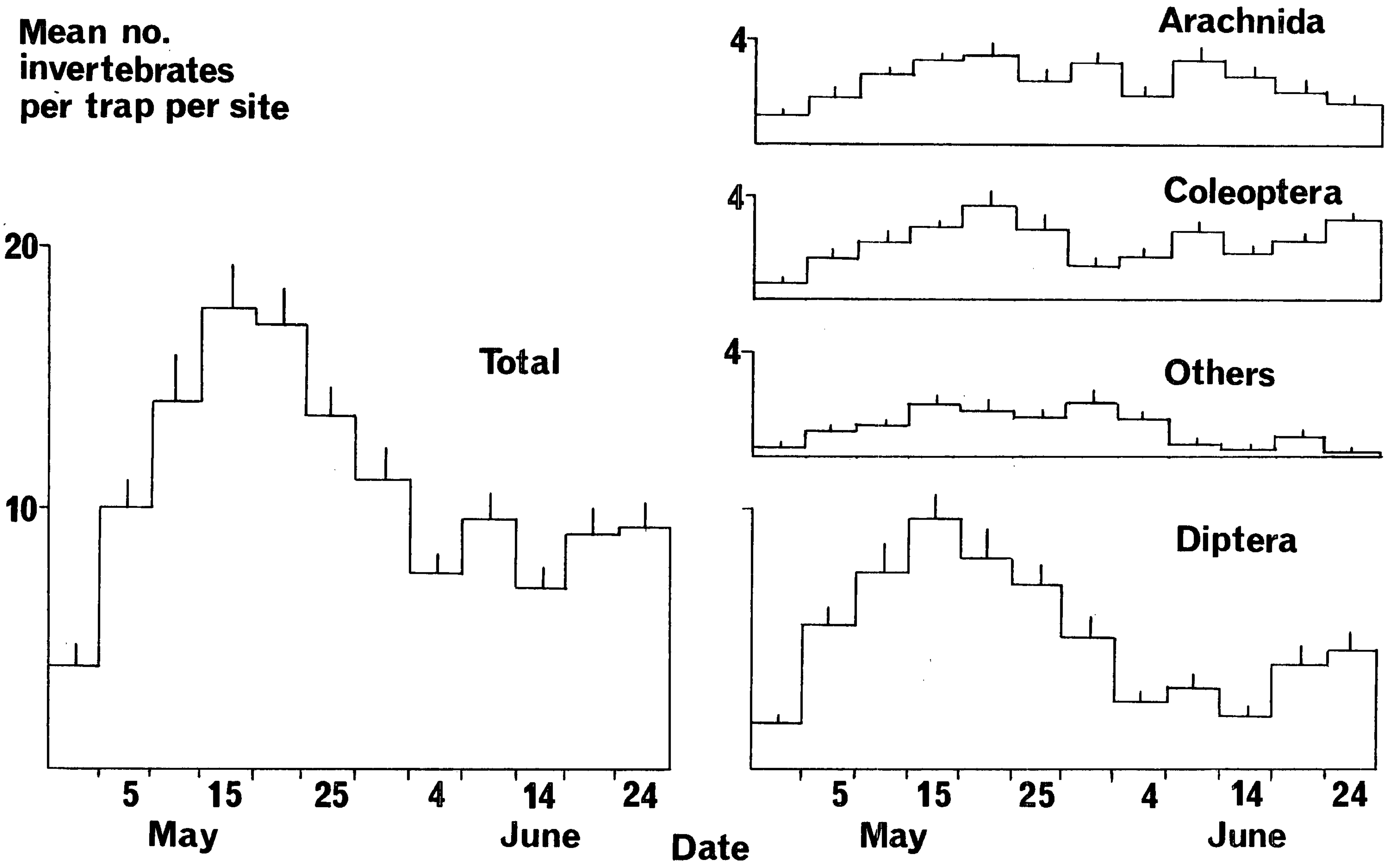

Mean no.
invertebrates
per trap per site
20
10
Total
5
15
25
4
14
24
May
June
Date
Arachnida
4
Coleoptera
4
Others
4
Diptera
5
15
25
4
14
24
May
June

Figure 9. Mean biomass (mg) of invertebrates (Arachnida, Diptera, Coleoptera, "others" and total) caught per pitfall trap per 5 days in each vegetation type, on Rockcliffe Marsh in 1976.

Error bars indicate one S.E. of mean. Numerals on abscissa indicate vegetation types 3 to 8. F is Field vegetation type.

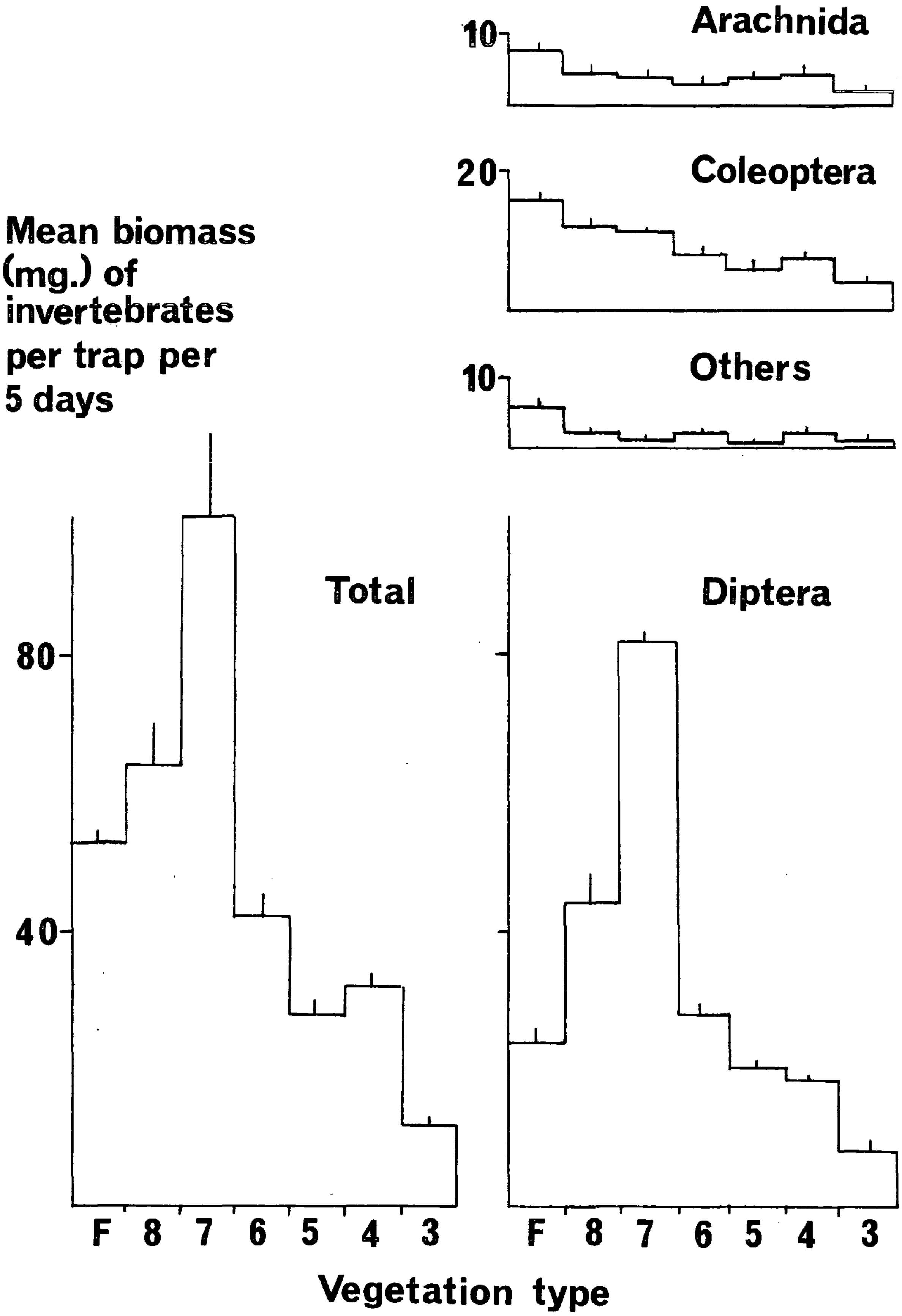
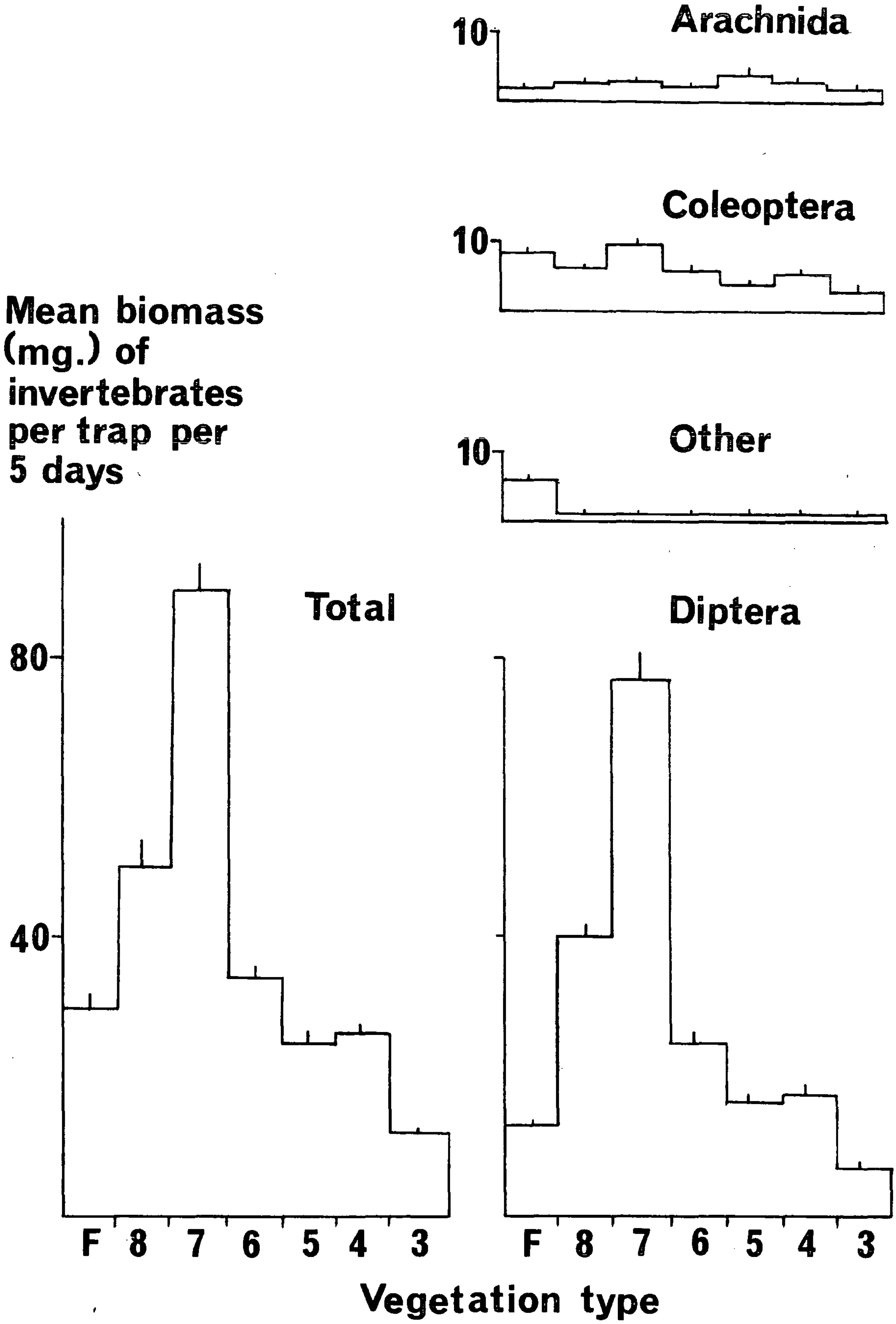

Arachnida
10
Coleoptera
20
Others
10
Mean biomass (mg.) of invertebrates per trap per 5 days
Total
80
40
Diptera
F
8
7
6
5
4
3
F
8
7
6
5
4
3
Vegetation type

Figure 10. Mean biomass (mg) of invertebrates (Arachnida, Diptera, Coleoptera, "others" and total) caught per pitfall trap per 5 days in each vegetation type, on Rockcliffe Marsh in 1977.

Error bars indicate one S.E. of mean. Numerals on abscissa indicate vegetation types 3 to 8. F is Field vegetation type.


Arachnida
10
Coleoptera
10
Other
10
Mean biomass (mg.) of invertebrates per trap per 5 days
Total
80
40
Diptera
F
8
7
6
5
4
3
F
8
7
6
5
4
3
Vegetation type

The proportion of dung-associated invertebrates

(a) Numbers

The majority (over 80%) of dung-associated Diptera were obligatory coprophiles and the proportion of total Diptera which were dung-associated (obligatory and facultative) varied from 64% to 96%, according to vegetation type, in 1976 and 1977 (table 6). The Coleoptera which were obligatory coprophiles, mainly Scarabaeidae and Hydrophilidae, comprised 14% to 84% of the total coleopterous fauna of different vegetation types in different years, the largest proportion occurring in T5, the water-logged area. Between 1% and 10% of the remaining invertebrates were dung-associated. These were mainly hymenopterous parasitoids whose hosts frequented dung. Of the total recorded invertebrates, between 34% and 73% were dung-associated, and of these obligatory coprophiles predominated.

(b) Biomass

During both years, in different vegetation types, over 80% of the total Diptera dry weight was derived from dung-associated species, 8-61% of Coleoptera biomass, and less than 12% of the biomass of the remaining invertebrates (table 7). Of the total invertebrate biomass in different vegetation types, 49-81% comprised dung-associated species.

The data for both invertebrate abundance and biomass indicated that dung-associated species, especially Diptera, comprised a significant part of the total invertebrate fauna.

Table 6. Percentage of invertebrates which were obligatory (O) and facultative (F) dung-associated species in each vegetation type on Rockcliffe Marsh in 1976 and 1977.

1976

VEGETATION TYPE		DIPTERA	COLEOPTERA	OTHERS	TOTAL
FIELD					
	O.	53.1	21.4	0.0	27.1
	F.	13.8	0.0	3.5	7.2
	O & F.	66.9	21.4	3.5	34.3
T8					
	O.	64.5	34.7	0.0	39.5
	F.	18.2	0.0	0.8	9.1
	O & F.	82.7	34.7	0.8	48.6
T7					
	O.	73.2	51.7	0.0	54.5
	F.	12.6	0.0	2.4	8.8
	O & F.	85.8	51.7	2.4	63.3
T6					
	O.	82.9	69.6	0.0	60.1
	F.	10.1	0.0	1.7	5.8
	O & F.	93.0	69.6	1.7	65.9
T5					
	O.	88.4	83.8	0.0	59.9
	F.	8.0	0.0	10.0	6.5
	O & F.	96.4	83.8	10.0	66.4
T4					
	O.	76.5	57.3	0.0	42.2
	F.	13.3	0.0	4.3	6.6
	O & F.	89.8	57.3	4.3	48.8
T3					
	O.	43.1	42.5	0.0	42.9
	F.	50.4	0.0	1.2	30.6
	O & F.	93.5	42.5	1.2	73.5

Table 6 (continued)

1977

VEGETATION TYPE		DIPTERA	COLEOPTERA	OTHERS	TOTAL
FIELD	O.	26.4	43.6	0.0	25.5
	F.	67.0	0.0	8.1	42.9
	O & F.	93.4	43.6	8.1	68.4
T8	O.	46.1	14.3	0.0	30.8
	F.	32.3	0.0	3.7	22.1
	O & F.	78.3	14.3	3.7	52.9
T7	O.	52.2	22.8	0.0	35.8
	F.	11.9	0.0	5.2	8.6
	O & F.	64.0	22.8	5.2	44.4
T6	O.	58.2	35.2	0.0	37.3
	F.	24.8	0.0	6.8	14.9
	O & F.	83.1	35.2	6.8	52.2
T5	O.	49.4	46.9	0.0	30.2
	F.	25.0	0.0	4.5	10.3
	O & F.	74.4	46.9	4.5	40.5
T4	O.	72.2	51.0	0.0	37.1
	F.	15.5	0.0	3.0	6.8
	O & F.	87.7	51.0	3.0	43.9
T3	O.	60.8	38.0	0.0	34.7
	F.	34.8	0.0	1.6	14.9
	O & F.	95.6	38.0	1.6	49.6

Table 7. Percentage biomass of invertebrates which were obligatory (O) and facultative (F) dung-associated species in each vegetation type on Rockcliffe Marsh in 1976 and 1977.

1976

VEGETATION TYPE		DIPTERA	COLEOPTERA	OTHERS	TOTAL
FIELD					
	O.	81.4	49.7	0.0	50.5
	F.	9.0	0.0	8.2	6.1
	O & F.	89.4	49.7	8.2	56.6
T8					
	O.	90.7	18.3	0.0	68.0
	F.	7.1	0.0	2.3	5.3
	O & F.	97.8	18.3	2.3	73.3
T7					
	O.	86.4	27.8	0.0	74.9
	F.	5.8	0.0	1.7	4.9
	O & F.	92.2	27.8	1.7	79.8
T6					
	O.	95.2	61.1	0.0	79.0
	F.	3.5	0.0	0.9	2.5
	O & F.	98.7	61.1	0.9	81.5
T5					
	O.	83.1	54.1	0.0	66.6
	F.	10.5	0.0	12.4	9.1
	O & F.	93.6	54.1	12.4	75.7
T4					
	O.	84.8	38.4	0.0	60.3
	F.	1.4	0.0	6.3	2.0
	O & F.	86.2	38.4	6.3	62.3
T3					
	O.	79.5	29.3	0.0	50.1
	F.	19.0	0.0	3.5	11.0
	O & F.	98.5	29.3	3.5	61.1

Table 7 (continued)

1977

VEGETATION TYPE		DIPTERA	COLEOPTERA	OTHERS	TOTAL
FIELD					
	O.	64.9	26.9	0.0	35.8
	F.	21.8	0.0	11.8	13.5
	O & F.	86.7	26.9	11.8	49.3
T8					
	O.	88.8	8.2	0.0	71.3
	F.	2.6	0.0	7.5	2.7
	O & F.	91.4	8.2	7.5	74.0
T7					
	O.	80.0	12.4	0.0	69.1
	F.	3.2	0.0	2.2	2.8
	O & F.	83.2	12.4	2.2	71.9
T6					
	O.	83.5	41.3	0.0	67.0
	F.	7.1	0.0	4.9	5.7
	O & F.	90.6	41.3	4.9	72.7
T5					
	O.	87.6	24.7	0.0	61.0
	F.	8.3	0.0	8.1	7.1
	O & F.	95.9	24.7	8.1	68.1
T4					
	O.	73.7	32.1	0.0	52.8
	F.	15.1	0.0	2.5	10.0
	O & F.	88.8	32.1	2.5	62.8
T3					
	O.	91.2	26.5	0.0	57.6
	F.	6.5	0.0	3.7	4.6
	O & F.	97.7	26.5	3.7	62.3

SECTION 6

THE CATTLE

Arnold & Dudzinski (1978), Hafez (1962), Hancock (1953) and Tribe (1950) have reviewed the behaviour of grazing mammals. In cattle, grazing activity follows a regularly repeated daily pattern which alternates with periods of rumination and rest; cattle prefer to graze during daylight, and lie down at night, although intermittent bouts of grazing still occur (e.g. Johnstone-Wallace & Kennedy 1944, Waite _et al_. 1951).

Grazing pressure is not solely related to stocking density. It may be influenced by the proximity of water, local floristic composition, vegetation height (cattle prefer leafy herbage less than 12cm high), topography and behavioural idiosyncracies of the cattle (e.g. American Society Range Management 1962, Arnold 1964).

The rhythm of faeces production by cattle varies between mean values of 8.4 and 16.8 defaecations per day (e.g. Castle _et al_. 1950, Wardrop 1953), with some seasonal variation (Macdiarmid & Watkin 1972). Dairy cattle tend to have a higher defaecation rate than beef cattle because their daily food intake is higher (Weeda 1967).

Although defaecation may occur while the animal is walking (resulting in strung-out pats) or laying down, it usually occurs when the cow is standing still, thereby producing the typical, discrete pat. Cattle deposit their faeces randomly with respect to location (Hafez 1962): they do not have group resting places, like sheep, at which large quantities of dung may be deposited (White 1960b), nor do they have particular defaecation sites, like some horses.

The most practical method for assessing range use by a species is to sample faecal distribution (e.g. Hansen 1972, Julander _et_ _al_. 1963). If there are no spatial, diurnal or seasonal variations in defaecation rate, the number of defaecations and the number of animals in an area are proportional (e.g. Neff 1968). Sample counts of faeces provide an index of a species' relative distribution within a diverse habitat, and have been extensively used to determine habitat use by ungulates, including cattle (e.g. Ares & Leon 1972, Cadwalladr & Morley 1973, Charles _et_ _al_. 1977, Julander 1955a, b, Rogers _et_ _al_. 1958).

The fundamental assumption of the faecal count method is that defaecation occurs in proportion to the length of time spent grazing under free range conditions. The method is more sensitive and reliable if the defaecation rate is high (e.g. Owen 1971). Cattle defaecate less than once an hour, on average, and may walk 2-4km each day, so the counts may be biased. However, at a high stocking rate, on a large area of pasture, in which cattle can select their own grazing areas, this potential error was minimised. The regular production of faeces during the grazing periods suggested that cowpat density could be used as a reliable index of relative grazing pressure under range conditions.

Between 900 and 1200 cattle are annually grazed on Rockcliffe Marsh between May and September (table 8). The herd includes dairy (Friesian) and beef (Hereford, Charolais hybrid, Galloway) cattle which are restricted to the marsh, but are free-ranging within its confines.

Table 8. The number of cattle grazed annually on Rockcliffe Marsh between May and September, 1974-1978. Information provided by Mr. T.J. Pattison, Castletown Estates.

Year	Number
1974	1044
1975	1160
1976	975
1977	1019
1978	909

Methods

Counts of fresh faeces subsequent to the marking of old faeces was used as the most accurate count technique applicable to cowdung (Welch 1971). The number of cowpats within 1 ha around each transect point was counted in the following manner. At each transect point, a perimeter stake was attached to a central stake by a rope 56.4m long. By moving the perimeter stake round the central one at a radius of 56.4m an area of one hectare was encompassed. A marker post was used to indicate the beginning of the circle and the perimeter post was initially placed by the marker. As the perimeter stake was advanced around the circle, cowpats were counted and simultaneously marked by piercing the centre of the pat with a stick. This prevented pats being counted twice, and also served to distinguish old from fresh pats during subsequent counts. Checks were made to ensure that all pats were marked in one sector before the perimeter stake was advanced several metres along the circumference prior to counting the next sector. The process was repeated until all the fresh cowpats in the circle had been counted and marked. Only those pats completely in the circumference were counted. Counts were made once every seven days over a period of 10 weeks, the first count being made seven days after the cattle were put on the marsh. These fresh pats were therefore less than seven days old. The counts are recorded in table 9.

Only normal cowpats were counted. Strung-out pats were ignored because they were difficult to count accurately, and were rapidly degraded. These comprised a small proportion of the total pats deposited (Gibbons 1968) and they were not more likely to be deposited more frequently in one sampling area than another.

Areas susceptible to heavy trampling and flooding were avoided, whenever possible, because they may cause an underestimation of total faeces counts (Riney 1957). The successive sampling at seven day intervals was at a

Table 9. Density (numbers per ha) of fresh cowpats, less than seven days old, at each transect point, sampled 10 times at seven day intervals between 11 May and 13 July, 1976, and between 12 May and 14 July, 1977, on Rockcliffe Marsh.

1976

Transect	Sampling Date											
Point	11/5	18/5	25/5	1/6	8/6	15/6	22/6	29/6	6/7	13/7	Mean	S.E.
A1	103	74	81	88	62	69	93	75	57	71	77.3	4.5
A2	69	90	114	83	89	77	71	85	97	72	84.7	4.4
A3	62	53	47	39	50	64	48	81	31	38	51.3	4.6
A4	50	29	36	47	41	55	73	68	53	44	49.6	4.3
A5	33	45	57	49	60	54	46	30	21	34	42.9	3.6
A6	42	37	60	52	45	38	21	39	54	62	45.0	3.4
A7	46	41	38	26	49	57	52	24	35	30	39.8	3.5
A8	11	17	13	24	18	28	31	25	17	11	19.5	2.2
FIELD	48	68	55	49	51	63	57	70	54	39	55.4	3.0
B1	77	84	72	55	101	83	69	71	95	61	76.8	4.0
B2	54	67	75	88	59	92	63	71	56	59	68.4	4.2
B3	65	58	67	43	62	39	82	40	54	32	54.2	4.9
B4	37	64	49	56	40	31	53	72	34	52	48.8	3.7
B5	54	46	59	33	48	57	62	36	75	41	51.1	4.1
B6	21	15	26	42	39	32	44	30	41	24	31.4	3.1
Mean	51.5	52.5	56.6	51.6	54.3	55.9	57.7	54.5	51.6	44.7		
S.E.	5.6	5.7	6.1	5.0	5.0	4.9	4.7	5.6	5.9	4.4		

1977

Transect Point	12/5	19/5	26/5	2/6	9/6	16/6	23/6	30/6	7/7	14/7		
A1	95	114	87	69	88	72	99	86	106	85	90.1	4.4
A2	69	82	120	76	67	93	87	85	74	91	84.4	4.8
A3	64	92	45	83	39	57	61	49	63	59	61.2	5.1
A4	47	52	65	58	44	39	71	50	46	63	53.5	3.3
A5	48	36	63	45	59	81	67	53	71	60	58.3	4.2
A6	33	47	58	48	52	61	40	52	66	42	49.9	3.2
A7	50	42	39	53	28	42	56	64	47	43	46.4	3.2
A8	25	30	28	42	29	34	31	51	26	34	33.0	2.5
FIELD	51	58	42	55	30	53	46	40	67	44	48.6	3.3
B1	93	79	84	100	89	72	77	65	83	76	81.8	3.2
B2	62	75	81	77	64	73	99	82	56	96	76.5	4.4
B3	74	82	79	60	76	64	58	65	81	72	71.1	2.8
B4	65	57	71	48	73	55	64	76	52	62	62.3	2.9
B5	48	66	39	54	42	70	46	55	53	41	51.4	3.3
B6	15	21	25	8	32	29	27	23	31	36	24.7	2.7
Mean	55.9	62.2	61.7	58.4	54.1	54.9	61.9	59.7	61.5	60.3		
S.E.	5.6	6.3	6.5	5.3	5.3	5.2	5.6	4.4	5.1	5.1		

short enough interval to preclude the possibility of pat degradation between counts. Estimates of the interval between pat deposition and complete disintegration vary from 14 to 510 days (e.g. Castle & MacDaid 1972, Marsh and Campling 1970, Nakamura 1975a), with marked seasonal differences, which have been attributed to weather (e.g. Dale 1963), but probably also involve changes in invertebrate activity. For instance, the main activity of earthworms is during autumn and spring (e.g. Barley 1964), which coincides with the usually rapid disappearance of pats in autumn. The absence of earthworms from most of Rockcliffe Marsh may account, in part, for the persistence of cowpats from late September, when the cattle are removed, until the following spring. Furthermore, the saltmarsh does not support many feeding birds in winter, so that the accelerated degradation of pats caused by foraging birds (Anderson & Merritt 1977) is minimal.

Before the cattle were introduced to the marsh during the first week of May, counts were also made of those cowpats remaining from the previous grazing season. The cattle are removed from the marsh at the end of September. These old pats had therefore persisted for at least 200 days after deposition. Counts were made 1-3 weeks before the new grazing season commenced (15 April 1976, 26 April 1977, and 28 April 1978). Pats only remained on the upper terraces. They were presumably removed by tidal action on the lower terrace (vegetation types T1-3). Therefore counts were only made at transect points Field, A1-7 and B1-5. In addition, counts were made in adjacent hectare plots to the transect points (table 11). These plots were of the same vegetation type as the neighbouring transect points, and were intended to provide some measure of the variation in old cowpat density at each transect point.

Sample counts of cattle in the vicinity of each transect point were not used as an index of grazing intensity because;

1) at any one sampling time, the numbers involved would have been small, or the cattle may have been absent from the sampling site due to chance or disturbance,
2) some cattle, e.g. Galloways, tended to graze in small groups (Williams *et al*. 1974), resulting in a clumped distribution, which would have increased sampling variability,
3) a large number of counts would have been required to accommodate this variability.

The use of faeces counts, which relied on cowpat density as a cumulative, relatively inert measure of grazing intensity over a given period was not subject to these vagaries, and therefore required a less intensive sampling procedure.

Figure 11. Relative grazing intensity across the halosere in 1976 and 1977 on Rockcliffe Marsh. Fresh cowpat (less than 7 days old) density ha^{-1} was used as an index of grazing intensity.

Error bars indicate one S.E. of mean. Numerals on abscissa indicate vegetation types 3 to 8. F is Field vegetation type.

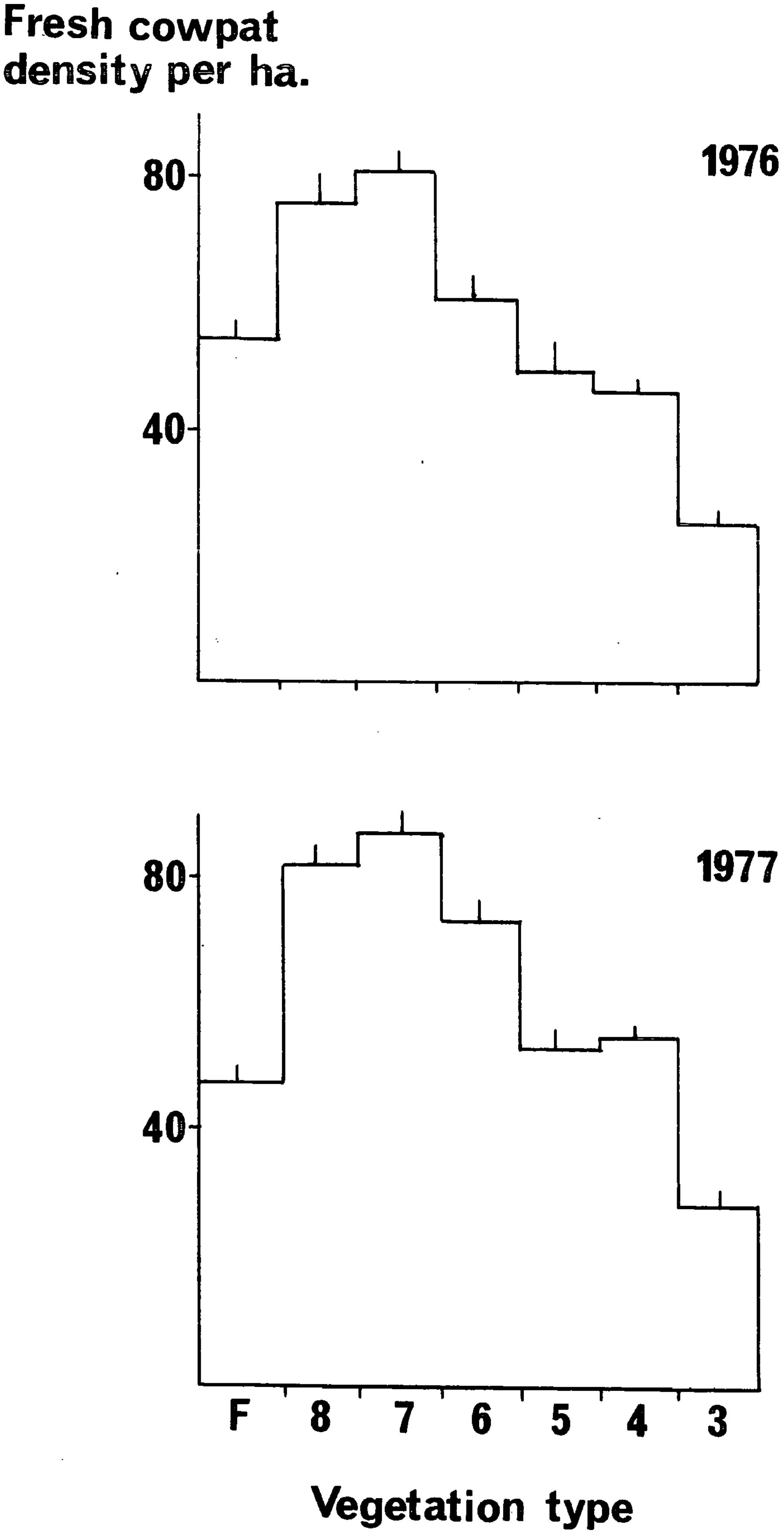

Fresh cowpat density per ha.
80
40
1976
80
40
1977
F
8
7
6
5
4
3
Vegetation type

Table 10. Density (numbers per ha) of old (previous year's) cowpats persisting at each transect point and adjacent plot, on 15 April, 1976, 26 April, 1977 and 28 April, 1978.
1 = transect sample, 2 = adjacent sample.

Transect Point	1976			1977			1978		
	1	2	Mean	1	2	Mean	1	2	Mean
A1	69	45	57.0	56	73	64.5	60	82	71.0
A2	72	50	61.0	47	39	43.0	63	48	55.5
A3	34	47	40.5	38	41	39.5	44	29	36.5
A4	28	22	25.0	33	27	30.0	22	36	29.0
A5	19	31	25.0	28	21	24.5	23	16	19.5
A6	25	22	23.5	23	18	20.5	19	25	22.0
A7	7	13	10.0	16	20	18.0	9	16	12.5
FIELD	31	44	37.5	34	53	43.5	31	26	28.5
B1	62	70	66.0	85	57	71.0	77	83	80.0
B2	36	49	42.5	51	44	47.5	46	44	45.0
B3	53	35	44.0	46	57	51.5	35	44	39.5
B4	19	26	22.5	32	46	39.0	28	34	31.0
B5	17	12	14.5	10	25	17.5	26	21	23.5

Relative grazing intensity

The transect data exhibited no consistent seasonal variation of fresh cowpat density (table 9). The data were grouped according to vegetation type to indicate the relative grazing pressure along the halosere (figure 11). In both years the pattern was similar. The density of fresh cowpats ha^{-1} (less than seven days old) in 1976 was positively and significantly correlated with that in 1977 at each transect point ($r = 0.92$, $df = 13$, $p < 0.01$) (figure 12). The slope of the relationship (0.97) deviated by 3% from the expected slope of 1.00, had the same number of cattle been grazed in both years. This was a similar percentage to the actual increased proportion of cattle (4%) in 1977 relative to 1976 (table 8).

This indicated that cowpat density was a consistent and reliable method of assessing relative grazing intensity.

The upper terrace (T8 & T7) was frequented more by the cattle than the lower terrace (T4 & T3): the cattle preferred the mature pasture to the less mature areas. Williams _et al_. (1974) found that cattle grazed where _Festuca rubra_ was dominant at Woodwalton Fen. Since this species predominated on Rockcliffe Marsh (table 2), its distribution did not explain the observed differences in relative grazing pressure. The percentage vegetation cover may have been involved, since this, in common with the grazing intensity, decreased across the halosere.

The comparatively low fresh cowpat density in the Field (figure 11, table 9), which was the most mature pasture, was due to the low number of cattle (usually less than a dozen) grazed there during the season. Furthermore, these cattle were not under range conditions, so the Field sampling site was not strictly comparable to the other transect points.

The significant positive correlations of fresh (figure 12) and old (figure 13) cowpat densities in different years, and between old and fresh cowpat densities in the same year (figure 14) indicated that cowpat density had a high predictability, both within, and between years; the pattern of grazing intensity was consistent. The potential importance of this predictability to the breeding waders will be examined later.

Figure 12. Relationship between fresh cowpat (less than 7 days old) density ha^{-1} in 1976 and 1977 at each transect point on Rockcliffe Marsh.

Regression equation:

$y = 0.97x + 8.11$
$r = 0.92$
$df = 13$
$p < 0.001$

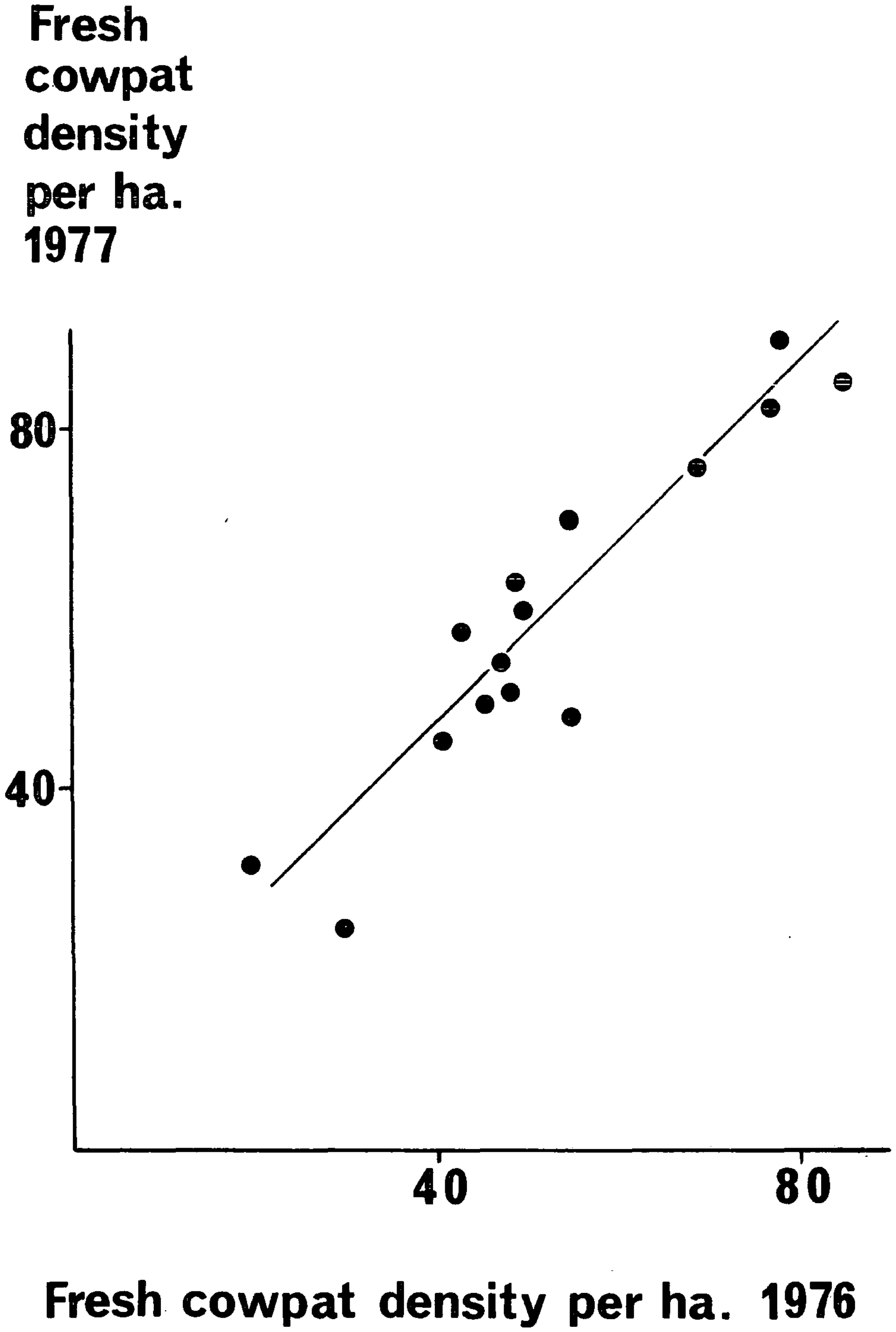

Fresh cowpat density per ha. 1977
80
40
40
80
Fresh cowpat density per ha. 1976

Figure 13. Relationships between density ha^{-1} of "old" cowpats (persisting since deposition the previous year) in years 1976, 1977 and 1978, at transect points, A1-A7, Field, B1-B5, on Rockcliffe Marsh.

a) 1976 with 1977

Regression equation: $y = 0.85 + 8.41$
S.E. of slope $= 0.13$
$r = 0.89$
df $= 11$
$p < 0.001$

b) 1976 with 1978

Regression equation: $y = 1.05x + 0.13$
S.E. of slope $= 0.13$
$r = 0.93$
df $= 11$
$p < 0.001$

c) 1977 with 1978

Regression equation: $y = 1.09x - 4.74$
S.E. of slope $= 0.14$
$r = 0.92$
df $= 11$
$p < 0.001$

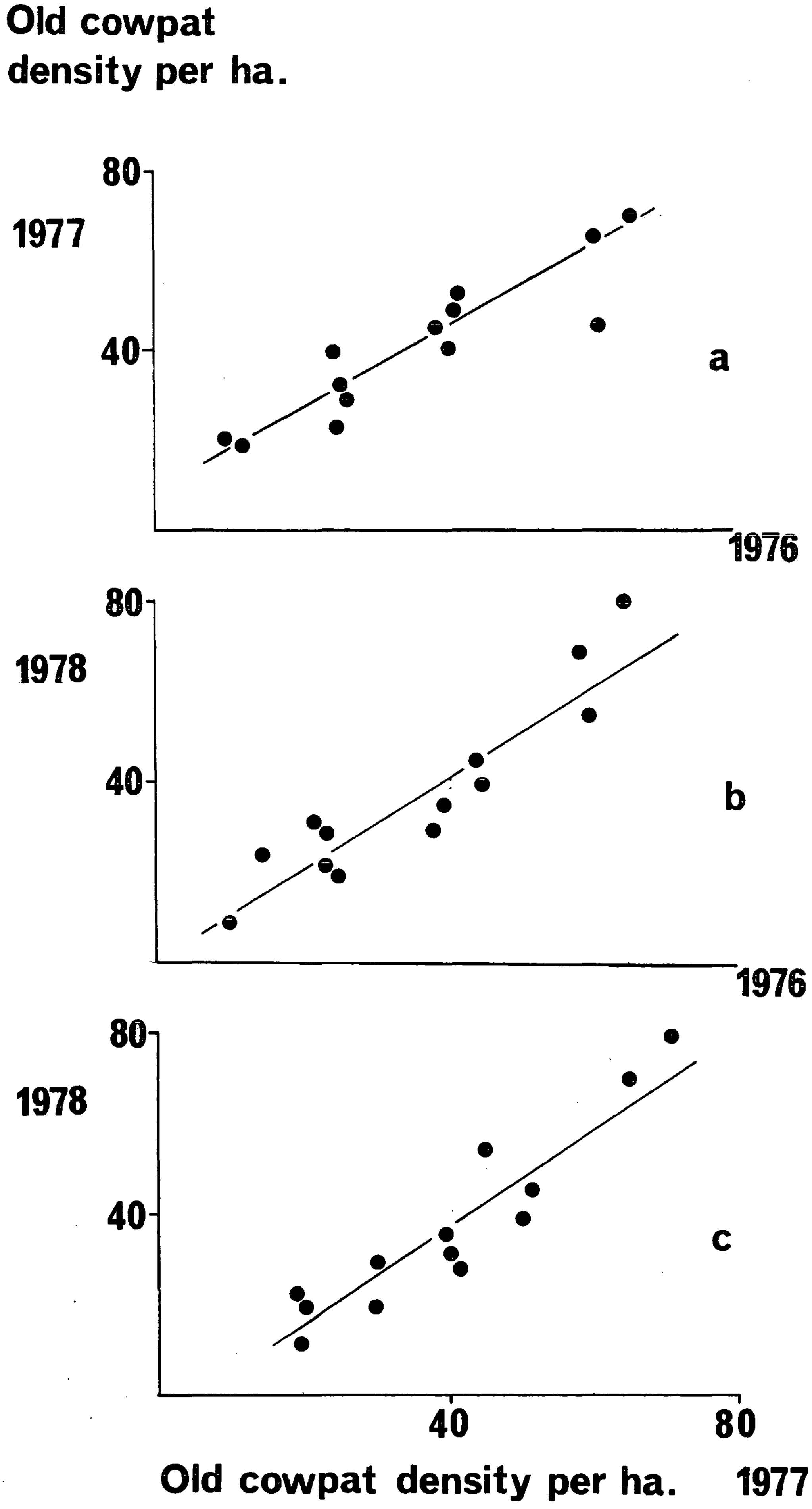

Old cowpat
density per ha.
80
1977
40
a
1976
80
1978
40
b
1976
80
1978
40
c
40
80
Old cowpat density per ha.
1977

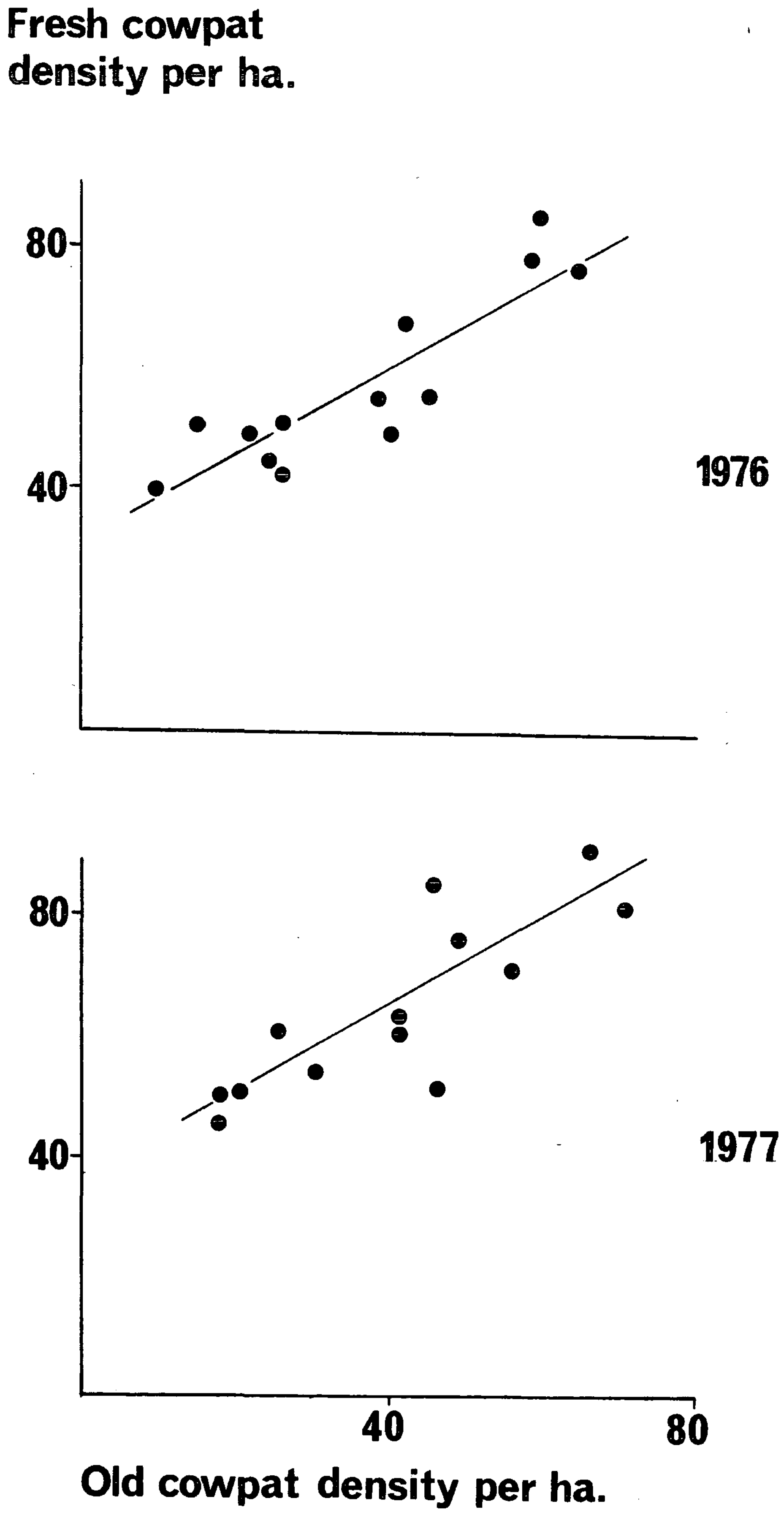
Figure 14. Relationships between old cowpat density ha^{-1} and fresh cowpat density ha^{-1} at transect points A1-A7, Field, B1-B5, on Rockcliffe Marsh in 1976 and 1977.

Regression equation 1976

$y = 0.74x + 30.79$
S.E. of slope = 0.10
$r = 0.90$
df = 11
p 0.001

1977

$y = 0.70x + 36.52$
S.E. of slope = 0.15
$r = 0.82$
df = 11
$p < 0.001$


Fresh cowpat
density per ha.
80
40
1976
80
40
1977
40
80
Old cowpat density per ha.

The proportion of fresh pats deposited at each transect point during the seven days prior to the removal of cattle in one year, which persisted until the April of the following year, when they were counted as old cowpats, was estimated. The proportion was not strictly that of fresh pats which persisted, since some pats which had been deposited in advance of the last week the cattle were on the marsh were included. Nevertheless, the proportions provided a relative measure of the persistence of pats at each transect point from the September of one year to the April of the following year (table 11). On average, 67% (between 34 and 95%) of cowpats persisted from September 1976 to April 1977, and 56% (27 to 98%) persisted during the corresponding interval from 1977 to 1978. There was a tendency during both periods for the proportion of cowpats persisting to be lower at those transect points (A6-7, B5) towards the tidal edge of the marsh than those nearer the sea wall. Tidal inundation, exposure and invertebrate activity, especially that of Coleoptera and Diptera larvae (e.g. Bornemissza 1960, Laurence 1954), were all implicated in the differential decomposition of dung at each transect point.

Table 11. Proportion of fresh cowpats assumed to be deposited in September at transect points A1-7, Field and B1-5, in one year, which persisted to the April of the following year as old cowpats. Percentages derived from density per ha at each transect point of fresh cowpats in 1976 and 1977, and of old pats in 1977 and 1978.

Transect Point	Percentage of cowpats persisting from: 1976-77	1977-78
A1	83	79
A2	51	66
A3	77	60
A4	60	54
A5	57	33
A6	46	44
A7	45	27
FIELD	78	59
B1	92	98
B2	69	59
B3	95	56
B4	80	50
B5	34	46

Cowpat density as an index of invertebrate abundance and biomass

Since, within normal limits, cowpat size has no influence on the number of flies attracted (Gibbons 1968), it was not necessary to distinguish between pats of different size during sampling. It was assumed that cowpat size did not affect the abundance of other dung-associated invertebrates at each pat.

In both 1976 and 1977, fresh cowpat density was positively and significantly correlated with total invertebrate abundance (figures 15 & 16) (r = 0.58 and 0.52 respectively) and biomass (figures 17 & 18) (r = 0.79 and 0.80 respectively) at each transect point. These correlations were primarily due to Diptera abundance and biomass (figures 15-18), which were more highly correlated with fresh cowpat density than were the total invertebrate data (table 12). In addition, the slopes of the relationships between fresh cowpat density and the abundance of total invertebrates and Diptera did not significantly differ for a given year. This also obtained for the biomass correlations with fresh cowpat density (table 13).

Fresh cowpat density was a better index of biomass than abundance; for both the total invertebrates and the Diptera, the correlation coefficient, r, was consistently higher when fresh cowpat density was correlated with biomass rather than abundance (table 12).

The total invertebrate data were comprised of Diptera and "others", which were largely Coleoptera and Arachnida. Fresh cowpat density was only significantly correlated with the biomass of "others" in 1976. There were no other significant correlations (table 14). The tendency for some Coleoptera to colonise dung older than 7 days (Koskela 1972) may have obscured the relationship between cowpat density and the abundance and biomass of "other" invertebrates.

A similar pattern of correlations existed between old cowpat density (deposited in the previous year) and the abundance and biomass of total invertebrates, Diptera and other invertebrates (table 15) as was observed between

Figure 15. Relationship between mean fresh cowpat density ha^{-1} and mean total invertebrate and Diptera abundance (numbers per trap per 5 days) at each transect point on Rockcliffe Marsh in 1976.

Regression equations

Total invertebrates:
$y = 0.19x + 1.99$
S.E. of slope = 0.07
$r = 0.58$
df = 13
$p < 0.05$

Diptera:
$y = 0.17x - 3.32$
S.E. of slope = 0.05
$r = 0.69$
df = 13
$p < 0.01$

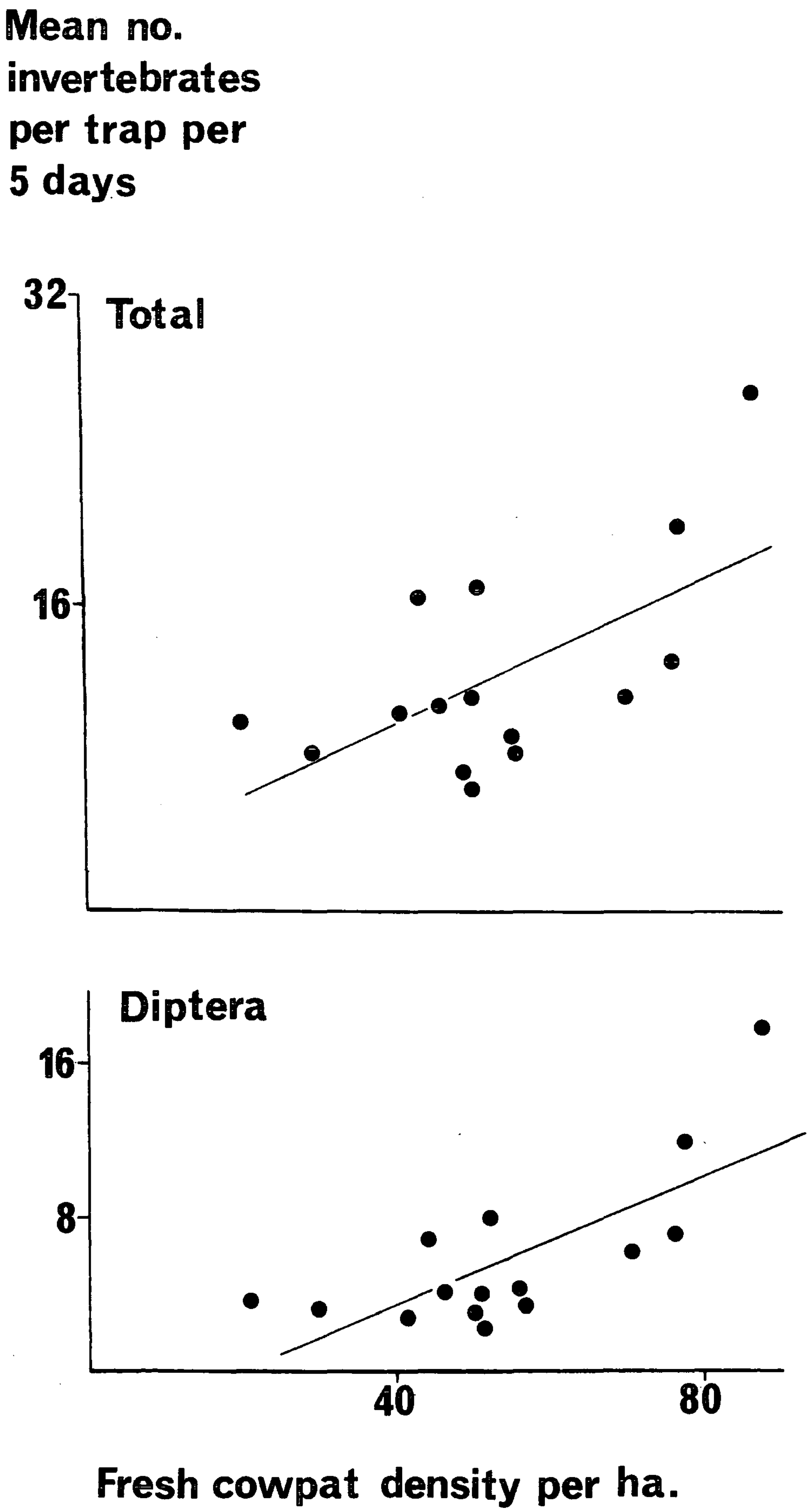

Mean no. invertebrates per trap per 5 days
32
Total
16
Diptera
16
8
40
80
Fresh cowpat density per ha.

Figure 16. Relationship between mean fresh cowpat density ha^{-1} and mean total invertebrate and Diptera abundance (numbers per trap per 5 days) at each transect point on Rockcliffe Marsh in 1977.

Regression equations

Total invertebrates:
$y = 0.18x + 0.13$
S.E. of slope $= 0.08$
$r = 0.52$
$df = 13$
$p < 0.05$

Diptera:
$y = 0.15x - 3.65$
S.E. of slope $= 0.05$
$r = 0.63$
$df = 13$
$p < 0.02$

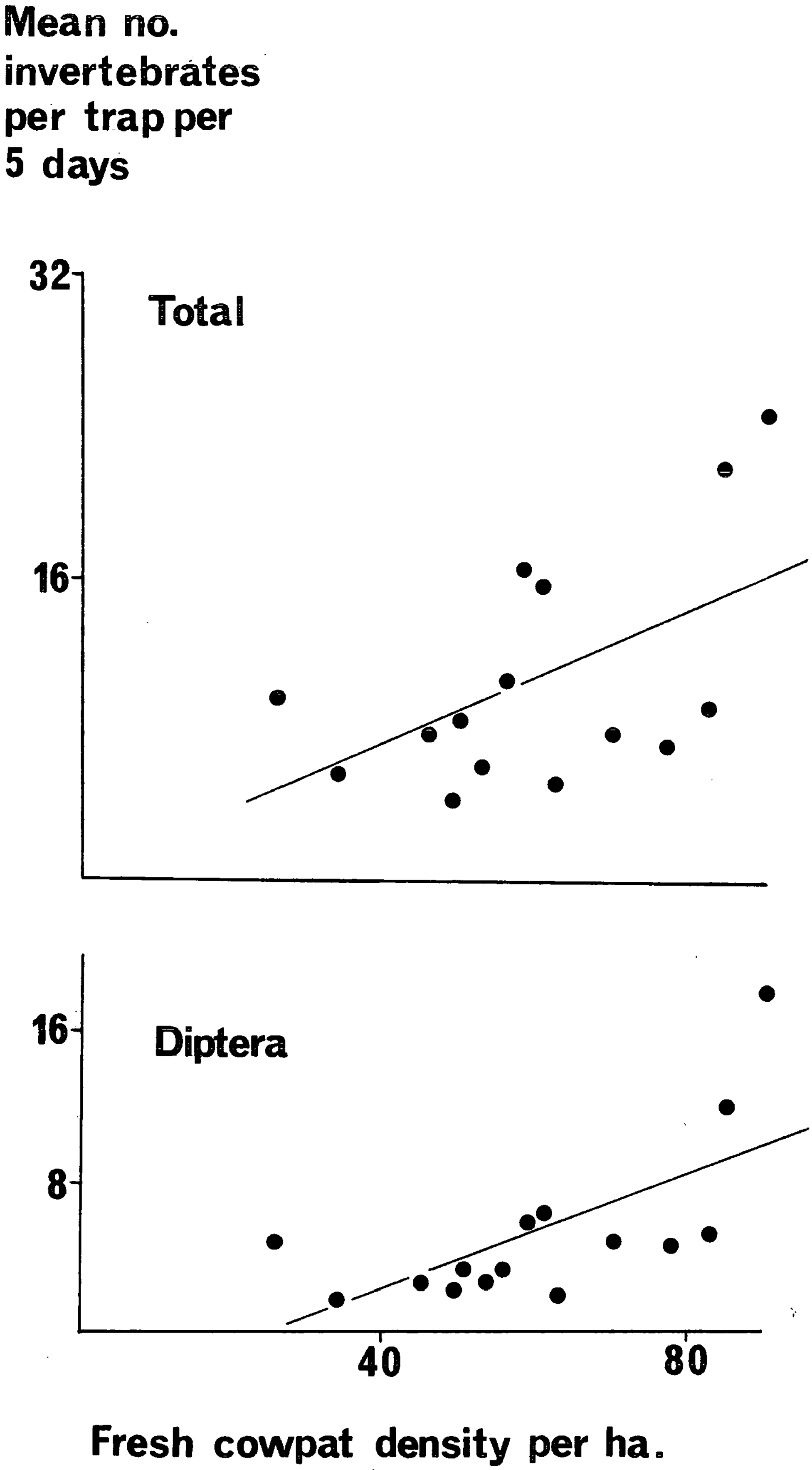

Mean no. invertebrates per trap per 5 days
32
Total
16
16
Diptera
8
40
80
Fresh cowpat density per ha.

Figure 17. Relationship between mean fresh cowpat density ha^{-1} and mean total invertebrate and Diptera biomass (mg per trap per 5 days) at each transect point on Rockcliffe Marsh in 1976.

Regression equations

Total invertebrates:
$y = 1.40x - 32.07$
S.E. of slope = 0.29
$r = 0.79$
df = 13
$p < 0.001$

Diptera :
$y = 1.21x - 34.07$
S.E. of slope = 0.24
$r = 0.81$
df = 13
$p < 0.001$

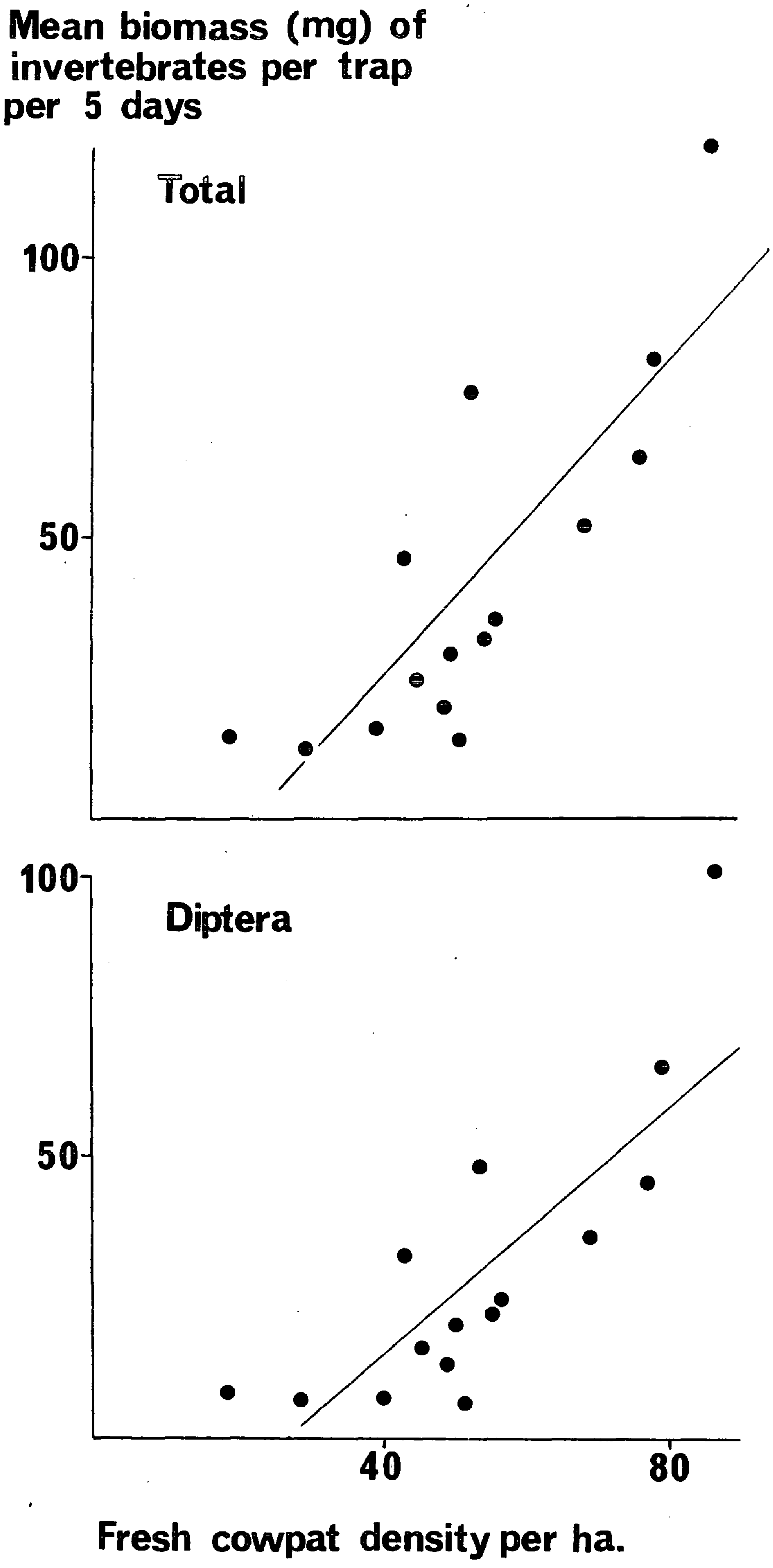

Mean biomass (mg) of invertebrates per trap per 5 days
Total
100
50
100
Diptera
50
40
80
Fresh cowpat density per ha.

Figure 18. Relationship between mean fresh cowpat density ha^{-1} and mean total invertebrate and Diptera biomass (mg per trap per 5 days) at each transect point on Rockcliffe Marsh in 1977.

Regression equations

Total invertebrates:

$y = 1.13x - 31.15$
S.E. of slope = 0.24
$r = 0.80$
df = 13
$p < 0.001$

Diptera:

$y = 1.01x - 34.51$
S.E. of slope = 0.21
$r = 0.81$
df = 13
$p < 0.001$

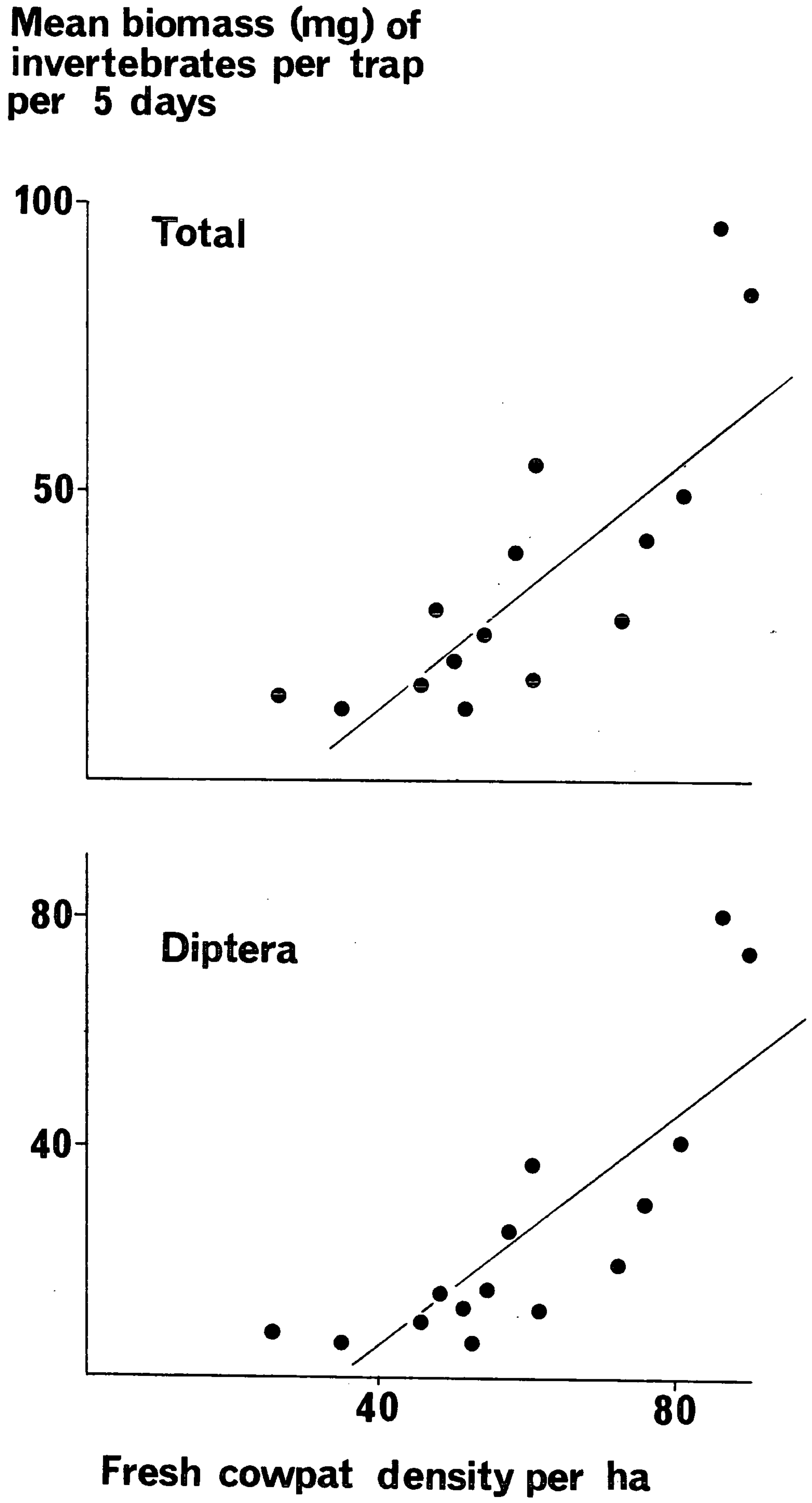

Mean biomass (mg) of invertebrates per trap per 5 days
100
50
Total
80
40
Diptera
40
80
Fresh cowpat density per ha

Table 12. Values of r for correlations of fresh cowpat density ha^{-1} with total invertebrate and Diptera abundance and biomass per trap per 5 day period, in 1976 and 1977, at transect points A1-8, Field B1-6, on Rockcliffe Marsh. In all cases, df = 13. * p 0.05, ** p 0.01, *** p 0.001.

	Total invertebrates	Diptera
Abundance of invertebrates		
1976	0.58*	0.69**
1977	0.52*	0.63*
Biomass of invertebrates		
1976	0.79***	0.81***
1977	0.80***	0.81***

Table 13. Slopes of the relationships between fresh cowpat density ha^{-1} and the abundance and biomass of total invertebrates and Diptera in 1976 and 1977, at transect points A1-8, Field B1-6, on Rockcliffe Marsh.

	Total invertebrates		Diptera			
	Slope	S.E. of slope	Slope	S.E. of slope	df	Student's "t"
Abundance of invertebrates						
1976	0.19	0.07	0.17	0.05	28	0.23
1977	0.18	0.08	0.15	0.05	28	0.32
Biomass of Invertebrates						
1976	1.40	0.29	1.21	0.24	28	0.50
1977	1.13	0.24	1.01	0.21	28	0.38

Table 14. Correlation coefficients, r, intercepts, C, and slopes, m, of correlations between fresh cowpat density ha^{-1} and the biomass and abundance of "other" invertebrates in 1976 and 1977, at transect points A1-8, Field, B1-6, on Rockcliffe Marsh.

	Correlation coefficient	Intercept	Slope	df
Abundance of "others"				
1976	0.18	5.28	0.02	13
1977	0.19	3.78	0.03	13
Biomass of "others"				
1976	0.62*	1.64	0.20	13
1977	0.47	3.36	0.11	13

fresh cowpat density and these dependent variables. It was not possible to elucidate the relative importance of old and fresh cowpat density in determining invertebrate abundance and biomass. Because of the extreme colinearity which existed between old and fresh cowpat density, a linear stepwise multiple regression could not be used (Nie *et al*. 1975). It was likely that the old cowpats provided a reservoir from which the fresh cowpats were infested by recently-emerged dung-associated invertebrates. The system was therefore perpetuated by the annual re-introduction of cattle which provided fresh sites, in the form of their excrement, for colonization by invertebrates which had overwintered, usually as pupae, in cowpats deposited during the previous grazing season.

Table 15. Correlation coefficients, intercepts and slopes of the correlations between "old" cowpat density ha^{-1} and the abundance and biomass of total invertebrates, Diptera, and "other" invertebrates, at transect points A1-7, Field and B1-5, on Rockcliffe Marsh in 1976 and 1977. df = 11, in all cases.

	Correlation Coefficient	Intercept	Slope
Abundance			
1976			
Total invertebrates	0.61*	5.16	0.21
Diptera	0.71**	-0.53	0.18
"Other" invertebrates	0.20	5.69	0.02
1977			
Total invertebrates	0.26	7.03	0.10
Diptera	0.50	-0.01	0.14
"Other" invertebrates	-0.17	7.04	-0.03
Biomass			
1976			
Total invertebrates	0.81***	-4.80	1.43
Diptera	0.81***	-10.49	1.22
"Other" invertebrates	0.61*	5.68	0.21
1977			
Total invertebrates	0.59 *	3.71	0.92
Diptera	0.59 *	-3.92	0.84
"Other" invertebrates	0.32	7.63	0.08

SECTION 7

ASPECTS OF THE BREEDING BIOLOGY OF WADING BIRDS: GENERAL METHODOLOGY

When a nest was found it was marked with a cane 2-3m from the nest to assist relocation (see Section 4, census methods). Each nest was individually coded, and the eggs were likewise numbered, in chronological order, where this was known, so that the fate of individual eggs could be followed. Newly-hatched chicks were ringed with an individually numbered Incoloy B.T.O. (British Trust for Ornithology) ring on the right leg. "Darvic" (semi-rigid P.V.C.) colour rings were used for individual identification at a distance. These rings are known to be durable, and their colours do not rapidly fade (Coulson 1963). One colour ring was placed above the B.T.O. ring on the right leg, and two were put on the left leg. By varying the colour and position of the colour rings, it was possible to create 216 different combinations of 6 colours (blue, white, grey, orange, yellow, green) in three positions. The time and date of each observation and measurement subsequently described were always noted. The measurements of time periods, e.g. the laying interval, was subject to a potential error of plus or minus 24 hours approximately, because nests were usually visited daily. Data for laying interval, and incubation, chipping and fledging periods are summarized, for each species, in Appendix 9.

Laying date

The date on which the first egg of a clutch was laid was considered to indicate the onset of breeding by a given pair. Equal effort was expended in finding nests throughout the season, so that bias in the analysis of breeding season data due to disproportionate searching intensity was minimised. Probability paper was used to assess the modality of the frequency distribution of laying date (Harding 1949).

In those cases where the date of laying of the first egg was not recorded, it was calculated by the methods of Newton (1964), in conjunction with estimates of the degree of egg or chick development. The degree of egg development was estimated by the flotation method (e.g. Schreiber 1970, Westerkov 1950), and by comparison of the weights of unaged eggs with those on a graph of egg weights of known age; egg weight declines during the incubation period (Ar _et al_. 1974, Rahn & Ar 1974). The ageing of chicks was accomplished by comparing the weight of an unaged chick with those of known age.

Laying interval

The laying interval was the period between the laying of one egg and a subsequent egg.

Clutch size

The clutch size was the number of eggs produced and incubated, usually by one pair. The number of eggs in the nest may not be the true clutch size due to unobserved losses. Abnormally large clutches, in excess of 5 eggs, were attributed to two hens depositing their eggs in the same nest. This may indicate polygyny, or may be due to the confusion arising from the close proximity of some nests. Clutch completion was assumed when the number of eggs had not increased at a second visit made more than one laying interval after the first visit.

Incubation period

The incubation period is the duration of embryonic development in the egg (e.g. Drent 1975). For practical purposes, it was the time elapsed between the laying of the last egg of the clutch and the hatching of the last chick (e.g. Kendeigh 1963, Nice 1954). This may not directly correspond to the period over which the parents actually exhibit incubation behaviour and during which embryonic development occurs, since incubation may occur prior to or be delayed until after the laying of the last egg (e.g. Baerends *et al*. 1970, Beer 1962).

Chipping period

The chipping period was the interval between the first chipping or "starring" of the egg and the complete removal of the chick from its shell.

Duration of the egg teeth

All neonatal chicks were examined for the presence of egg teeth at the tips of both upper and lower mandibles. Daily examinations of chicks revealed how long the egg teeth persisted.

Fledging period

The fledging period was the interval between hatching and the first observed flight of a juvenile. Flight was arbitrarily classified as aerial locomotion by wing flapping for at least ten metres by a juvenile bird.

Distance moved by broods during the fledging period

Whenever broods of known age were relocated, the distance they had moved from the nest was measured to the nearest metre with a 300m rule.

Hatching success

The study area was divided into sub-areas, representative of each vegetation type, which were intensively searched for nests and scrapes. Most nests were found during the laying of the clutch or shortly after, and they were usually visited daily. Unsuccessful nests were easily found during systematic searching, and egg losses could be estimated from the remains of any predated or trampled eggs in or near the nest. It was unlikely that nests were initiated and destroyed between searches, so that there was little, if any, overestimation of hatching success due to unrecorded, failed nests; a potential bias usually associated with periodic searching at relatively long intervals (e.g. Coulson 1956, Mayfield 1975, Miller & Johnson 1978).

Because many nests suffered partial losses of the clutch during incubation, rather than complete clutch mortality, it was decided to use the proportion of eggs which successfully hatched, rather than the proportion of clutches which suffered total mortality, as a measure of hatching success. This permitted a more sensitive analysis of the differential influence of each mortality factor on hatching success. Only the data for those nests whose complete history was known were included.

Most studies of hatching success implicitly assume that visiting the nest does not significantly affect egg mortality. However, visits may attract the attention of predators or the curiosity of grazing animals, although Willis (1973) found no difference between the survival rates of visited and unvisited nests of Bicolored Antbirds. It was not possible to determine the extent to which nest marking and visiting influenced hatching success in this study.

Fledging success

Fledging success was the proportion of chicks hatching which survived to fledge. All the chicks ringed within four days of hatching were used to obtain estimates of fledging success. Chicks whose origins were not known were not included in the analyses. Many chicks were presumed dead, although a proportion of these undoubtedly survived. Fledging success was, therefore, underestimated.

Breeding success and the production of fledged young per nest

Breeding success was the product of hatching and fledging success. This was also expressed in terms of the mean number of young reared per nest. Only single broods are reared per annum by the Lapwing (Klomp 1951), Oystercatcher (Harris 1967) and Redshank (Grosskopf 1958, 1959).

Life tables of eggs and chicks

The life tables were constructed, as described by Krebs (1972), where;

x is the age interval,
l_x is the number of survivors at the start of age interval x,
d_x is the number dying during the age interval x to x+1,
L_x is the number of individuals alive, on average, during the age interval,
q_x is the rate of mortality during the age interval,
e_x is the mean expectation of further life for individuals alive at the start of age x,

to provide an age-specific summary of the mortality rates of eggs and chicks.

The rate of population increase

Using the formulae and tables provided by Capildeo & Haldane (1954), it was possible to calculate the rate, λ, at which each wader breeding population of Rockcliffe Marsh would increase or decrease, assuming that the population was closed. The net fertility, $\underline{f}$, assuming that the sex-ratio was at parity, was calculated from the equation:

$$\underline{f} = cbs_1/2s$$

where;

c is the mean number of eggs laid each year,
b is the fraction of eggs laid which fledge,
s is the mean annual adult survival rate,
s_1 is the survival rate during the first year.

The net fertility, in conjunction with the mean age at first breeding, was used to determine λ from the tables.

Nest dispersion

The location of each nest was plotted on a large scale (1m:1mm) map of the sub-areas. The nesting density was measured by counting the number of contemporaneous nests within a 49m radius (0.75ha) of each nest. A radius of 49m was selected because wader nests were usually less than this distance apart, and a variable frequency of nests per 0.75ha was therefore encountered. The observed frequencies were compared with those expected by a Poisson distribution with the same mean and sample size. Classes in which the expected frequencies were less than 5 were grouped with adjacent classes to prevent the generation of spuriously high chi-square values.

Further tests were used to assess the significance of apparently non-random distributions of nests. The coefficient of variation (CV; the variance-mean ratio) for a Poisson distribution is unity; a coefficient less than unity occurs in a uniform distribution, and a value greater than unity indicates aggregation. The significance of the coefficient was tested by the index of dispersion, I (Greig-Smith 1964), which is distributed approximately as chi-square, with n-1 degrees of freedom:

$$I = S^2 (n-1)/\bar{x}$$

where; S^2 is the variance,
$\underline{n}$ is the number of samples,
$\bar{x}$ is the arithmetic mean.

If the dispersion is random, chi-square (I) should lie between the values $0.95 \geq p \geq 0.05$. If it lies above 0.95, the dispersion is uniform; below 0.05 it is aggregated. Since the index of dispersion was not influenced by the grouping of data which occurred during comparison of the Poisson and observed distributions, it was used as the most sensitive measure of significance.

SECTION 8

ASPECTS OF THE BREEDING BIOLOGY OF LAPWING, OYSTERCATCHER AND REDSHANK

Laying season

(i) LAPWING

The percentage cumulative frequency of the laying date of the first egg (figure 19), indicated that the breeding season was consistently earlier in 1976 than in 1977. In 1976, 50% of the laying dates preceded 15 April, whilst in 1977, the median was 11 May; this difference of 26 days was highly significant (median test; $X_1^2 = 36.2$, $p < 0.001$). The 1976 percentage cumulative frequency curve exhibited positive skewness, indicating that the rate of onset of laying was at its highest earlier in the season, whilst the negatively skewed 1977 ogive indicated that the rate was greater during the latter part of the breeding season. The last clutches of each season were commenced within a day of each other, on 6 June 1976 and 7 June 1977. Breeding refractoriness corresponded to the onset of the post-nuptial moult, which commences with the primaries during early June (e.g. Appleton & Minton 1978, Beser 1972, Snow & Snow 1976). On Rockcliffe Marsh, the first Lapwing in primary moult was observed between 3 and 9 June in 1974-1978. The coincidence of refractoriness and the onset of moult is typical of many species (e.g. Murton & Kear 1978, Richards 1976), although some arctic breeding waders, e.g. Dunlin, undergo primary moult during the breeding season so that migration is not delayed at the cessation of breeding (Holmes 1966).

The variation of the mean laying date in different vegetation types in each year was examined by an analysis of variance (table 16). There were significant differences between the mean laying dates in different vegetation types in both 1976 ($F_{5,47} = 3.42$, $p < 0.05$) and 1977 ($F_{3,51} = 3.62$, $p < 0.05$), consequent on the tendency for the mean laying date to be earlier in the successionally more mature vegetation types (e.g. Field, T8) than in the less mature vegetation types (T4 & T3) in each year. Significant differences between the mean laying dates in paired vegetation types during each year are indicated in table 16. The 1977 mean laying dates for each vegetation type were all significantly later than their 1976 counterparts (table 17); the laying season was delayed in 1977 relative to 1976 in all vegetation types.

(ii) OYSTERCATCHER

There was a bimodal laying date distribution in both 1976 and 1977 (figure 20). In 1976, the main peak was in late April to early May, whilst in 1977 it was

Figure 19. Percentage cumulative frequency (on a probability scale) of laying date of first egg of each Lapwing clutch in 1976 and 1977, at 3 day intervals on Rockcliffe Marsh.

N is 54 in 1976 and 63 in 1977.

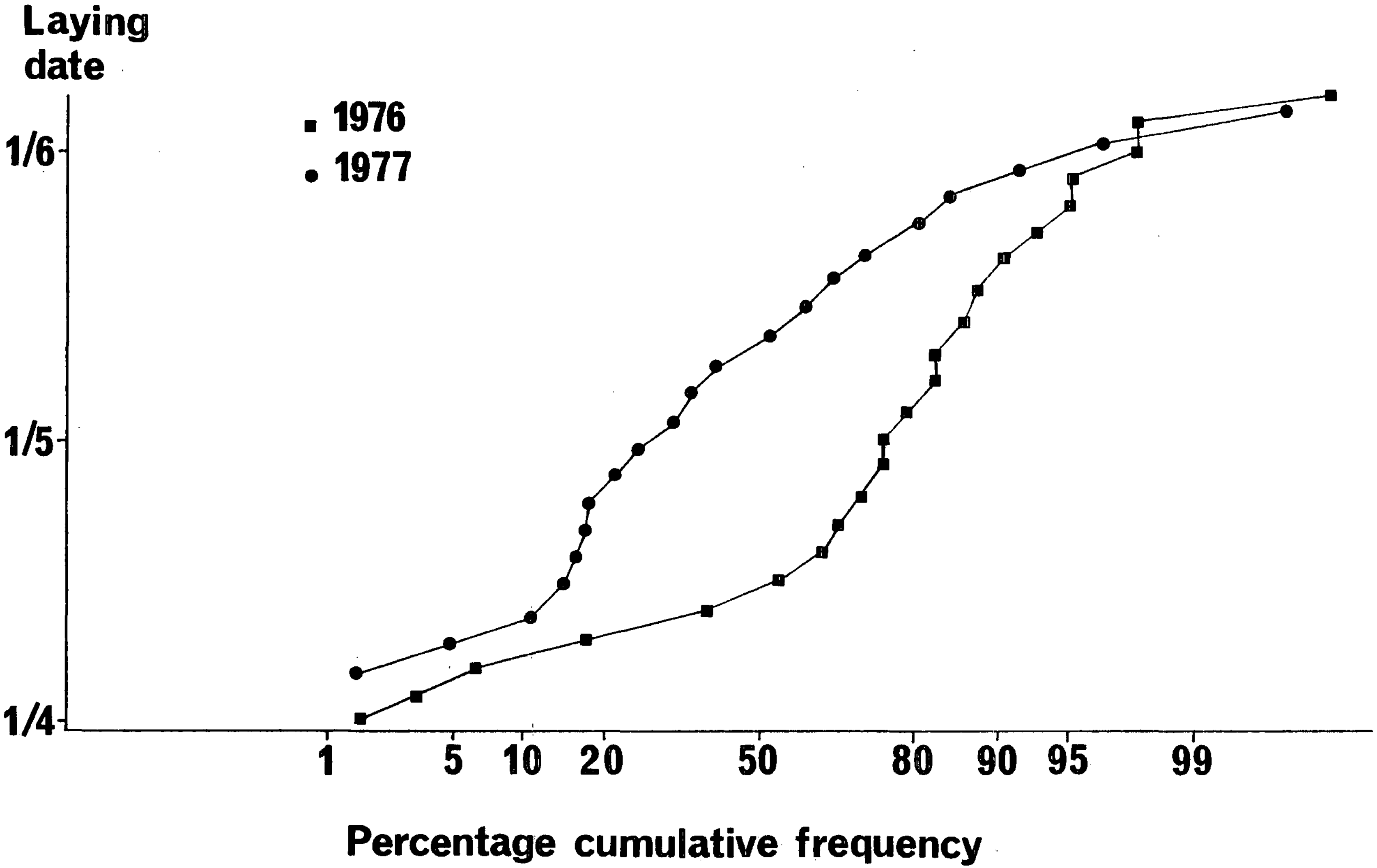

Laying date
■ 1976
● 1977
1/6
1/5
1/4
1
5
10
20
50
80
90
95
99
Percentage cumulative frequency

Table 16. Mean laying date of Lapwings on Rockcliffe Marsh in 1976 and 1977 in different vegetation types. Standard errors were derived from the table of analysis of variance for each year. Laying date was measured from 1 April, which was given a value of 1. Data for gravel areas were omitted in both years, as were those for Field and T_3 (single and double observations) in 1977.

1976

Vegetation Type	No. of observations	x	x^2	Mean date of laying	S.E. (days)
Field	3	26	238	8.67	5.51
T8	16	215	3363	13.44	2.38
T7	8	114	1792	14.25	3.36
T6	13	290	8202	22.31	2.64
T4	10	201	5233	20.10	3.01
T3	3	95	3693	31.67	5.51
Totals	53	941	22521	17.75	

Analysis of variance for 1976 data

Source of variation	Sum of squares	d.f.	Mean square	Variance ratio (F)
Between vegetation types	1549.4	5	309.9	3.42
Residual	4264.4	47	90.7	-
Totals	5813.8	52	-	-

Values of Student's "t" for mean laying dates and standard errors in paired vegetation types in 1976. * $p < 0.05$
** $p < 0.01$

Vegetation Type	T8	T7	T6	T4	T3
Field	0.79	0.86	2.23*	1.82	2.95**
T8		0.20	2.49*	1.74	3.03**
T7			1.88	1.29	2.70*
T6				0.55	1.53
T4					1.84

1977

Vegetation Type	No. of observations	x	x^2	Mean date of laying	S.E. (days)
T8	22	683	28997	31.04	3.35
T7	5	164	6614	32.80	7.01
T6	22	948	43312	43.09	3.35
T4	6	302	16302	50.33	6.41
Totals	55	2097	95225	38.13	

Analysis of variance for 1977 data

Source of variation	Sum of squares	d.f.	Mean square	Variance ratio (F)
Vegetation types	2681.2	3	893.7	3.62
Residual	12590.9	51	246.9	-
Totals	15272.1	54	-	-

Table 16 (continued)

Values of Student's "t" for mean laying dates and standard errors in paired vegetation types in 1977.
* p $<$ 0.05

Vegetation Type	T7	T6	T4
T8	0.23	2.54*	2.67*
T7		1.32	1.89
T6			1.00

Table 17. Values of Student's "t" for paired mean laying dates and standard errors in similar vegetation types in 1976 and 1977.

Vegetation Type	"t"	df	p
T8	4.28	36	0.001
T7	2.39	11	0.05
T6	4.87	33	0.001
T4	4.26	14	0.001

slightly delayed until early to mid-May. In 1976, a second peak occurred in late May, but the second peak was much less marked in 1977 and occurred in mid-June. Although the laying season commenced and terminated later in 1977 (3 May - 22 June) than in 1976 (26 April - 10 June), and the range of laying dates was similar in both years (46 days in 1976, and 50 days in 1977), the median laying date was the same, 18 May, in both years (median test; $X_1^2 = 0.01$, n.s.), because the rate of onset of laying was more rapid prior to this date in 1977 than in 1976.

There were differences between the mean laying dates on the "old" (T8-4) and "new" marsh (T3) in 1976 (table 18). The laying season was earlier on the old than the new marsh by an average of 10.5 days in 1976 ($t = 2.3$, $df = 28$, $p < 0.05$), but in 1977 there was no significant difference ($t = 0.5$, $df = 47$, n.s.), because the start of laying was delayed on the old marsh in 1977, perhaps due to the lower availability of food in 1977, relative to 1976 (Section 5). The mean date of first laying was significantly earlier in 1976 than 1977 on the old marsh by almost 10 days ($t = 2.8$, $df = 45$, $p < 0.05$). The laying date of the first nest on the old marsh was 26 April in 1976 and 9 May in 1977. There was no significant difference between years for the laying dates on the new marsh ($t = 0.2$, $df = 30$, n.s.); the laying season on the new marsh was not delayed in 1977 relative to 1976.

Figure 20. Percentage cumulative frequency (on a probability scale) of laying date of first egg of each Oystercatcher clutch in 1976 and 1977, at 3 day intervals, on Rockcliffe Marsh.

N is 33 in 1976 and 52 in 1977.

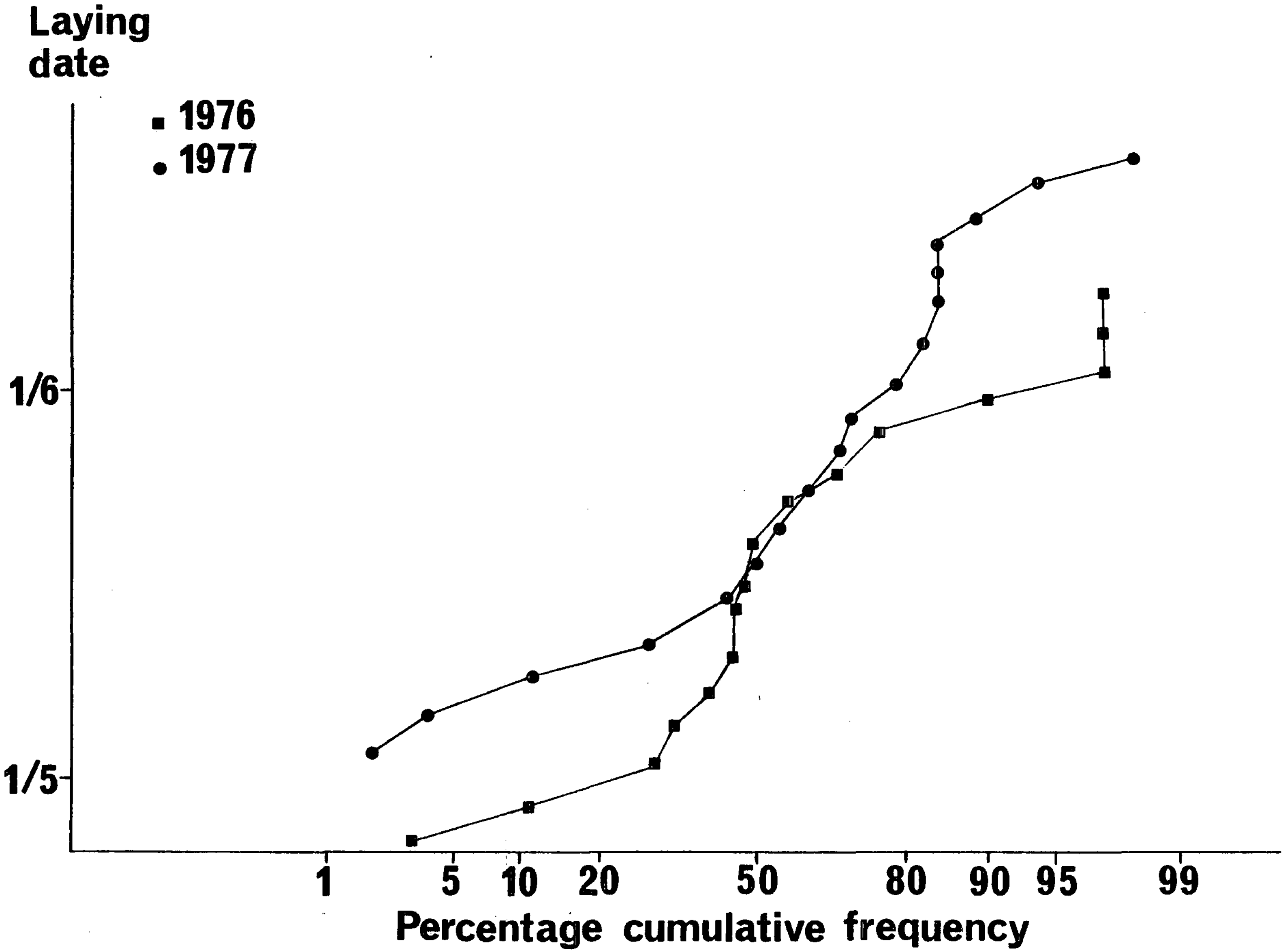

Laying date
■ 1976
● 1977
1/6
1/5
1
5
10
20
50
80
90
95
99
Percentage cumulative frequency

Table 18. Mean date, in May, of the laying of the first egg of Oystercatcher clutches on the "old" (T8-4) and "new" (T3)marsh, on Rockcliffe Marsh in 1976 and 1977.

1976	Old marsh	New marsh
Mean laying date of 1st egg	11.17	21.75
S.E. (days)	3.22	3.23
No. of clutches	15	15
1977		
Mean laying date of 1st egg	21.07	22.95
S.E. (days)	1.85	3.70
No. of clutches	32	17

(iii) REDSHANK

During both 1976 and 1977, there was a bimodal distribution of laying date frequency (figure 21). In 1976, the main peak occurred from mid-April to mid-May, whilst in 1977 it was delayed until mid-May. The second peak occurred in late May in 1976 and early June in 1977. The breeding season was consistently earlier in 1976 than 1977. The median laying date in 1976 was 28 April and in 1977 it was 14 May. This difference of 16 days was highly significant (median test; $X_1^2 = 24.0$, $p < 0.001$). The negative skewness of the percentage cumulative frequency distributions indicated that, during both years, the rate of onset of laying was highest during the early part of the season.

The mean laying date was significantly earlier on the "old" (T8-6) than the "new" (T4-3) marsh by 7 days in 1976 ($t = 2.1$, $df = 40$, $p < 0.05$) and 9 days in 1977 ($t = 2.9$, $df = 38$, $p < 0.01$) (table 19). The mean laying date was significantly earlier on the old marsh in 1976 than 1977 by 15 days ($t = 5.0$, $df = 32$, $p < 0.001$), and by 17 days on the new marsh ($t = 4.9$, $df = 46$, $p < 0.001$); the delay in the laying season of the Redshank occurred over the whole study area in 1977 relative to 1976.

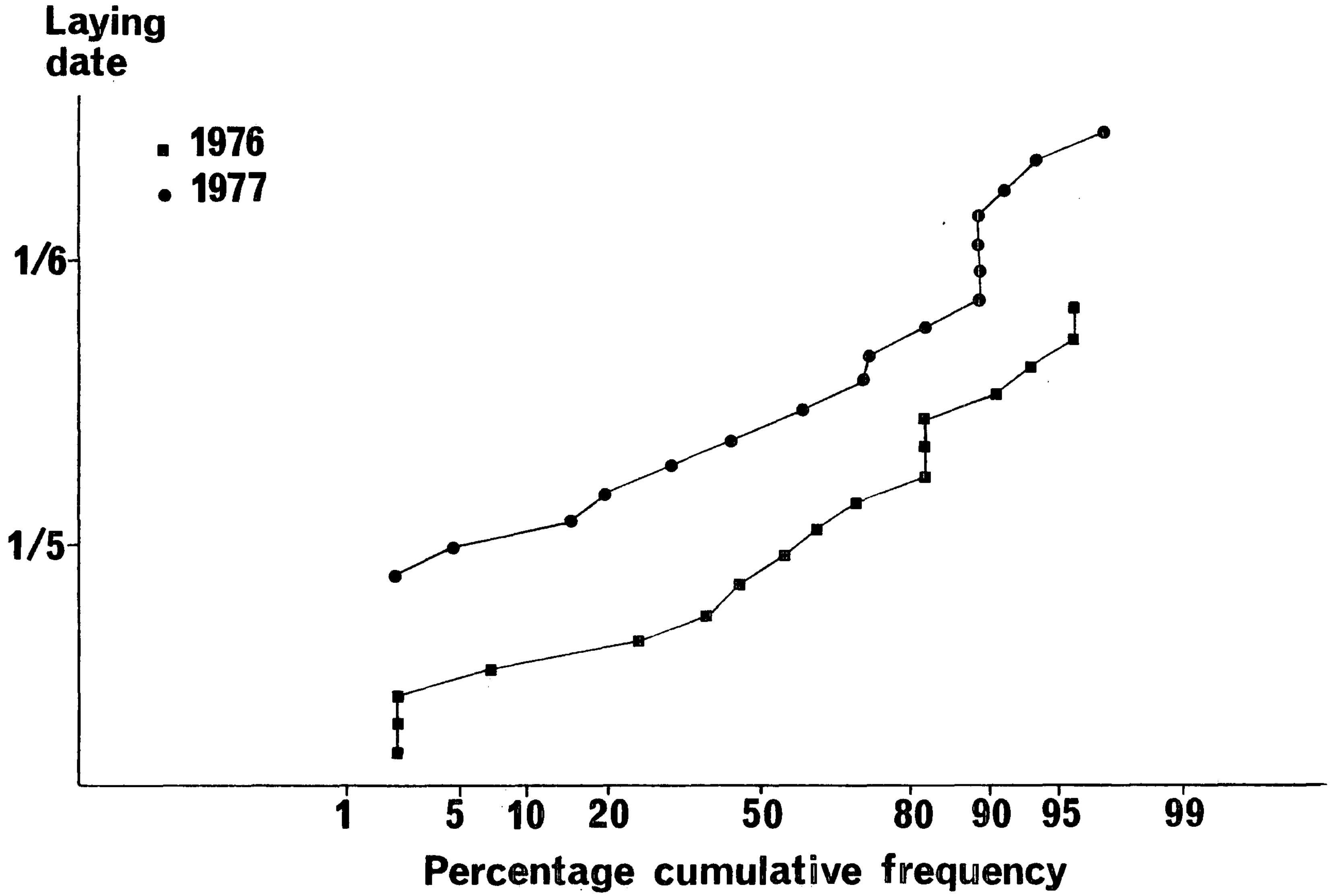
Table 19. Mean laying date of the first egg of Redshank clutches on the "old" (T8-6) and "new" (T4-3) marsh, on Rockcliffe Marsh in 1976 and 1977.

1976	Old marsh	New marsh
Mean laying date of 1st egg	26.07 (April)	3.07 (May)
S.E. (days)	2.47	2.37
No. of clutches	15	27
1977		
Mean laying date of 1st egg	11.32 (May)	19.95 (May)
S.E. (days)	1.76	2.45
No. of clutches	19	21

In Redshanks, the female lays progressively earlier by 2-5 days for each year during her first four breeding seasons (Grosskopf 1970). This tendency for young birds to breed later than older ones occurs in many species (e.g. Coulson 1966, Perrins 1965), although it has not been documented in the Lapwing and Oystercatcher. The bimodality of the Redshank's laying date frequency

Figure 21. Percentage cumulative frequency (on a probability scale) of laying date of first egg of each Redshank clutch in 1976 and 1977 at 3 day intervals, on Rockcliffe Marsh.

N is 43 in 1976 and 42 in 1977.


Laying date
■ 1976
● 1977
1/6
1/5
1
5
10
20
50
80
90
95
99
Percentage cumulative frequency

distribution may be due to the later laying of young birds, and of replacement clutches.

(iv) DISCUSSION

Gonad development is influenced in birds by photoperiod, temperature (Lofts & Murton 1968) and food availability (e.g. Huxley 1976, Jones & Ward 1976). The laying dates of each wader species were not correlated with invertebrate abundance or biomass across the halosere in any year. Moller (1978) suggested that breeding may be delayed on saltmarshes by a high water table. On Rockcliffe Marsh, the intermittent tidal inundation of the lower terrace, especially in late March and early April, may delay the laying season in less mature areas. In the Oystercatcher, the laying season does not commence inland until suitable nest sites (on tilled ground) are available (Heppleston 1972). On Rockcliffe Marsh, nest sites were apparently available throughout the year, for all wader species, except in those areas where tidal inundation regularly occurred. The annual differences in the laying dates of Lapwing and Redshank may have been related to the colder mean temperatures and higher precipitation in 1977 than in 1976 (Appendix 8).

In both years, the laying seasons of the three species were staggered in the chronological order, Lapwing, Redshank and Oystercatcher (table 20). The median laying date and the laying date of the first nest of the season were successively later in this sequence in both 1976 and 1977.

Table 20. Median laying dates and range of laying dates of Lapwing, Redshank and Oystercatcher, in 1976 and 1977, on Rockcliffe Marsh. A is April, M is May and J is June.

	1976			1977		
	Median laying date	Range of laying dates	No. of clutches	Median laying date	Range of laying dates	No. of clutches
Lapwing	15A	1A- 6J	54	11M	6A- 7J	63
Redshank	28A	9A-29M	43	14M	28A-18J	42
Oystercatcher	18M	26A-10J	33	18M	3M-22J	52

There were significant differences between the median laying dates of each species in 1976, but in 1977 the only significant difference between the median laying dates of paired species was that between the Lapwing and the Oystercatcher (table 21). In 1977, the earliest breeding species (Lapwing and Redshank) had a later laying season than in 1976, whereas that of the Oystercatcher was similar in both years.

Table 21. The significance of differences between the laying date distributions of paired wader species (Lapwing, Oystercatcher and Redshank) on Rockcliffe Marsh, in 1976 and 1977. Chi-square values were determined by the median test; p is the significance level of these values.

		Oystercatcher		Redshank	
		1976	1977	1976	1977
Lapwing	X^2_1	31.1	14.8	18.7	0.1
	p	0.001	0.001	0.001	n.s.
Redshank	X^2_1	7.9	1.3		
	p	0.01	n.s.		

Clutch size

The clutch sizes of the Lapwing, Redshank and Oystercatcher on Rockcliffe Marsh are summarized in table 22. The modal clutch size of the Lapwing and Redshank was 4 eggs, and exhibited no seasonal decline.

The modal clutch size of the Oystercatcher was 3 eggs, and a seasonal decline of mean clutch size was observed in 1976 and 1977, from approximately 3.0 eggs in late April to 2.3 eggs in late June (table 23). A similar decline was observed on Skokholm by Harris (1967), in which clutch size decreased from 3.2 eggs in April to 1.9 eggs in late May. There is no evidence that older birds lay larger clutches and breed earlier than young birds (Harris 1967). A seasonal decline in clutch size occurs in many species (see Klomp 1970), and may be related to a seasonal decline in food availability.

Duration of the egg tooth

The maximum and minimum duration of the upper egg tooth of each species are tabulated in table 24. The Lapwing and Redshank shed their upper egg tooth within two days, and usually within one day, of hatching. The scanty published information for the Lapwing concurred with this estimate; the egg tooth is retained for at least 15 hours (Spencer 1953) and less than 24 hours (Thomas 1939). In marked contrast, the egg tooth of the Oystercatcher persisted for 5 to 13 days after hatching, and was usually shed between 8 and 10 days post hatching. Webster (1941, 1942) noted that the egg tooth persisted for 7 to 12 days in the American Black Oystercatcher, and Dewar (1920) recorded an egg tooth on a 6 day old European Oystercatcher chick. The persistence of the upper egg tooth may be related to the feeding activity of the chicks, since it is presumably sloughed during foraging. Lapwing and Redshank chicks commence foraging within a day of leaving the nest, whereas foraging by the Oystercatcher chick may not commence for four or five days, since parental feeding occurs in this species (e.g. Lind 1965, Norton-Griffiths 1969, pers. obs.).

Table 22. The clutch sizes of the Lapwing, Oystercatcher and Redshank on Rockcliffe Marsh, 1974-78. Data for 1975 from Elliott (1975).

		Clutch size							No. of
	Year	1	2	3	4	5	6	Mean	clutches
Lapwing									
	1974		1	3	11			3.67	15
	1975		1	5	9			3.53	15
	1976			7	44			3.86	51
	1977	1	1	4	40		1	3.85	47
	1978			2	16			3.89	18
	TOTAL	1	3	21	120		1	3.81	146
Oystercatcher									
	1974		4	10				2.71	14
	1975		10	12	2			2.67	24
	1976	2	6	26	2	1		2.84	37
	1977	3	10	20				2.52	33
	1978		3	15	1			2.89	19
	TOTAL	5	33	83	5	1		2.72	127
Redshank									
	1974			2	10			3.83	12
	1975		1	3	13			3.71	17
	1976			1	37			3.97	38
	1977			2	31			3.94	33
	1978			1	17			3.94	18
	TOTAL		1	9	108			3.91	118

Table 23. Variation of Oystercatcher clutch size in relation to laying date on Rockcliffe Marsh, in 1976 and 1977.

	Laying date of first egg		
	26 April-10 May	11-25 May	26 May-22 June
1976			
Mean clutch size	3.12	2.78	2.45
S.E.	0.14	0.21	0.24
Number of clutches	17	9	11
1977			
Mean clutch size	2.80	2.67	2.23
S.E.	0.18	0.14	0.22
Number of clutches	5	15	13

Table 24. The maximum and minimum durations (hours) of the upper egg tooth of Lapwing, Oystercatcher and Redshank chicks.

	Maximum duration (Mean ± S.E.)	Minimum duration (Mean ± S.E.)	No. of observations
Lapwing	17.8 ± 1.6	8.4 ± 1.2	27
Oystercatcher	246.0 ±18.0	185.4 ±18.6	8
Redshank	30.9 ± 5.6	10.0 ± 2.0	10

Neonatal chicks, which were still damp, were examined for the presence of an egg tooth on the lower mandible. Three (12%) of 24 Lapwing, 1 (5%) of 20 Oystercatcher and 2 (6%) of 31 Redshank neonates had a lower egg tooth. The lower mandible egg tooth is lost so rapidly that the incidence of this structure may be underestimated. Clark (1961) reported a Lapwing chick with an egg tooth on its lower mandible, and they appear to be typical of the Scolopacidae (Jehl 1968). The function of the lower egg tooth is obscure, but it may be protective of the lower rhamphotheca during hatching.

Distance moved by broods during the fledging period

The distances moved by Lapwing, Oystercatcher and Redshank broods are illustrated in figures 22, 23 and 24 respectively. Lapwing broods remained within 100m of the nest for at least the first 18 days, and strayed no further than 200m during the whole fledging period. Klomp (1953) found that where food was abundant, adult and chick Lapwings tended to remain and feed in the territory, but in areas of low food availability, the adults led their chicks to the nearest meadow which was rich in food.

Oystercatcher broods exhibited less motility than Lapwing broods, and remained within 100m of the nest site throughout most of the fledging period. On the new marsh (T3), some broods were led by their parents from the breeding territory to an adjacent feeding territory, near the shores of the rivers Esk and Eden; these movements were all less than 100m and occurred during the first week after hatching.

Redshank broods travelled less than 200m from the nest during the fledging period. The fastest moving broods, which travelled at least 100m during the first 5-6 days after hatching (marked T3 in figure 24), hatched in vegetation type T3, but moved to T4 on the next highest terrace, where food availability was higher (Section 5). Redshank chicks may travel prodigious distances to the nearest available source of freshwater, or to the nearest suitable feeding ground (Grosskopf 1959, Hale 1955), but on Rockcliffe Marsh, such large scale movements were not observed, presumably because adequate feeding sites were locally available.

As the wader chicks move from the vicinity of the nest, the parents defend a mobile "chick area" (Hale 1956) or "juvenile distance" (Conder 1949) around the brood. The distance moved by wader chicks during the

Figure 22. Distances (m) moved by Lapwing broods during the first 36 days after hatching, on Rockcliffe Marsh, in 1976 and 1977. Successive sightings of the same brood are joined, except from the initial location in or near the nest.

The number of broods followed from the nest in both years was 64.

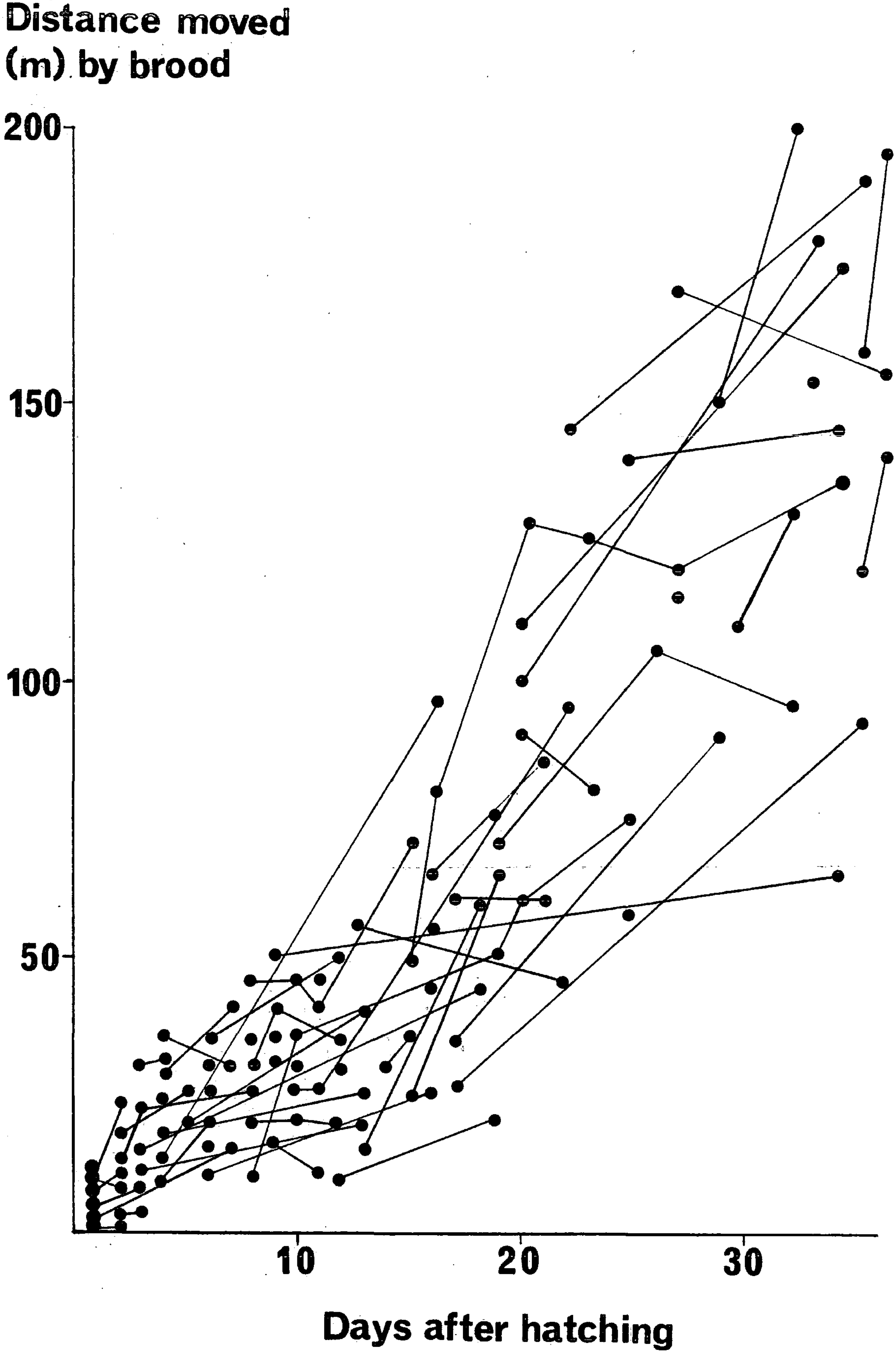

Distance moved
(m) by brood
200
150
100
50
10
20
30
Days after hatching

Figure 23. Distance (m) moved by Oystercatcher broods during the first 36 days after hatching, on Rockcliffe Marsh, in 1976 and 1977. Successive sightings of the same brood are joined, except from the initial location in or near the nest.

The number of broods followed from the nest in both years was 38.

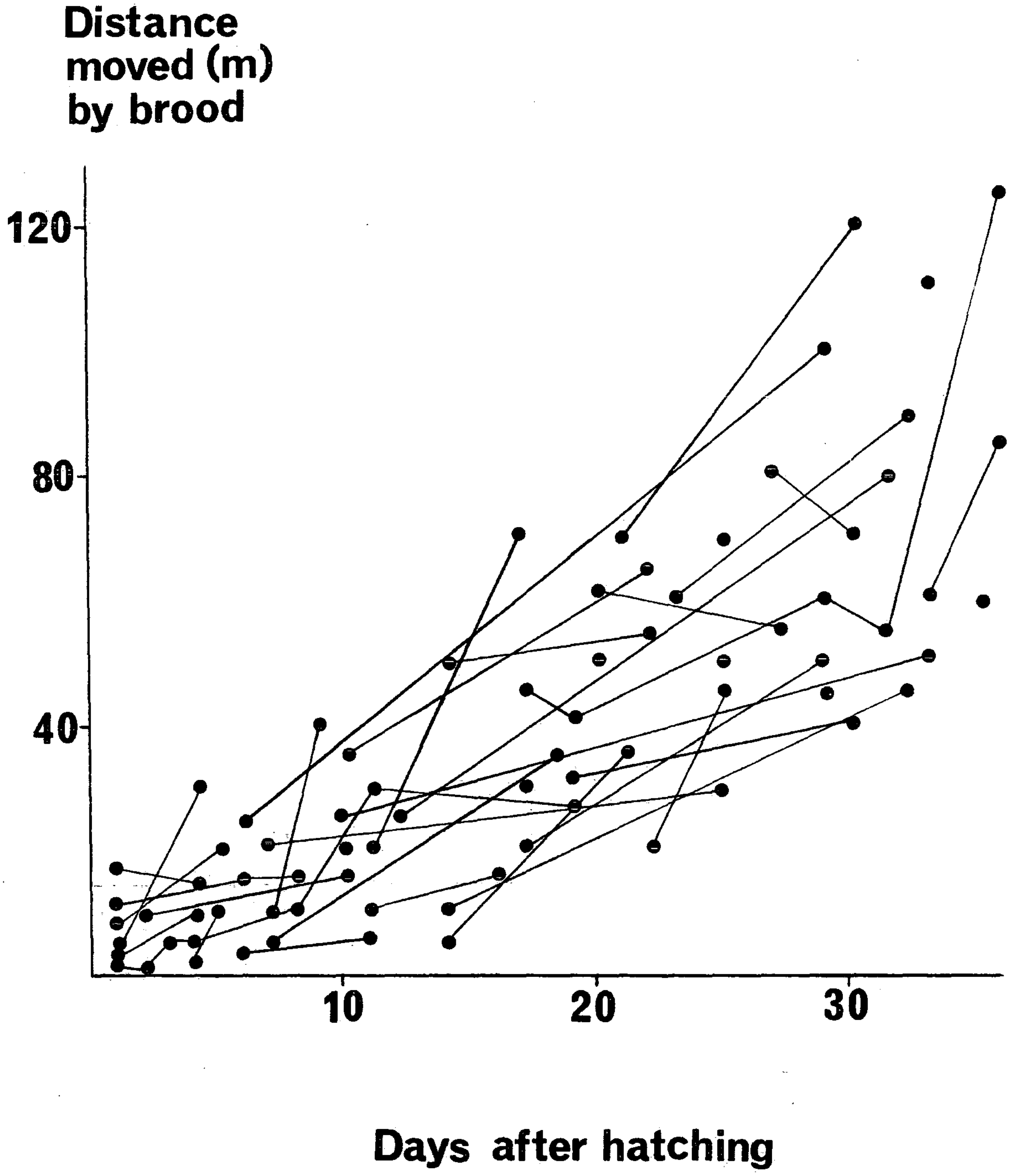
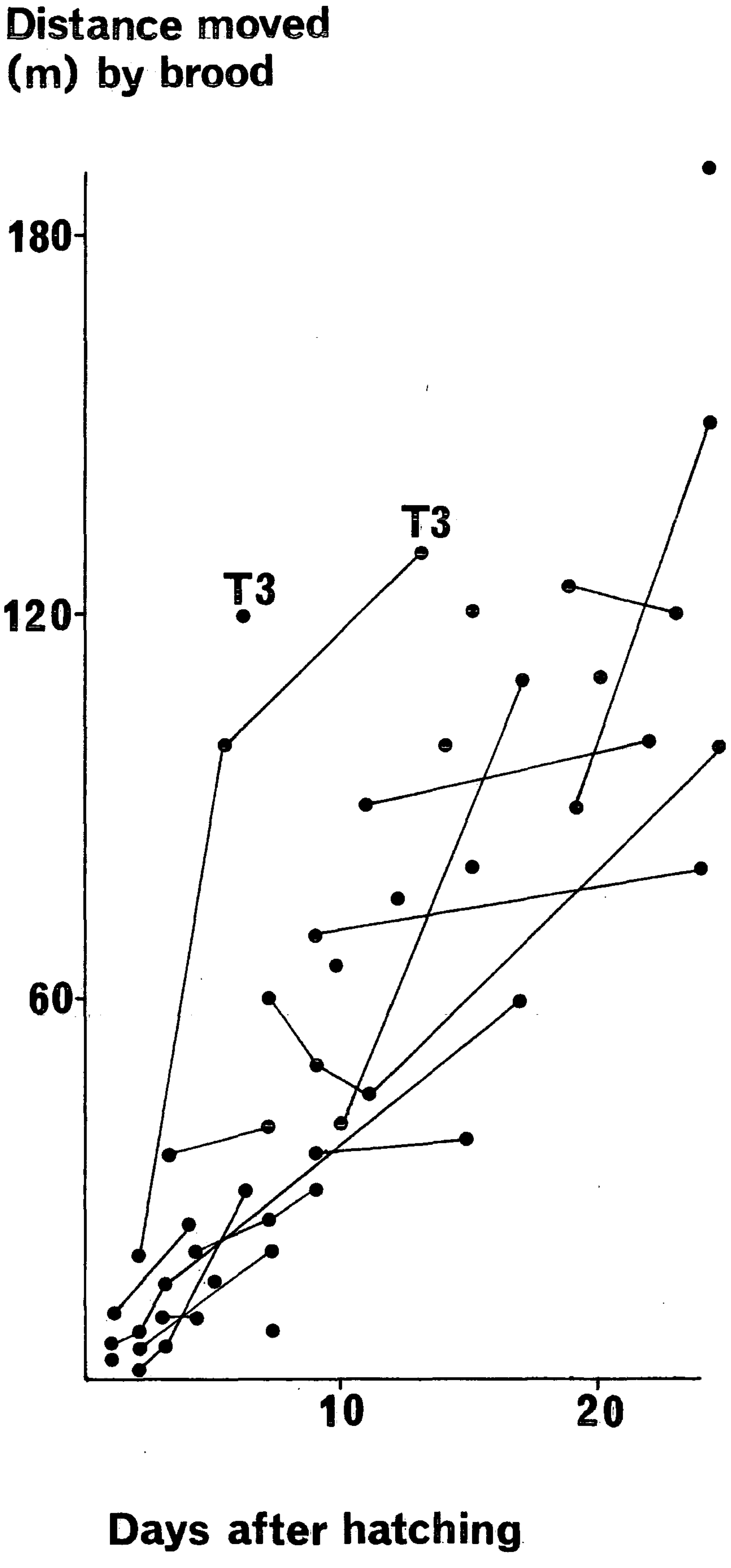

Distance moved (m) by brood
120
80
40
10
20
30
Days after hatching

Figure 24. Distance moved by Redshank broods during the first 24 days after hatching, on Rockcliffe Marsh in 1976 and 1977. Successive sightings of the same brood are joined, except from the initial location in or near the nest.

The number of broods followed from the nest in both years was 26.

Broods marked T_3 indicates those hatched in vegetation type T_3.


Distance moved
(m) by brood
180
120
60
T3
T3
10
20
Days after hatching

fledging period is inversely related to the local availability of food (Safriel 1975). On Rockcliffe Marsh, the food availability in the vicinity of the nest site was sufficient to restrict the movements of the broods to within 100m of the nest for at least the first 10 days after hatching, and no wader broods were observed to move further than 200m from the nest site during the fledging period. Oystercatcher broods tended to remain within 100m of the nest site throughout the fledging period, but Redshank and Lapwing broods attained a maximum of twice this distance during the fledging period. The maximum rates of movement of Lapwing and Redshank broods (7 and 8m day^{-1}, respectively) during the fledging period, were approximately twice as high as that of Oystercatcher broods (4m day^{-1}) (Table 25). The minimum rates of movement of Lapwing and Redshank broods (2 and 3m day^{-1}, respectively) were two to three times greater than that of Oystercatcher broods (1m day^{-1}). The lower motility of Oystercatcher broods may have been related to parental feeding, which was observed in this species, but not in the Lapwing and Redshank. For this reason, foraging movements by Oystercatcher chicks were presumably less extensive than those of Lapwing and Redshank chicks, which fed themselves within a day of hatching.

Table 25. Maximum and minimum rates of movement of wader broods (m day^{-1}) on Rockcliffe Marsh in 1976 and 1977, based on the most rapid and least rapid recorded movements during the fledging period for each species. Data derived from figures 22-24 inclusive.

	Rates of movement (m day^{-1})	
Species	Maximum	Minimum
Lapwing	7	2
Oystercatcher	4	1
Redshank	8	3

Breeding data

(i) LAPWING

Breeding success was almost twice as high in 1976 than 1977 (table 26). The difference was largely due to the higher proportion of eggs and chicks trampled by cattle in 1977 than 1976. Although there were only 4% more cattle on the marsh in 1977 than 1976, a higher proportion of nests were commenced after the cattle had been introduced in 1977 (65%) than in 1976 (20%). In different vegetation types, breeding success varied from 0% to 34% in 1976 and from 0% to 75% in 1977. There was no consistent variation of breeding success across the halosere in either 1976 or 1977.

There was a seasonal decline of breeding success in 1976 from a productivity of 0.9 chicks fledged per nest prior to 17 April, to one of 0.5 chicks fledged per nest on and subsequent to that date (table 27). In 1977,

Table 26. Summary of breeding data for the Lapwing on Rockcliffe Marsh, in different vegetation types, in 1976 and 1977. Losses due to predation and unknown causes were grouped, as were those due to infertility and putrifaction (embryonic death).

	VEGETATION TYPES							
	Gravel	Field	T8	T7	T6	T4	T3	Total
1976								
No. of nests	1	3	16	8	13	10	3	54
No. of eggs	3	12	44	28	38	39	12	176
No. hatch	0	7	14	16	21	27	8	93
No. fledge	0	2	6	4	11	13	1	37
% hatch	0	58	32	57	55	71	67	53
% fledge	0	29	43	25	52	48	12	40
% breeding success	0	17	14	14	29	34	8	21
Mean no. fledged/nest	0.0	0.7	0.4	0.5	0.8	1.3	0.3	0.7
Mortality								
EGGS								
No. infertile		1			1	1		3
% infertile		8			3	3		2
No. flooded						1	2	3
% flooded						3	17	2
No. deserted				1	1			2
% deserted				4	3			1
No. predated		3	21	7	12	8	2	53
% predated		25	48	25	32	21	17	30
No. trampled	3	1	9	4	3	2		22
% trampled	100	8	20	14	8	5		13
CHICKS								
No. predated		4	6	11	8	12	7	48
% predated		57	43	69	38	44	87	52
No. trampled		1	2	1	2	2		8
% trampled		14	14	6	9	7		9
No. of eggs and chicks trampled	3	2	11	5	5	4	0	30
% of eggs subsequently trampled during egg or chick stage	100	17	25	18	13	10	0	17

Table 26 (continued)

			VEGETATION TYPES					
	Gravel	Field	T8	T7	T6	T4	T3	Total
1977								
No. of nests	3	1	22	4	22	6	2	60
No. of eggs	9	4	73	14	74	20	8	202
No. hatch	3	4	29	8	43	8	0	95
No. fledge	1	3	9	3	5	4	0	25
% hatch	33	100	40	57	58	40	0	47
% fledge	33	75	31	37	12	50	0	26
% breeding success	11	75	12	21	7	20	0	12
Mean no. fledged/nest	0.3	3.0	0.4	0.7	0.2	0.7	0.0	0.4
Mortality								
EGGS								
No. infertile	1		1		1	1		4
% infertile	11		1		1	5		2
No. flooded							8	8
% flooded							100	4
No. deserted			1	1				2
% deserted			1	7				1
No. predated	4		16	1	19	9		49
% predated	44		25	7	28	45		24
No. trampled	1		26	4	11	2		44
% tramples	11		33	29	15	10		22
CHICKS								
No. predated	1		14	3	32	4		54
% predated	33		48	38	74	50		57
No. trampled	1	1	6	2	6			16
% trampled	33	25	21	25	14			17
No. of eggs and chicks trampled	2	1	32	6	17	2	0	60
% of eggs subsequently trampled during egg or chick stage	22	25	44	43	23	10	0	30

Table 27. The breeding statistics of Lapwings in relation to laying date on Rockcliffe Marsh in 1976 and 1977. Different laying date ranges were selected in each year to equilibrate sample sizes.

	Laying date			
	1976		1977	
	1-16 April	17 April -9 June	1 April -11 May	12 May- 9 June
No. nests	28	26	29	31
No. eggs	89	87	106	96
No. hatch	52	41	52	43
No. fledge	24	13	14	11
% hatch	58	47	49	45
% fledge	46	32	27	26
% breeding success	27	15	13	11
Mean no. fledged/nest	0.9	0.5	0.5	0.4
% of total eggs lost due to:				
predation	56	59	48	54
trampling	8	26	25	31

Table 28. Breeding statistics of the Lapwing on Rockcliffe Marsh, 1975-78, with comparative data from published sources.

Locality	Hatching success (%)	Fledging success (%)	Breeding success (%)	No. fledged per nest	Authority
Switzerland	70	64	45		Glutz(1959)
"				0.6	Imboden(1970)
Germany	5	67	3		Laven(1941)
British Isles (various sites)	100-46				Spencer(1953)
Essex	49				Steuart(1939)
Hampshire	90-67	34-14	31-9	1.2-0.5	Jackson & Jackson(1975)
Devonshire			81		Reynolds (1946)
Stokholm	52				Vernon(1953)
Morecambe Bay	53-38				Squires(1976, 1978)
Rockcliffe Marsh 1975	77				Elliott(1975)
1976	53	40	21	0.7	This study
1977	47	26	12	0.4	"
1978	61				"

the seasonal decline was much less marked, possibly because the laying season was delayed in that year; productivity decreased from 0.5 chicks fledged per nest prior to 12 May to 0.4 after that date. This seasonal decline was largely due to the incidence of trampling after the cattle were introduced during the first week of May in each year. In addition, there was a slightly higher percentage of losses due to predation in the latter half of the laying season in 1976 (3%) and 1977 (16%), than in the first half (table 27).

Klomp & Speek (1971) suggested that late ringed chicks had a slightly higher survival rate up to 1 September of the first year than those ringed earlier in the season. However, the survival rates may have been biased by the average age at which the chicks of late and early breeders were ringed, and on which Klomp & Speek had no information.

The breeding success of Lapwings on Rockcliffe Marsh was similar to that encountered in other studies of Lapwing breeding biology (table 28).

(ii) OYSTERCATCHER

Breeding success was approximately two-thirds greater in 1976 than in 1977 (table 29), due to the larger proportion of eggs and chicks trampled by cattle in the latter year. A higher proportion of clutches ~~were~~ was laid after the introduction of cattle in 1977 (96%) than in 1976 (65%). Breeding success in different vegetation types varied from 6% to 67% in 1976 and from 0% to 24% in 1977. Comparative breeding data from published sources and B.T.O. nest record cards (table 30) indicated that the breeding success of Oystercatchers on Rockcliffe Marsh was within the range previously recorded.

Harris (1967, 1969) showed that concomitant with the seasonal decline in clutch size was a seasonal decline in breeding success from 67% prior to 20 May to 33% after 30 June on Skokholm. Due to a paucity of data, breeding statistics for Rockcliffe Marsh could only be grouped into three seasonal periods, and to increase the sample sizes for each period, the data for 1976 and 1977 were combined (table 31). Early breeders (26 April-10May) produced twice as many fledged young per nest than did late breeders (26 May - 22 June). Breeders during the middle period were only slightly more productive of fledged young than late breeders. The proportion of eggs trampled, fluctuated between 20 and 24%, and showed a slight seasonal increase. As the earliest laying date was only 9 or 10 days in advance of the cattle being introduced to the marsh, most of the nests were subject to the risk of being trampled for the greater part of the incubation period even during the earliest part of the Oystercatchers laying season. The percentage of eggs predated showed a slight, but consistent seasonal increase.

Clutches of 3 or more eggs had a percentage breeding success over twice as high as that of 2 and 1 egg clutches, and produced six times more fledged young per pair than did the smaller clutches (table 32).

Table 29. Summary of breeding data for the Oystercatcher on Rockcliffe Marsh, in different vegetation types in 1976 and 1977. Losses due to unknown causes and predation were grouped, as were those due to embryonic putrefaction and infertility.

	VEGETATION TYPES						
	Gravel	T8	T7	T6	T4	T3	Total
1976							
No. of nests	3	1	2	7	7	15	35
No. of eggs	9	3	6	16	23	37	94
No. hatch	4	3	2	4	7	16	36
No. fledge	2	2	1	1	5	8	19
% hatch	44	100	33	25	30	43	38
% fledge	50	67	50	25	71	50	53
% breeding success	22	67	17	6	22	22	20
Mean no. fledged/nest	0.7	2.0	0.5	0.1	0.8	0.5	0.5
Mortality							
EGGS							
No. infertile	1		1		1	2	5
% infertile	11		17		4	5	5
No. flooded						6	6
% flooded						16	6
No. deserted	1			1		2	4
% deserted	11			6		5	4
No. predated	3		1	5	13	9	31
% predated	33		17	31	56	24	33
No. trampled			2	6	2	2	12
% trampled			33	37	9	5	13
CHICKS							
No. predated	2		1	3	1	7	14
% predated	50		50	75	14	44	39
No. trampled		1			1	1	3
% trampled		33			14	6	8
No. of eggs and chicks trampled	0	1	2	6	3	3	15
% of eggs subsequently trampled during egg or chick stage	0	33	33	37	13	8	16

Table 29 (continued)

	Gravel	T8	T7	T6	T4	T3	Total
1977							
No. of nests	3	2	3	8	15	15	46
No. of eggs	7	5	5	16	33	33	99
No. hatch	2	2	0	5	11	10	30
No. fledge	1	0	0	3	8	2	14
% hatch	29	40	0	31	33	30	30
% fledge	50	0	0	60	73	20	47
% breeding success	14	0	0	19	24	6	14
Mean no. fledged/nest	0.3	0.0	0.0	0.4	0.5	0.1	0.3
Mortality							
EGGS							
No. infertile		1					1
% infertile		20					1
No. flooded					2	7	9
% flooded					6	21	9
No. deserted	1		1		1	1	4
% deserted	14		20		3	3	4
No. predated	3		1	4	12	10	30
% predated	43		20	25	36	30	30
No. trampled	1	2	3	7	7	5	25
% trampled	14	40	60	44	21	15	25
CHICKS							
No. predated	1	2		1	3	7	14
% predated	50	100		20	27	70	47
No. trampled				1		1	2
% trampled				20		10	7
No. of eggs and chicks trampled	1	2	3	8	7	6	27
% of eggs subsequently trampled during egg or chick stage	14	40	60	50	21	18	27

Table 30. Breeding statistics of the Oystercatcher, derived from published sources, B.T.O. nest record cards 1944-74, and this study.

LOCALITY	Hatching success (%)	Fledging success (%)	Breeding success (%)	Source
Scotland:				
coastal	63			B.T.O.
	47	27	13	Heppleston(1972)
inland	77			B.T.O.
	50	46	22	Heppleston(1972)
N.England:				
coastal	40			B.T.O.
	68	65	44	Greenhalgh(1973)
	8			Squires(1976)
	17			Squires(1978)
	78			This study;1975
	38	53	20	1976
	30	47	14	1977
	49			1978
inland	63			B.T.O.
	53	61	32	Greenhalgh(1973)
Stokholm:				
coastal	74			B.T.O.
1948	66	75	49	Keighley(1949)
1939-1965	82-44			Harris(1967)
1963	64	37	23	"
1964	64	60	38	"
Anglesey:				
coastal	59	28	16	Mercer(in Heppleston,1972)
S.England:				
coastal	58			B.T.O.
N.Ireland:				
coastal	83			B.T.O.
Finland:				
coastal	92	78	72	Nordberg(1950)
Germany:				
coastal	79	5	4	Dircksen(1932)
	41-35	26-22	c. 9	Schnakenwinkel (1970)

Table 31. The breeding statistics of Oystercatchers in relation to laying date on Rockcliffe Marsh. Data for 1976 and 1977 are combined.

	LAYING DATE OF FIRST EGG		
	26 April-10 May	11-25 May	26 May-22 June
No. nests	24	30	27
No. eggs	66	69	58
No. hatch	25	22	19
No. fledge	15	11	7
% hatch	38	32	33
% fledge	60	50	37
% breeding success	23	16	12
Mean no. fledged/nest	0.6	0.4	0.3
% of total eggs lost due to:			
predation	42	46	50
trampling	20	24	22

Table 32. The breeding success of Oystercatchers on Rockcliffe Marsh in relation to clutch size. Data for 1976 and 1977 are combined.

	CLUTCH SIZE	
	c/5, c/4 & c/3	c/2 & c/1
No. nests	39	21
No. eggs	121	37
No. hatch	38	11
No. fledge	24	3
% hatch	31	30
% fledge	63	27
% breeding success	20	8
No. fledged per pair	0.6	0.1

Percentage hatching success was similar for the different clutch sizes, but fledging success was twice as high as that of smaller clutches. Oystercatchers which produced the largest clutches tended to breed earlier in the season and more successfully than those producing smaller clutches. Harris (1967) suggested that the earlier part of the season was the most "suitable", presumably in terms of food availability. On Rockcliffe Marsh, the decline in clutch size and breeding success of the Oystercatcher corresponded to the seasonal decline in the abundance of terrestrial invertebrates after mid-May (Section 5; figures 7 & 8). It is not known if older, more experienced birds breed earlier in the season, as occurs for example in the Kittiwake (Coulson & White, 1958), but if this does occur it may largely explain the tendency for early breeders to be more successful in the Oystercatcher. Breeding experience is likely to be of particular importance to the Oystercatcher, since it is one of the few wader species in which parental feeding of the chicks is well developed (e.g. Buxton 1939, von Frisch 1959, Lind 1965).

(iii) REDSHANK

The breeding success of Redshanks was similar in both 1976 and 1977 at 11% (table 33). Breeding success in different vegetation types in each year, varied from 0% to

19% and there was a tendency for breeding success to be higher in vegetation types T8-6 than in T4-3 in both years; 13% and 9% respectively in 1976, and 17% and 3% in 1977. This difference was due to the incidence of flooding on the lower terraces, which destroyed those vulnerable Redshank nests constructed in tussocks along the banks of creeks. A higher proportion of eggs was trampled in 1977 (27%) than in 1976 (17%) because a higher proportion of Redshanks laid their eggs after the cattle were introduced to the marsh in 1977 (85%) than in 1976 (32%).

There was a seasonal decline in the breeding success of the Redshank (table 34). In 1976, the difference in breeding success during the two halves of the laying season was not marked, but in 1977, breeding success was almost three times higher in the first half of the laying season (prior to 15 May) than in the latter half. In both years, the proportions of eggs predated and trampled showed a seasonal increase. Since older birds tend to breed earlier than younger birds (Grosskopf 1970), this difference in breeding success may be due to the greater experience of the earlier, and presumably older, breeding birds, as it is in the Kittiwake (Coulson 1966).

Comparative data from published sources (table 35) indicated that the annual breeding success of 11% of Redshanks on Rockcliffe Marsh, was very low, at approximately one quarter of the breeding success recorded in Germany and Finland.

Table 33. Summary of breeding data for the Redshank on Rockcliffe Marsh, in different vegetation types, in 1976 and 1977. Losses due to predation and unknown causes were combined, as were those due to embryonic putrefaction and infertility.

	VEGETATION TYPES					
	T8	T7	T6	T4	T3	Total
1976						
No. of nests	3	8	2	12	5	30
No. of eggs	10	28	8	39	19	104
No. hatch	4	7	4	17	7	39
No. fledge	0	5	1	4	1	11
% hatch	40	25	50	44	37	38
% fledge	0	71	25	23	14	28
% breeding success	0	18	12	10	5	11
Mean no. fledged/nest	0.0	0.6	0.5	0.3	0.2	0.4
Mortality						
EGGS						
No. infertile				2		2
% infertile				5		2
No. flooded					4	4
% flooded					21	4
No. deserted	3	4				7
% deserted	30	14				7
No. predated	1	10	2	15	8	36
% predated	10	36	25	38	42	35
No. trampled	2	7	2	5		16
% trampled	20	25	25	13		15
CHICKS						
No. predated	4		3	9	6	22
% predated	100		75	53	86	56
No. drowned				4		4
% drowned				24		10
No. trampled		2				2
% trampled		29				5
No. of eggs and chicks trampled	2	9	2	5	0	18
% of eggs subsequently trampled during egg or chick stage	20	32	25	13	0	17

Table 33 (continued)

	VEGETATION TYPES					
1977	T8	T7	T6	T4	T3	Total
No. of nests	5	7	6	7	4	29
No. of eggs	17	22	21	23	13	96
No. hatch	5	7	4	3	4	23
No. fledge	3	3	4	1	0	11
% hatch	29	32	19	13	31	24
% fledge	60	43	100	33	0	48
% breeding success	18	14	19	4	0	11
Mean no. fledged/nest	0.6	0.4	0.7	0.1	0.0	0.4
Mortality						
EGGS						
No. flooded				7	8	15
% flooded				30	61	16
No. deserted		2		3		5
% deserted		9		13		5
No. predated	7	6	9	6	1	29
% predated	41	27	43	26	8	30
No. trampled	5	7	8	4		24
% trampled	29	32	38	17		25
CHICKS						
No. predated	1	3		2	4	10
% predated	20	43		67	100	43
No. trampled	1	1				2
% trampled	20	14				9
No. of eggs and chicks trampled	6	8	8	4	0	26
% of eggs subsequently trampled during egg or chick stage	35	36	38	17	0	27

Table 34. The breeding success of Redshanks in relation to laying date on Rockcliffe Marsh, in 1976 and 1977.

	1976		1977	
	1-30 April	1-30 May	25 April -14 May	15 May- 20 June
No. nests	16	14	16	13
No. eggs	59	45	47	49
No.hatch	23	16	17	6
No.fledge	7	4	8	3
% hatch	39	36	36	12
% fledge	30	25	47	50
% breeding success	12	9	17	6
Mean no. fledged/nest	0.4	0.3	0.5	0.2
% of total eggs lost due to:				
predation	54	58	38	47
trampling	15	20	17	33

Table 35. Breeding statistics of the Redshank derived from published sources, B.T.O. nest record cards 1939-44, and this study.

LOCALITY		Hatching success (%)	Fledging success (%)	Breeding success (%)	Source	
Britain:						
North;	coastal	30-17			Squires (1976, 1978)	
		51			B.T.O.	
		77			Elliott (1975)	1975
		38	28	11	This study;	1976
		24	48	11		1977
		49				1978
	inland	65			B.T.O.	
South;	coastal	33			Steuart (1939)	
		48			B.T.O.	
	inland	46			B.T.O.	
Germany:						
	coastal	86	c.50	43	Grosskopf (1958)	
Finland:						
	coastal	96	41	39	Nordberg (1950)	

(iv) DISCUSSION

All three species exhibited a seasonal decline of breeding success. Many species have an optimum timing of breeding, with regard to breeding success (Perrins 1970), among which, for example, the Oystercatcher (Harris 1967), Fulmar (Ollason & Dunnet 1978) and Arctic Skua (O'Donald et al. 1974) have a seasonal decline of breeding success, which is usually attributed to a declining availability of food (e.g. Lack 1966). The seasonal decline of Oystercatcher breeding success was related to the decreasing availability of food by Heppleston (1972) and Safriel (1967). White (1978) has emphasized the importance of a relative shortage of food, especially nitrogeneous food, in reducing the breeding success of many species. On Rockcliffe Marsh, the declining breeding success of the three species corresponded to the seasonal decline in the abundance of terrestrial invertebrates in late May (Section 5). The main advantage of breeding earlier on Rockcliffe Marsh, apart from the greater availability of food, was the reduced risk of trampling of eggs and chicks. Those nests whose laying date preceded 3-5 May in 1976 and 1977 had a lower risk of being trampled, at least during part of the incubation period, than those nests commenced after the cattle were introduced on 3-5 May. There was also a slight tendency for the proportion of predated eggs and chicks to show a seasonal increase. This occurred in all three species in both 1976 and 1977. Chicks may have been more susceptible to predation later in the season because of the relative shortage of food. Safriel (1975) suggested that the foraging movements of nidifugous young become more extensive when food availability is low. As the brood becomes more dispersed, the adults become less able to deter predators as effectively as they can when the brood is less dispersed. The predation rate of Oystercatcher chicks was related to the duration that foraging adults were absent from their offspring, which was, in turn, inversely related to the local availability of suitable prey (Safriel 1967). The differential risk of predation early and late in the laying season may also have been due to the earlier breeding of older birds (e.g. Grosskopf 1970), whose greater experience enabled them to deter potential predators more effectively than could less experienced birds. Alternatively, there may have been a seasonal increase in the intensity of predation; families of Carrion Crows, which frequented the marsh after early May, and several gull species, which had growing chicks to feed after late May, were the major predators.* Although predation may cause significant mortality, of eggs and chicks, there is no evidence that predation is a density-dependent mortality factor in shore birds (Jehl 1971). In this study there was no significant relationship between

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* The predators of eggs and chicks of waders recorded on Rockcliffe Marsh are listed in Appendix 10.

the nest densities of any of the species and the proportions of eggs predated during the egg and chick stage. The unsuccessful clutches or broods of earlier breeders had a higher chance of being replaced than those of later breeders since a higher proportion of the laying season was available to earlier breeders during which replacement clutches could be initiated.

The incidence of predation and trampling during the incubation period

(i) LAPWING

Egg predation occurred almost three times more frequently during the first quarter of the incubation period than was expected by chance, in both 1976 ($X^2_3 = 20.0$, $p \angle 0.001$) and 1977 ($X^2_3 = 20.7$, $p \angle 0.001$) (table 36). Over 60% of egg predation occurred during the first quarter of the incubation period in both years. There were no significant differences between the relative proportions of eggs predated during each stage of the incubation period in 1976 and 1977 ($X^2_3 = 0.9$, n.s.).

In contrast, there was no significant tendency for eggs to be trampled during a particular stage of incubation, neither in 1976 ($X^2_3 = 1.6$, n.s.), nor in 1977 ($X^2_3 = 2.4$, n.s.). There was no significant difference between the proportion of eggs trampled during each stage in different years ($X^2_3 = 1.4$, n.s.). The percentage of eggs trampled did not appreciably decrease during the incubation period, indicating that trampling was a random mortality factor, unlike predation, which occurred when the adults were least attentive of the nest, just after laying.

(ii) OYSTERCATCHER

Egg predation occurred more than twice as frequently during the first five days of the incubation period than was expected by chance, in both 1976 ($X_4^2 = 12.0$, $p < 0.02$) and 1977 ($X_4^2 = 39.7$, $p < 0.001$) (table 37). There was no significant difference between the relative frequency of predation during each stage in different years ($X_4^2 = 1.8$, n.s.).

There was no significant tendency for trampling to occur during a particular stage of the incubation period in either 1976 ($X_4^2 = 0.3$, n.s.) or 1977 ($X_4^2 = 5.2$, n.s.), and this pattern did not significantly vary between years ($X_4^2 = 0.2$, n.s.).

(iii) REDSHANK

The proportion of eggs predated during each quarter of the incubation period significantly deviated from that expected by chance, in both 1976 ($X_3^2 = 10.5$, p 0.02) and 1977 ($X_3^2 = 11.9$, $p < 0.01$); the highest proportion of egg predation occured during the first 6 days after laying (67% in 1976 and 76% in 1977). The relative incidence of predation in each stage of the incubation period did not significantly differ between the years ($X_3^2 = 2.4$, n.s.).

Table 36. The proportion of Lapwing eggs trampled and predated during each quarter of the 24 day incubation period on Rockcliffe Marsh, in 1976 and 1977.

	Stage of incubation (days)			
	0-6	7-12	13-18	19-24
1976				
No. of eggs at beginning of stage	176	125	105	97
No. of eggs predated during stage	32	14	5	1
% of eggs predated during stage	18	11	5	1
No. of eggs trampled during stage	10	6	3	3
% of eggs trampled during stage	6	5	3	3
1977				
No. of eggs at beginning of stage	202	140	116	101
No. of eggs predated during stage	33	10	4	2
% of eggs predated during stage	16	7	3	2
No. of eggs trampled during stage	17	12	11	4
% of eggs trampled during stage	8	9	9	4

Table 37. The proportion of Oystercatcher eggs trampled and predated during each fifth of the incubation period on Rockcliffe Marsh, in 1976 and 1977.

	Stage of incubation (days)				
	0-5	6-10	11-15	16-20	21-25
1976					
No. of eggs at beginning of stage	94	66	53	44	39
No. of eggs predated during stage	17	9	3	1	1
% of eggs predated during stage	18	14	6	2	3
No. of eggs trampled during stage	4	3	2	2	1
% of eggs trampled during stage	4	5	4	5	3
1977					
No. of eggs at beginning of stage	99	67	52	42	35
No. of eggs predated during stage	19	7	2	2	0
% of eggs predated during stage	19	10	4	5	0
No. of eggs trampled during stage	8	7	5	3	2
% of eggs trampled during stage	8	10	10	7	6

Table 38. The proportion of Redshank eggs trampled and predated during each quarter of the incubation period on Rockcliffe Marsh, in 1976 and 1977.

	Stage of incubation (days)			
	0-6	7-12	13-18	19-24
1976				
No. of eggs at beginning of stage	104	64	51	44
No. of eggs predated during stage	24	7	3	2
% of eggs predated during stage	23	11	6	4
No. of eggs trampled during stage	6	3	4	3
% of eggs trampled during stage	6	5	8	7
1977				
No. of eggs at beginning of stage	96	52	35	29
No. of eggs predated during stage	22	6	1	0
% of eggs predated during stage	23	11	3	0
No. of eggs trampled during stage	10	7	5	2
% of eggs trampled during stage	10	13	14	7

There was no significant tendency for the trampling of eggs to occur during a particular stage of incubation, in 1976 (X^2_3 = 0.5, n.s.) or 1977 (X^2_3 = 0.9, n.s.), nor did the relative frequency of trampling in each stage differ between years (X^2_3 = 0.9, n.s.).

(iv) DISCUSSION

In all three species, significantly more eggs were predated during the initial stage of incubation than was expected by chance (tables 36-38). Predation mostly occurs during and shortly after the laying period in many species (e.g. Drent 1970, Vermeer 1967), including the Black-tailed Godwit (Lind 1961). These losses coincided with the time at which the attentiveness of the adults was minimal (Drent 1975). Many species are known to become increasingly attentive at the nest as the incubation period progresses (e.g. Baerends et al. 1970, Cullen 1956, Sears 1978). The eggs were therefore at their most vulnerable to predation because the anti-predatory behaviour of the adults (e.g. "mobbing") was not as vigorous and effective as it becomes later during the incubation period, when parental investment (Trivers 1972) in the eggs has substantially increased.

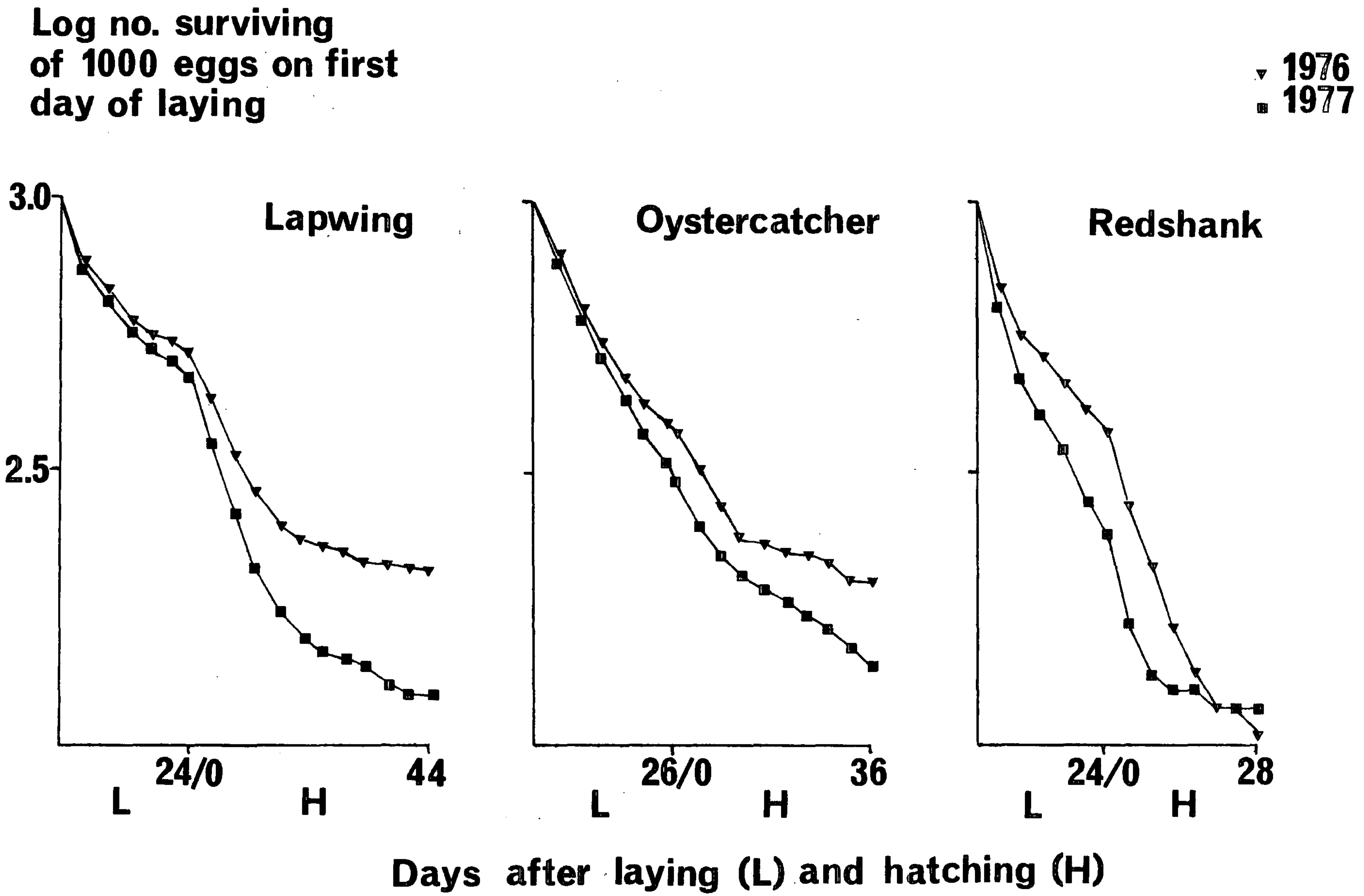
In contrast, the incidence of trampling underwent no appreciable decline during the incubation period, which suggests that trampling was an essentially random egg mortality factor, and that the response of breeding waders to intruding cattle was not very effective.

Cohort life tables of wader eggs and chicks

The life tables of the eggs and chicks of Lapwing, Oystercatcher and Redshank are summarized in Appendices 11, 12 and 13, respectively. The l_x data were converted to the log number of survivors of a cohort of 1000 eggs to permit direct comparisons of the survival rates of the eggs and chicks of each species.

The survival rate of eggs and chicks was consistently higher in 1976 than 1977 for each species (figure 25). The lowest survival rates of Lapwing and Redshank eggs were encountered in the early part of the incubation period and the early part of the fledging period,

Figure 25. Survivorship curves of Lapwing, Oystercatcher and Redshank eggs and chicks on Rockcliffe Marsh in 1976 and 1977, expressed as the log number of survivors of a cohort of 1000 eggs alive on the date of laying.


Log no. surviving of 1000 eggs on first day of laying
▽ 1976
■ 1977
3.0
2.5
Lapwing
Oystercatcher
Redshank
24/0
44
26/0
36
24/0
28
L
H
L
H
L
H
Days after laying (L) and hatching (H)

especially within the first eight days of these periods. This tendency was also apparent in the 1976 Oystercatcher data, but not in the 1977 survivorship curve. Although predation usually occurs during or shortly after the laying period in many species (e.g. Drent 1973, see above), Patterson (1965) noted a second peak of losses, which he attributed to predation, at hatching time in the Black-headed Gull. The lower rate of survival exhibited by the wader chicks within a week of hatching, was also attributed to an increased predation rate at this period, which was presumably due to the relative vulnerability of naive chicks, unfamiliar with their immediate cover, even though at this stage parental attentiveness appeared to be high.

The Redshank had the consistently lowest survival rate of eggs and chicks of the three species in a given year (figure 25), as expected from the low breeding success of the Redshank on Rockcliffe Marsh, relative to those of the Lapwing and Oystercatcher.

The rate of increase of the breeding wader populations

Using the formulae and tables provided by Capildeo & Haldane (1954), it was possible to calculate the rate, λ , at which each breeding wader population on Rockcliffe Marsh would increase or decrease, assuming that the population was closed, and that no non-breeding, sexually mature "floaters" (Brown 1969) occurred. Small flocks, of approximately 10-12 Oystercatchers and Lapwings were occasionally observed at the margins of the marsh, but these were immatures.

The values of <u>c</u>, the mean number of eggs laid per year, were underestimated, since the modal clutch size of each species was used for this value, and the number of replacement nests were not included.

(i) LAPWING

The mean adult mortality rate of Lapwings is known to be 34% in Britain (Haldane 1953, Lack 1943), giving a survival rate of 0.66. Boyd (1962) tentatively suggested a first year survival rate of 0.58. This may be an overestimate, but was the only approximation available. From this information, in conjunction with the modal clutch size of 4 eggs (table 22), and a breeding success of 21% in 1976 and 12% in 1977 (table 26), a net fertility of 0.37 was calculated for 1976, and of 0.21 for 1977. If the age at first breeding is 1 year old, $\lambda = (1 + f)s$, which at equilibrium is unity. In 1976, λ was 0.90 and in 1977 it was 0.80. The rates may have been as low as 0.86 and 0.77 respectively, since some Lapwings do not breed until their second year (Kraak <u>et al</u>. 1940). In both years, therefore, the population was apparently not self-maintaining.

(ii) OYSTERCATCHER

The mean adult annual survival rate in Britain is 88% (Harris 1967) and the first year survival rate has been estimated at 64% (Boyd 1962). The modal clutch size was 3 eggs (table 23), and the annual breeding success was 20% in 1976 and 14% in 1977 (table 29). From the information above, the net fertility was 0.22 in 1976 and 0.15 in 1977. Breeding may occur for the first time in the third year (e.g. Anderson & Minton 1978, Dircksen 1932), but the age at first breeding is usually 4 years (e.g. Grosskopf 1964, Harris 1967, Jungfer 1954, Schnakenwinkel 1970), although the male does not breed, on average, until 5 years (Harris 1970a). A value of 4 years for the age at first breeding was used during this analysis. The predicted rate of change, λ , in a closed population was 1.01 in 1976 and 0.98 in 1977. Since these values fluctuated around unity, the population was in equilibrium.

(iii) REDSHANK

From several studies, Boyd (1962) concluded that the annual adult mortality rate did not exceed 30%, and that the first year survival rate was 45%. The modal clutch size was 4 eggs (table 23) and breeding success was 11% in both 1976 and 1977 (table 33). From the above information, the net annual fertility was 0.30. Redshanks usually breed for the first time when they are two years old, and occasionally when they are one (Grosskopf

1959). For a closed population with a net fertility of 0.3, and a mean age at first breeding of 2 years, the rate of population change, λ , was 0.9, which was insufficient to maintain the population at equilibrium.

(iv) DISCUSSION

From the calculations presented above only the Oystercatcher population was at equilibrium. The Lapwing and Redshank breeding populations were not apparently self-maintaining. It was assumed that immigration was occurring to maintain the local populations, because the annual nest censuses (Section 4) showed no evidence that these populations were declining.

The dispersion of nests

(i) LAPWING

Nest density was higher in 1976 than 1977 by at least 50% in the grouped vegetation types (T3-6 and T7-Field), and for the total area (table 39). In 1976, the dispersion (measured as described in Section 7) of the total nests significantly deviated from a Poisson distribution, i.e. the nests were non-randomly distributed. This was confirmed (table 40) by the coefficient of variation (CV) and the index of dispersion (I), which indicated that, for the total data, Lapwing

Table 39. Density of Lapwing nests within 0.75 ha. around each nest, in different vegetation types on Rockcliffe Marsh, 1976 and 1977.

1976

Vegetation Type	No.of nests within each 0.75 ha. 0	1	2	3	4	5	Total	Mean Density	Variance
T3	3						3	0.00	
T4	3	5	3	1			12	1.17	
T6	3	2	6	4			15	1.73	
T7	2	0	0	2	2	3	9	3.22	
T8	8	1	6	2	2		19	1.42	
Field	0	3					3	1.00	
T3-T6									
Observed	9	7	9	5			30	1.33	1.19
Expected	7.9	10.5	11.6				30	1.33	
								$X_2^2=1.84$,	n.s.
T7-Field									
Observed	10	4	6	4	4	3	31	1.90	3.02
Expected	13.5		8.4		9.1		31	1.90	
								$X_2^2=1.11$,	n.s.
Total									
Observed	19	11	15	9	4	3	61	1.62	2.17
Expected	12.1	19.6	15.8		13.5		61	1.62	
								$X_3^2=8.22$,	$p \angle 0.05$
1977									
T3	2						2	0.00	
T4	6	1					7	0.14	
T6	12	7	4	1			24	0.75	
T7	0	2	1	1			4	1.75	
T8	3	13	3	3	1		23	1.39	
Field	0	1					1	1.00	
T3-T6									
Observed	20	8	4	1			33	0.58	0.69
Expected	18.5		14.5				33	0.58	
								$X_1^2=0.28$,	n.s.
T7-Field									
Observed	3	16	4	4	1		28	1.43	0.99
Expected	6.7	9.6		11.7			28	1.43	
								$X_2^2=6.98$,	$p \angle 0.05$
Total									
Observed	23	24	8	5	1		61	0.97	1.00
Expected	23.1	22.4		15.5			61	0.97	
								$X_2^2=0.25$,	n.s.

Table 40. Coefficients of variation (CV), indices of dispersion (I), probability levels of I, and degrees of freedom (df) of Lapwing nest dispersion in vegetation types T3-6, T7-Field, and total vegetation types on Rockcliffe Marsh, in 1976 and 1977.

	CV	I	d.f.	P
1976				
T3-T6	0.90	26.10	29	n.s.
T7-Field	1.59	47.70	30	≤ 0.05
Total	1.34	80.41	60	≤ 0.05
1977				
T3-T6	1.19	38.1	32	n.s.
T7-Field	0.69	18.7	27	n.s.
Total	1.03	61.90	60	n.s.

nests were aggregated or clumped. In T3-6, Lapwing nests tended to be uniformly distributed (CV less than unity, table 40), but this tendency was not significant. In T7-Field, the observed distribution did not significantly deviate from a Poisson distribution (table 39), but CV indicated that the nests had a clumped distribution, which was significant (table 40).

In 1977, the dispersion of Lapwing nests in T7-Field was significantly different from a Poisson distribution (table 39), but the index of dispersion indicated that this tendency to a uniform distribution was not significant (table 40), nor did the nest distributions in any of the remaining vegetation type groupings differ significantly from a random distribution.

Table 41. Density of Oystercatcher nests within 0.75ha of each nest in different vegetation types on Rockcliffe Marsh, 1976 and 1977.

Vegetation Type	No.of nests within 0.75ha. 0	1	2	3	Total	Mean Density	Variance
1976							
T8 & T7	1	3			4	0.75	0.25
T6	4	2	2		8	0.75	0.79
T4	3	3	2		8	0.87	0.70
T3 & Gravel	7	7	4		18	0.83	0.62
T8-4							
Observed	8	8	4		20	0.80	0.59
Expected	9.0	11.0			20	0.80	
						$X_1^2=0.19$,	n.s.
T3 & Gravel							
Observed	7	7	4		18	0.83	0.62
Expected	7.9	10.1			18	0.83	
						$X_1^2=0.16$	n.s.
Total							
Observed	15	15	8		38	0.82	0.59
Expected	16.7	13.7	7.5		38	0.82	
						$X_1^2=0.33$,	n.s.
1977							
T8 & T7	3	2	1		6	0.67	0.67
T6	4	5			9	0.56	0.28
T4	9	6	2		17	0.59	0.51
T3 & Gravel	10	6	3	1	20	0.75	0.83
T8-4							
Observed	16	13	3		32	0.59	0.44
Expected	17.7	14.3			32	0.59	
						$X_1^2=0.38$	n.s.
T3 & Gravel							
Observed	10	6	3	1	20	0.75	0.82
Expected	9.5	10.5			20	0.75	
						$X_1^2=0.06$,	n.s.
Total							
Observed	26	19	6	1	52	0.65	0.58
Expected	27.1	17.6	7.2		52	0.65	
						$X_1^2=0.16$,	n.s.

Table 42. Coefficients of variation (CV), indices of dispersion (I), probability levels of I, and degrees of freedom (df) of Oystercatcher nest dispersion in vegetation types T8-4, T3 & Gravel, and all vegetation types, on Rockcliffe Marsh in 1976 and 1977.

	CV	I	df	P
1976				
T8-T4	0.74	14.0	19	n.s.
T3 & Gravel	0.75	12.7	17	n.s.
Total	0.72	27.3	37	n.s.
1977				
T8-T4	0.75	23.1	31	n.s.
T3 & Gravel	1.09	20.8	19	n.s.
Total	0.89	45.5	51	n.s.

(ii) OYSTERCATCHER

The dispersion of Oystercatcher nests (table 41) did not significantly deviate from a random distribution in the grouped vegetation types (T8-4 and T3 & Gravel), nor over the whole marsh, in both 1976 and 1977, as indicated by the values of CV and I (table 42). The values of CV, which were usually less than unity, but not significantly so, indicated that Oystercatcher nests tended to be uniformly distributed, and this was probably consequent on territorial behaviour; the flexibility of territoriality in the Oystercatcher (Heppleston 1972, Lind 1965) may have reduced this tendency to insignificance. During both years the mean density of Oystercatcher nests only varied from 0.56 to 0.87 within 0.75ha of each nest.

Table 43. Density of Redshank nests within 0.75ha of each nest in different vegetation types on Rockcliffe Marsh, 1976 and 1977.

Vegetation Type	No.of nests within 0.75ha. 0	1	2	3	4	5	6	Total	Mean Density	Variance
1976										
T8-T6	2	6	1	2	4	0	1	16	2.25	3.13
T4	4	2	2	2	5	5		20	2.85	3.71
T3	5	2	2					9	0.66	0.75
T8-T6										
Observed	2	6	1	2	4	0	1	16	2.25	3.13
Expected	5.5				10.7			16	2.25	
									$X^2_1=1.8$	n.s.
T4-T3										
Observed	9	4	4	2	5	5		29	2.17	3.79
Expected	10.5		7.8		10.7			29	2.17	
									$X^2_2=2.6$	n.s.
Total										
Observed	11	10	5	4	9	5	1	45	2.20	3.48
Expected	15.9		12.0		17.0			45	2.20	
									$X^2_2=6.0$	n.s.
1977										
T8-T7	2	3	2	4	1	1		13	2.15	2.31
T6	2	3	1	1	1			8	1.50	2.00
T4	4	7	2	2	2			17	1.47	1.76
T3	2	2						4	0.50	0.33
T8-T6										
Observed	4	6	3	5	2	1		21	1.90	2.19
Expected	9.1		5.7		6.2			21	1.90	
									$X^2_2=1.9$	n.s.
T4-3										
Observed	6	9	2	2	2			21	1.29	1.61
Expected	5.8	7.4		7.8				21	1.29	
									$X^2_2=0.7$	n.s.
Total										
Observed	10	15	5	7	4	1		42	1.59	1.95
Expected	8.6	13.6	10.9		8.6			42	1.59	
									$X^2_2=4.6$	n.s.

(iii) REDSHANK

The dispersion of Redshank nests did not significantly deviate from a Poisson distribution in any of the vegetation type groupings in 1976 and 1977 (table 43). However, in 1976, the coefficients of variation significantly differed from unity in T4-T3, and for the total data, indicating that Redshank nests were clumped (table 44).

Table 44. Coefficients of variation (CV), indices of dispersion (I), probability levels of I, and degrees of freedom (df) of Redshank nest dispersion in vegetation types T8-6, T4-3, and all vegetation types on Rockcliffe Marsh, in 1976 and 1977.

	CV	I	df	P
1976				
T8-T6	1.39	20.8	15	n.s.
T4-T3	1.75	48.9	28	<0.05
Total	1.58	69.6	44	<0.01
1977				
T8-T6	1.15	23.0	20	n.s.
T4-T3	1.25	24.9	20	n.s.
Total	1.23	50.2	41	n.s.

(iv) DISCUSSION

The total data for Redshank and Lapwing nest distribution in 1976 indicated that the nests were significantly clumped, although no significant differences were obtained for the total nest data for these species in 1977. Both the Redshank and the Lapwing are known to be sub-colonial (e.g. Rinkel 1940, Thomas 1942, Williamson 1951). The breeding dispersion of Lapwings had features of coloniality and territoriality (Nethersole-Thompson 1951, Wynne-Edwards 1962), although it has been suggested that the apparent coloniality may be due to preferences for a particular habitat (Lack 1966). However, the social organisation involves more than a mere aggregation of nests in favoured sites, because although territoriality persists within the "colony", territory size is greatly restricted and there is presumably much overlap of individual territories. Further, the colony as a whole is usually involved in mutual anti-predatory behaviour, so that the colony, rather than individual territories, is protected. Spacing out is of survival value (Croze 1970, Goransson et al. 1976, Tinbergen et al. 1967), especially if the nest, eggs and chicks are cryptic (Taylor 1976), but the effects of aggregation may also be beneficial, if as in the cases of the Fieldfare and Black-headed Gull, and presumably in the Lapwing, parental attacks on some predators are more effective en masse (Anderson & Wiklund 1978, Kruuk 1964). The Lapwing's social organisation appears, at times, to incorporate both of these advantages, nesting at a density low enough to reduce predation pressure, especially from ground predators, and high enough to facilitate social "mobbing" of predators. The social reality of these colonies, despite their diffuse nature, in contrast for example to some Larid colonies, was suggested by Kraak *et al*. (1940), who found a tendency for first year birds to breed on the edge of colonies. A similar tendency for young and low quality individuals to nest on the edge of colonies was observed by Coulson (1968) in the Kittiwake.

The aggregated breeding dispersion of the Redshank may be possible because of its apparent lack of territoriality (Hale 1956), or the flexibility of its territorial system (Grosskopf 1963), whether one accepts that its display flight is principally involved in pair-formation and courtship (Hale 1956) or territoriality (Bocker 1958, Rueppel 1962).

The territorial behaviour of Oystercatchers tends to distribute their nests uniformly, although on Rockcliffe Marsh, the flexibility of the territorial system, for example the use of separate feeding and breeding territories on vegetation type T3, may have obscured the tendency to a uniform distribution. Oystercatcher nest distribution did not significantly differ from a Poisson distribution in any vegetation type, in any year.

SECTION 9

ECOLOGICAL INTERACTIONS BETWEEN WADING BIRDS AND CATTLE

Food availability

Between 34% and 73% of the total recorded invertebrates in different vegetation types on Rockcliffe Marsh were dung-associated, and comprised 49% to 81% of the total invertebrate biomass (Section 5). It was therefore necessary to identify the main prey species of the breeding waders and their chicks, to assess if their diets corresponded to the relative availability of potential prey in the habitat.

Casual observations of adult waders probing cowpats, and the discovery of chicks with dung-coated bills indicated that cowpats provided a readily available source of invertebrate prey, which was accessible to both long- and short-billed wader species. Foraging in cowpats, usually for Coleoptera and the larvae of Diptera, by, for example, Rooks, Starlings, Meadowlarks and Killdeer Plovers, has been frequently observed (e.g. Anderson & Merritt 1977, Hammer 1941, Laurence 1954, Valiela 1969b). It was not usually possible to determine from observations alone what particular prey were featuring in the diets of the waders, so information was obtained from pellets, faeces and gizzard contents.

Many waders egest pellets containing the indigestible remains of their prey (e.g. Goss-Custard & Jones 1976, Swennen 1971), and these were occasionally found in the area from which a feeding bird has been flushed. It was possible to distinguish the pellets of Redshank and Oystercatcher on the basis of size (no Lapwing pellets were found); Redshank pellets were approximately 20 x 10mm, whilst those of Oystercatcher were about 30 x 15mm. Most of the pellets consisted largely of black chitinous remains, although some Oystercatcher pellets were pale because the chitinous remains were embedded in a sandy matrix. Faeces were collected whilst a bird was being handled, and gizzards were excised from recently-killed birds that had died of natural causes (e.g. trampling, predation).

It was only intended to obtain information on the major components of the diet. The rate of digestion of different prey species vary, and the incidence of soft-bodied prey may be underestimated (Goss-Custard 1973), but these potential biases were not considered to significantly affect the general conclusions concerning the proportion of dung-associated species in the diet. However, adult Coleoptera were likely to be over-estimated, due to the extensive remains of their chitinous exoskeleton.

Each pellet, faecal and gizzard sample was examined under a binocular microscope, and fragments which occur only once or twice in the prey (e.g. head capsule, elytra) were counted. Particularly distinctive features, which were considered diagnostic of some families, included the head capsules of Curculionidae, wing venation of some Diptera and Hymenoptera, spiracles of Tipulidae larvae, legs of Carabidae and Scarabaeidae, and elytra of some Hydrophilidae. Searching for chaetae failed to provide any evidence that annelids, which occurred at very low densities on Rockcliffe Marsh (Section 5) featured in the diets of waders, although they are known to be important prey in some areas (e.g. Hogstedt 1974, Safriel 1967). The identifiable prey of Lapwing, Oystercatcher and Redshank are summarised in table 45, with some information from published sources. Dung-associated invertebrates have been previously recorded in the diet of all three species.

In all the samples, there were traces of sand and vegetable matter. All the gizzard samples, except those of very young (less than three days old) chicks, contained gastroliths, apparently of quartz. This hard, brittle mineral is also preferred by Red Grouse as an aid to digestion (Selden & Smith 1978). Fragments of quartz presumably originated from the gravel areas and the banks of the River Esk. Gastroliths were occasionally present in pellets. All the samples contained minute, unidentifiable, chitinous remains, including the faeces of Redshank, in the winter samples of which Goss-Custard & Jones (1976) detected no hard fragments.

Table 45. Recorded invertebrate prey of Lapwing, Oystercatcher and Redshank, with particular reference to the insect prey

	LAPWING									OYSTERCATCHER							REDSHANK						
	A	B	D	E	H	K	M	N	O	E	F	G	I	L	N	O	A	C	D	E	J	N	O
Annelida		x	x	x	x		x	x		x	x	x	x	x	x		x		x	x		x	
Mollusca	x		x	x	x			x		x		x		x	x	x		x	x	x		x	x
Crustacea	x							x		x		x			x				x	x		x	x
Myriapoda								x															
Arachnida	x					x		x	x							x	x			x		x	x
Insecta	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Odonata																						x	
Orthoptera	x			x																			
Dermaptera								x														x	
Hemiptera								x														x	
Lepidoptera	x	x			x		x	x						x	x								
Trichoptera								x			x												
Hymenoptera								x														x	
Diptera	x	x		x	x		x	x	x		x		x	x	x	x		x			x	x	x
*Tipulidae				x				x	x		x		x	x	x	x						x	x
*Chironomidae																					x		
*Stratiomyidae									x							x							x
Rhagionidae																		x					
*Syrphidae								x															
*Calliphoridae							x																
*Anthomyiidae								x															
*Calyptrates									x							x							x
Coleoptera	x	x		x	x	x	x	x	x						x	x		x		x		x	x
Carabidae	x			x		x		x	x							x							x
Dytiscidae				x																		x	
*Hydrophilidae									x							x							x
Silphidae																						x	
*Staphylinidae						x		x	x														x
*Scarabaeidae	x					x		x	x							x						x	x
Elateridae	x	x						x														x	x
Chrysomelidae																						x	
Curculionidae	x			x		x	x	x	x							x							

* indicates a dung-associated family.

Key to sources:

A	Bent (1927)	I	Heppleston (1972)
B	Brown (1936)	J	Larsson (1976)
C	Campbell (1946)	K	Murton (1971)
D	Collinge (1924-27)	L	Safriel (1967)
E	Dement'ev *et al.* (1969)	M	Vepsalainen (1968)
F	Dewar (1920)	N	Witherby *et al.* (1940)
G	Dircksen (1932)	O	This study
H	Ennion (1949)		

Small hydrophilid beetles, carabids, tipulids (adults and larvae), small calyptrates and Scathophaga larvae were the main prey items of chicks. In addition, adults took larger carabid and staphylinid beetles, as well as dung-beetles (Aphodius spp.). Although the data derived from pellet, gizzard and faecal analyses may be biased, the available evidence did suggest that dung-associated invertebrates comprised 48-69% of the diet of adult waders (by frequency) and 67-80% of that of the chicks (table 46), which suggested that the chicks may be slightly more dependent on dung as a source of invertebrate prey than their parents. The incidence of dung-associated prey in the diets of wader adults and chicks reflected their availability in the habitat. Oystercatchers usually feed their chicks on tipulid larvae in inland areas (e.g. Dewar 1920, Heppleston 1972), and seemed to do so on Rockcliffe Marsh, as did terrestrially feeding Oystercatchers on Skokholm (Safriel 1967). On disturbing parental feeding on two occasions, the prey in both cases were found to be Tipula paludosa larvae, and Tipula paludosa larvae were present in the few adult (1) and chick (3) gizzard samples obtained. Cowpats may be of particular importance on this dry, well-drained saltmarsh as refuges for such invertebrates as tipulid larvae, which require a moist environment (Coulson 1962).

Table 46. Frequency of occurrence of adults and larvae of Diptera and Coleoptera, and total invertebrates, and the proportions which were dung-associated, in the diets of adult and chick Lapwing, Oystercatcher and Redshank on Rockcliffe Marsh, 1976-1978, as indicated by faecal (f), pellet (p) and gizzard (g) samples.

Species	LAPWING		OYSTERCATCHER		REDSHANK	
Age	Adult	Chick	Adult	Chick	Adult	Chick
Source of material	2g	23f,4g	3p,1g	19f,3g	5p,1g	13f,1g
Diptera;						
larvae	29	60	11	37	15	26
adults	9	7	1	1	2	0
Coleoptera;						
larvae	8	16	12	3	13	17
adults	23	101	15	14	36	22
Other invertebrates	1	0	7	1	3	0
Total invertebrates	70	184	46	56	69	65
% of invertebrates which were dung-associated;						
Diptera	95	97	100	100	88	100
Coleoptera	39	51	37	41	45	59
Total	69	67	48	80	54	75

The gizzard and faecal samples obtained from very young chicks (less than two days old) did not usually contain any invertebrate remains. The yolk sac was still providing nourishment at this early stage, and no data pertaining to these young chicks have been included in table 46.

The influence of cattle on avian feeding ecology has been previously emphasized by several studies. As Nicholson (1938-39) and Williamson (1951) suggested, the droppings of ungulates provide a source of food for breeding Lapwings and their young. Similarly, the diet of breeding Black-tailed Godwits in Siberian pastures largely consists of predacious and coprophagous insects taken from cowpats (Tolchin & Melnikov 1974). North (1937) suggested that the highest breeding densities of the Crested Wattled Plover were associated with the herds of Somali sheep and cattle whose droppings provided suitable insect prey for the plover. From July to October, the Curlew frequents pastures where its diet is principally composed of dung-beetles probed from cowpats (Hibbert-Ware & Ruttledge 1944). The ontogeny of food preferences has been little studied (Rabinovitch 1968). Presumably food preferences develop on the basis of early feeding experience, so that relevant search-images (Tinbergen 1960), such as that for cowpats, are formed.

Trampling

Trampling was a significant mortality factor of the eggs and chicks of Lapwing, Redshank and Oystercatcher (Section 8), accounting for 15-17% of eggs laid in 1976 and 26-30% in 1977. The higher losses in 1977 were associated with the later breeding season of 1977, which resulted in a higher proportion of the eggs and chicks of each species being exposed to trampling in 1977 than 1976, after the introduction of the cattle during the

Figure 26. Relationship between percentage mortality of Lapwing eggs due to trampling and mean fresh cowpat density ha^{-1} in each vegetation type on Rockcliffe Marsh in 1976 and 1977.

Regression equations

1976
$y = 0.37x - 7.68$
S.E. of slope $= 0.10$
$r = 0.91$
df $= 4$
$p < 0.05$

1977
$y = 0.70x - 19.48$
S.E. of slope $= 0.15$
$r = 0.89$
df $= 4$
$p < 0.05$

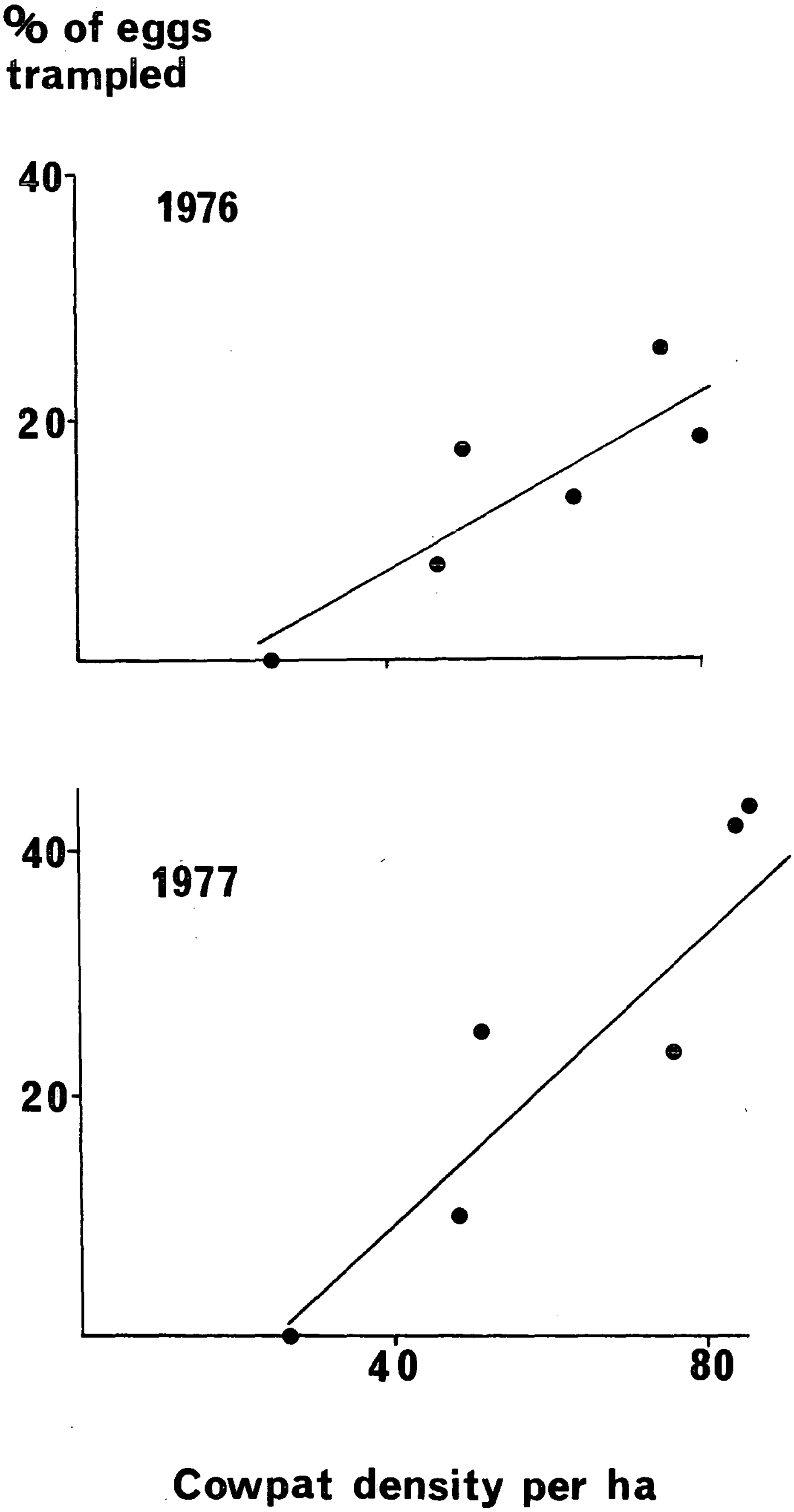

% of eggs trampled
40
1976
20
40
1977
20
40
80
Cowpat density per ha

Figure 27. Relationship between percentage mortality of Oystercatcher and Redshank eggs due to trampling and mean fresh cowpat density ha^{-1} in each vegetation type on Rockcliffe Marsh in 1976 and 1977.

Regression equations

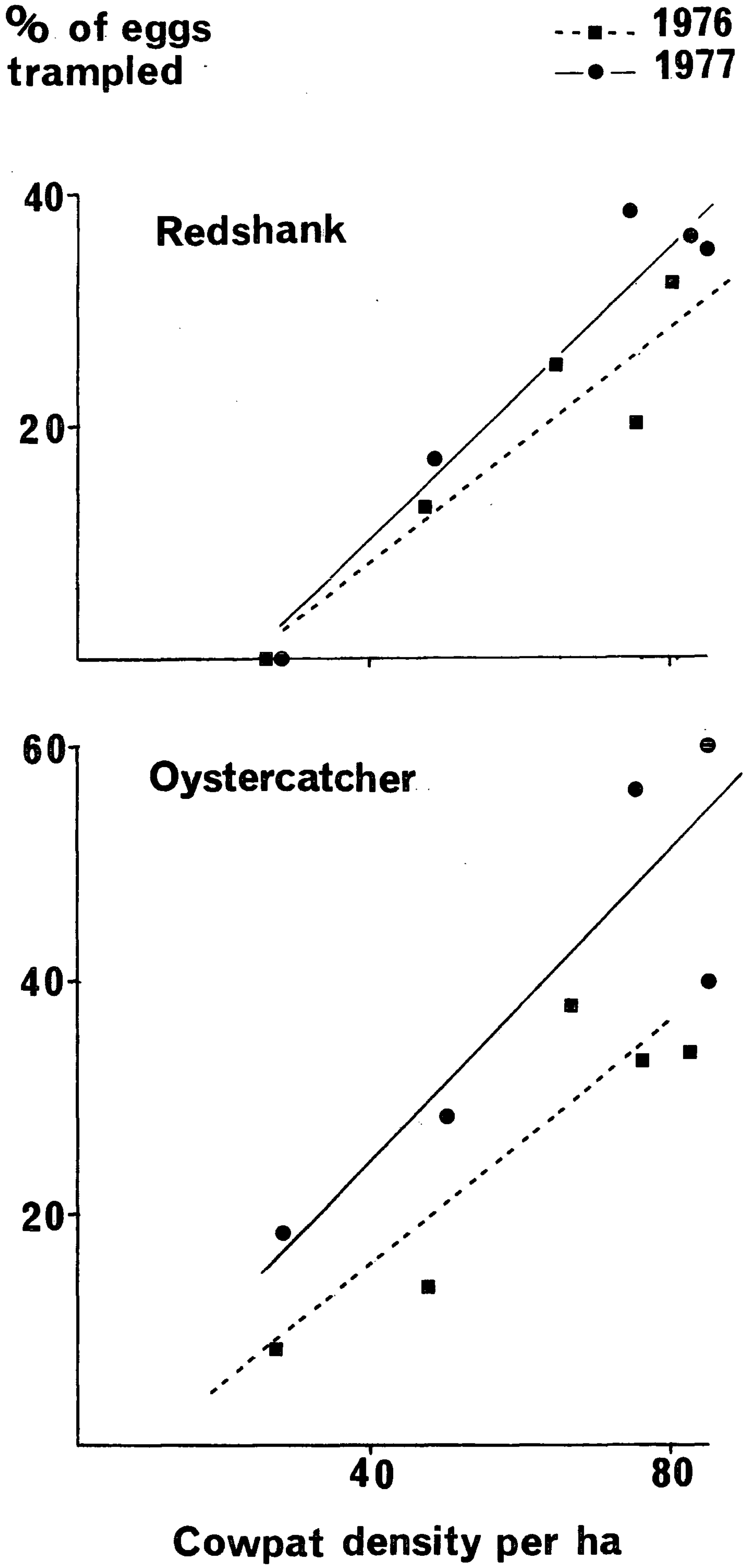
Redshank 1976
$y = 0.51x - 12.49$
S.E. of slope $= 0.11$
$r = 0.94$
$df = 3$
$p < 0.02$

1977
$y = 0.63x - 15.17$
S.E. of slope $= 0.08$
$df = 3$
$p < 0.01$

Oystercatcher

1976
$y = 0.52x - 4.90$
S.E. of slope $= 0.17$
$r = 0.88$
$df = 3$
$p < 0.05$

1977
$y = 0.67x - 6.04$
S.E. of slope $= 0.21$
$r = 0.88$
$df = 3$
$p < 0.05$


% of eggs trampled
- -■- - 1976
—●— 1977
Redshank
40
20
Oystercatcher
60
40
20
40
80
Cowpat density per ha

first week of May in both years. A higher mortality of Oystercatcher eggs than of Lapwing and Redshank eggs was expected, since the laying season of the Oystercatcher was later than that of those two species in both years. No such difference was apparent, perhaps because a higher proportion of Oystercatcher nests (approximately 35%, table 57) were on the new marsh (T3), where cowpat density was low, than were Lapwing nests (approximately 5%, table 59) and Redshank nests (approximately 15%, table 55).

For each species, the relative incidence of trampling in each vegetation type was significantly and positively correlated with fresh cowpat density per ha in both 1976 and 1977 (figures 26 and 27). This provided corroboration that cowpat density was a reliable index of cattle activity across the marsh. For each species, the slopes of the relationship between percentage egg mortality and fresh cowpat density per ha, in each vegetation type, in 1976 and 1977, did not significantly differ (Lapwing, t = 1.8, df = 10, n.s.; Oystercatcher, t = 0.6, df = 8, n.s.; Redshank, t = 0.9, df = 8, n.s.), and the data for both years were combined (table 47).

Table 47. Slopes (m), standard errors of slopes (S.E. of m), intercepts (I) and correlation coefficients (r) of the relationship between fresh cowpat density ha^{-1} and the percentage egg mortality of Lapwing, Oystercatcher and Lapwing, in 1976, 1977 and 1976 & 1977, on Rockcliffe Marsh.

Correlation of fresh cowpat density per ha with the % egg mortality of;		Slope (m)	S.E. of m	I	r	df	p
LAPWING	1976	0.37	0.10	- 7.68	0.91	4	<0.05
	1977	0.70	0.15	-19.48	0.89	4	<0.05
	1976 & 1977	0.56	0.12	-14.47	0.83	10	<0.001
OYSTERCATCHER	1976	0.52	0.17	- 4.90	0.88	3	<0.05
	1977	0.67	0.21	- 6.04	0.88	3	<0.05
	1976 & 1977	0.63	0.14	- 7.57	0.85	8	<0.01
REDSHANK	1976	0.51	0.11	-12.49	0.94	3	<0.02
	1977	0.63	0.08	-15.17	0.98	3	<0.01
	1976 & 1977	0.59	0.07	-14.85	0.94	8	<0.001

The proportion of eggs likely to be trampled could be predicted if the fresh cowpat density of an area was known. The relationship for all three species was very similar; the slope of each relationship for combined years only varied from 0.56 to 0.63. For each species, a unit increase in fresh cowpat density ha^{-1} corresponded to an increase in the percentage of eggs trampled of approximately 0.6%, at cowpat densities in excess of $25ha^{-1}$ (intercept on the abscissa) in the Lapwing, $10ha^{-1}$ in the Oystercatcher, and $25ha^{-1}$ in the Redshank (figures 26 & 27).

Additional damage by cattle included predation of eggs. This was only directly observed on two occasions, when cows were licking out the contents of Lapwing eggs.

The habit did not appear to be widespread. Wilson (1978) suggested that cattle were eating as well as trampling wader eggs on South Uist. Although sheep may lick, and inadvertently roll an egg out of a nest (Greenhalgh 1969b), they are not known to eat the contents.

Heppleston (1971, 1972) emphasized the extensive egg losses due to cattle at inland sites in Scotland; in grassland 61% of nests were destroyed by trampling, and a further 34% were deserted as a result of non-fatal interference, so that only 5% of nests in grazed fields reached the hatching stage. Desertion of nests could not be definitely attributed to disturbance by cattle in this study. The use of wire frames over nests may minimise damage by cattle (Heppleston 1971). It is evident that the behavioural interactions, such as distraction displays, by waders against cattle or sheep (e.g. Coomber 1978, Penrose & Penrose 1959, Took 1936, pers. obs.) are not very effective.

Cowpat density as a potential proximate factor in nest-site selection

To assess if cowpat density was a potential proximate factor involved in nest-site selection by wading birds, the mean fresh cowpat density ha^{-1} around each nest in a given vegetation type was compared with the mean cowpat density for that vegetation type. If there was no selection on the basis of cowpat density, it was expected that the slope of this relationship would not significantly deviate from unity, as indicated by 95% confidence limits (± 2 S.E.).

For all three species, the slope of the relationship in 1976 did not significantly differ from that in 1977 (Lapwing, t = 1.4, df = 10, n.s., figure 28; Oystercatcher, t = 1.7, df = 8, n.s. figure 29; Redshank, t = 1.1, df = 8, n.s., figure 30), according to the means and standard errors of the slopes. The data for both years were therefore combined. Using these combined data, for all three species the slope of the regression significantly deviated from the expected slope of unity (slope ± S.E.; Lapwing, 0.69 ± 0.07; Oystercatcher, 0.82 ± 0.06; Redshank, 0.82 ± 0.08).

In the Lapwing, the slope of the regression significantly differed from a slope of unity in 1976 (0.59 ± 0.12) and 1977 (0.77 ± 0.04). The fresh cowpat density ha^{-1} around Lapwing nests (table 48) was significantly lower in vegetation type T7 than was expected by chance in 1976, and significantly higher in T3 than was expected by chance in both 1976 and 1977 (table 49). The deviation of the slope from unity therefore occurred in areas of both high and low cowpat density; Lapwings selected to nest in areas of lower than average fresh cowpat density in regions where the mean cowpat density was high (e.g. T7) and in areas of higher than average cowpat density in vegetation types where the mean cowpat density was low (T3).

Figure 28. Relationship between mean fresh cowpat density ha^{-1} around transect samples and Lapwing nest samples, grouped according to vegetation type, on Rockcliffe Marsh in 1976 and 1977. Interrupted line indicates a slope of unity. Uninterrupted line indicates correlation for 1976 & 1977.

Regression equations:

1976 $y = 0.59x + 23.43$
S.E. of slope $= 0.12$
$r = 0.92$
$df = 4$
$p < 0.01$

1977 $y = 0.77x + 14.52$
S.E. of slope $= 0.04$
$r = 0.99$
$df = 4$
$p < 0.001$

1976 & 1977 $y = 0.69x + 18.37$
S.E. of slope $= 0.07$
$r = 0.96$
$df = 10$
$p < 0.001$

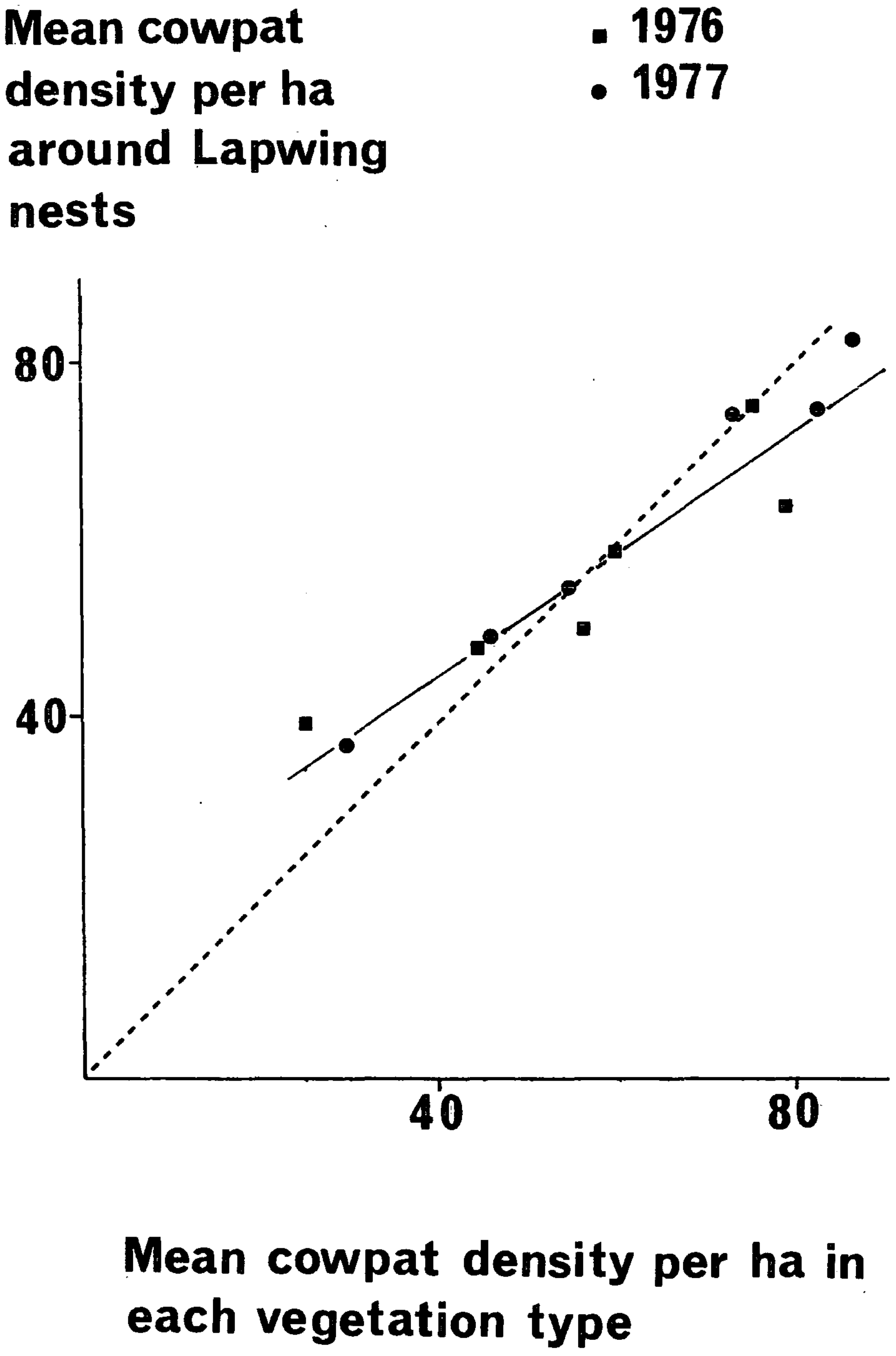

Mean cowpat density per ha around Lapwing nests
■ 1976
● 1977
80
40
40
80
Mean cowpat density per ha in each vegetation type

Figure 29. Relationship between mean fresh cowpat density ha^{-1} around transect samples and Oystercatcher nest samples, grouped according to vegetation type, on Rockcliffe Marsh, in 1976 and 1977. Interrupted line indicates a slope of unity. Uninterrupted line indicates correlation for 1976 & 1977.

Regression equations:

1976
$y = 0.72x + 17.41$
S.E. of slope $= 0.09$
$r = 0.98$
$df = 3$
$p < 0.01$

1977
$y = 0.93x + 2.99$
S.E. of slope $= 0.08$
$r = 0.99$
$df = 3$
$p < 0.01$

1976 and 1977
$y = 0.82x + 10.68$
S.E. of slope $= 0.06$
$r = 0.98$
$df = 8$
$p < 0.001$

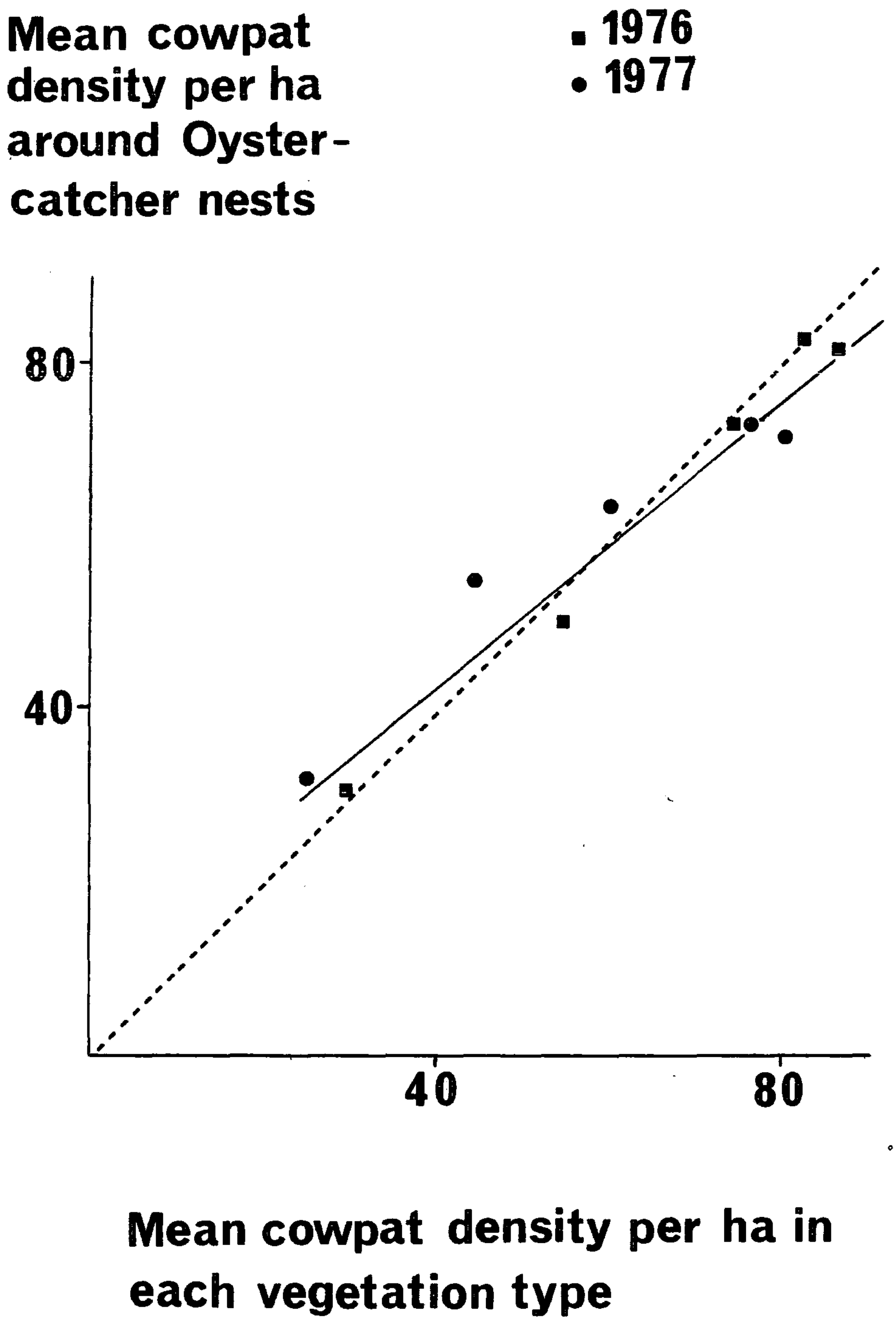

Mean cowpat density per ha around Oyster-catcher nests
■ 1976
● 1977
80
40
40
80
Mean cowpat density per ha in each vegetation type

Figure 30. Relationship between mean fresh cowpat density ha^{-1} around transect samples and Redshank nest samples, grouped according to vegetation type, on Rockcliffe Marsh, in 1976 and 1977. Interrupted line indicates a slope of unity. Uninterrupted line indicates correlation for 1976 & 1977.

Regression equations:

1976
$y = 0.72x + 18.14$
S.E. of slope = 0.16
$r = 0.93$
df = 3
$p < 0.05$

1977
$y = 0.92x + 5.09$
S.E. of slope = 0.10
$r = 0.98$
df = 3
$p < 0.01$

1976 & 1977
$y = 0.82x + 11.88$
S.E. of slope = 0.08
$r = 0.96$
df = 8
$p < 0.001$

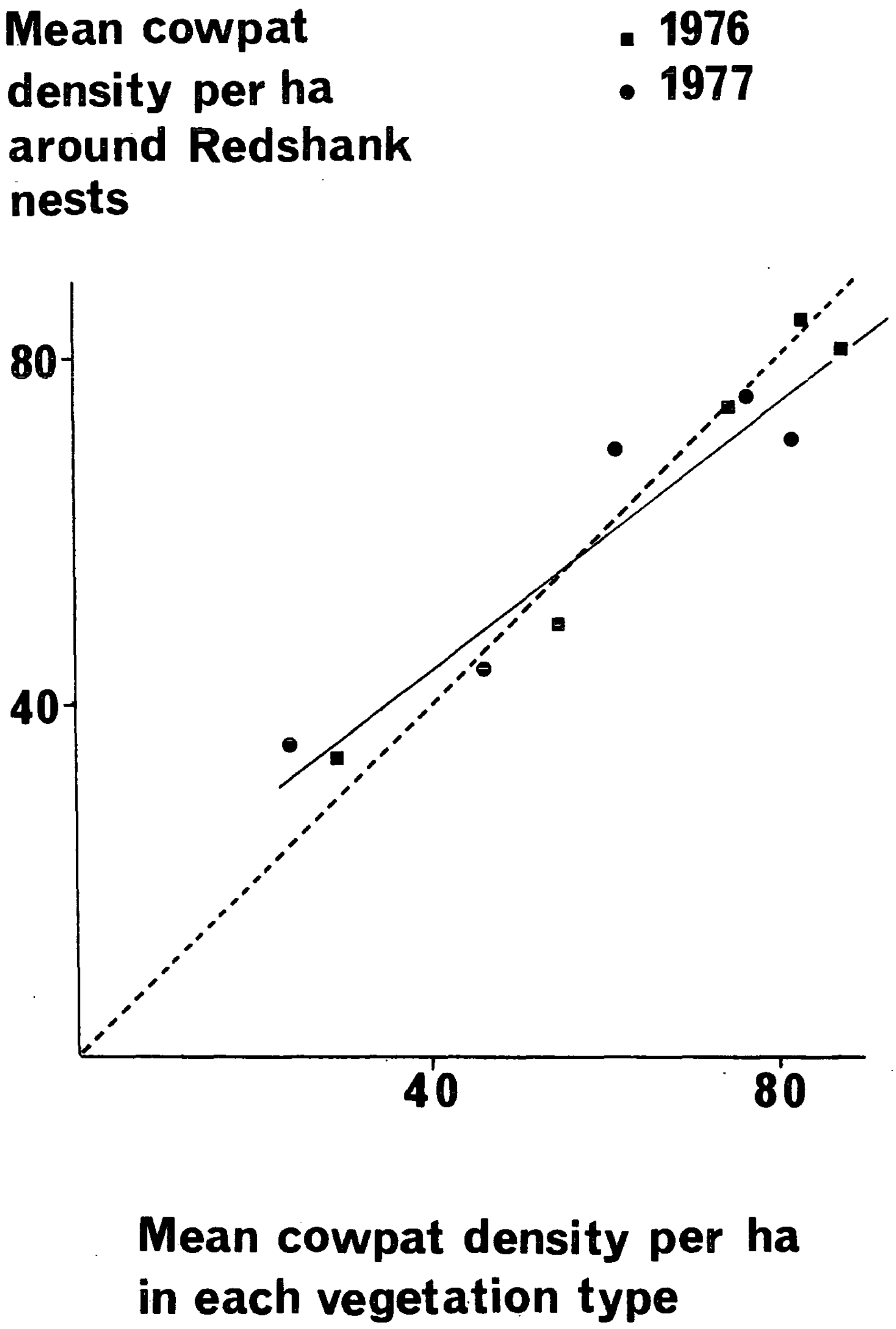

Mean cowpat density per ha around Redshank nests
■ 1976
● 1977
80
40
40
80
Mean cowpat density per ha in each vegetation type

Table 48. Mean fresh cowpat density ha^{-1} around each wader nest and transect point, grouped according to vegetation type, on Rockcliffe Marsh in 1976 and 1977. Two measurements of cowpat density were made at each nest site, (Appendix 15) and the transect data were derived from table 10. The sample size is N.

Cowpat density ha^{-1} around;		VEGETATION TYPES					
		FIELD	T8	T7	T6	T4	T3
1976							
Transect points	Mean	55.4	76.8	81.0	61.3	46.5	25.4
	S.E.	3.0	4.0	3.2	3.5	1.8	2.8
	N.	10	10	20	20	60	20
Lapwing nests	Mean	51.2	76.1	65.2	62.2	48.9	40.0
	S.E.	7.7	1.9	4.4	1.2	1.4	7.6
	N.	6	38	18	30	24	6
Oystercatcher nests	Mean		73.0	72.2	64.2	55.4	32.0
	S.E.		6.1	7.0	2.7	4.1	1.7
	N.		2	6	16	16	30
Redshank nests	Mean		75.9	70.9	71.0	44.7	37.1
	S.E.		5.4	3.5	3.6	0.9	1.9
	N.		6	22	4	40	18
1977							
Transect points	Mean	48.6	81.8	87.2	73.8	54.9	28.8
	S.E.	3.3	3.2	3.3	2.7	1.7	2.1
	N.	10	10	20	20	60	20
Lapwing nests	Mean	50.0	75.4	82.7	74.2	56.0	38.1
	S.E.	4.1	0.6	2.1	0.9	1.2	4.0
	N.	2	46	8	48	14	4
Oystercatcher nests	Mean		83.0	81.2	72.8	50.5	31.1
	S.E.		1.4	1.2	1.0	1.8	1.1
	N.		4	8	18	34	34
Redshank nests	Mean		84.6	81.8	75.0	49.8	33.7
	S.E.		2.9	1.1	1.3	0.9	1.8
	N.		10	16	16	34	8

In the Oystercatcher, the slope of the regression of fresh cowpat density around nests and around transect points in different vegetation types significantly differed from a slope of unity in 1976 (0.72 ± 0.09) but not in 1977 (0.93 ± 0.06). In neither year did the mean fresh cowpat density around nests significantly differ from that expected by chance in each vegetation type (table 49). For this reason, no selection of nest sites on the basis of local cowpat densities was considered to occur in the Oystercatcher, although the slope of the regression for combined years significantly differed from unity (figure 29).

Table 49. Values of Student's "t" and degrees of freedom (df) of paired mean fresh cowpat densities ha^{-1} around the nests of three wader species and around transect points in each vegetation type on Rockcliffe Marsh in 1976 and 1977. Significant values ($p < 0.05$) are indicated by *.

Cowpat density ha^{-1}: transect data compared with;	VEGETATION TYPES					
	FIELD	T8	T7	T6	T4	T3
Lapwing nests						
1976 t	0.5	0.3	2.9*	0.2	1.1	3.2*
df	14	46	36	48	82	24
1977 t	0.3	1.9	1.2	0.1	0.5	2.1*
df	10	54	26	66	72	22
Oystercatcher nests 1976 t		0.5	1.1	0.7	1.9	2.0
df		10	24	34	74	48
1977 t		0.3	1.7	0.3	1.7	1.0
df		12	26	36	92	52
Redshank nests 1976 t		0.1	2.1*	1.8	0.9	3.4*
df		14	40	22	98	36
1977 t		0.6	1.5	0.4	2.6*	1.8
df		18	34	34	92	26

In the Redshank, the slope of the regression of fresh cowpat density around nests and around transect points in different vegetation types did not significantly differ from unity in either 1976 (0.72 ± 0.16) or 1977 (0.92 ± 0.10), although for combined years the slope did significantly deviate from unity (figure 30). The fresh cowpat density ha^{-1} around Redshank nests (table 48) was significantly lower than expected by chance in vegetation type T7 in 1976, and significantly higher than was expected by chance in T4 in 1977 and T3 in 1976 (table 49). The deviation of the slope from unity therefore occurred in areas of both high and low cowpat density; Redshanks selected to nest in areas of lower than average fresh cowpat density where the mean cowpat density was high (T7), and in areas of higher than averate cowpat density in vegetation types where the mean cowpat density was low (T4, T3).

Fresh cowpat density was known to be positively correlated with percentage egg mortality due to trampling (figures 26-28) and also with Diptera and total invertebrate biomass and abundance (Section 6). Two selective pressures may, therefore, be influencing the location of a nest-site with regard to cowpat density; those of food availability and the mortality of eggs due to trampling. The Lapwing and Redshank, in areas of high mean cowpat density, where food availability was high, minimised losses due to trampling by nesting in a locality with a slightly lower than average cowpat density. Conversely,

Figure 31. Relationship between mean fresh cowpat density ha^{-1} and Lapwing nest density per 0.75ha in different vegetation types on Rockcliffe Marsh in 1976 and 1977. Lapwing nest density derived from table 39. Regression line indicates relationship for 1976 & 1977.

Regression equations:

1976 $y = 0.04x - 1.13$
S.E. of slope $= 0.01$
$r = 0.86$
$df = 4$
$p < 0.05$

1977 $y = 0.03x - 0.75$
S.E. of slope $= 0.01$
$r = 0.83$
$df = 4$
$p < 0.05$

1976 & 1977 $y = 0.03x - 0.78$
S.E. of slope $= 0.01$
$r = 0.72$
$df = 10$
$p < 0.01$

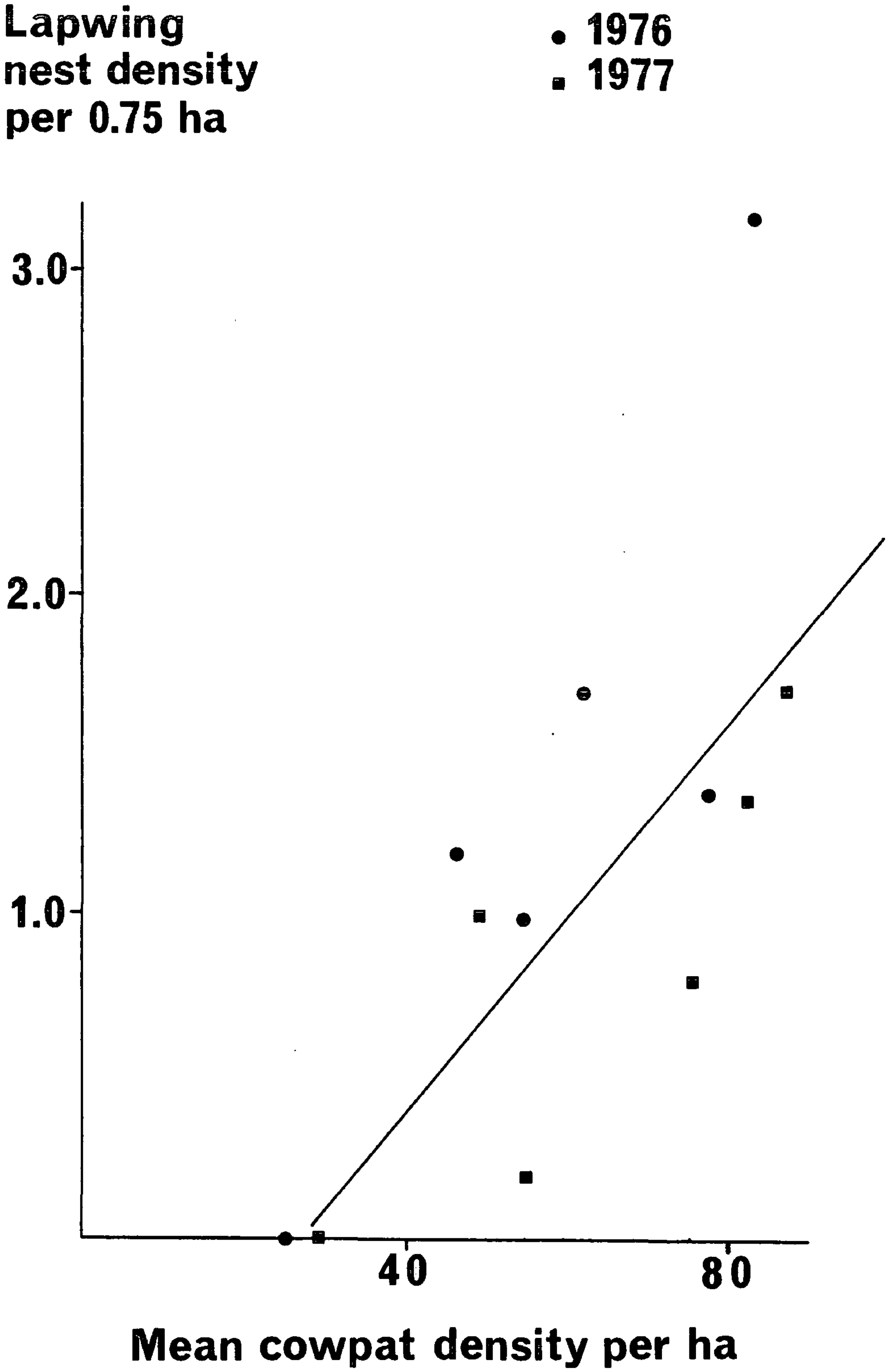

Lapwing nest density per 0.75 ha
● 1976
■ 1977
3.0
2.0
1.0
40
80
Mean cowpat density per ha

Figure 32. Relationship between Lapwing nest density per 0.75 ha and (a) log mean Diptera biomass (mg per trap per 5 days) x 10, and (b) log mean total invertebrate biomass (mg per trap per 5 days) x 10, in each vegetation type on Rockcliffe Marsh in 1976 and 1977. The regression lines for 1976 & 1977 are depicted.

Regression equations:

(a) 1976 $y = 2.90x - 5.65$
S.E. of slope = 0.49
$r = 0.93$
df = 4
$p < 0.05$

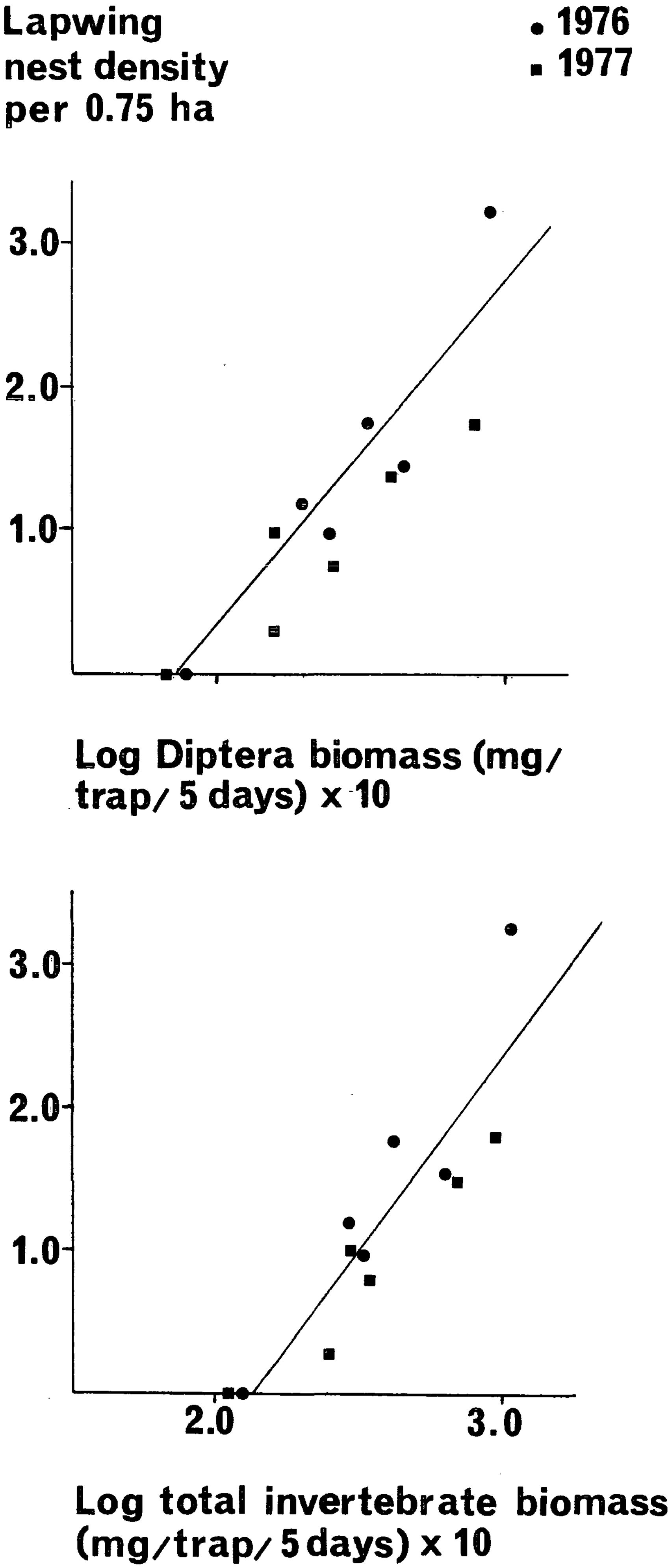
1977 $y = 1.72x - 3.13$
S.E. of slope = 0.36
$r = 0.90$
df = 4
$p < 0.05$

1976 & 1977 $y = 2.56x - 4.91$
$r = 0.87$
df = 10
$p < 0.001$

(b) 1976 $y = 3.15x - 6.61$
S.E. of slope = 0.54
$r = 0.92$
df = 4
$p < 0.06$

1977 $y = 2.10x - 4.52$
S.E. of slope = 0.42
$r = 0.93$
df = 4
$p < 0.05$

1976 & 1977 $y = 2.85x - 6.13$
$r = 0.87$
df = 10
$p < 0.001$


Lapwing
nest density
per 0.75 ha
● 1976
■ 1977
3.0
2.0
1.0
Log Diptera biomass (mg/trap/ 5 days) x 10
3.0
2.0
1.0
2.0
3.0
Log total invertebrate biomass (mg/trap/ 5 days) x 10

in areas of low mean cowpat density, where the incidence of trampling was low, food availability was maximised, both for the adults and the chicks, by nesting where the cowpat density was higher than average. The motility of the wader broods (Section 8), which usually remained within 100m of the nest for at least the first 10 days, indicated that the locally available food supply was adequate, and that long journeys to suitable feeding areas, as described for example by Klomp (1953), were not necessary. Cowpats are not only an index of food availability, they are also sources of invertebrate prey for the wading birds. Nutrition may be the most critical niche dimension for birds, and patch selection (Baker 1977) of higher than average cowpat densities presumably enabled the wading birds to obtain a higher proportion of food items within the nest vicinity than their occurrence over the whole vegetation type would suggest was available.

Since a proportion of the nests of each species were selected prior to the introduction of cattle, selection of the site may have involved old, rather than new, cowpat density. The mean old cowpat density ha^{-1} around these nests of each species did not significantly differ from that around the transect points in each vegetation type in either 1976 or 1977 (Appendix 14), but the data were scanty. However, the linear correlation between old and new cowpat density was very high in both years (Section 6), and for those nests commenced prior to the introduction of the cattle, old cowpat density was a reliable index of subsequent fresh cowpat density.

Lapwing nest density was positively correlated with fresh cowpat density in both 1976 and 1977 (figure 31). There was no significant difference between the slopes of this relationship in different years, ($t = 1.2$, df = 10, n.s.), and the data for both years were combined ($r = 0.72$, df = 10, $p < 0.01$). Fresh cowpat density was positively correlated with the abundance and biomass of Diptera and total invertebrates (table 13), and Lapwing nest density was also positively correlated with the biomass of Diptera and total invertebrates, expressed as the log of the mean biomass multiplied by 10 for each vegetation type (figure 32), in both 1976 and 1977. The slopes of the relationship between Lapwing nest density and log Diptera biomass x 10 did not significantly differ between years ($t = 1.9$, df = 10, n.s.), and neither did that between nest density and log total invertebrate biomass x 10 ($t = 1.6$, df = 10, n.s.). In both years, therefore, Lapwing nest density appeared to be adjusted to the available food supply (ultimate factor) on the basis of cowpat density (proximate factor), which was an index of the potential abundance and biomass of Diptera and total invertebrates. An increase in cowpat density of 20 pats ha^{-1} was associated with a unit increase of Lapwing nest density within 0.75 ha of each nest (figure 31).

Diptera constituted 41% of the adult and 33% of the chick diet of Lapwing, by frequency, and at least 95% of these Diptera were dung-associated (table 46). Of the total prey items, 69% of the diet of adults and 67% of that of chicks comprised dung-associated invertebrates. Dung-associated prey were also important in the diets of Oystercatcher and Redshank adults and chicks, but in these species nest density was not correlated with food availability or cowpat density, perhaps because the availability of suitable nest-sites was a more important influence on nest density; Redshanks required tussocks and Oystercatchers required a loose substrate for their nest-site (Section 10). Furthermore, in the Redshank and Oystercatcher, a lower proportion of the adult than the chick diet was composed of dung-associated invertebrates and adults may have fed at some distance from the nest (some Oystercatchers had feeding territories separate from their breeding territories) so that it was not necessary for the area surrounding the nests of these species to provide the adults with adequate food, in contrast to Lapwing adults which appeared to feed exclusively around their nests. A similar relationship between nest density and food availability as observed in the Lapwing occurs in arctic breeding Dunlin. Breeding density and food abundance were positively correlated in those areas where adult feeding occurred on the territory, and the abundance, availability and predictability of the food supply was high (Holmes 1970). There is a correlation of territory size and food availability in many avian species (e.g. Schoener 1968), and Simon (1975) temporarily reduced territory size in the iguanid lizard, <u>Sceloporus jarrovi</u>, by the provision of extra food.

It was not possible to relate absolute changes in the breeding density of the Lapwing to differences in the local availability of food, because Lapwing nest density was measured in terms of the mean number of nests in an area of 0.75 ha around each nest in each vegetation type (table 39). This was, therefore, an index of density rather than an absolute measure, but was more representative of local differences of breeding density, since the measurement was based on the density of nests around each nest, which maximised the sample size, rather than a count per unit area which may have been biased by arbitrary divisions between vegetation types and differences in the area which each vegetation type occupied.

Nest-sites

Many waders make use of dry cow dung as a nest site (Hall 1958, Pitman 1965, Spencer 1953, Wilson 1978), either because it is friable and easy to scrape, or, as Cott (1940) suggested for the Lapwing, it provides better camouflage for the eggs than does a grass sward. Stubbs (1907), who commented on the resemblance of downy Lapwing chicks to the colour of cowdung, implied that this camouflage may extend to the chick as well as the egg stage.

If cowpats were not being selected as nest-sites, it would be expected that their incidence as nest-sites would not markedly deviate from the observed occurrence of cowpats. The area of a cowpat varies from 0.04 to $0.06m^2$ (Castle & MacDaid 1972, Johnstone-Wallace & Kennedy 1944). Only old cowpats were used as nest sites, and the maximum number recorded per hectare was 85 (table 12). Using this maximum figure, an area of $3\text{-}5m^2$ ha^{-1} would be covered by old cowpats, or less than 0.001% of the available ground.

It was likely that Lapwings and Oystercatchers selected old cowpats as suitable nesting sites (table 50), since their total percentage occurrence as nest-sites exceeded the maximum recorded percentage availability of old cowpats by a factor of 20,000 in the Lapwing and 13,000 in the Oystercatcher. Although the remaining species used cowpats as nest-sites, the data for Ringed Plover (16 nests) and Dunlin (9 nests) were comparatively scanty, and the three nest-sites and one scrape of the Redshank on cowpats may have been selected on the basis of the surrounding tall vegetation rather than the cowpat *per se*. The nests of Dunlin and Redshank which were on old cowpats were all encircled by lush vegetation, due to the rejection of fouled herbage by cattle (Castle & MacDaid 1972). This type of enclosed nest-site was favoured by these two species. Of 87 Redshank nests, 86% were canopied by vegetation and 60% of Dunlin nests were fully covered. However, not all old cowpats were surrounded by lush vegetation; some had not been deposited long enough for sufficient growth to have occurred. The single Ringed

Table 50. The number of nests and scrapes of Lapwing, Oystercatcher, Redshank, Dunlin and Ringed Plover, which were on cowpats on Rockcliffe Marsh in 1976 and 1977.

	No.of nests/scrapes			No. and % of nests/scrapes on cowpats			
	1976	1977	1976 & 1977	1976	1977	1976 & 1977	% Total
Lapwing							
nests	62	62	124	13	12	25	20
scrapes	15	19	34	2	2	4	12
Oystercatcher							
nests	38	52	90	5	7	12	13
scrapes	14	19	33	1	2	3	9
Redshank							
nests	45	42	87	3	0	3	3
scrapes	19	17	36	1	0	1	3
Ringed Plover							
nests	10	6	16	0	1	1	6
scrapes	4	3	7	0	0	0	0
Dunlin							
nests	3	6	9	0	1	1	11
scrapes	0	1	1	0	0	0	0

Plover nest on a cowpat was in vegetation type T4, successionally the most mature type in which this species nested, and an area in which there was very little bare ground available for scraping. The mechanical ease of scraping dry, old cowpats was considered to be the main factor involved in their use as nest-sites by several wader species, and cryptic coloration of the eggs and newly-hatched young may also have been important to the Lapwing.

SECTION 10

HABITAT AND NEST-SITE SELECTION BY WADING BIRDS (LAPWING, OYSTERCATCHER, REDSHANK, DUNLIN AND RINGED PLOVER)

Many authors have attempted to determine the factors involved in habitat selection by describing the apparent preferences of a species for certain ranges of habitat variables (e.g. Asbirk & Dybbro 1978, Brown & Goertz 1978, Donaldson & Bergerud 1974, Dunker 1974). It is, however, not sufficient to merely describe these apparent preferences. It is necessary to relate them to the availability of the whole range of each habitat variable in a given location. If the relative frequency of occurrence of a species in relation to a habitat variable does not significantly deviate from the observed relative frequency of that variable in the habitat, then selection is not occurring.

Comparisons of the observed frequency distribution of a species in various habitats and the distribution of random samples, or the relative availability of habitats, have been made by, for example, Heppleston (1971), White & James (1978) and Loman (1979) to elucidate the selection process. Jackson & Burchfield (1975) compared the characteristics of bridges under which Barn Swallows nested, and those under which they did not nest. Similarly, Reichert (1976) delineated the process of web-site selection by the desert spider, Agelenopsis aperta, and used discriminant function analysis to compare web and non-web sites. This method of comparing sites at which a structure (web or nest) is absent or present may be particularly valuable, since it maximises potential differences between the two categorisations, and it is possible to estimate the extent to which they are dissimilar.

Multivariate techniques permit the simultaneous mathematical combination and analysis of several variables; the formation of a prediction equation, with an assessment of its accuracy; and an evaluation of the relative contribution of a specific variable, or set of variables, to the equation (Nie *et al*. 1975). They are, therefore, particularly suited to the analysis of the response of one or several species to a range of habitat variables, and have, for example, been extensively used in determining the niche segregation of congeners (Gochfeld 1978, James 1971).

Methods

Discriminant function analysis was used to determine if nest and non-nest (random samples) groups could be distinguished, i.e. that nest-site selection was occurring. To distinguish between nest and non-nest samples, a collection of putative discriminating variables was selected that measured habitat characteristics in which the groups were considered to potentially differ.

The methods of measuring habitat variables which were considered of potential importance as proximate habitat or nest-site factors are summarised in Appendix 15. This array of factors was measured around each nest and around each random point to provide two series of nest and non-nest variables which could be compared by discriminant function analysis. In 1976 and 1977, random samples were obtained by walking along 8 transects, approximately parallel to the sea wall, at intervals of about 250m. The non-nest samples were selected at every 250th pace taken along each transect. One hundred samples were obtained in each year. Vegetation types T1 and T2 were not sampled in either year, because they were inundated daily and no birds nested in these areas.

There were no significant differences between the relative frequency of random samples in each vegetation type in different years (X^2_3 = 1.6, n.s., in which the groups were Field-T7, T6-5, T4, and T3 and Gravel), and neither distribution differed markedly from the percentage availability of each vegetation type, as determined from the vegetation map, figure 4 (table 51).

Table 51. The relative frequency of occurrence of 100 random samples in different vegetation types in 1976 and 1977, and the percentage availability of each vegetation type, which was the same in both 1976 and 1977, on Rockcliffe Marsh.

	VEGETATION TYPES								
	FIELD	T8	T7	T6	T5	T4	T3	GRAVEL	Total
Random samples:									
1976	1	1	5	7	2	51	32	1	100
1977	1	2	8	10	2	47	29	1	100
% availability	2	3	6	12	3	43	30	1	100%

The correlation matrices of a selection of the habitat variables (Appendix 16) indicated that the random samples obtained in both years were comparable. The significantly correlated variables of 1976 were also significantly correlated in 1977, except for debris abundance (DEB), which varied annually according to tidal inundation and deposition of debris. More debris was deposited near the sea wall in 1976 than 1977, hence the additional correlations of debris abundance with PLE, TU and TUHT (see Appendix 15 for symbols for each variable) in 1976, the values of which all increased towards the sea wall. Similar correlations also obtained in 1976 and 1977 between vegetation types and habitat variables (Appendix 17). Therefore the random samples were representative of the relative occurrence of each habitat variable across the marsh, and were consistent between years, with the exception of debris abundance (DEB), noted above. In the discriminant function analysis, interdependence or covariation of the variables was automatically taken into account.

Rao's V, a generalized distance measure along discriminant function axes in geometrical space, was used as the stepwise criterion. The variables were sequentially selected to maximise Rao's V, until the addition to Rao's V became insignificant; the change in V has a chi-square distribution with 1 df. On this basis, all the discriminating variables selected in each of the subsequent analyses were highly significant ($p < 0.01$).

The optimal combination of the least number of significant variables which achieved maximum discrimination was used, since habitat selection was considered to be mediated by only a few proximate factors. Although it did not necessarily follow that the selected discriminating variables were the proximate factors, or indeed the only proximate factors, involved, they did provide the most parsimonious explanation of the discrimination between nest and non-nest samples. The degree of this discrimination corresponded to the degree of habitat selection exhibited by the species concerned, assuming that no important proximate factors had inadvertantly been omitted from consideration.

The discriminating power of the function was inversely related to the value of Wilk's lambda, which the programme transformed into a chi-square statistic. The group centroids were the mean discriminant scores for each group along a function, and the mid-point between these values represented the borderline discriminant score for nests and non-nests. Each case was classified as a nest or non-nest on the basis of its discriminant score. The classification routine therefore identified each case into a group, and the percentage of cases correctly classified indicated the degree of discrimination achieved. The relative contribution of the variables to the discriminant function was indicated by the magnitude (but not the direction) of the standardized discriminant function coefficients. The unstandardized coefficients, together with the constant, were incorporated into a prediction equation.

The data for 1976 and 1977 were combined to increase the sample sizes of nest and non-nest data.

(i) LAPWING

Lapwing nests occurred in vegetation types Field, T8, T7, T6, T4, T3 and Gravel (table 52). The data were combined into the vegetation groups, Field & T8-5 and T4-3 & Gravel, for analysis. There was no significant difference between the distribution of nests in 1976 and 1977 in different vegetation types ($X_1^2 = 0.5$, n.s.). Significantly more nests occurred in the successionally mature vegetation types (Field, T8-6) than was expected by chance in both 1976 ($X_1^2 = 52.4$, $p < 0.001$) and 1977 ($X_1^2 = 51.0$, $p < 0.001$), when the nest data were compared with the distribution of random samples in each vegetation type (table 51).

Table 52. Distribution of Lapwing nests in vegetation types on Rockcliffe Marsh in 1976 and 1977

	VEGETATION	TYPES						
	Gravel	T3	T4	T6	T7	T8	Field	TOTAL
1976	1	3	12	15	4	19	3	62
1977	3	2	7	24	9	23	1	64

The discrimination between nest and non-nest samples was highly significant (final Wilk's lambda = 0.53, $X_3^2 = 209.5$, $p < 0.001$). Those cases with a discriminant score of less than -0.17 were classed as nests, and those above that score as non-nests. Of 126 nests, 120 (95%) were correctly classified (discriminant scores of -0.18 to -1.63), and 84% of non-nests were also correctly classified. The significant discriminating variables were cowpat density and the distances to the nearest Lapwing nest and creek edge. Of these, cowpat density and the distance to the nearest Lapwing nests were approximately twice as important to the discrimination as the remaining variable (standardized discriminant function coefficients in table 53). The incorrectly classified nests were either at a higher than average (for Lapwings) distance to the nearest creek edge (nests 4, 30, 32 and 33, at over 66m) or Lapwing nest (nest 45 at 322m), or in areas of very low cowpat density (nest 15 at 29 cowpats ha^{-1}).

The Lapwing prefers open, flat, treeless areas with sparse or absent ground vegetation, generally in the vicinity of marshy ground or surface water (e.g. Imboden 1970, 1971a, 1971b, Lister 1964, Venables 1937). Marshy areas are, however, avoided for nest building, and sandy soils, as on Rockcliffe Marsh, are preferred since they are well-drained and produce the low vegetation which is attractive to Lapwings (Klomp 1953). Sites on shingle and gravel are occasionally used (Rooke 1950). In 1976 and 1977, a total of 4 nests were situated on gravel on

Rockcliffe Marsh (table 52). One of the three 1977 nests was situated on the exact site that the 1976 nest had been located.

Klomp (1953) found that in ungrazed areas the ultimate vegetation height determined Lapwing breeding; differences in ultimate height were detected by Lapwings on the basis of field colour. Grey-green vegetation, as on Rockcliffe Marsh, was preferred to green vegetation because it was not only a predictor of low ultimate vegetation height, but may also have provided the best camouflage for the eggs (Klomp 1953).

Short vegetation is conducive to food location by Lapwings, since epigeic prey predominate in the diet. The mobility of both adults and chicks may be impeded by tall vegetation, since the locomotion of the Lapwing is adapted to low vegetation; whilst walking or running, the Lapwing does not raise its legs very high, and its toes are hardly retracted, so that they may get entangled in tall vegetation (Klomp 1953).

Botanical composition did not influence Lapwing nest-site selection on Rockcliffe Marsh. Klomp (1953) found no influence of botanical composition on Lapwing breeding density in the Netherlands, although Nicholson (1938-39), Squires (1976) and Taylor (1974) found a correlation with Juncus spp. cover. This, and other relatively tall, unpalatable (to cattle) plants, may provide cover for nests and chicks in an otherwise closely-cropped pasture.

Table 53. Summary table of discriminant function analysis of Lapwing nest and non-nest samples for 1976 and 1977 on Rockcliffe Marsh.

Step No.	Variable entered*	Wilk's lambda	Change in Rao's V	Discriminant function coefficients; Standardized	Unstandardized
1	Lapwing nest	0.68	149.8	0.627	0.006
2	Cowpat density	0.59	77.0	-0.531	-0.026
3	Creek edge	0.53	53.3	0.330	0.012
				CONSTANT:	-0.031

Prediction results

Actual group	No. of cases	Predicted group membership; Non-nests	Nests
Non-nests	200	168	32
% classified		84	16
Nests	126	6	120
% classified		5	95

Percentage of grouped cases correctly classified: 88%

Centroids of groups in reduced space

	Function 1
Non-nests	0.54
Nests	-0.88

Mean, standard deviation (S.D.) and sample size (N.) of each significant discriminating variable in the nest and non-nest samples

	Non-nests			Nests		
Variable	Mean	S.D.	N.	Mean	S.D.	N.
Lapwing nest	175.1	109.7	200	49.5	40.6	126
Cowpat density	46.1	18.9	200	67.6	16.5	126
Creek edge	37.7	28.6	200	21.6	19.6	126

* Lapwing nest = distance to nearest Lapwing nest (m)
Cowpat density = cowpat density ha^{-1}
Creek edge = distance to nearest creek edge (m)

The presence of other Lapwings was a proximate factor involved in nest-site selection on Rockcliffe Marsh. The distances to the nearest Lapwing and Redshank nests from random points were highly correlated ($r = 0.63$, $df = 198$, $p < 0.001$). However, the variable, distance to nearest Lapwing nest, was preferentially selected in the analysis because it had a much greater F value ($F_{1,324} = 146.1$) than that of the distance to the nearest Redshank nest ($F_{1,324} = 101.4$). The variation due to the former variable largely explained that due to the latter variable in the analysis of Lapwing nest and non-nest data. The significance of sociality in the Lapwing has been discussed in Section 8, where it was noted that Lapwing nests had a significantly clumped dispersion. Klomp (1953) found no tendency for Lapwings to be intra-specifically aggregated, but Taylor (1974) demonstrated that the presence of Lapwings was a positive proximate factor involved in Lapwing nest-site selection. To determine if there was a selective advantage to Lapwings which nested in the vicinity of other Lapwings, the breeding success of Lapwings nesting less than and greater than 50m from the nearest Lapwing nest in 1976 and 1977 were compared (table 54). Of 77 Lapwing nests less than 50m from the nearest Lapwing nest, breeding success data were available for 68 of them. Breeding success data were available for 46 of the 49 Lapwing nests greater than 50m from the nearest Lapwing nest. Those Lapwing nests less than 50m from the nearest nest of the same species were approximately twice as successful as those nests greater than 50m from the nearest Lapwing nest. This difference was largely due to the higher hatching success of nests in the former category, which was reflected by the lower predation rate of these nests, especially in the egg stage. Thus, the presence of other breeding Lapwings was a proximate factor which ultimately reduced the predation rate of Lapwing eggs and chicks; mobbing of potential predators by Lapwings was presumably more effective when several pairs of Lapwings were involved in the attack than when one or a few pairs were involved.

<u>Table 54.</u> Breeding statistics of Lapwings nesting less than 50m from the nearest Lapwing nest (A) and greater than 50m from the nearest Lapwing nest (B), on Rockcliffe Marsh in 1976 and 1977.

	A	B
No. nests	68	46
No. eggs	231	147
No. hatch	136	51
No. fledge	46	16
% hatch	59	35
% fledge	34	31
% breeding success	20	11
Mean no./fledged/nest	0.7	0.3
No. of eggs predated	44	58
No. of chicks predated	68	34
% of eggs predated	19	39
% of chicks predated	50	67

The inter-relationships of Lapwings and cattle have been well documented. Nicholson (1938-39) considered that large herbivores could exert important effects on Lapwing distribution by grazing, disturbance of nesting and dung-deposition, which would provide suitable invertebrate prey and potential nest-sites. Klomp (1953) compared the effects of strewn cowdung and the application of sodium chlorate (a graminicide), which produced areas of equal attraction to Lapwings with regard to colour. The dung-treated area supported 8 pairs of Lapwings, but the chlorate treated site had only one pair. Klomp concluded that the unevenness due to dung application rendered an area more attractive to Lapwings. However, differences in food availability may also have been involved. Taylor (1974) and Squires (1976) observed a preference by Lapwings for rough terrain. On Rockcliffe Marsh, terrain evenness was positively correlated with cowpat density in 1976 and 1977 (Appendix 16), but the unevenness was a feature of the terrain, rather than due to the presence of cowpats, as it was in Klomp's experiment. The discriminant function analysis indicated that the discrimination of nest and non-nest samples due to terrain evenness was largely explained by that due to cowpat density. Robson (1974) observed that Lapwings bred where manure had been spread, and Klomp (1951) suggested that "chemical manure" (presumably manufactured fertilizer) could be of use in the management of Lapwing habitats. This circumstantial evidence would indicate that the influence of dung or fertilizer on the invertebrate fauna is of importance, rather than the presence of the dung, per se. On Rockcliffe Marsh, Lapwing nest density was positively correlated with the biomass of Diptera and total invertebrates (Section 9, figure 32). Taylor (1974), using linear multiple regression, found that Lapwing breeding density was positively correlated with the abundance of surface invertebrates in upland pastures. Klomp (1953), however, found no such correlation, but his population occupied a highly heterogeneous habitat, in contrast to upland pastures (Taylor 1974) and saltmarsh (this study), and some feeding occurred far outside some territories, although in areas of high prey abundance Klomp found that this did not occur. It may be significant that, around London, sewage farms, which combined a "damp environment, abundant food and some freedom from disturbance", supported the highest density of breeding Lapwings in the London area (Homes et al. 1960).

To summarize, Lapwings tended to nest closer to the edges of creeks than was expected by chance, which presumably reduced the risk of flooding, because these sites were slightly elevated (Section 2); in the vicinity of other Lapwings, as an anti-predation strategy; and at a higher than average cowpat density, where food availability was high. The tendency for Lapwings to nest in the successionally mature vegetation types (table 51) was largely due to the selection of areas with a higher than average cowpat density.

(ii) OYSTERCATCHER

Oystercatcher nests occurred in vegetation types T3, T4, T6, T7, T8 and Gravel (table 55). The data were combined into the vegetation groups, Field & T8-5 and T4-3 & Gravel, for analysis. There was no significant difference between the distribution of nests in each vegetation type in 1976 and 1977 ($X^2_1 = 0.1$, n.s.). When compared with the random samples (table 51), the distribution of nests showed no significant difference from that of the random samples in each vegetation type in either 1976 ($X^2_1 = 3.2$, n.s.) or 1977 ($X^2_1 = 0.4$, n.s.).

Table 55. Distribution of Oystercatcher nests in vegetation types on Rockcliffe Marsh in 1976 and 1977.

	VEGETATION TYPES						
	Gravel	T3	T4	T6	T7	T8	Total
1976	3	15	8	8	3	1	38
1977	3	17	17	9	4	2	52

The discrimination between nests and non-nests was highly significant (final Wilk's lambda = 0.45, $X^2_5 = 225.5$, $p \angle 0.001$). Those cases with a discriminant score of less than -0.30 were classed as nests, and those above that score as non-nests. Of 90 Oystercatcher nests, 85 (94%) were classified correctly (discriminant scores of -0.36 to -2.32) and 90% of the non-nests were also assigned to their correct group (table 56). The significant discriminating variables were the distances to the nearest creek and plateau edges and Oystercatcher nest, substrate consistency, and the Gravel vegetation type. Nest numbers 13, 27, 32, 36 and 38 were incorrectly classified because they were located at a higher than average (for Oystercatchers) distance from the nearest creek edge (nest 38 at 69m), Oystercatcher nest (nest 27 at 117m, 32 at 109m, and 36 at 110m) and plateau edge (nest 13 at 483m, 27 at 542m, and 32 at 600m).

On Rockcliffe Marsh, the selection of nesting areas closer to plateau and creek edges than was expected by chance reduced the risk of flooding of Oystercatcher nests because these sites were slightly elevated (Section 2). The preferential location of Oystercatcher nests less than 10m from the nearest creek was also noted by Elliott (1975) and Squires (1976). The choice of a raised area for the nest-site to avoid inundation by high spring tides has been previously documented in both the European Oystercatcher and the congeneric Black Oystercatcher (Haematopus moquini) (Hall 1959, Hausmann & Hausmann 1972).

The ancestral coastal breeding habitat of the Oystercatcher is sand or shingle (Heppleston 1972). Approximately 7% of Oystercatcher nests were in gravel habitats, which comprised less than 1% of the available vegetation types on Rockcliffe Marsh (table 51). Gravel was a significant discriminating variable, indicating the preference for the ancestral habitat. When such sites are

Table 56. Summary table of discriminant function analysis of Oystercatcher nest and non-nest samples for 1976 and 1977 on Rockcliffe Marsh.

Step No.	Variable entered*	Wilk's lambda	Change in Rao's V	Discriminant function coefficients;	
				Standardized	Unstandardized
1	Creek edge	0.80	70.0	0.453	0.017
2	Oystercatcher nest	0.67	68.5	0.296	0.003
3	Substrate consistency	0.62	38.2	-0.328	-0.656
4	Plateau edge	0.49	90.4	0.545	0.002
5	Gravel	0.45	51.3	-0.290	-1.768
				CONSTANT	0.192

Prediction results

Actual groups	No. of cases	Predicted group membership;	
		Non-nests	Nests
Non-nests	200	179	21
% classified		90	10
Nests	90	5	85
% classified		6	94

Percentage of grouped cases correctly classified: 91%

Centroids of groups in reduced space

	Function 1
Non-nests	0.49
Nests	-1.10

Mean, standard deviation (S.D.) and sample size (N.) of each significant discriminating variable in the nest and non-nest samples

Variable	Non-nests Mean	Non-nests S.D.	Non-nests N.	Nests Mean	Nests S.D.	Nests N.
Creek edge	37.68	28.64	200	11.66	10.32	90
Oystercatcher nest	153.97	101.17	200	62.94	33.20	90
Substrate consistency	0.43	0.50	200	0.78	0.42	90
Plateau edge	330.21	218.17	200	154.42	181.81	90
Gravel	0.01	0.10	200	0.07	0.25	90

* Creek edge = distance to nearest creek edge (m)
Oystercatcher nest = distance to nearest Oystercatcher nest (m)
Substrate consistency = Firm/Loose; 0 = Firm, 1 = Loose
Plateau edge = distance to nearest plateau edge (m)
Gravel = Gravel vegetation type; Gravel = 1, other vegetation

of limited availability, alternative sites, such as grassland, may be used (Wilson 1978), as they are on Rockcliffe Marsh, especially if the soil substrate is loose.

Heppleston (1971, 1972) considered that Oystercatchers selected a loose substrate for their nest-site for three reasons:

(i) eggs were laid where they were most effectively camouflaged;

(ii) the mechanical ease of scraping;

(iii) to avoid cattle and sheep disturbance, since this was more frequent on grassland.

On Rockcliffe Marsh, the "loose" sites included the bare, sandy substrate (47 nests), old cowpats (12 nests), tidal debris (10 nests) and gravel (6 nests). The remaining 15 nests were located on turf with a sandy substrate. The old cowpats and debris (usually dried, matted grass) were bleached, and like the other "loose" sites matched the background colour of the Oystercatcher eggs. These sites therefore provided camouflage and were easy to scrape.

Oystercatchers did not significantly prefer particular vegetation types (table 55), although Gravel was a significant discriminating variable (table 56). Twenty-six (68%) nests in 1976 and 37 (71%) nests in 1977 were in vegetation types T3, T4 and Gravel (table 55). Vegetation types T3 and T4 had the lowest mean cowpat density ha^{-1} (Section 6), and these vegetation types, in addition to Gravel, suffered the least egg and chick mortality due to trampling in both 1976 (0%-13%) and 1977 (14%-21%) in the Oystercatcher (table 29). There was, therefore, circumstantial evidence for Heppleston's (1972) supposition that Oystercatchers tended to avoid cattle disturbance.

Oystercatcher nests occurred in closer proximity to other Oystercatcher nests than was expected by chance (table 56). This may have been partly due to the limited availability of suitable nest-sites, although Oystercatcher nests did not have a clumped distribution (Section 8). However, Oystercatcher nests were not clustered, but tended to be located sequentially along creek and plateau edges, occasionally as little as 5m apart (figure 33). Nethersole-Thompson (1961) reported similar instances where, for example, 7 nests were concentrated along a stretch of river beach 223m long, with two nests only 2m apart. To assess if there was any selective advantage to Oystercatchers nesting in the vicinity of other Oystercatchers, the breeding success of nests less than and greater than 50m from the nearest Oystercatcher nest were compared (table 57). Of 39 Oystercatcher nests less than 50m from the nearest Oystercatcher nest, breeding success data were available for 37 nests. Breeding success data were available for 44 of 51 nests greater than 50m from the nearest Oystercatcher nest. There was no significant difference between the breeding success of nests in the two categories, although there was a slight tendency for nests less than 50m from the nearest Oystercatcher nest to be more successful than those greater than 50m away. Oystercatchers do not exhibit a concerted mobbing response comparable to that made by Lapwings, which might have reduced the predation rate of nests located close together. The limited availability of suitable nest sites may have resulted in Oystercatchers nesting in closer proximity to each other than was expected by chance.

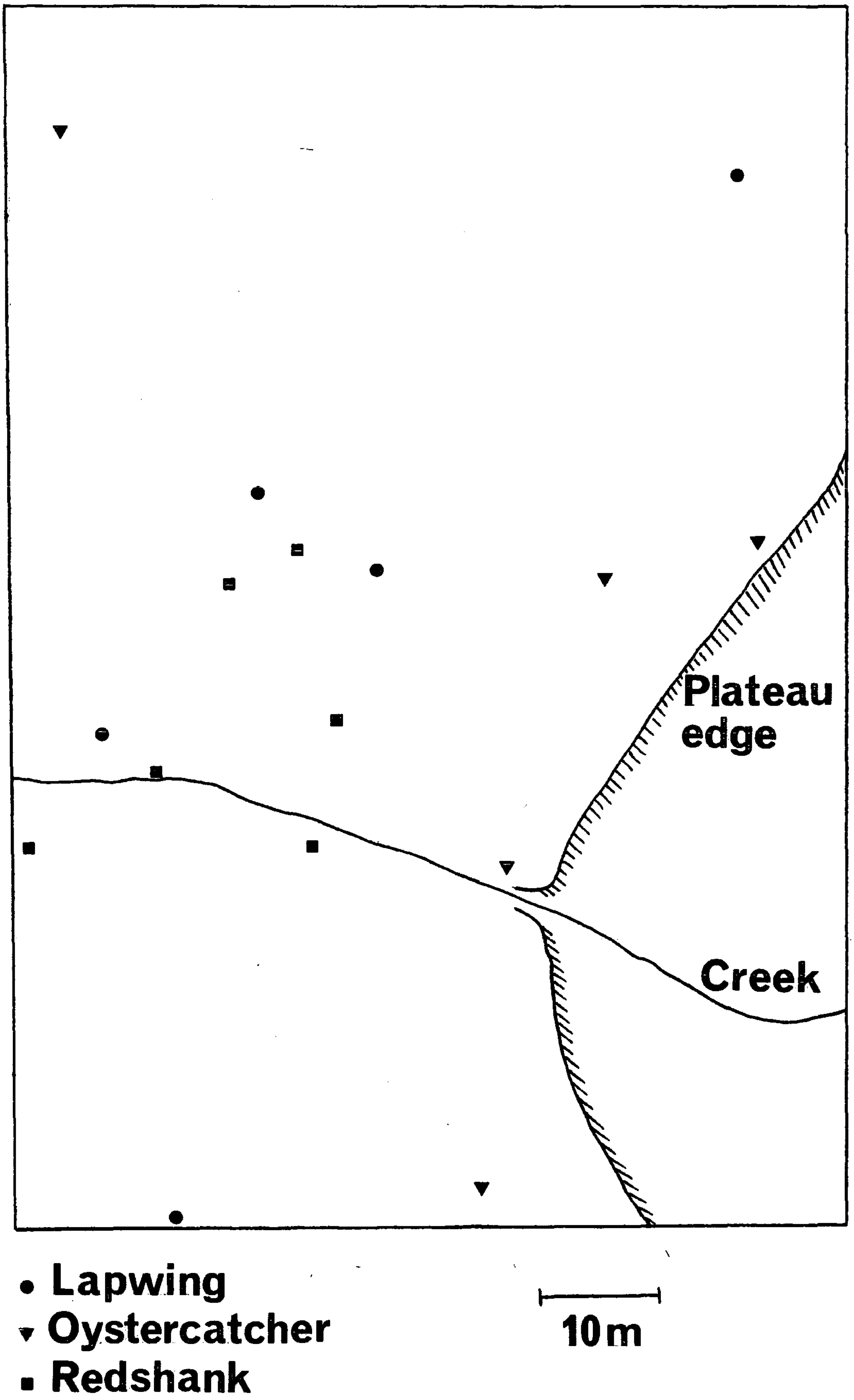
Table 57. Breeding statistics of Oystercatchers nesting less than 50m from the nearest Oystercatcher nest (A) and greater than 50m from the nearest Oystercatcher nest (B) on Rockcliffe Marsh in 1976 and 1977.

	A	B
No. nests	37	44
No. eggs	84	109
No. hatch	35	31
No. fledge	16	17
% hatch	42	28
% fledge	46	55
% breeding success	19	16
Mean no. fledged/nest	0.4	0.4
No. of eggs predated	27	39
No. of chicks predated	15	13
% of eggs predated	32	36
% of chicks predated	43	42

Heppleston (1972) observed interspecific aggression between inland breeding Oystercatchers and Lapwings, and of 27 direct attacks by Lapwings, 23 (85%) were successful. Heppleston suggested that this was evidence of interspecific competition, but Oystercatchers are known predators of eggs and chicks (e.g. Burger & Lesser 1978, Jamieson 1925, Rutten 1931), and these interactions may have been anti-predatory, rather than competitive. The potentially limited resources for which competition could occur between these two species were food and breeding space. Although the diets of Oystercatchers and Lapwings showed some overlap, in that dung-associated prey featured largely in the diets of both species (Section 9), their foraging behaviour differed. Competition may, therefore, involve territorial space. However, Hepplestone (1972) found no evidence of an inverse correlation between Lapwing and Oystercatcher breeding densities, and no such correlation was apparent on Rockcliffe Marsh. Interspecific competition between these two species was not considered to be a major influence on nest-site selection by either species.

To summarize, Oystercatchers selected to nest near to creek and plateau edges. These areas were slightly elevated and therefore less susceptible to flooding and better drained than those at a slightly lower elevation. Areas of loose substrate consistency, including gravel, provided an approximation to the ancestral habitat. The presence of other Oystercatchers as a proximate factor affecting the settling reaction may have been due to a degree of sociality, although the breeding success of Oystercatchers nesting less than and greater than 50m from the nearest Oystercatcher nest did not significantly differ. Alternatively, the availability of suitable breeding sites may have been a limiting factor.

Figure 33. Map of part of study area on Rockcliffe Marsh, in vegetation type T4, illustrating location of Lapwing, Oystercatcher and Redshank nests in 1976.


Plateau edge
Creek
● Lapwing
▼ Oystercatcher
■ Redshank
10 m

(iii) REDSHANK

Redshank nests occurred in vegetation types T3, T4, T6, T7 & T8 (table 58). Data were pooled into two categories (Gravel & T3-4 and T5-8 & Field) for analysis, due to the low numbers of nests occurring in some vegetation types. The distribution of nests in each vegetation type did not significantly differ between years ($X_1^2 = 1.3$, n.s.). A significantly greater proportion of nests occurred in the successionally more mature vegetation types (T6-8) than was expected by chance (comparison with random samples, table 51) in both 1976 ($X_1^2 = 5.8$, $p < 0.05$) and 1977 ($X_1^2 = 8.9$, $p < 0.01$).

Table 58. Distribution of Redshank nests in vegetation types on Rockcliffe Marsh in 1976 and 1977

	VEGETATION TYPES					
	T3	T4	T6	T7	T8	Total
1976	9	20	2	11	3	45
1977	4	17	8	8	5	42

The discrimination between nests and non-nests was highly significant (final Wilk's lambda = 0.34, $X_5^2 = 303.7$, $p < 0.001$). Of 87 Redshank nests, 83 (95%) were correctly classified (discriminant scores of -0.42 to -2.39). Of 200 non-nest samples, 92% were correctly classified.

Samples with discriminant scores of less than -0.35 were categorised as nests, and those with scores in excess of this value were classed as non-nests. The significant discriminating variables were distance to the nearest Lapwing nest, tussock density, distance to the nearest creek and plateau edges, and cowpat density. The four incorrectly classified nests had discriminant scores of -0.21 to -0.29. These high scores were largely due to the distances of these nests from the nearest plateau edge; these distances (in excess of 600m) were more than three times the mean distance (166m) at which Redshanks nested from a plateau edge (table 59).

The tendency for Redshanks to nest in the vicinity of Lapwings was either due to a similar habitat preference by the two species, or the presence of Lapwings in an area increased the attractiveness of that area to Redshanks, within the limits set by inter-specific aggressive interactions. Furthermore, there was a significant correlation between the distances from random samples to the nearest Lapwing and Redshank nests ($r = 0.63$, $df = 198$, $p < 0.001$), indicating that Redshank tended to nest in the vicinity of other Redshanks, in addition to Lapwings, as illustrated in a map of nest distribution on part of Rockcliffe Marsh (figure 33). Because of the high correlation, noted above, either variable (distances to nearest Lapwing or Redshank nest), but not both, was incorporated into the analysis. The variable, distance to nearest Lapwing nest, was preferentially selected during the analysis because it had a slightly higher F value than that of the distance to

Table 59. Summary table of discriminant function analysis of Redshank nest and non-nest samples for 1976 and 1977, on Rockcliffe Marsh.

Step No.	Variable entered*	Wilk's lambda	Change in Rao's V	Discriminant function coefficients; Standardized	Unstandardized
1	Lapwing nest	0.72	111.2	0.375	0.003
2	Tussock density	0.56	97.7	-0.429	-0.162
3	Plateau edge	0.46	122.6	0.519	0.002
4	Creek edge	0.38	136.0	0.342	0.013
5	Cowpat density	0.34	82.3	-0.292	-0.015
				CONSTANT:	-0.384

Prediction results

Actual results	No. of cases	Predicted group membership; Non-nests	Nests
Non-nests	200	184	16
% classified		92	8
Nests	87	4	83
% classified		5	95

Percentage of grouped cases correctly classified: 93%

Centroids of groups in reduced space

	Function 1
Non-nests	0.53
Nests	-1.23

Mean, standard deviation (S.D.) and sample size (N.) of each significant discriminating variable in the nests and non-nest samples

	Non-nests			Nests		
Variable	Mean	S.D.	N.	Mean	S.D.	N.
Lapwing nest	175.1	109.7	200	46.1	47.4	87
Tussock density	1.4	1.9	200	4.5	2.8	87
Plateau edge	330.2	218.2	200	166.0	175.5	87
Creek edge	37.7	28.6	200	16.2	14.9	87
Cowpat density	46.1	18.9	200	58.0	18.3	87

* Lapwing nest = distance to nearest Lapwing nest (m)
Tussock density = tussock density m^{-2}
Plateau edge = distance to nearest plateau edge (m)
Creek edge = distance to nearest creek edge (m)
Cowpat density = cowpat density ha^{-1}

the nearest Redshank nest ($F_{1, 285}$ = 149.8 and 138.9, respectively). It was not possible to distinguish which of the two potential proximate factors was involved in nest-site selection, and they may both have been involved.

To assess the selective advantages of Redshank nests being located in the vicinity of Lapwing nests and other Redshank nests, the breeding success of Redshanks nesting less than or greater than 50m from the nearest Lapwing or Redshank nests, and Lapwing and Redshank nests, were compared (table 60). Redshank nests less than 50m from the nearest Lapwing or Redshank nest, or Lapwing and Redshank nest, were approximately twice as successful, in terms of breeding success, than those Redshank nests over 50m from the nearest Lapwing and Redshank nests. It was not possible to separate the affect of proximity to Lapwing and Redshank nests, as most Redshank nests were in the vicinity of other Redshank and Lapwing nests. The presence of either breeding Lapwings or Redshanks (or both species) were proximate factors in the nest-site selection of Redshanks, which ultimately reduced the predation rate of Redshank eggs and chicks. It was not considered likely that Lapwings and Redshanks were independently selecting to nest in similar areas, as the nest-site requirements of these species differed, and none of these requirements appeared to be of limited availability.

Table 60. Breeding statistics of Redshanks nesting less than 50m (A) and greater than 50m (B) from the nearest Lapwing, Redshank, and Lapwing & Redshank nests on Rockcliffe Marsh in 1976 and 1977.

	LAPWING		REDSHANK		LAPWING & REDSHANK	
	A.	B.	A.	B.	A.	B.
No. nests	39	20	49	10	54	5
No. eggs	132	68	168	32	184	16
No. hatch	43	19	54	8	59	3
No. fledge	18	4	20	2	21	1
% hatch	33	28	32	25	32	19
% fledge	42	21	37	25	36	33
% breeding success	14	6	12	6	11	6
Mean no. fledged/pair	0.5	0.2	0.4	0.2	0.4	0.2
No. eggs predated	34	31	45	20	56	9
No. chicks predated	20	12	27	5	30	2
% eggs predated	26	45	27	62	30	56
% chicks predated	46	63	50	62	51	67

Redshank nests have been frequently recorded in very close proximity to Lapwing nests (Campbell 1974, von Frisch 1957, Nicholson 1938-39, Thomas 1942). This may be an anti-predator strategy, as Bub (1957) and Lack (1968) suggested. Evidence for this proposition has been adduced by this study and Goransson *et al*. (1975). The Redshank lays, on average, later than the Lapwing (Section 8), and presumably most Redshanks select to nest in the vicinity of Lapwing nests, and not *vice versa*. Lind (1961) noted mixed sub-colonies of Lapwings, Redshanks, Oystercatchers, Ruffs and Arctic Terns, the existence of which, he considered, was due to interspecific aggression being less pronounced than intraspecific aggression. The tendency to form mixed species nesting groups may also reduce the predation rate of the eggs of one species if predators form a specific searching image for another species' eggs. The ability of Redshanks to nest close together may be due to their lack of territorial behaviour (Hale 1956). They exhibit a communal reaction against potential predators (Grosskopf 1959, pers. obs.), although the attack tendencies of the Redshank are lower than those of larger waders, such as the Black-tailed Godwit and Lapwing, whose attack flights are pressed more closely home (Simmons 1955).

The Redshank usually breeds in dense ground vegetation, in or near marshy areas (Larsson 1976, Venables 1937), although exposed nest-sites, e.g. a shingle beach, have occasionally been reported (Rooke 1950). Tussock nest-sites, with good cover, are usually selected (Squires 1978, Thomas 1942). On Rockcliffe Marsh, 89% (94) of 106 Redshank nests were in tussocks. The remaining 11% were situated along creeks and runnels. Similarly, on the Dutch polders, the partial concealment afforded by drain sides, where the grass was not as closely cropped as on the marsh surface, was preferred by Redshanks (Bent 1927).

Larsson (1976) concluded that tussocks less than 10cm high were preferentially used as nest-sites. On Rockcliffe Marsh, the mean tussock height was 102.0 ± 3.3mm (n = 77), and the mean height of tussocks in which Redshanks nested was 108.7 ± 3.3mm (n = 74). No selection on the basis of tussock height was occurring, and the range of tussock heights was within the preferred range cited by Larsson (1976).

Tussock density was a significant discriminating variable; Redshanks nested at a higher than average tussock density of 4.5 tussocks m^{-2}, three times higher than the average for the whole marsh (table 59). The preferred tussock densities on Rockcliffe Marsh corresponded to the low-medium tussock densities which Squires (1976) found were preferred by Redshanks on Morecambe Bay saltmarshes. They were, however, higher than the tussock densities of less than $2m^{-2}$, which Larsson (1976) considered the Redshank to prefer on Swedish shore meadows. Unfortunately, Larsson (1976) did not statistically relate the observed distribution of Redshank nests, according to tussock density, to the relative availability of tussock densities, although he did state that there were few areas of his study sites where tussock density exceeded $2m^{-2}$. His results were biased by the restricted range of tussock densities available, from which the Redshanks made their selection, in his study areas. The Redshank is associated during the breeding season with grazed habitats, and tolerates a wide range of grazing intensity (Bergman 1946, Larsson 1969). Tussock formation is engendered by grazing, and suitable nest-sites for the Redshank are, therefore, produced under a grazing regime.

The tendency to nest near creek and plateau edges may have been due to the slight elevation of such sites (Section 2), which were, in consequence, less liable to be inundated. In addition, some nests were situated just below the edge of creeks (see above), where the vegetation was largely inaccessible to grazing cattle, and was ranker than that on the marsh surface. Apart from containing suitable nest-sites for Redshanks, these areas were also unlikely to be trampled by cattle; none of the 12 Redshank nests located below the edges of creeks in 1976 and 1977 incurred any losses of eggs due to trampling. This reduced risk of trampling offset the increased risk of inundation; of the 12 nests, 4 were flooded.

The selection of areas of higher than average cowpat densities may ultimately have been related to food availability or to the density of suitable nest-sites (tussocks); cowpat density was highly correlated with food availability (Section 6) and tussock density (Appendix 16: $r = 0.44$, $df = 198$, $p < 0.001$). However, tussock density was itself a significant discriminating variable, in addition to cowpat density. The selection of areas with a higher than average cowpat density largely explained the tendency for more mature vegetation types to be occupied (table 58), since vegetation types T8-6 had the highest cowpat densities on the marsh (Section 6).

(iv) RINGED PLOVER

Ringed Plover nests only occurred in vegetation types T3, T4 and Gravel (table 61). Significantly more nests occurred in gravel areas than were expected by chance in both 1976 ($X_1^2 = 76.7$, $p < 0.001$) and 1977 ($X_1^2 = 37.4$, $p < 0.001$), in which data were grouped into two categories (Gravel and T3-8 & Field) for comparison with the random samples (table 51), which were likewise grouped.

Table 61. Distribution of Ringed Plover nests in vegetation types on Rockcliffe Marsh in 1976 and 1977.

	VEGETATION TYPES			
	Gravel	T3	T4	Total
1976	9	1		10
1977	3	2	1	6

The discrimination between nest and non-nest samples was highly significant (final Wilk's lambda = 0.71, $X_4^2 = 70.8$, $p < 0.001$). Of 16 nests, 15 (94%) were correctly classified (discriminant scores of -0.96 to -2.93). Of 200 non-nests, 11% were categorised as nests because their discriminant scores were less than -0.87 (mid-point between centroids) (table 62). Nest number 9 was incorrectly classified because it was in an area of zero debris abundance, where the mean grass height (23mm) was over twice as tall as the average vegetation height (8.9mm) in which the Ringed Plover nested; the discriminant score of -0.56 classified the nest as a non-nest. Ringed Plovers selected to nest in areas of lower than average grass height; at a higher than average debris abundance; in close proximity to creek edges; and on loose substrate. Of these discriminating variables, the standardized coefficients indicated that grass height was more than twice as important to the discrimination as the remaining variables in the analysis (table 62).

Lack (1933) suggested that the specificity of habitat selection by the Ringed Plover restricted the distribution of the species to gravel areas, although the species was structurally adapted to short vegetation. Sluiters (1954) concluded that the main factor influencing the occupation of a habitat was the availability of suitable nest-sites, rather than the food supply or the presence and salinity of water. In addition to gravel and shingle areas, the Ringed Plover is known to nest in dense turf where there is broken ground, such as wheel ruts, or where it is possible to scrape through to bare sand (Wilson 1978). One site on Rockcliffe Marsh was on a cowpat on turf, 2 were on bare sand, and one was on tidal debris (dried grass). The remaining 12 nest-sites were on gravel.

Walters (1956) suggested that the physical features of the nest-sites chosen by the Kentish and Little Ringed Plovers (which are congeners of the Ringed Plover), such as

Table 62. Summary table of discriminant function analysis of Ringed Plover nest and non-nest samples in 1976 and 1977 on Rockcliffe Marsh.

Step No.	Variable entered*	Wilk's lambda	Change in Rao's V	Discriminant function coefficients; Standardized	Unstandardized
1	Grass height	0.80	53.8	0.80	0.05
2	Debris abundance	0.76	13.0	-0.35	-0.32
3	Creek edge	0.73	11.3	0.33	0.01
4	Substrate consistency	0.71	6.8	-0.27	-0.53
				CONSTANT:	-1.66

Prediction results

Actual group	No. of cases	Predicted group membership; Non-nests	Nests
Non-nests	200	178	22
% classified		89	11
Nests	16	1	15
% classified		6	94

Percentage of grouped cases correctly classified: 89%

Centroids of groups in reduced space

	Function 1
Non-nests	0.15
Nests	-1.88

Mean, standard deviation (S.D.) and sample size (N.) of each significant discriminating variable in the nest and non-nest samples

	Non-nests			Nests		
Variable	Mean	S.D.	N.	Mean	S.D.	N.
Grass height	37.7	13.9	200	8.9	10.9	16
Debris abundance	0.7	1.1	200	1.1	1.1	16
Creek edge	37.7	28.6	200	17.3	7.9	16
Substrate consistency	0.4	0.5	200	1.0	0.0	16

* Grass height = grass height (mm)
Debris abundance within 20m radius of site, on 0-5 scale
Creek edge = distance to nearest creek edge (m)
Substrate consistency = Firm/Loose; 0 = Firm, 1 = Loose

debris or conspicuous adjacent objects, were used in nest recognition. However, Maclean & Moran (1965) thought the prime function of these sites was to render the eggs less conspicuous to predators by the visually disruptive effect of extraneous objects. Nevertheless, if the nest-site is covered by wind-blown sand, the Ringed Plover can locate its position by visual orientation to local landmarks (Koehler 1940), so the use of debris as a nest-site, or its presence in the nest vicinity, may, secondarily, provide reference for orientation. On Rockcliffe Marsh, Ringed Plovers tended to nest in areas of a higher than average debris abundance (table 62), presumably for the reasons outlined above. The actual location of a nest on a visually prominent feature, such as debris or a cowpat, rather than in the vicinity of such features, may have been for the ease of scraping (Section 9), rather than to facilitate camouflage or site recognition. On Rockcliffe Marsh, such sites were only used in areas other than the Gravel vegetation type, where the substrate consistency was not as friable as gravel.

Sluiters (1954) suggested that the Ringed Plover tended to be colonial, but Mason (1947) considered it to a territorial and solitary-nesting species, albeit with small territories (approximately $30m^2$). The apparent coloniality may be due to a shortage of suitable nest-sites, although at high densities, several birds may jointly mob potential predators (Mason 1947, pers. obs.), and thus act colonially. On Rockcliffe Marsh, there was no tendency to colonial nesting, and the presence of a pair of Ringed Plovers in an area was not a proximate factor inducing other pairs to nest in that area.

On Rockcliffe Marsh, habitat selection was for areas of short grass, to which the Ringed Plover is structurally adapted, and a loose substrate, which was easily scraped. The selection of areas of higher than average debris abundance may have enhanced the natural camouflage of the nest and eggs, and facilitated nest relocation by the adults when the wind-blown, loose substrate, on which they nested, concealed the nest. Debris abundance may also have indicated the highest level that the previous high tides have reached, as it does to the Laughing Gull (Bongiorno 1970).

(v) DUNLIN

Of 11 Dunlin nests found in 1976 and 1977, 6 were located in vegetation type T6 and 5 were in T4. The habitat variables of only 9 of these nests were measured. A highly significant discrimination was achieved (final Wilk's lambda = 0.72, $X^2_3 = 40.8$, $p < 0.001$), by which all Dunlin nests were correctly classified, but 6% of the non-nest samples were classified on the basis of their discriminant scores, as Dunlin nests (table 63). For each case, discriminant scores of less than -0.86 were classified as nests, and those above this score as non-nests.

Dunlin selected areas with a higher than average tussock density, and nested closer to creek and plateau edges than was expected by chance (table 63). All Dunlin nests were in tussocks, so a suitable breeding habitat contained at least one tussock. Larsson (1976) found that Dunlin preferred areas in which tussock density was less than 1 tussock m^{-2}, and in which tussock height was shorter than 10cm. Such short tussocks are characteristic of intensively grazed areas. On Rockcliffe Marsh, the mean tussock height was 103.0 ± 3.3mm ($n = 77$), so the range of tussock heights was within that over which Larsson (1976) considered that no selection would occur. The only requirement for the nest-site appeared to be the presence of tussocks, and this discriminant variable was the most important contributor to the discrimination of Dunlin nests and non-nests, as indicated by the standardized function coefficients (table 63).

The Dunlin prefers breeding areas interspersed by small pools, creeks or damp areas (Bannerman 1961). On Rockcliffe Marsh, vegetation type T4, in which Dunlin nested, surrounded the waterlogged area T5, and Dunlin nests were situated closer to the edges of creeks than was expected by chance. Creeks and waterlogged areas provide suitable feeding grounds, where the main prey of Dunlin, Chironomidae and Tipulidae larvae, occur (Holmes 1966). In the Peak District, Dunlin breeding distribution was correlated with the distribution of Eriophorum vaginatum, which characterized poorly-drained regions (Yalden 1974).

Table 63. Summary table of discriminant function analysis of Dunlin nests and non-nests on Rockcliffe Marsh, in 1976 and 1977.

Step No.	Variable entered*	Wilk's lambda	Change in Rao's V	Discriminant function coefficients; Standardized	Unstandardized
1	Tussock density	0.87	15.7	-0.719	-0.334
2	Creek edge	0.78	14.1	0.524	0.016
3	Plateau edge	0.72	12.1	0.427	0.002
				CONSTANT:	-0.324

Prediction results

Actual group	No. of cases	Predicted group membership; Non-nests	Nests
Non-nests	100	189	11
% classified		94	6
Nests	9	0	9
% classified		0	100

Percentage of grouped cases correctly classified: 95%

Centroids of groups in reduced space

	Function 1
Non-nests	0.17
Nests	-1.88

Mean, standard deviation (S.D.) and sample size (N.) of each significant variable in the nest and non-nest samples

	Non-nests			Nests		
Variable	Mean	S.D.	N.	Mean	S.D.	N.
Tussock density	1.4	1.9	200	4.2	2.0	9
Creek edge	37.7	28.6	200	18.3	16.0	9
Plateau edge	330.2	218.2	200	198.5	176.5	9

* Tussock density = tussock density m^{-2}
Creek edge = distance to nearest creek edge (m)
Plateau edge = distance to nearest plateau edge (m)

On Rockcliffe Marsh, E. vaginatum was restricted to T5. Although Dunlin were frequently observed feeding there, no nests were recorded from this vegetation type, perhaps because there was a high risk of flooding in this low-lying area. The risk of flooding was further minimised by nesting closer to creek and plateau edges than was expected by chance; the ground towards the edged of creeks and plateaux were slightly elevated (Section 2). These slightly raised areas were not considered to afford improved visibility to this tussock-nesting species.

The Dunlin is characteristic as a breeding species in grazed habitats. As Larsson (1969) indicated, the selection of habitats with tussocks and a short sward is equivalent to the selection of intensively grazed areas. This preference for grazed habitats has also been noted by Brown (1938), Soikkeli (1964) and Wilson (1978).

The selection of nest-sites by Dunlin on Rockcliffe Marsh presumably occurred in two stages. The general breeding area was selected on the bases of the distances to the nearest creek and plateau edges, and the exact nest-site was determined by the presence of tussocks in the vicinity of creeks or waterlogged ground. The requirements of the nest-site outweighed those of the breeding area.

(vi) DISCUSSION

It was assumed that the significant discriminating variables selected in each analysis corresponded to the most important proximate factors involved in habitat and nest-site selection. However, when discriminating variables were highly correlated, e.g. the distances to the nearest Lapwing and Redshank nest, it was not possible to determine which variable was primarily involved in nest-site selection. The problem of extreme co-linearity is common to all multivariate techniques (Nie _et_ _al_. 1975), and the interpretation of results in which several variables are highly interdependent becomes difficult.

_A_ _priori_, few proximate factors should be involved in the selection of habitat and nest-site (Section 1), and the maximum number of significant variables in any one function was five. For each analysis, 94%-100% of the nests of each species were correctly classified, and 88%-95% of the total nest and non-nest cases were assigned to their correct group. The high degree of discrimination between nest and non-nest samples indicated that nest-site selection was occurring. The prediction equation (summation of unstandardized discriminant function coefficients and the constant) enabled the probability of a given site being a nest or non-nest to be determined for each species. This prediction equation was analagous to the formula for the selection mechanism presented in Section 1. The internal motivation of the bird (b_k) and the accumulated level of stimuli required for the settling reaction to occur were not known, but were assumed to have been adequate for the settling reaction to have occurred. The summation of the unstandardized discriminant function coefficients multiplied by their respective variable values was comparable to the summation of proximate factor values (y_i). The standardized discriminant function coefficients were equivalent to the weighting factors in the formula (a_i).

Probably all wader species which nested on Rockcliffe Marsh selected the saltmarsh as a breeding habitat because it is flat, exposed and treeless. The song-flights of most waders are adapted for delivery in such habitats (Dabelsteen 1978), and their anti-predatory behaviour is most effective in those circumstances (Klomp 1953). Furthermore, as Bergman (1946), Partridge (1974) and Klomp (1953) have indicated, different habitats may be preferred by birds due to anatomical and locomotory adaptations. This initial stage of habitat selection was not examined during the present study.

The second stage involved the selection of a suitable breeding area within the habitat. This area usually encompassed several potential nest-sites. For the 5 species studied, the habitat variables, distances to creek and plateau edges; cowpat density; substrate consistency; and grass height were typically important at this stage. The apparent preference for certain vegetation types was explicable, not in terms of plant species or community distribution, but with regard to tendencies to nest, for example, nearer to creek and plateau edges than was expected by chance, or at a higher than average cowpat density. The ultimate reasons for the selection of each proximate factor, by each species, were previously discussed in this section.

The third stage involved the selection of nest-sites within the breeding area. The discriminant function analyses indicated that the relative importance of nest-site characteristics, based on the standardized discriminant function coefficients, was usually high. The nest-site requirements of Dunlin (table 63) and Redshank (table 59) was for tussocks, and tussock density was one of the most important proximate factors to these species.

Proximity to the nests of the same or a different species may have been involved in either breeding area or nest-site selection, or both. Redshanks tended to nest in the vicinity of Lapwings and other Redshanks, (table 59) whereas Oystercatchers (table 56) and Lapwings (table 53) had a tendency to nest near members of their own species. However, Oystercatcher nests were usually in linear proximity, along creek and plateau edges, whereas Lapwing nests typically had a clumped distribution (Section 8). The presence of the same or a different species as a proximate factor was ultimately of anti-predatory value, except in the case of the Oystercatcher, and was comparable to the nesting of anatids in gulleries (Koskimies 1957).

The Lapwing, Redshank and Dunlin, and to some extent the Oystercatcher, are all species which are characteristic of grazed habitats. Some of the proximate factors to which these species responded were associated with grazed habitats. Redshank and Dunlin selected to nest where tussock density was higher than average. Lapwing and Redshank selected to nest in areas of higher than average cowpat density, and coupat density was also implicated in the finer levels of nest-site selection by these species (Section 9), especially that of the Lapwing, whose nest density was correlated with cowpat density, and hence invertebrate abundance and biomass. Ringed Plovers may also be considered to be potentially adapted to heavily grazed areas, since they selected areas where grass height was lower than average in which to nest (table 62). The congeneric Kittlitz's Plover also nests where vegetation is kept short by grazing and trampling (Hall 1958).

Many wader species exhibit natal-site and nest-site tenacity, to varying degrees (e.g. Cadbury & Olney 1978, Grosskopf 1963, Soikkeli 1970). Nest-site tenacity was not considered to influence the conclusions concerning nest-site selection of this study, because selection must have occurred initially, although the initial choice may have been perpetuated by nest-site tenacity.

The quality of a breeding habitat was readily measured by the breeding success of the birds within it. The breeding data of Lapwing, Oystercatcher and Redshank (tables 26, 29 and 33, respectively) were combined for both 1976 and 1977 to eliminate annual pertubations of breeding success and to increase sample size. The data for each species were analysed according to breeding success in the vegetation type groupings Field & T8-6 (old marsh) and T4-3 & Gravel (new marsh). The former grouping comprised the preferred vegetation types of Lapwings and Redshanks, but the Oystercatcher showed no apparent preference for particular vegetation types, although the latter grouping contained 70% of all Oystercatcher nests.

The percentage breeding success of Lapwings was higher in the new marsh (21%) than in the old marsh (15%), and the number of fledged young reared per pair was almost twice as high in the new marsh (0.8) than in the old marsh (0.5). Breeding success and productivity were, therefore, higher in those areas which were less preferred, but this difference was not statistically significant, according to the proportion of eggs laid which fledged in the old marsh (287 eggs, 43 fledged) and the new marsh (91 eggs, 19 fledged) (X_1^2 = 1.2, n.s.).

The percentage breeding success of Oystercatchers was slightly higher in the new (18%) than in the old marsh (14%), as was the number of chicks successfully fledged per pair (0.4 and 0.3, respectively). The proportion of eggs laid which fledged in the old marsh (51 eggs, 7 fledged) and the new marsh (126 eggs, 23 fledged) did not significantly differ (X_1^2 = 0.4, n.s.).

The proportion of Redshank eggs laid which fledged was almost three times higher in the old marsh (106 eggs, 16 fledged) at 15%, than in the new marsh (94 eggs, 6 fledged) at 6%, but this difference was not significant (X_1^2 = 2.4, n.s.). The number of fledged chicks reared per pair was more than twice as high on the old than the new marsh (0.5 and 0.2, respectively). Breeding success and productivity were higher in the preferred vegetation types than in those less preferred. This difference was largely due to differences in fledging success between the two areas. Hatching success was 29% on the old and 32% on the new marsh, but fledging success was over twice as high on the old marsh (52%) than the new marsh (19%). Of a total of 32 chicks predated, 21 (66%) were killed in the new, and 11 (34%) in the old marsh. The higher predation rate on the new than the old marsh was related to the higher breeding success of Redshanks nesting in the vicinity of Lapwing nests than those nesting greater than 50m from the nearest Lapwing nest (table 60). Of 20 Redshank nests greater than 50m from the nearest Lapwing nest, for which complete breeding data were available, 17 (65%) were in vegetation types T3 and T4. There was, therefore, a degree of overlap between the categories of Redshank nests greater than 50m from the nearest Lapwing nest and the Redshank nests on the new marsh, and between Redshank nests less than 50m from the nearest Lapwing nest and the Redshank nests on the old marsh. A similar overlap occurred with those Redshank nests less than 50m from the nearest Redshank nest, whose breeding success was also presented in table 60.

The higher breeding success of Redshanks in the preferred vegetation types (T8-6) was, in part, associated with the seasonal decline in breeding success and the tendency for nests on the new marsh (T4-3) to be commenced later (according to the laying date of the first egg) than those on the old marsh (Section 8). Thus, Redshank nests on the old marsh tended to be commenced earlier, and have a higher breeding success, than those on the new marsh.

Lapwings and Oystercatchers also exhibited a seasonal decline in breeding success and tended to lay earlier on the old than the new marsh (Section 8). However, the expected result of syllogistic reasoning (viz. that breeding success in these species would, therefore, be higher on the old than the new marsh, as it is in the Redshank) was obscured. This was due to the annual variability of the seasonally declining breeding success of the Lapwing and Oystercatcher (tables 27 and 31, respectively) and of their respective mean laying dates in each vegetation type (tables 16 and 18).

It was predicted (Section I) that those habitats which were preferred (i.e. evoked the settling reaction most strongly) would be those in which breeding success was highest. Only the breeding success of the Redshank markedly differed between vegetation type groupings, although this was not significant and the highest breeding success was in the most preferred habitat (old marsh). In the Lapwing and Oystercatcher, no significant differences were apparent, and the data may have been biased by the disproportionately high incidence of nests in the old and new marsh respectively. In contrast, the Redshank sample sizes were more homogeneous, and the observed differences were not, therefore, likely to be due to chance. It is axiomatic that natural selection will result in habitat preferences, assuming that differential breeding success occurs, because those pairs breeding in optimum habitats will, on average, successfully rear more offspring than those pairs breeding in sub-optimal sites. There will, therefore, be strong selective pressures for young birds to subsequently breed in an area approximating to the one in which they were reared. This may be achieved by an innate response, by habitat imprinting, or by a combination of both processes. Decision making during habitat selection occurs to maximise an individual's chance of survival and reproductive success (McFarland 1977). The decision involves the evocation of the settling response, and this reaction is delicately adjusted to a few, key proximate factors (Miller 1942).

There was no evidence of interspecific competition for breeding areas and nest-sites between the wader species. Although the species exhibited niche differences, as indicated by the proximate factors, these were not necessarily related to competitive interactions, but may have been due to adaptations to different, contiguous habitats. For example, the nesting distributions of the Ringed Plover was largely determined by the availability of gravel habitat; this species was not restricted to that habitat by interspecific competition, but by the nature of its habitat selection response. Furthermore, in each discriminant function analysis, there was a proportion of non-nest samples which were classed as nests. This indicated that, for each species, there were some suitable nest sites which were not occupied. Nest-site availability was not a limiting resource over which different wader species were competing.

SECTION 11

THE CONSERVATION AND MANAGEMENT OF THE HABITATS OF BREEDING WADERS

Studies of habitat and nest-site selection are essential to the effective management of the habitats of breeding waders. The adaptability of the members of a species may be such that a wide variety of habitats may be occupied. However, the range of occupied habitats may be influenced by inter- and intra-specific competition. Inter-specific competition may modify habitat selection to the extent that only optimal habitats are utilized, whereas intra-specific competition may cause a greater variety of habitats, including sub-optimal ones, to be adopted (Svardson 1949).

The settling reaction of meadow birds is primarily determined by the ground topography or habitat structure (Larsson 1976). This initial response may be related to the locomotory adaptations of the species concerned (e.g. Klomp 1953, Klopfer & Hailman 1965). Most wader species appear to prefer large expanses of exposed, closely-cropped pasture. It will therefore be necessary to conserve large areas of suitable breeding habitat.

Grazing is an important management tool in wader habitats (Fog 1976), and features of grazed habitats may be proximate factors in the selection of breeding areas (Section 10). The main effects of a grazing regime are on vegetation height, plant species composition, vegetation structure, especially the formation of tussocks and the loss of the litter layer (Section 3), and food availability (Section 6).

Grazing and trampling reduce vegetation height. On Rockcliffe Marsh, the mean vegetation height was 38mm (Section 10), which was suitable for breeding waders with regard to locomotion, foraging and nest site selection. Hogstedt & Larsson (1971) found that the frequency of foraging waders was inversely related to vegetation height at foraging sites in coastal meadows. Tall vegetation may hamper the movements of adults, and especially of young chicks. A lack of sufficient grazing may reduce the diversity of the wader fauna (Larsson 1976, Mitchell 1977); the proximate factor mediating this response may be vegetation height, and the ultimate factor may be the affect of vegetation height on locomotion and foraging behaviour. Grazing also encourages tussock formation, thereby providing suitable nest-sites for Dunlin and Redshank. The decline in the breeding populations of many wader species in Fenno-Scandia has been attributed to marked changes in vegetation height and species composition, consequent on the abandonment of coastal grazing (von Haartman 1975, Hilden 1978, Larsson 1969). Conversely, a high species diversity of nesting waders on saltmarshes may be maintained by cattle grazing (Moller 1975).

Safriel (1975) considered that the habitat in which precocial young are raised should be selected by the parents to provide the chicks with food items at densities which minimise the foraging movements of the young and hence exposure to predation. On Rockcliffe Marsh, cowpats provided a reliable index of food availability, as well as a source of prey (Section 6), and most adult waders and their chicks fed in the vicinity of the nest. The movements of chicks during the fledging period indicated that for the Lapwing, Oystercatcher and Redshank, sufficient food was locally available to preclude the necessity of travelling further than 100m from the nest, for at least the first 16 days after hatching (Section 8). In contrast, Soikkeli (1965) found that on lightly grazed coastal meadows in Finland, most species fed outside the meadow habitat, in the littoral zone and on the shoreline, and that after hatching the chicks were led to the dampest areas. The meadow therefore only served as a breeding area, and not a feeding area, because there was insufficient food available. The Finnish coastal meadows which Soikkeli surveyed were similar to Rockcliffe Marsh in that they had a sandy substrate. The differences in food availability may have been due to the different grazing intensities obtaining at the two sites; Rockcliffe Marsh is more intensively grazed than the coastal meadows of Finland, and dung-associated invertebrates, rather than intertidal ones, were the staple of the breeding waders and their chicks on Rockcliffe Marsh (Section 9). The importance of cattle grazing in providing suitable invertebrate prey, especially Diptera larvae, for breeding waders was emphasized by Harrison (1973), who recommended the application of cow slurry to those areas of a habitat which were not grazed. At inland sites, where salinity does not reduce or eliminate the lumbricid fauna, Curry (1976c) found that the application of cattle slurry resulted in earthworm numbers 41% higher and biomass 56% higher than in control plots.

The detrimental impact of cattle varies according to grazing intensity (figures 26 and 27) and the timing of grazing. Klomp (1953) implicated the destruction of eggs and chicks by cattle in the decline of the Netherlands breeding Lapwing population, and Heppleston (1971) recorded a hatching success of 5% for Oystercatcher nests in grazed fields in Scotland. The 95% nest failure rate was due to a combination of trampling and desertion due to disturbance by stock. In the Uists, losses of Lapwing eggs to cattle were negligible since most eggs had hatched prior to late May, when the cattle were introduced. The timing of the introduction of cattle may be critical, and it is usually recommended that it should not be performed until the end of the birds' breeding season (Moller 1975). On Rockcliffe Marsh, this delay may not be advisable. The increasing availability of invertebrates coincided with the introduction of cattle in early May (Section 5), when Lapwings, Oystercatchers and Redshanks have commenced to lay eggs (Section 8), so that newly-hatched chicks experience a high, but declining, availability of food. If the cattle were not introduced until later in the season, e.g. early to mid-June, the chicks would probably experience a relative shortage of food. Dung-associated invertebrates comprised 34-73% of the available invertebrates, and the main reservoir of these organisms was the old cowpats which persisted from the previous grazing season. After the emergence of the larvae and pupae from these old pats, the availability of dung-associated invertebrates will decline unless there are suitable oviposition sites available (i.e. fresh cowpats) to the newly-emerged adults. On Rockcliffe Marsh, it is, therefore, advisable to introduce the cattle no later than mid-May. This will incur losses of 16 to 30% of eggs due to trampling, depending on the annual variation in the timing of the waders' breeding seasons (Section 8). Heppleston (1971) suggested that these losses could be alleviated by the use of wire frames placed over the nest which would prevent cattle treading on the eggs. Limited use of these frames on Rockcliffe Marsh proved to be of dubious value. Cattle were attracted to them as scratching posts, although the frames were camouflaged by being painted green, and succeeded, in two of three cases, in displacing them. The provision of frames does not, of course, confer protection to the chicks, once they have left the nest. Cowpat density was used as an index to determine the optimum grazing intensity, with reference to the preferences of the breeding waders. The Lapwing, Oyster-catcher and Redshank, all tended to nest at higher than average cowpat density in those areas where the mean cow-pat density was low (to maximise food availability), and at a lower than average cowpat density where the mean cowpat density was high (to minimise trampling) (figures 28-30, Section 9). The behaviour of the free-ranging cattle resulted in a differential grazing intensity across the halosere (Section 6). Therefore, the stocking rate, and the resultant cowpat density, could only be reduced to that level at which the individual wader species were responding, during nest site selection, by nesting at a lower than average cowpat density, within the context of their habitat preferences. This assumes that their response to cowpat density does not change when the range of cowpat densities is reduced.

Lapwings and Redshanks tended to occur in the more mature vegetation types because they selected to nest in breeding areas with a high overall cowpat density (Section 10), but within these breeding areas (T8-T6) they nested at a lower than average cowpat density (figures 28 and 30, respectively). To maintain the present breeding densities of these two species, stocking rate could only be marginally reduced, so that cowpat density approximated to 70-80 ha^{-1} in T8 and T7, instead of the present annual densities of 77-87 ha^{-1} in these vegetation types, (figure 11). This would be effected by a reduction in stocking rate of approximately 10%, assuming that the differential grazing intensity was maintained. A reduction in excess of 10% would presumably render the preferred vegetations less acceptable, and there would be a concomitant decline in breeding density. This would be especially likely in the Lapwing, whose breeding density was correlated with cowpat density (figure 31). A 10% decrease in cowpat density would be accompanied by a decline in nest density of 0.3

Lapwing nests per 0.75ha around each nest, on average. A reduction of stocking rate, and hence cowpat density, of 10% would not markedly influence the breeding densities of Lapwing and Redshanks, but would reduce the proportion of eggs trampled by approximately 6% in both these species (figures 26 and 27). These losses would be further reduced by a delay of 1-2 weeks in the introduction of cattle, so that on average more nests would be incubated for a higher proportion of the incubation period before they were at risk to trampling. The efficacy of this delay would be dependent on the annual timing of the laying season of these species (Section 8). The earlier the breeding season (within the limits set by photoperiod, temperature and food availability), the fewer would be the losses of eggs and chicks due to trampling.

Approximately 70% of Oystercatcher nests were in T4, T3 and Gravel (table 58), and nests tended to be in areas of a higher than average cowpat density in these vegetation types (figure 29). Because the mean fresh cowpat density around Oystercatcher nests did not significantly differ from that expected by chance in each vegetation ty (table 49), it was not considered likely that a major reduction of fresh cowpat density would be detrimental to the breeding Oystercatcher population of Rockcliffe Marsh. A minimum stocking rate would need to be determined which would provide sufficient cowpats as a source of invertebrate prey. This latter requirement would militate against the use of mowing and burning as alternative management techniques to grazing on saltmarshes, like Rockcliffe, where cowpats are the main source of invertebrate prey for the breeding waders.

The importance of the distances to the nearest creek and plateau edges as proximate factors in the selection of breeding areas by Dunlin (table 63), Redshank (table 59), Oystercatcher (table 56), Ringed Plover (table 62) and Lapwing (table 53), suggested that these species tended to nest in slightly elevated areas which were less susceptible to inundation and were better-drained than lower lying areas. All 5 species nested closer to creek and/or plateau edges than was expected by chance; these sites tended to be marginally higher than those further from the edges (Section 2). Although many wader species are associated with damp habitats (Witherby _et_ _al_. 1940), they nevertheless nest on dry sites to prevent, for example, chilling of the eggs, and to reduce the energetic costs of incubation to the adult (Drent 1975, Ricklefs 1974).

Hald-Mortensen (1972) considered that significant decreases in the breeding populations of Redshank and Dunlin were associated with the drainage of previously suitable habitats. In the Outer Hebrides, a lowering of the water table could have disastrous consequences for the wader communities, since damp meadows are their most important breeding zone (Fuller 1978, Wilson 1973). These damp areas presumably provide foraging sites. However, on Rockcliffe Marsh, which is largely well-drained, the provision and maintenance of damp areas is not critical, because dung-associated invertebrates provide the main prey items for the breeding waders (Section 9).

Olney (1965) recommended that the water level in Avocet nesting habitats should be manipulated. By raising the water level in spring, Avocets nested on higher ground, thereby reducing the risk of subsequent flooding. By gradually lowering the water level as the young hatched, the available feeding area for the chicks was maximised. To some extent, this process occurred naturally on Rockcliffe Marsh, where the lower marsh was inundated too frequently to be available as a breeding area in March to April; the laying season of Lapwings (table 16), Oystercatchers (table 18) and Redshanks (table 19) was therefore retarded in these areas beyond the time at which equinoctial spring tides occurred (Section 8).

The local control of predators, especially corvids, has been frequently suggested as a measure to reduce mortality due to predation (Olney 1965, Squires 1976). This is unlikely to be effective, since the influx of predators may be from a wider area than that over which control can be operated.

Disturbance by humans, dogs and cattle may cause desertion (Heppleston 1971, Olney 1965). Disturbance by people and dogs can be minimised by limiting human access. On Rockcliffe Marsh, which is a local nature reserve, authorised access is by permit only, and only small numbers (usually less than a dozen) of visitors are escorted round the reserve at a given time. In contrast, the cattle constitute an integral part of the ecosystem with respect to the breeding waders. Heppleston (1971) found that desertion due to disturbance by cattle accounted for 34% of Oystercatcher nest failures in inland pastures. On Rockcliffe Marsh, no desertions could be definitely attributed to this cause. Cattle were not considered to be an important source of disturbance to waders, and it is possible that the waders were habituated to the presence of cattle. Desertion only accounted for 1-7% of the egg losses of Lapwing, Oystercatcher and Redshank annually (tables 26, 29 and 33, respectively), and these desertions usually involved partially predated clutches.

To maximise wader species diversity, a mosaic of habitats should be created and managed. For example, the provision of gravel areas, of at least 10ha (the approximate area of gravel on Rockcliffe Marsh), may encourage the nesting of Ringed Plovers, and possibly Little Ringed Plovers (especially in the southern half of Britain - Sharrock 1976), in an otherwise unsuitable area. The transition between plant communities, grazing intensity and hydrology should be maintained. On Rockcliffe Marsh, the gently sloping terraces, separated by erosion edges, contribute to this gradient with respect to salinity, drainage and plant communities. The grazing intensity of the cattle sustains the close-cropped sward at a pre-climactic successional stage, and the behaviour of the cattle perpetuates the differential grazing intensity across the halosere. In addition, cowdung constitutes an annually renewable resource which is the main food reservoir of the breeding waders.

Shrubs and trees should be removed to circumvent their use as vantages by predators. Such vantages may deter, for example, Lapwings from breeding in their vicinity (Klomp 1953). On Rockcliffe Marsh, the removal of tide-borne dead trees, which provided Carrion Crows and Rooks with elevated perches, should be effected for this reason.

A management plan should only be implemented when the conditions peculiar to a habitat, especially with respect to food availability, have been elucidated. On Rockcliffe Marsh, the importance of cattle, in this and other respects, has already been emphasized.

As a corollary to the requirements of many wader species for exposed expanses of suitable breeding habitat, large areas must be conserved and managed. This is especially necessary on saltmarsh, which is an ecologically unstable habitat, whose flora and fauna are increasingly threatened by large-scale reclamation.

SUMMARY

1. Aspects of the breeding biology of wading birds were studied on a dry, cattle-grazed saltmarsh, Rockcliffe Marsh, in Cumbria.
2. A phytosociological survey, using a simplified Braun-Blanquet method, enabled 11 vegetation types to be distinguished, 9 of which were arranged in order of increasing successional maturity along a sere-climax, from a predominantly halophytic to a largely glycophytic community. The species composition and the growth form of plant species in each vegetation type were influenced by the processes of trampling and grazing by cattle.
3. Historical sources indicated that the status of the avifauna of Rockcliffe Marsh had undergone marked changes during the period 1870-1978. The numbers of breeding Oystercatchers and Black-headed, Lesser Black-backed and Herring Gulls have increased, and the numbers of breeding Dunlins have decreased.
4. The breeding birds' numbers were censused using the technique of nest counts in 1970-1978. During that period the avian species composition did not markedly change, although individual species exhibited fluctuations in numbers.
5. The invertebrate fauna was sampled by pitfall trapping and soil sampling, although so few invertebrates were obtained by the latter method that pitfall trapping was used as the main relative index of food availability to the waders. The invertebrate fauna comprised dung-

associated, maritime and marshland invertebrates. Dung-associated species, especially Diptera, comprised between 34% and 73% of the total number of recorded invertebrates, and 49% to 81% of their biomass. The upper marsh supported approximately twice the number and biomass of invertebrates that were on the lower marsh. Both biomass and numbers of total invertebrates were slightly larger in 1976 than 1977 at each transect point. There was a seasonal decline of invertebrate abundance from May to July in both years.

6. Approximately 1000 cattle are grazed annually on Rockcliffe Marsh between May and September. Faecal counts, expressed as cowpat density ha^{-1}, provided an index of relative grazing intensity across the halosere. On this basis, the upper terrace (T8 & T7) was frequented more by the cattle than the lower terrace (T4 & T3), in both 1976 and 1977. In both years, cowpat density was positively correlated with the abundance and biomass, of Diptera and total invertebrates.
7. In the Lapwing, Oystercatcher and Redshank, the laying date of the first egg of a clutch tended to be later in 1977 than 1976; these annual differences may have been related to the colder mean temperatures and higher precipitation in 1977 than 1976. Laying date in these species tended to be later on the new than the old marsh; intermittent tidal inundation of the lower

terrace during March and early April may delay the breeding in the less successionally mature vegetation types.

8. The modal clutch size of the Lapwing and Redshank was 4 eggs, and their clutch size did not exhibit a seasonal decline. The modal clutch size of the Oystercatcher was 3 eggs, and this species' clutch size exhibited a seasonal decline, in 1976 and 1977, from approximately 3.0 eggs in late April to 2.3 eggs in late June.
9. The upper egg tooth of the Lapwing and Redshank was shed within two days of hatching. In contrast, that of the Oystercatcher persisted for 5-13 days after hatching. The persistence of the upper egg tooth may have been related to the feeding activity of the chicks. Lapwing and Redshank chicks began to forage within a day of leaving the nest, whilst Oystercatcher chicks did not do so until 4-5 days post-hatching since parental feeding occurs in this species. A small, but probably underestimated, proportion of the neonatal chicks of the 3 wader species also had a lower egg tooth, which may have been protective of the lower rhamphotheca during hatching.
10. The broods of Lapwing, Oystercatcher and Redshank were not observed to move further than 200m from the nest-site during the fledging period, presumably because food availability was sufficiently high to restrict the foraging movements of the chicks.
11. The breeding success of the Lapwing and Oystercatcher was approximately twice as high in 1976 than 1977,

whereas that of the Redshank showed no annual variation. All three species exhibited a seasonal decline of breeding success, which may have been related to food availability and the rates of trampling and predation of eggs and chicks. The seasonal decline of Oystercatcher breeding success was concomitant with the seasonal decline of clutch size; and larger clutches had a higher breeding success than smaller clutches.

12. The predation rate of the eggs of each species was higher during the initial stage of incubation, when the parents were least attentive of the nest, than during the latter stage. In contrast, trampling was an essentially random egg mortality factor.
13. Cohort life tables of eggs and chicks indicated that the greatest losses occurred during the early parts of the incubation and fledging periods of the three wader species.
14. The Lapwing and Redshank breeding populations were not self-maintaining, and it was assumed that immigration was occurring to maintain the local populations, since there was no evidence that these breeding populations were declining. In contrast, the Oystercatcher breeding population was at equilibrium; breeding success was sufficient to maintain the population at its present level.
14. Lapwing and Redshank nests were significantly clumped in 1976, but not in 1977, and the dispersion of Oyster-

catcher nests did not deviate from a random distribution in both 1976 and 1977. The advantages of territoriality and sub-colonial nesting were discussed.

15. Using gizzard, pellet and faecal samples of adult and chick waders, it was determined that dung-associated invertebrates comprised 48-80% of the diets adults and chicks.

16. For each wader species, the relative incidence of egg and chick mortality due to trampling in each vegetation type was positively correlated with cowpat density in both 1976 and 1977, indicating that cowpat density was a reliable index of cattle activity across the marsh.

17. Cowpat density was involved in the selection of nest-sites by Lapwings and Redshanks. In areas of high cowpat density, these species nested at a lower than average cowpat density, thereby minimising losses of eggs and chicks due to trampling. Conversely, in areas of low mean cowpat density, where the incidence of trampling was low, food availability was maximised by nesting in areas of higher than average cowpat density. In addition, Lapwing nest density was positively correlated with cowpat density, and with the biomass of total invertebrates and Diptera; Lapwing nest density was therefore adjusted to the available food supply (ultimate factor) on the basis of cowpat density (proximate factor).

18. Lapwings and Oystercatchers selected to nest on old cowpats. Old cowpats were also used as nest-sites by

Redshanks, Dunlins and Ringed Plovers because they were easy to scrape.

19. The proximate factors involved in nest-site and habitat selection by wading birds were determined from a discriminant function analysis of nest and non-nest samples. For the 5 species studied (Lapwing, Oystercatcher, Redshank, Ringed Plover and Dunlin), the significant habitat variables included the distances to the nearest creek and plateau edges and cowpat density. The nests of those species which tended to nest closer to creek and plateau edges than was expected by chance were less likely to be inundated by a high tide because these sites were slightly elevated. Lapwing and Redshank tended to nest in areas of a higher than average cowpat density, where food availability was higher. The behavioural requisites of some species also influenced nest-site selection. For example, the use of tussocks as nest-site by Redshank and Dunlin involved tussock density in the selection process. The tendency of some species, e.g. Lapwing, and Redshank, to nest in the vicinity of the same or a different species, was an anti-predator strategy.

20. The implications of the cattle-wading birds interactions and the habitat and nest-site requirements of wading birds were discussed with reference to the management and conservation of breeding waders and their habitats.

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APPENDICES

Appendix 1. The scientific names of birds and mammals mentioned in the text, based on the check lists of K.H. Voous (1977). "List of Recent Holarctic Bird Species" and G.B. Corbet & H.N. Southern (1977) "The Handbook of British Mammals".

BIRDS Common name	Scientific name
Fulmar	Fulmarus glacialis
Shag	Phalacrocorax aristotelis
Grey Heron	Ardea cinerea
Pink-footed Goose	Anser brachyrhynchus
Barnacle Goose	Branta leucopsis
Shelduck	Tadorna tadorna
Teal	Anas crecca
Mallard	A. platyrhynchos
Shoveler	A. clypeata
Red-breasted Merganser	Mergus serrator
Sparrowhawk	Accipiter nisus
Buzzard	Buteo buteo
Kestrel	Falco tinnunculus
Merlin	F. columbarius
Peregrine	F. peregrinus
Red Grouse	Lagopus lagopus
Blue Grouse	Dendragapus obscurus
Grey Partridge	Perdix perdix
Moorhen	Gallinula chloropus
European Oystercatcher	Haematopus ostralegus
African Black Oystercatcher	Haematopus moquini
Little Ringed Plover	Charadrius dubius
Ringed Plover	C. hiaticula
Killdeer Plover	C. vociferus

Appendix 1. (continued)

Common name	Scientific name
Kittlitz's Sandplover	C. pecuarius
Kentish Plover	C. alexandrinus
Crested Wattled Plover	Hoplopterus tectus
Lapwing	Vanellus vanellus
Dunlin	Calidris alpina
Ruff	Philomachus pugnax
Black-tailed Godwit	Limosa limosa
Curlew	Numenius arquata
Redshank	Tringa totanus
Common Sandpiper	Actitis hypoleucos
Arctic Skua	Stercorarius parasiticus
Great Skua	S. skua
Laughing Gull	Larus atricilla
Black-headed Gull	L. ridibundus
Common Gull	L. canus
Lesser Black-backed Gull	L. fuscus
Herring Gull	L. argentinus
Greater Black-backed Gull	L. marinus
Kittiwake	Rissa tridactyla
Common Tern	Sterna hirundo
Arctic Tern	S. paradisaea
Guillemot	Uria aalge
Puffin	Fratercula arctica
Adelie Penguin	Pygoscelis adeliae
Barn Owl	Tyto alba
Little Owl	Athene noctua

Appendix 1. (continued)

Common name	Scientific name
Short-eared Owl	Asio flammeus
Skylark	Alauda arvensis
Meadowlark	Sturnella neglecta
Sand Martin	Riparia riparia
Swallow	Hirundo rustica
Tawny Pipit	Anthus campestris
Meadow Pipit	A. pratensis
Yellow Wagtail	Motacilla flava
Pied Wagtail	Motacilla alba
Magpie	Pica pica
Rook	Corvus frugilegus
Carrion Crow	C. corone
Starling	Sturnus vulgaris
Linnet	Carduelis cannabina
Bicoloured Antbird	Gymnopithys bicolor
MAMMALS	
Water Vole	Arvicola terrestris
Dog (domestic)	Canis
Fox	Vulpes vulpes
Stoat	Mustela erminea
Weasel	M. nivalis
Horse (domestic)	Equus
Cow (domestic)	Bos
Sheep (domestic)	Ovis

Appendix 2. The invertebrates of Rockcliffe Marsh, collected from pitfall traps and soil samples 1976-1977.

ANNELIDA		
Chaetopoda		
Oligochaeta	*Enchytraeidae	
	*Lumbricidae	
MOLLUSCA		
Lamellibranchiata	Tellinidae	Tellina tenuis (L.)
ARTHROPODA		
Crustacea		
Isopoda	Sphaeromatidae	Sphaeroma rugicauda Leach
	Porcellionidae	Porcellio scaber (Latr.)
	Armadillidiidae	Armadillidium vulgare (Latr.)
Amphipoda	Corophidae	Corophium volutator (Pallas)
	Gammaridae	Gammarus duebeni Liljeborg
	Talitridae	Orchestia spp.
Decapoda	Portunidae	Carcinus maenas Pennant
Diplopoda	Iulidae	Tachypodoiulus niger (Leach)
Arachnida		
Acari	Nemastomatidae	Mitostoma chrysomelas (Herm.)
Opiliones	Phalangiidae	Mitopus morio (Fab.)
Araneae	Linyphiidae	Silometopus elegans (Camb.)
		Agyneta decora (Camb.)
		Erigone dentipalpis (Wider)
	Argiopidae	Araneus diadematus Clerck
	Theridiidae	Theridion bimaculatum (L.)
	Lycosidae	Pardosa purbeckensis (Camb.)
		P. monticola (Clerck)
		P. palustris (L.)
		P. amentata (L.)
		Trochosa ruricola (Degeer)
	Pisauridae	Pisaura mirabilis (Clerck)
	Salticidae	Salticus cingulatus (Panzer)
	Tetragnathidae	Pachygnatha clercki (Sund.)
		P. degeeri Sund.
Insecta		
Protura		
Collembola		
Odonata	Coenagriidae	Pyrrhosoma nymphula (Sulzer)
Orthoptera	Acrididae	Chorthippus spp.
Dermaptera	Forficulidae	Forficula auricularia (L.)
Hemiptera	Corixidae	Sigara sahlbergi (Fieb.)
	Rhopalidae	
	Miridae	
	Saldidae	Salda littoralis L.
		S. pallipes Fab.
	Cicadellidae	
Mecoptera	Panorpidae	Panorpa communis L.
Lepidoptera	Pieridae	Artogeia napi (L.)
		Anthocharis cardamines (L.)
	Nymphalidae	Inachis io (L.)
		Vanessa atalanta (L.)
		V. cardui (L.)
		Aglais urticae (L.)

* indicates a dung-associated family or species.

Appendix 2 (continued)

	Satyridae	Hipparchia semele (L.)
		Maniola jurtina (L.)
		Coenonympha pamphilus (L.)
		Lasiommata megera (L.)
Lepidoptera	Lycaenidae	Polyommatus icarus (Rott.)
	Zygaenidae	Zygaena filipendulae (L.)
	Noctuidae	Cerapteryx graminis (L.)
		Autographa gamma (L.)
		Agrotis vestigialis (Rott.)
Trichoptera	Limnephilidae	Limnephilus affinis Curtis
Hymenoptera	Tenthredinidae	
	Cynipidae	
	*Ichneumonidae	
	Platygasteridae	
	Aphelinidae	
	Chrysididae	Chrysis ignita (L.)
	*Formicidae	Myrmica rubra (L.)
	Vespidae	Vespula vulgaris (L.)
		V. germanica (Fab.)
	Apidae	Bombus lucorum L.
		B. terrestris L.
Diptera	*Tipulidae	Nephrotoma quadrifaria(Meig.)
		Tipula nigra L.
		T. rufina Meig.
		T. cava Riedel
		*T. vernalis Meig.
		T. oleracea L.
		*T. paludosa Meig.
	*Trichoceridae	Trichocera spp.
	*Psychodidae	*Psychoda spp.
	*Ptychopteridae	Ptychoptera spp.
	Culicidae	Aedes cinereus Meig.
		Anopheles spp.
	*Ceratopogonidae	
	*Chironomidae	Pentapedilum flavipes Meig.
		*Smittia spp.
	*Anisopodidae	*Anisopus punctatus (Fab.)
	Bibionidae	Bibio marci (L.)
		Dilophus febrilis (L.)
	*Mycetophilidae	Phronia flavipes Winn.
	*Sciaridae	Sciara autumnalis (Winn.)
	*Cecidomyiidae	
	*Scatopsidae	*Scatopse notata (L.)
	*Stratiomyidae	Nemotelus notatus Zett.
		N. uliginosus (L.)
		*Chloromyia formosa (Scop.)
		*Microchrysa flavicornis Meig.
	*Rhagionidae	*Rhagio scolopacea (L.)
	*Tabanidae	Chrysops relictus Meig.
		Haematopota pluvialis (L.)
	*Empididae	Rhamphomyia sulcata (Meig.)
		Megacyttarus maculipennis Zett.

Appendix 2 (continued)

Diptera		Pachymeria tessellata Fab.
		Hilara litorea (Fall.)
		H. lundbecki Frey
	*Dolichopodidae	Dolichopus brevipennis Meig.
		D. clavipes Hal.
		D. nubilus Meig.
		D. plumipes (Scop.)
		D. rupestris Hal.
		*D. ungulatus (L.)
		Macrodolichopus diadema Hal.
		Medetera dendrobaena Kw.
	Lonchopteridae	Lonchoptera spp.
	*Phoridae	
	*Syrphidae	*Rhingia campestris Meig.
		Cheilosia spp.
		*Eristalis pertinax (Scop.)
		*Syrvita spp.
	Tephritidae	
	Otitidae	Melieria omissa (Meig.)
	*Dryomyzidae	
	Chamaemyiidae	
	*Lauxaniidae	
	*Heleomyzidae	
	*Sepsidae	Themira putris (L.)
		*Sepsis duplicata Hal.
		S. punctum (Fab.)
	Sciomyzidae	
	*Sphaeroceridae	*Copromyza similis (Collin)
		*Limosina spp.
	*Lonchaeidae	Lonchaea spp.
	Opomyzidae	
	Anthomyzidae	Anthomyza spp.
	Ephydridae	Ephydra riparia Fall.
	*Milichidae	*Madiza glabra Fall.
	Agromyzidae	Phytomyza spp.
	Chloropidae	
	*Calliphoridae	*Calliphora vomitoria (L.)
		*Lucilia caesar (L.)
	*Scathophagidae	Scathophaga litorea Fall.
		*S. stercoraria (L.)
	*Anthomyiidae	
	*Fanniidae	*Fannia spp.
	*Muscidae	*Polietes lardaria (Fab.)
		*Mesembrina meridiana (L.)
		*Dasyphora cyanella (Meig.)
		*Musca domestica L.
		M. autumnalis Deg.
		*Hydrotaea spp.
		*Phaonia spp.
		*Stomoxys calcitrans (L.)

Appendix 2 (continued)

Coleoptera	Carabidae	Leistus fulvibarbis Dej.
		Nebria brevicollis (Fab.)
		N. salina Fair. & Lab.
		Notiophilus biguttatus (Fab.)
		Loricera pilicornis (Fab.)
		Dyschirius globosus (Hbst.)
		D. politus (Dej.)
		D. salinus Schaum
		*Clivina fossor (L.)
		Broscus cephalotes (L.)
		Trechus quadristriatus(Schr.)
		Asaphidion flavipes (L.)
		Bembidion aeneum Germ.
		B. atrocoeruleum Steph.
		B. bipunctatum (L.)
		B. guttula (Fab.)
		B. lampros (Hbst.)
		B. litorale (Ol.)
		B. lunulatum (Fourc.)
		B. minimum (Fab.)
		Pterostichus diligens(Sturm)
		P. madidus (Fab.)
		P. niger (Sch.)
		P. nigrita (Payk.)
		P. vernalis (Panz.)
		Calathus fuscipes (Goeze)
		Agonum marginatum (L.)
		A. muelleri (Hbst.)
		Amara aenea (Deg.)
		A. familiaris (Duft.)
		A. plebeja (Gyll.)
		Dicheirotrichus gustavi Crotch
		Badister bipustulatus (Fab.)
	Dytiscidae	Agabus bipustulatus (L.)
		A. conspersus (Marsh.)
	Gyrinidae	Orectochilus villosus (Mull.)
	*Hydrophilidae	Helophorus griseus Hbst.
		H. flavipes (Fab.)
		*Sphaeridium bipustalatum Fab.
		*S. scarabaeoides (L.)
		*Cercyon haemorrhoidalis(Fab.)
	*Histeridae	*Hister unicolor L.
	Silphidae	Nicrophorus humator (Gled.)
		Thanatophilus rugosus (L.)
		Silpha atrata L.
	*Staphylinidae	Lesteva spp.
		Bledius spp.
		*Platystethus arenarius(Fourc.
		*Anotylus tetracarinatus(Block
		*Stenus spp.
		*Philonthus marginatus(Str.)
		*Quedius spp.

Appendix 2 (continued)

	*Tachyporus chrysomelinus(L.)
	*T. hypnorum (Fab.)
	Tachnius spp.
*Geotrupidae	*Geotrupes stercorarius(L.)
*Scarabaeidae	*Aphodius ater (Deg.)
	*A. depressus (Kug.)
	*A. fossor (L.)
	*A. prodromus (Brahm)
	*A. rufipes (L.)
	Hoplia philanthus(Fuess.)
Byrrhidae	Byrrhus pilula (L.)
Dryopidae	Dryops ernesti des Gozis
Elateridae	Athous haemorrhoidalis(Fab.)
	Agriotes lineatus (L.)
Cantharidae	Cantharis livida L.
	C. nigricans (Mull.)
	C. rufa L.
	C. rustica Fall.
Coccinellidae	Subcoccinella vigintiquattuorpunctata (L.)
	Adalia bipunctata (L.)
	A. decempunctata (L.)
	Coccinella septempunctata L.
	C. undecimpunctata L.
	Thea vigintiduopunctata (L.)
Cerambycidae	Rhagium mordax (Deg.)
Chrysomelidae	Chrysolina staphylaea (L.)
	C. polita (L.)
	Hydrothassa marginella (L.)
	Psylliodes spp.
Apionidae	Apion spp.
Curculionidae	Otiorhynchus spp.
	Sitona spp.
	Ceutorhynchus spp.

Appendix 3. The main keys used for invertebrate identification.

General		Authority
Seashore invertebrates		Barrett & Yonge (1958)
Land invertebrates		Cloudsley-Thompson & Sankey (1961)
Insects		Chinery (1973)
Arachnida		
Opiliones		Sankey & Savory (1974)
Araneae		Locket & Millidge (1951, 1953) Locket, Millidge & Merrett (1974)
Insecta		
Dermaptera		Brindle (1977)
Hemiptera		
	Corixidae	Macan (1939)
Lepidoptera		Higgins & Riley (1970) South (1961)
Trichoptera		Macan (1973)
Hymenoptera		Richards (1956)
	Formicidae	Bolton & Collingwood (1975)
Diptera		Colyer & Hammond (1951)
	Nematocera	Coe *et al.* (1950)
	Mycetophilidae	Edwards (1924)
	Sciaridae	Edwards (1924)
	Tabanoidea	Oldroyd (1960)
	Empididae	Collin (1961)
	Dolichopodidae	Parent (1938)
	Syrphidae	Coe (1953)
	Agromyzidae	Spencer (1972)
	Calliphoridae	van Emden (1954)
	Muscidae	Fonseca (1968)
Coleoptera		Crowson (1956) Joy (1932)
	Carabidae	Lindroth (1974)

Appendix 4. Sources of references to recorded dung-associated invertebrates

General	Authority
	Hafez (1939)
	Legner & Olton (1970)
	Merritt & Anderson (1977)
	Mohr (1943)
	Nakamura (1975b)
	Olechowicz (1974)
	Valiela (1969a)
Oligochaeta	Cernosvitov & Evans (1947)
	Svendsen (1957a,b)
Diptera	Coe (1953)
	Coe *et al*. (1950)
	van Emden (1954)
	Fonseca (1968)
	Gibbons (1968)
	Hammer (1941)
	Laurence (1954)
	Papp (1971)
	Wingo *et al*. (1974)
Coleoptera	Hanski & Koskela (1977)
	Joy (1932)
	Koskela (1972)
	White (1960a,b)

Appendix 5. Mean numbers of invertebrates per trap per 5 day period at each transect point, on Rockcliffe Marsh in 1976 and 1977.

1976

Transect Number		Mean ($\bar{x}$)	Standard Error (S.E.)	Sample Size (n)
A1	Arachnida	2.98	0.46	48
	Diptera	12.71	1.54	48
	Coleoptera	2.17	0.51	48
	Other	1.71	0.36	48
	Total	19.56	1.86	48
A2	Arachnida	4.00	0.78	45
	Diptera	17.96	1.30	45
	Coleoptera	3.58	0.52	45
	Other	1.58	0.37	45
	Total	27.11	1.42	45
A3	Arachnida	3.45	0.42	47
	Diptera	7.98	0.44	47
	Coleoptera	4.02	0.42	47
	Other	1.57	0.24	47
	Total	17.02	2.13	47
A4	Arachnida	1.39	0.32	48
	Diptera	4.46	0.38	48
	Coleoptera	2.77	0.46	48
	Other	1.85	0.39	48
	Total	10.48	1.73	48
A5	Arachnida	4.15	0.50	46
	Diptera	6.63	0.66	46
	Coleoptera	3.22	0.49	46
	Other	2.83	0.60	46
	Total	16.83	2.29	46
A6	Arachnida	2.02	0.48	48
	Diptera	3.46	0.79	48
	Coleoptera	2.56	0.58	48
	Other	2.10	0.57	48
	Total	10.15	2.50	48
A7	Arachnida	1.17	0.28	47
	Diptera	2.36	0.46	47
	Coleoptera	2.72	0.48	47
	Other	3.51	0.51	47
	Total	9.77	1.29	47
A8	Arachnida	2.57	0.49	42
	Diptera	4.12	0.54	42
	Coleoptera	3.24	0.52	42
	Other	0.33	0.10	42
	Total	10.26	1.39	42

Appendix 5 (continued)

1976

Transect Number		Mean ($\bar{x}$)	Standard Error (S.E.)	Sample Size (n)
FIELD	Arachnida	2.35	0.40	47
	Diptera	3.26	0.37	47
	Coleoptera	1.57	0.38	47
	Other	0.45	0.15	47
	Total	7.62	0.99	47
B1	Arachnida	3.12	0.31	43
	Diptera	6.09	0.57	43
	Coleoptera	2.86	0.50	43
	Other	0.39	0.16	43
	Total	12.46	2.02	43
B2	Arachnida	2.29	0.40	45
	Diptera	5.87	0.84	45
	Coleoptera	1.95	0.47	45
	Other	1.09	0.34	45
	Total	11.20	1.21	45
B3	Arachnida	0.98	0.27	44
	Diptera	4.14	0.61	44
	Coleoptera	2.61	0.51	44
	Other	1.54	0.32	44
	Total	9.27	1.10	44
B4	Arachnida	1.34	0.26	47
	Diptera	2.70	0.42	47
	Coleoptera	1.96	0.43	47
	Other	0.53	0.43	47
	Total	6.45	0.88	47
B5	Arachnida	2.04	0.38	48
	Diptera	1.81	0.42	48
	Coleoptera	0.75	0.20	48
	Other	1.38	0.31	48
	Total	5.98	0.70	48
B6	Arachnida	0.83	0.20	46
	Diptera	2.95	0.55	46
	Coleoptera	1.59	0.48	46
	Other	1.98	0.34	46
	Total	7.35	1.19	46

Appendix 5 (continued)

1977

Transect Number		Mean ($\bar{x}$)	Standard Error (S.E.)	Sample Size (n)
A1	Arachnida	3.88	0.55	43
	Diptera	18.21	1.45	43
	Coleoptera	1.67	0.25	43
	Other	1.60	0.29	43
	Total	25.37	1.01	43
A2	Arachnida	3.24	0.48	45
	Diptera	11.58	2.73	45
	Coleoptera	5.07	0.46	45
	Other	2.33	0.36	45
	Total	22.22	1.56	45
A3	Arachnida	5.19	0.62	48
	Diptera	6.13	0.90	48
	Coleoptera	2.95	0.39	48
	Other	1.81	0.46	48
	Total	16.08	1.68	48
A4	Arachnida	3.44	0.59	48
	Diptera	3.90	0.82	48
	Coleoptera	3.19	0.74	48
	Other	0.79	0.21	48
	Total	11.32	1.89	48
A5	Arachnida	4.29	0.70	48
	Diptera	5.64	1.15	48
	Coleoptera	4.77	0.98	48
	Other	2.52	0.66	48
	Total	17.23	1.99	48
A6	Arachnida	2.21	0.55	48
	Diptera	3.06	0.58	48
	Coleoptera	1.44	0.39	48
	Other	1.04	0.31	48
	Total	7.75	1.33	48
A7	Arachnida	2.39	0.73	47
	Diptera	2.46	0.68	47
	Coleoptera	1.94	0.57	47
	Other	0.78	0.32	47
	Total	7.72	1.10	47
A8	Arachnida	1.69	0.41	48
	Diptera	2.06	0.49	48
	Coleoptera	2.23	0.53	48
	Other	0.92	0.22	48
	Total	6.90	1.24	48

Appendix 5 (continued)

1977

Transect Number		Mean ($\bar{x}$)	Standard Error (S.E.)	Sample Size (n)
FIELD	Arachnida	0.11	0.04	45
	Diptera	2.15	0.39	45
	Coleoptera	0.71	0.17	45
	Other	0.51	0.15	45
	Total	3.49	0.38	45
B1	Arachnida	1.49	0.28	47
	Diptera	5.44	0.47	47
	Coleoptera	1.28	0.28	47
	Other	0.55	0.19	47
	Total	8.76	1.08	47
B2	Arachnida	1.21	0.31	47
	Diptera	3.30	0.38	47
	Coleoptera	1.06	0.30	47
	Other	0.87	0.23	47
	Total	6.44	1.00	47
B3	Arachnida	1.59	0.30	46
	Diptera	4.26	0.58	46
	Coleoptera	1.85	0.43	46
	Other	0.30	0.11	46
	Total	8.00	1.09	46
B4	Arachnida	1.65	0.32	48
	Diptera	1.35	0.20	48
	Coleoptera	0.79	0.22	48
	Other	0.71	0.19	48
	Total	4.50	0.60	48
B5	Arachnida	1.58	0.34	48
	Diptera	2.71	0.40	48
	Coleoptera	1.10	0.25	48
	Other	0.98	0.24	48
	Total	6.37	0.85	48
B6	Arachnida	1.94	0.39	48
	Diptera	4.88	0.79	48
	Coleoptera	2.06	0.32	48
	Other	1.08	0.26	48
	Total	9.96	0.94	48

Appendix 6. Mean numbers of invertebrates per trap per transect point during each 5 day period, on Rockcliffe Marsh in 1976 and 1977.

1976

Collection Date		Mean ($\bar{x}$)	Standard Error (S.E.)	Sample Size (n)
30/4	Arachnida	1.65	0.34	49
	Diptera	4.24	0.49	49
	Coleoptera	1.02	0.13	49
	Other	0.76	0.17	49
	Total	7.67	0.90	49
5/5	Arachnida	3.15	0.37	53
	Diptera	9.23	0.78	53
	Coleoptera	2.34	0.45	53
	Other	1.74	0.28	53
	Total	16.45	1.71	53
10/5	Arachnida	2.38	0.40	58
	Diptera	11.07	0.86	58
	Coleoptera	3.14	0.49	58
	Other	2.34	0.42	58
	Total	18.93	2.23	58
15/5	Arachnida	2.87	0.41	60
	Diptera	7.83	0.90	60
	Coleoptera	4.78	0.43	60
	Other	3.33	0.57	60
	Total	18.82	2.00	60
20/5	Arachnida	2.29	0.36	59
	Diptera	6.66	1.14	59
	Coleoptera	3.64	0.41	59
	Other	2.93	0.40	59
	Total	15.52	1.43	59
25/5	Arachnida	1.82	0.36	60
	Diptera	3.78	0.74	60
	Coleoptera	2.95	0.34	60
	Other	0.93	0.20	60
	Total	9.48	0.98	60
30/5	Arachnida	1.65	0.23	58
	Diptera	3.43	0.35	58
	Coleoptera	1.43	0.20	58
	Other	1.53	0.37	58
	Total	8.05	0.97	58
4/6	Arachnida	2.71	0.25	58
	Diptera	4.45	0.77	58
	Coleoptera	2.00	0.24	58
	Other	1.97	0.39	58
	Total	11.12	0.75	58

Appendix 6 (continued)

Collection Date		Mean ($\bar{x}$)	Standard Error (S.E.)	Sample Size (n)
9/6	Arachnida	1.59	0.19	56
	Diptera	5.13	0.85	56
	Coleoptera	1.34	0.26	56
	Other	1.11	0.24	56
	Total	9.16	1.06	56
14/6	Arachnida	2.89	0.33	60
	Diptera	3.42	0.46	60
	Coleoptera	2.20	0.32	60
	Other	0.80	0.18	60
	Total	9.28	0.94	60
19/6	Arachnida	2.60	0.30	60
	Diptera	5.18	0.68	60
	Coleoptera	2.67	0.27	60
	Other	0.42	0.12	60
	Total	10.87	0.72	60
24/6	Arachnida	1.93	0.36	60
	Diptera	4.73	0.75	60
	Coleoptera	2.05	0.30	60
	Other	0.52	0.10	60
	Total	9.23	0.89	60
1977				
30/4	Arachnida	0.95	0.21	57
	Diptera	1.88	0.29	57
	Coleoptera	0.68	0.14	57
	Other	0.44	0.13	57
	Total	3.84	0.57	57
5/5	Arachnida	1.81	0.40	59
	Diptera	5.56	0.70	59
	Coleoptera	1.46	0.29	59
	Other	1.03	0.21	59
	Total	9.86	0.97	59
10/5	Arachnida	2.71	0.29	55
	Diptera	7.62	1.11	55
	Coleoptera	2.25	0.42	55
	Other	1.33	0.22	55
	Total	13.91	1.75	55
15/5	Arachnida	3.21	0.34	58
	Diptera	9.71	0.92	58
	Coleoptera	2.78	0.36	58
	Other	2.00	0.41	58
	Total	17.69	1.89	58

Appendix 6 (continued)

Collection Date		Mean $(\bar{x})$	Standard Error (S.E.)	Sample Size (n)
20/5	Arachnida	3.42	0.51	60
	Diptera	7.92	1.07	60
	Coleoptera	3.55	0.48	60
	Other	1.76	0.42	60
	Total	17.15	1.52	60
25/5	Arachnida	2.36	0.44	56
	Diptera	6.96	0.85	56
	Coleoptera	2.57	0.48	56
	Other	1.55	0.30	56
	Total	13.45	1.63	56
30/5	Arachnida	2.93	0.46	59
	Diptera	4.86	0.87	59
	Coleoptera	1.34	0.28	59
	Other	2.03	0.43	59
	Total	13.45	1.24	59
4/6	Arachnida	1.85	0.32	60
	Diptera	2.70	0.28	60
	Coleoptera	1.58	0.31	60
	Other	1.35	0.30	60
	Total	7.48	0.73	60
9/6	Arachnida	3.30	0.49	60
	Diptera	3.18	0.50	60
	Coleoptera	2.52	0.29	60
	Other	0.60	0.13	60
	Total	9.60	1.00	60
14/6	Arachnida	2.67	0.37	60
	Diptera	2.07	0.33	60
	Coleoptera	1.73	0.28	60
	Other	0.37	0.11	60
	Total	6.83	0.78	60
19/6	Arachnida	2.02	0.27	60
	Diptera	3.93	0.70	60
	Coleoptera	2.33	0.31	60
	Other	0.82	0.13	60
	Total	9.10	0.99	60
24/6	Arachnida	1.53	0.30	60
	Diptera	4.62	0.74	60
	Coleoptera	2.90	0.29	60
	Other	0.18	0.11	60
	Total	9.23	0.97	60

Appendix 7. Mean Biomass (mg.) of invertebrates per trap per 5 day period at each transect point, on Rockcliffe Marsh in 1976 and 1977.

1976

Transect Number		Mean ($\bar{x}$)	Standard Error (S.E.)	Sample Size (n)
A1	Arachnida	4.35	1.15	48
	Diptera	65.41	8.26	48
	Coleoptera	10.93	2.61	48
	Other	0.44	0.14	48
	Total	81.13	5.56	48
A2	Arachnida	4.57	1.28	45
	Diptera	100.93	9.19	45
	Coleoptera	13.89	2.92	45
	Other	0.27	0.10	45
	Total	119.67	10.17	45
A3	Arachnida	6.75	1.20	47
	Diptera	48.14	10.88	47
	Coleoptera	18.31	2.69	47
	Other	2.46	0.50	47
	Total	75.66	7.62	47
A4	Arachnida	4.02	0.60	48
	Diptera	20.92	1.74	48
	Coleoptera	4.78	0.75	48
	Other	0.25	0.11	48
	Total	29.97	1.92	48
A5	Arachnida	7.91	0.79	46
	Diptera	32.14	3.17	46
	Coleoptera	6.47	1.00	46
	Other	0.45	0.10	46
	Total	46.97		
A6	Arachnida	4.29	0.73	48
	Diptera	15.76	1.68	48
	Coleoptera	4.55	0.79	48
	Other	0.24	0.11	48
	Total	24.85	1.77	48
A7	Arachnida	2.65	0.55	47
	Diptera	6.92	1.08	47
	Coleoptera	5.07	1.16	47
	Other	1.38	0.24	47
	Total	16.02	1.63	47
A8	Arachnida	3.12	0.64	42
	Diptera	8.11	1.20	42
	Coleoptera	3.76	0.65	42
	Other	0.10	0.06	42
	Total	15.09	2.11	42

Appendix 7 (Continued)

1976

Transect Number		Mean ($\bar{x}$)	Standard Error (S.E.)	Sample Size (n)
FIELD	Arachnida	8.31	1.76	47
	Diptera	24.00	2.38	47
	Coleoptera	15.74	2.68	47
	Other	6.09	1.83	47
	Total	54.14	3.11	47
B1	Arachnida	5.34	0.56	43
	Diptera	45.44	5.32	43
	Coleoptera	12.45	1.51	43
	Other	0.72	0.14	43
	Total	63.96	6.97	43
B2	Arachnida	3.80	0.80	45
	Diptera	35.56	4.03	45
	Coleoptera	10.72	1.17	45
	Other	1.38	0.20	45
	Total	51.47	6.26	45
B3	Arachnida	2.41	0.37	44
	Diptera	22.85	2.38	44
	Coleoptera	6.17	0.74	44
	Other	0.54	0.09	44
	Total	31.97	4.49	44
B4	Arachnida	2.57	0.36	47
	Diptera	12.19	2.01	47
	Coleoptera	3.84	0.53	47
	Other	0.91	0.14	47
	Total	19.51	2.16	47
B5	Arachnida	2.86	0.45	48
	Diptera	5.43	0.77	48
	Coleoptera	2.75	0.42	48
	Other	1.52	0.19	48
	Total	12.56	1.46	48
B6	Arachnida	1.92	0.30	46
	Diptera	7.27	1.11	46
	Coleoptera	3.14	0.62	46
	Other	1.02	0.21	46
	Total	13.35	1.01	46

Appendix 7 (continued)

1977

Transect Number		Mean ($\bar{x}$)	Standard Error (S.E.)	Sample Size (n)
A1	Arachnida	3.61	0.51	43
	Diptera	74.02	8.18	43
	Coleoptera	8.54	1.24	43
	Other	0.30	0.17	43
	Total	86.47	7.08	43
A2	Arachnida	3.14	0.52	45
	Diptera	80.31	12.22	45
	Coleoptera	11.65	1.41	45
	Other	0.72	0.21	45
	Total	95.82	7.81	45
A3	Arachnida	5.14	0.82	48
	Diptera	37.42	4.80	48
	Coleoptera	11.02	1.42	48
	Other	1.87	0.26	48
	Total	55.45	7.14	48
A4	Arachnida	4.36	0.59	48
	Diptera	16.19	1.90	48
	Coleoptera	3.64	0.64	48
	Other	0.51	0.19	48
	Total	24.70	3.79	48
A5	Arachnida	6.83	0.89	48
	Diptera	25.72	3.83	48
	Coleoptera	7.13	1.10	48
	Other	0.68	0.11	48
	Total	40.36	5.13	48
A6	Arachnida	3.91	0.58	48
	Diptera	13.14	1.76	48
	Coleoptera	2.78	0.46	48
	Other	0.19	0.07	48
	Total	20.02	2.19	48
A7	Arachnida	3.26	0.45	47
	Diptera	8.73	1.38	47
	Coleoptera	4.04	0.71	47
	Other	0.75	0.12	47
	Total	16.78	1.98	47
A8	Arachnida	2.48	0.38	48
	Diptera	5.92	0.79	48
	Coleoptera	1.85	0.28	48
	Other	1.17	0.19	48
	Total	11.40	1.02	48

Appendix 7 (continued)

1977

Transect Number		Mean ($\bar{x}$)	Standard Error (S.E.)	Sample Size (m)
FIELD	Arachnida	2.87	0.37	45
	Diptera	13.67	1.78	45
	Coleoptera	7.31	2.44	45
	Other	6.43	1.35	45
	Total	30.28	3.51	45
B1	Arachnida	3.06	0.39	47
	Diptera	39.71	4.49	47
	Coleoptera	6.41	0.76	47
	Other	1.14	0.23	47
	Total	50.32	6.05	47
B2	Arachnida	2.25	0.42	47
	Diptera	30.18	3.98	47
	Coleoptera	6.53	1.01	47
	Other	1.81	0.29	47
	Total	40.77	4.90	47
B3	Arachnida	3.47	0.50	46
	Diptera	19.53	3.03	46
	Coleoptera	4.82	0.66	46
	Other	0.40	0.12	46
	Total	28.22	4.00	46
B4	Arachnida	1.95	0.31	48
	Diptera	9.62	1.60	48
	Coleoptera	2.58	0.41	48
	Other	1.13	0.32	48
	Total	15.28	2.21	48
B5	Arachnida	2.24	0.34	48
	Diptera	6.07	1.08	48
	Coleoptera	1.99	0.42	48
	Other	0.41	0.14	48
	Total	10.71	1.43	48
B6	Arachnida	1.54	0.24	48
	Diptera	8.10	1.14	48
	Coleoptera	2.83	0.52	48
	Other	0.47	0.18	48
	Total	12.94	1.39	48

Appendix 8.

METEOROLOGICAL OBSERVATIONS

METHODS

(i) RAINFALL

Daily measurements were taken, at 9.00 hours, of the depth of water, in mm, in a glass jar. The jar was embedded in the soil with its lip 50mm above ground level to prevent raindrops splashing into the vessel from adjacent areas. Overhanging vegetation was removed when necessary to preclude the possibility of water dripping into the jar.

(ii) AIR TEMPERATURE

A "Zeal" maximum and minimum registering thermometer was suspended in a shaded position 1m above ground level. The instrument was sensitive to 1°C. Readings were made twice daily, at 9.00 hours and 21.00 hours, and after each reading the thermometer was reset.

RESULTS

The mean maximum and minimum temperatures (°C) and mean rainfall (mm) over 5 day periods in 1976 and 1977, between April and July are illustrated in Figure 1.

During both 1976 and 1977 there was a decrease in monthly precipitation and an increase in mean monthly temperatures, both maximum and minimum, between April and July (Table 1).

TABLE 1. Annual and monthly climatic variation between April and July.

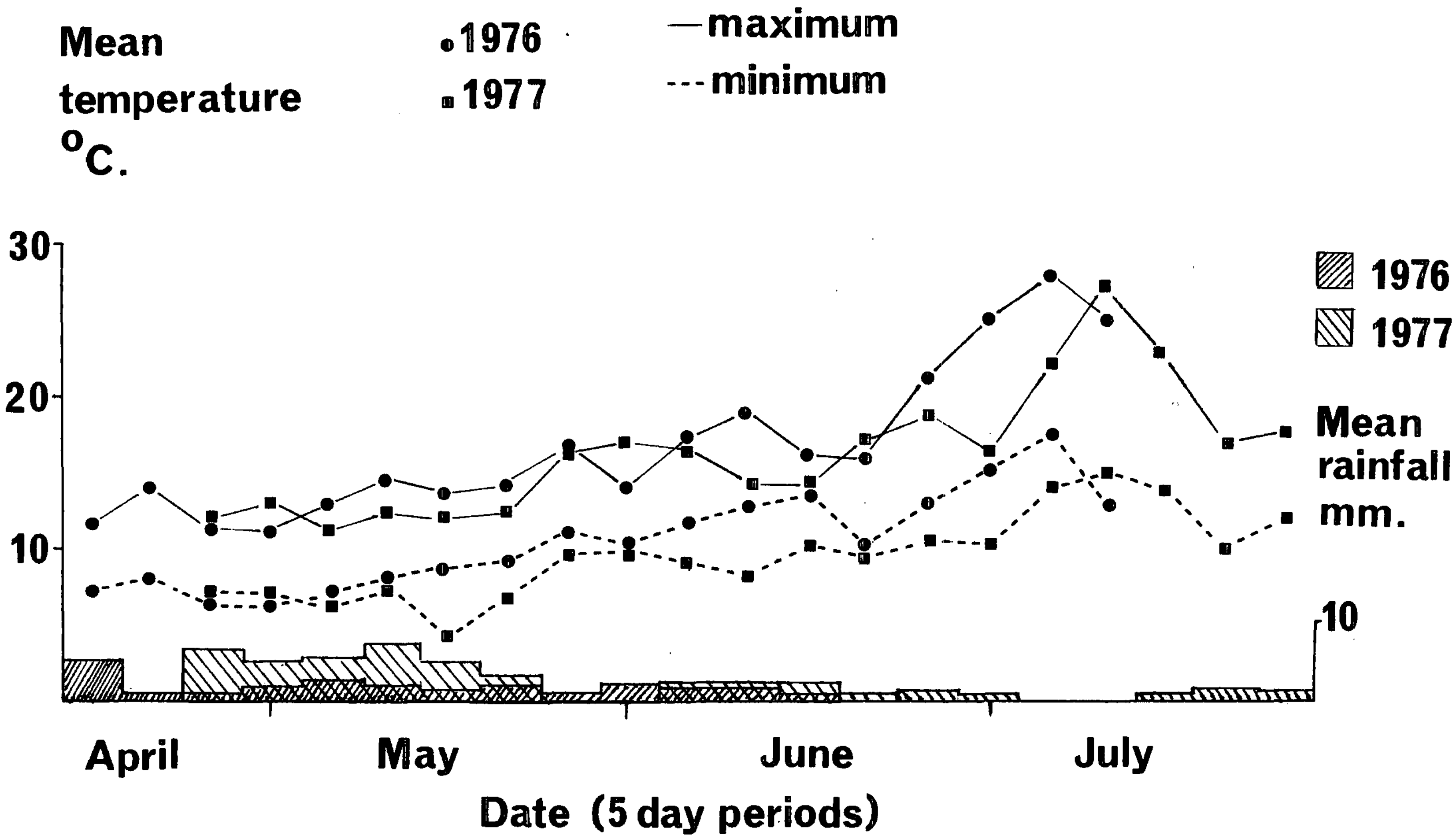
	MONTH	MEAN MAX. TEMP. (^{o}C)	MEAN MIN. TEMP. (^{o}C)	RAINFALL (mm)	ARIDITY INDEX
1976	APRIL	11.97	6.47	129	80.54
	MAY	13.51	7.83	123	71.41
	JUNE	18.97	12.04	79	37.17
	JULY	27.12	16.53	6	2.26
1977	APRIL	11.55	6.30	238	150.91
	MAY	14.06	6.84	133	78.04
	JUNE	16.45	10.75	108	55.15
	JULY	20.65	12.89	63	28.24

Martonne's (1926) Aridity Index, I, was used to provide a simple, relative monthly indication of aridity: $I = \frac{12p}{t+10}$

where p = monthly rainfall (mm.)
and t = mean monthly temperature (^{o}C)

It is not possible to statistically compare the aridity indices, but for the four months the aridity indices were consistently lower, in April and July markedly so, in 1976 than in 1977.

Figure 1. Mean maximum and minimum temperatures (^{o}C) and mean rainfall (mm) over 5 day periods between April and July, in 1976 and 1977 on Rockcliffe Marsh. Measurements were taken between 13 April and 11 July in 1976 and 23 April to 26 July in 1977.


Mean temperature °C.
● 1976
▪ 1977
— maximum
--- minimum
30
20
10
▨ 1976
▧ 1977
Mean rainfall mm.
10
April
May
June
July
Date (5 day periods)

Appendix 9. Summary of information on laying interval, incubation period, chipping period and fledging period of Lapwings, Oystercatchers and Redshanks on Rockcliffe Marsh, 1974 and 1976-1978.

	Mean	S.E.	Sample size	Range
Laying interval				
Lapwing	40.8	2.1	25	30-72 hours
Oystercatcher	38.7	3.5	19	24-72 "
Redshank	37.5	3.0	14	24-48 "
Incubation period				
Lapwing	23.9	0.3	48	19-29 days
Oystercatcher	26.1	0.2	36	24-30 "
Redshank	23.7	0.2	34	21-27 "
Chipping period				
Lapwing	64.3	4.1	21	42-100 hours
Oystercatcher	70.5	3.6	18	42-108 "
Redshank	70.9	9.4	8	36-110 "
Fledging period				
Lapwing	40.1	0.6	27	32-46 days
Oystercatcher	33.4	0.9	15	27-39 "
Redshank	26.8	0.5	14	24-30 "

Appendix 10. Potential predators of the eggs, young and adults of wading birds recorded on Rockcliffe Marsh, 1974-1978, with published records and personal observations of predation during the breeding season.
Numerals refer to the authorities, and letters to the stage predated; adult (a), chick (y), egg (e).

	Prey species				
Predator	Lapwing	Oyster-catcher	Redshank	Dunlin	Ringed Plover
Sparrowhawk	16a,17a	16a	16a	16a	
Buzzard	16a				
Peregrine	16a,17a	16a	16a,17a	16a,17a	16a
Merlin	9y,16ay, 17a		9a,16a 17a	9a,16a	16a
Kestrel	16ay,17y		16a,17y	12y	
Black-headed Gull	11e, 17ey	17e	14e		
Lesser Black-backed Gull	16a,17ey	17e	14e,39a		
Great Black-backed Gull	15y,17y	6y	6y		
Herring Gull	2e,7ey, 17ey	7ey,13ey, 17ey	2e,16a, 17ey		
Barn Owl	3a			16a	
Short-eared Owl	3a,16y		3a	3a,16a	3a
Little Owl	3a,16a				
Grey Heron	10y		16y	16y	
Rook	16ey,17e	17e	14e		
Carrion Crow	16e,17ey	17e	14e, 16e,17e	12y	
Magpie			14e		
Stoat	1e,17y	17y	17y	12ay	4a
Weasel	17y				
Fox	5a	8e		12y	8e

Appendix 10 (continued)

Predator	Lapwing	Oyster-catcher	Prey species Redshank	Dunlin	Ringed Plover
Dog	17ey				17y
Cow	17e	17e			
Water Vole				12e	

Authorities

1. Baldwin (1903)
2. Bruyns (1958)
3. Glue (1972)
4. Graham (1890)
5. Groszczynski (1974)
6. Groundwater (1974)
7. Harris (1965)
8. Kruuk (1964)
9. Newton *et al.* (1978)
10. Owen (1955)
11. Robson & Williamson (1972)
12. Soikkeli (1967)
13. Spaans (1971)
14. Thomas (1942)
15. Wilson (1973)
16. Witherby *et al.* (1940)
17. Pers. obs.

Appendix 11. Cohort life table for Lapwing eggs and chicks, with age intervals of 4 days, on Rockcliffe Marsh, in 1976 and 1977. Symbols explained in Section 7.

1976		l_x	d_x	L_x	e_x	q_x
Days after laying	0	176	38	157.0	6.9	0.22
	4	138	20	128.0	7.7	0.14
	8	118	12	112.0	7.9	0.10
	12	106	6	103.0	7.8	0.06
	16	100	4	98.0	7.2	0.04
	20	96	3	94.5	6.5	0.03
	24/0	93	18	84.0	5.7	0.19
Days after hatching	4	75	15	67.5	5.9	0.20
	8	60	9	55.5	6.3	0.15
	12	51	7	48.0	6.3	0.14
	16	44	3	42.5	6.2	0.07
	20	41	1	40.5	5.6	0.02
	24	40	1	39.5	4.8	0.03
	28	39	1	38.5	3.9	0.03
	32	38	1	38.0	3.0	0.00
	36	38	0	37.5	2.0	0.03
	40	37	1	37.0	1.0	0.00
	44	37	-	-	-	-
1977						
Days after laying	0	202	48	178.0	5.8	0.24
	4	154	23	142.5	6.5	0.15
	8	131	15	123.5	6.6	0.11
	12	116	9	111.5	6.3	0.08
	16	107	8	103.0	5.8	0.07
	20	99	4	97.0	5.3	0.04
	24/0	95	24	83.0	4.5	0.25
	4	71	18	56.0	4.8	0.25
	8	53	10	48.0	5.4	0.19
	12	43	8	39.0	5.5	0.19
	16	35	3	33.5	5.7	0.09
	20	32	2	31.0	5.2	0.06
	24	30	1	29.5	4.5	0.03
	28	29	2	28.0	3.6	0.07
	32	27	1	26.5	2.9	0.04
	36	26	1	25.5	1.9	0.04
	40	25	0	25.0	1.0	0.00
	44	25	-	-	-	-

Appendix 12. Cohort life table for Oystercatcher eggs and pulli, with age intervals of 4 days, (and 2 days around hatching date), on Rockcliffe Marsh, in 1976 and 1977. Symbols explained in Section 7.

1976		l_x	d_x	L_x	e_x	q_x
Days after laying	0	94	19	84.5	6.9	0.20
	4	75	15	67.5	7.4	0.20
	8	60	8	56.0	7.7	0.13
	12	52	8	48.0	7.8	0.15
	16	44	4	42.0	7.8	0.09
	20	40	3	38.5	7.4	0.08
	24	37	1	36.5	6.7	0.03
Days after hatching	26/0	36	6	33.0	6.4	0.17
	4	30	4	28.0	6.3	0.13
	8	26	3	24.5	6.1	0.12
	12	23	1	22.5	5.5	0.04
	16	22	1	21.5	4.7	0.05
	20	21	0	21.0	3.8	0.00
	24	21	1	20.5	2.9	0.05
	28	20	1	19.5	2.0	0.05
	32	19	0	19.0	1.0	0.00
	36	19	-	-	-	-

1977						
Days after laying	0	99	21	88.5	6.1	0.21
	4	78	17	69.5	6.5	0.22
	8	61	10	56.0	6.8	0.16
	12	51	9	46.5	7.0	0.18
	16	42	5	39.5	7.1	0.12
	20	37	5	34.5	6.9	0.14
	24	32	2	31.0	6.6	0.06
Days after hatching	26/0	30	5	27.5	6.3	0.17
	4	25	3	23.5	6.2	0.12
	8	22	2	21.0	5.9	0.09
	12	20	1	19.5	5.2	0.05
	16	19	1	18.5	4.5	0.05
	20	18	1	17.5	3.7	0.06
	24	17	1	16.5	2.8	0.06
	28	16	1	15.5	1.9	0.06
	32	15	1	14.5	1.0	0.07
	36	14	-	-	-	-

Appendix 13. Cohort life table for Redshank eggs and chicks, with age intervals of 4 days, on Rockcliffe Marsh in 1976 and 1977. Symbols explained in Section 7.

1976		l_x	d_x	L_x	e_x	q_x
Days after laying	0	104	32	88.0	5.4	0.31
	4	72	13	65.5	5.9	0.18
	8	59	6	56.0	5.8	0.10
	12	53	5	50.5	5.3	0.09
	16	48	5	45.5	4.8	0.10
	20	43	4	41.0	4.2	0.09
	24/0	39	11	33.5	3.9	0.28
Days after hatching	4	28	6	25.0	3.9	0.21
	8	22	5	19.5	3.7	0.22
	12	17	3	15.5	3.3	0.18
	16	14	2	13.0	2.8	0.14
	20	12	0	12.0	2.0	0.00
	24	12	1	11.5	1.0	0.08
	28	11	-	-	-	-

1977						
Days after laying	0	96	36	78.0	4.5	0.38
	4	60	15	52.5	5.3	0.25
	8	45	7	41.5	5.4	0.16
	12	38	5	35.5	5.1	0.13
	16	33	6	30.0	4.9	0.18
	20	27	4	25.0	4.7	0.15
	24/0	23	7	19.5	4.7	0.30
Days after hatching	4	16	3	14.5	5.0	0.19
	8	13	1	12.5	4.6	0.08
	12	12	0	12.0	3.8	0.00
	16	12	1	11.5	2.9	0.08
	20	11	0	11.0	2.0	0.00
	24	11	0	11.0	1.0	0.00
	28	11	-	-	-	-

Appendix 14. Mean old cowpat density ha^{-1} around each nest commenced prior to 4 May in 1976 and 5 May in 1977 (the dates on which the cattle were introduced) of each wader species, and around each transect point, grouped according to vegetation type, in 1976 and 1977 on Rockcliffe Marsh. Transect data were derived from table 11. No Oystercatcher nests were commenced in vegetation types Field and T8-4, prior to 5 May in 1977. The sample size is N.

Cowpat density ha^{-1} around;	VEGETATION TYPES				
	FIELD	T8	T7	T6	T4
1976					
Transect points	37.5	66.0	59.0	43.2	22.7
Mean	6.5	4.0	6.7	4.5	3.2
S.E.	2	2	4	4	12
N.					
Lapwing nests					
Mean	31.5	59.2	52.3	48.0	30.9
S.E.	6.2	2.4	5.3	2.5	3.3
N.	3	16	7	8	11
Oystercatcher					
nests Mean	-	60	-	37	29.4
S.E.	-	-	-	-	4.8
N.	-	1	-	1	6
Redshank nests					
Mean	-	61.3	55.6	40	26.6
S.E.	-	5.1	4.8	-	3.0
N.	-	3	8	1	12
1977					
Transect points					
Mean	43.5	71.0	53.7	49.5	26.5
S.E.	9.5	14.0	7.3	2.9	3.1
N.	2	2	4	4	12
Lapwing nests					
Mean	46.7	68.5	55.8	-	-
S.E.	3.5	6.6	5.4	-	-
N.	13	2	6	-	-
Redshank nests					
Mean	-	63	52.0	47.5	-
S.E.	-	-	3.0	2.5	-
N.	-	1	2	2	-

Appendix 15. Measurement and scoring of habitat variables around each nest and non-nest site on Rockcliffe Marsh.

FACTOR	SYMBOL	SCORING/MEASUREMENT
Distance to nearest plateau (terrace) edge	PLE	Measured with 300m tape measure or paced (1 pace approximately 0.75m) to nearest metre.
Distance to nearest creek edge	CRE	As above.
Distance to nearest nests of:		
Black-headed Gull	BHG	As above, in some cases using 1m:1mm scale map
Lapwing	LAP	"
Oystercatcher	OIK	"
Redshank	RED	"
Dunlin	DUN	"
Ringed Plover	RP	"
Substrate at site	SUB	Scored; soil as 0, gravel as 1.
Substrate consistency at site	CON	Scored; firm as 0, loose as 1.
Flat or slope at site	FLS	Scored; flat as 0, slope as 1 (slopes were very gentle on Rockcliffe Marsh).
Raised or hollow at site	RH	Scored; raised as 0, hollow as 1.
Humus content of substrate at site	HU	An increasing, subjective scale of 0-3, from no humus to a high humus content.
Evenness of terrain at site	EV	An increasing, subjective scale of 1-4, from flat to many undulations, excluding vegetation profile.
Debris abundance within 20m radius of site	DEB	An increasing, subjective scale of 0-5.
Tussock density m^{-2} at site	TU	Counts of tussocks m^{-2}; range 0-12.
Mean tussock height at site	TUHT	Mean height of nearest tussocks, measured to top of dense tussock mat, within an area of $1m^2$ at site, to nearest mm. If no tussocks were present, tussock height was 0mm.

Appendix 15 (continued)

FACTOR	SYMBOL	SCORING/MEASUREMENT
Maximum grass height at site	GRHT	Greatest height of grass (excluding tussocks) from substrate to height of naturally standing sward; measured to nearest mm.
Cowpat density ha^{-1} (fresh only)	NOC	Measured as in Section 6, but with only two intervals of 7 days at each site.
Vegetation Type	VEG	Each vegetation type was treated as a separate variable; the programme constructed a matrix such that, for example when VEG = T3, T3 = 1, and all other vegetation types were scored as 0.

Appendix 16. Correlation matrices of a selection of habitat variables on Rockcliffe Marsh in 1976, 1977 and 1976 and 1977. The correlation coefficients are based on random samples. The degrees of freedom were 98 in each year and 198 in 1976 and 1977. Significant values (p ∠0.05) are indicated by *. The symbols of the habitat variables are explained in Appendix 15.

Habitat variables	Habitat variables					
	PLE	CRE	SUB	CON	HU	DEB
1976						
RH	-0.10	-0.08	0.07	0.05	0.03	-0.00
PLE		0.01	0.04	-0.23*	0.28*	0.25*
CRE			0.03	0.05	-0.04	0.05
SUB				0.14	-0.22*	0.01
CON					-0.62*	-0.18
HU						0.26*

	FLS	EV	TU	TUHT	GRHT	NOC
RH	0.13	-0.07	0.02	-0.07	-0.08	-0.07
PLE	0.14	0.19	0.40*	0.27*	0.16	0.46*
CRE	-0.06	-0.02	-0.05	-0.11	0.03	-0.14
SUB	-0.03	-0.11	-0.08	-0.11	0.06	-0.57*
CON	-0.04	-0.18	-0.19	-0.17	-0.11	-0.35*
HU	-0.07	0.13	0.53*	0.66	0.57*	0.56*
DEB	0.09	0.10	0.24*	0.02	0.05	0.21*
FLS		0.16	-0.12	0.09	0.04	0.08
EV			0.16	0.18	0.14	0.33*
TU				0.67*	0.16	0.38*
TUHT					0.17	0.60*
GRHT						0.42*

1977	PLE	CRE	SUB	CON	HU	DEB
RH	-0.10	-0.16	0.06	0.06	0.03	-0.04
PLE		0.08	0.09	-0.25*	0.42*	0.12
CRE			0.07	-0.08	-0.01	0.18
SUB				0.11	-0.29*	0.06
CON					-0.53*	0.04
HU						0.03

	FLS	EV	TU	TUHT	GRHT	NOC
RH	-0.14	-0.06	-0.13	-0.13	0.06	-0.03
PLE	0.07	0.02	0.28*	0.25*	-0.01	0.49*
CRE	0.12	-0.13	0.10	0.18	-0.01	0.06
SUB	0.01	0.04	-0.12	-0.16	-0.06	-0.27*
CON	-0.06	-0.13	-0.02	-0.03	0.04	-0.21*
HU	-0.04	0.17	0.42*	0.47*	0.33*	0.65*
DEB	-0.11	0.05	0.11	0.03	-0.01	0.20*
FLS		0.11	0.15	0.17	-0.05	-0.01
EV			0.17	0.15	0.10	0.21*
TU				0.71*	0.13	0.34*
TUHT					0.19	0.46*
GRHT						0.23*

1976 & 1977

	PLE	CRE	SUB	CON	HU	DEB
RH	-0.12	-0.09	0.03	0.06	0.03	-0.03
PLE		0.04	0.13	-0.19*	0.35*	0.13
CRE			0.05	0.03	-0.03	0.08
SUB				0.12	-0.34*	0.00
CON					-0.40*	-0.03
HU						0.09

	FLS	EV	TU	TUHT	GRHT	NOC
RH	0.03	-0.11	-0.10	-0.08	-0.04	-0.12
PLE	0.04	0.12	0.46*	0.33*	0.08	0.45*
CRE	0.05	-0.04	0.11	0.11	-0.02	-0.05
SUB	0.01	-0.03	-0.12	-0.17	-0.07	-0.27*
CON	-0.05	-0.22*	-0.18	-0.24*	-0.09	-0.25*
HU	-0.08	0.32*	0.37*	0.46*	0.41*	0.51*
DEB	-0.03	0.19*	0.13	0.07	0.08	0.13
FLS		0.12	-0.01	-0.00	-0.00	0.05
EV			0.27*	0.20*	0.09	0.27*
TU				0.63*	0.13	0.44*
TUHT					0.25*	0.34*
GRHT						0.21*

Appendix 17. Correlation coefficients between each vegetation type and a selection of habitat variables on Rockcliffe Marsh in 1976, 1977 and 1976 & 1977. Significant correlations (p ∠ 0.05) were indicated by *; df was 98 in both years, and 198 in 1976 & 1977. Symbols are explained in Appendix 14.

Habitat variables								
1976								
RH	0.07	0.03	0.07	0.08	0.10	0.03	0.08	0.07
PLE	0.26*	0.39*	0.20*	0.35*	0.18	-0.17	-0.32*	0.04
CRE	0.12	0.05	-0.17	0.00	-0.12	0.07	0.02	0.03
SUB	-0.01	-0.01	-0.03	-0.02	-0.01	-0.08	-0.05	1.00*
CON	-0.05	-0.09	0.10	-0.14	-0.06	-0.43*	0.52*	0.14
HU	0.07	0.15	0.19	0.23*	0.10	0.33*	-0.61*	-0.22*
DEB	-0.06	0.06	-0.01	0.13	0.17	0.15	-0.28*	0.01
FLS	-0.03	0.17	-0.08	-0.02	0.09	-0.11	0.06	-0.03
EV	0.01	0.24*	0.29*	0.21	0.17	0.03	-0.40*	-0.11
TU	0.03	0.12	0.26*	0.11	0.19	0.07	-0.38*	-0.08
TUHT	-0.01	0.15	0.43*	0.13	0.04	0.13	-0.62*	-0.12
GRHT	-0.08	0.05	0.33*	0.23*	0.14	0.09	-0.25*	-0.23*
NOC	-0.07	0.33*	0.53*	0.32*	0.15	-0.03	-0.64*	-0.11
1977								
RH	-0.09	0.00	0.01	0.01	0.00	-0.17	0.15	0.10
PLE	0.27*	0.42*	0.38*	0.47*	0.12	-0.19	-0.33*	0.08
CRE	0.00	-0.16	0.10	0.06	-0.05	0.18	-0.15	-0.09
SUB	-0.12	-0.03	-0.05	-0.06	-0.03	-0.08	-0.03	1.00*
CON	-0.12	0.10	0.02	0.05	0.11	-0.44*	0.34*	0.15
HU	0.14	0.19	0.26*	0.38*	0.19	0.21*	-0.47*	-0.30*
DEB	-0.07	0.38*	0.16	0.06	-0.03	0.10	0.16	0.01
FLS	-0.06	0.06	0.04	-0.07	0.06	0.14	-0.15	-0.02
EV	-0.06	0.22*	0.24*	0.24*	0.02	0.14	-0.32*	-0.05
TU	0.03	0.02	0.33*	0.18	0.22*	0.01	-0.38*	-0.13
TUHT	0.11	0.11	0.37*	0.19	0.14	0.12	-0.47*	-0.18
GRHT	0.03	0.01	0.23*	0.11	0.02	0.15	-0.30*	-0.26*
NOC	0.04	0.26*	0.51*	0.45*	0.05	0.06	-0.59*	-0.17
1976 & 1977								
RH	-0.03	-0.03	-0.09	-0.01	0.04	0.00	0.09	0.03
PLE	0.27*	0.54*	0.17*	0.24*	0.09	-0.14*	-0.32*	0.12
CRE	0.06	-0.05	-0.05	-0.05	-0.07	0.13	-0.09	0.05
SUB	-0.01	-0.06	-0.04	-0.08	-0.00	-0.10	-0.08	1.00*
CON	-0.06	-0.10	0.04	-0.06	0.01	-0.22*	0.30*	0.16*
HU	0.08	0.21*	0.11	0.21*	0.12	0.24*	-0.39	-0.34*
DEB	-0.08	0.04	-0.06	0.07	0.06	0.10	-0.17*	0.00
FLS	-0.04	0.00	-0.02	0.02	0.13	0.01	-0.04	0.01
EV	0.12	0.18*	0.19*	0.05	0.09	-0.01	-0.21*	-0.03
TU	0.04	-0.01	0.31*	0.01	0.20*	0.10	-0.20*	-0.11
TUHT	-0.00	-0.01	0.24*	0.08	0.09	0.12	-0.33*	-0.16*
GRHT	-0.01	0.02	0.25*	0.03	0.07	0.10	-0.27*	-0.27*
NOC	-0.07	0.35*	0.37*	0.31*	0.07	0.11	-0.56*	-0.19*