

**INDIVIDUAL DIFFERENCES IN FORAGING BEHAVIOUR,
HABITAT SELECTION AND BILL MORPHOLOGY OF
WINTERING CURLEW, *NUMENIUS ARQUATA*.**

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To Julianne, for making it all complete.

*" Half of the people can be part right all of the time,
Some of the people can be all right part of the time,
But all of the people can't be all right all of the time.'
I think Abraham Lincon said that.
'I'll let you be in my dream if I can be in yours'
I said that."*

BOB DYLAN 1963.

DECLARATION

**I hereby declare that this thesis has been composed
by myself and the work described within it is my
own except where duly acknowledged.**

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ABSTRACT

The foraging and roosting behaviour of wintering curlew, *Numenius arquata*, were studied between August 1984 and April 1987, on a rocky shore in S.E. Scotland. In all 140 birds were individually colour-ringed. On capture standard biometrics were recorded and a close up photographic transparency of the bill was taken laterally to allow precise measurement of bill decurvature to be made. Within-sex coefficients of variation of bill measurements were extremely high (20.8% for bill-shape index ~~index~~ in females). Radio-transmitters were attached to five birds to obtain detailed information on ranging behaviour and habitat selection. Individual birds specialised in the microhabitat they exploited. Bill shape was important in determining niche utilisation; birds with relatively short, thick, straight bills tended to feed in field habitats, whilst birds with long, thin, decurved bills tended to be intertidal specialists. The diversity of bill use exhibited by intertidal specialists was greater than that shown by field-feeding specialists. The area exploited by field feeders was far greater than that used by intertidal specialists. Birds on the intertidal zone tended to feed solitarily, sometimes defending territories, whilst those which fed on fields formed flocks. It was concluded that the variation in phenotype and foraging behaviour between individual birds was probably the result of disruptive selection and could be explained by the niche variation hypothesis.

Vigilance behaviour in roosting flocks was investigated. As expected, the proportion of birds vigilant at any given time decreased with flock size, but reached an asymptote at about 30 birds; thereafter vigilance levels were constant and predictable. To test whether vigilance levels were being regulated in some way, decoy birds in 'look up' postures were positioned at roost sites. This had the effect of significantly reducing vigilance levels of live birds. It was concluded that curlew can assess the number of vigilant birds in their flock and adjust their own behaviour accordingly.

CHAPTER 1.

GENERAL INTRODUCTION AND STUDY SITE.

*"Take me disappearin' through the smoke rings of my mind,
Down the foggy ruins of time, far past the frozen leaves,
The haunted, frightened trees, out to the windy beach,
Far from the twisted reach of crazy sorrow.
To dance beneath the diamond sky with one hand waving free,
Silhouetted by the sea, circled by the circus sands,
With all memory and fate driven deep beneath the waves,
Let me forget about today until tomorrow."*

BOB DYLAN, 1964.

During the past 20 years or so there has been a dramatic increase in the volume of research on wintering waders (shorebirds). This period has also seen a dichotomy in the approach of behavioural scientists to these birds. At one level qualitative and quantitative data have accumulated on foraging behaviour and feeding ecology (*e.g.* Drinnan 1957, Norton-Griffiths 1967, Goss-Custard 1969, 1970a, Heppleston 1971, Baker 1974, Smith 1975 and Hulscher 1981). As this research progressed, the complexity of the relationship between waders and their environment became increasingly obvious. Many more recent studies have concentrated on the identification and detailed measurement of the biotic and abiotic variables that affect wader foraging behaviour (*e.g.* Evans 1976, 1979, Goss-Custard 1977a, Pienkowski 1981, 1983, Rands & Barkham 1981). Other researchers have investigated in more detail specific problems such as optimality in foraging (Goss-Custard 1977b), or survival in severe conditions (Davidson 1981, Davidson & Evans 1982). One might ask why so much attention has been paid to the ecology of wintering waders: there are two reasons. First, the estuarine ecosystem (to which most studies have been confined) affords easy access to the inquisitive. Few other habitats provide the opportunity for prolonged observation and precise measurement of predatory behaviour. Both biotic and abiotic variables, although complex, can be relatively easily measured; for instance predator dispersion can be determined (*e.g.* Goss-Custard 1976), prey availability can be sampled (*e.g.* Dugan 1981, Evans 1987), and the effect of temperature on both assessed (*e.g.* Clark 1983). In this way, by continued research our understanding of the operation of an entire ecosystem –and the effect of *Homo sapiens* upon it– will become more complete.

This leads to the second, more sinister reason for the recent proliferation of wader research. The threat to the ecological balance of estuaries, not just in the developed, but also, perhaps more seriously, in developing countries

(Parish 1987), is increasing. Well publicised hazards include reclamation schemes, industrial pollution and tidal barrage schemes. Waders, as predators, are good indicators of habitat 'quality' and several studies have been designed specifically to assess the environmental impact of reclamation schemes (*e.g.* Goss-Custard 1977c, Evans *et al.* 1979).

Recently there have been several useful reviews of the topics outlined above (Evans 1981, Burger 1984, Goss-Custard 1984, Pienkowski *et al.* 1984, Puttick 1984, Piersma 1987). These serve both to highlight the successes of the past two decades in unravelling the complex web of environmental variables that determine shorebird behaviours and to emphasise the need for further research. One area in particular stands out as requiring more attention and here lies the dichotomy mentioned earlier.

Studies of other birds have revealed differences in feeding behaviour and foraging efficiency between intraspecific classes of individuals. Young birds are often less efficient than adults in locating and/or harvesting prey (Ashmole & Tovar 1968, Orians 1969, Recher & Recher 1969, Buckley & Buckley 1974). Differences in the feeding patterns of male and female conspecifics have been documented in diverse groups of birds (*e.g.* woodpeckers, Selander 1966, Kilham 1970, Hogstad 1976, Peters & Grubb 1983; finches, Newton 1967; warblers, Morse 1968; crows, Holyoak 1970 and hawks, Newton 1986). Further, differences in the foraging abilities of individuals within age/sex classes have been recorded (Partridge 1976a). Techniques for catching and colour marking waders have improved tremendously since the development of cannon-netting in the mid 1960's. With the ability to identify individuals in the field came the discovery among waders of variation in foraging behaviour between intraspecific age (Groves 1978 Burger 1980), and sex (Puttick 1981) classes similar to that found in other species of bird. Additionally individual variation has been documented in spacing behaviour (Myers 1984) and foraging ability

(Goss-Custard & Durell 1983, Goss-Custard & Sutherland 1984, Whitfield 1985a, and Goss-Custard 1986).

The question of why individuals should vary so dramatically in their behaviour can only be answered through further research. Over the past 25 years the thesis that selection occurs predominantly at the level of the individual has become central to evolutionary thought, therefore to comprehend evolutionary processes more fully it is necessary to look at differences between individuals. The measurement of phenotypic variation in a behaviour, especially if this can be related to morphological variation and habitat utilization, can help us understand the selective forces in operation (Van Valen 1965, Grant *et al* 1976, Roughgarden 1972). It has been suggested that individual differences in foraging technique may serve to reduce intraspecific competition and thus permit a greater population size (e.g. Van Valen 1965, Smith 1987). Partridge & Green (1985) indicate that individual feeding specialisations may have a profound effect on the population dynamics of both predator and prey.

Although there now exist two distinct levels of research (population and feeding ecology vs. individual ethology) it must be borne in mind that the two will always be inter-dependent. To recapitulate then, individual variation in the foraging behaviour of waders has been identified as a biotic variable that may affect the population biology of the waders themselves, as well as their prey. As such it is a subject worthy of further study, but why choose curlew, *Numenius arquata*, as the study species and why on a rocky shore? I shall deal with these questions in turn.

Curlew exhibit a large degree of sexual dimorphism (Cramp & Simmons 1983). in fact sex can be assigned to the vast majority of individuals on measurement of bill length alone (Prater *et al* 1977, Cramp & Simmons 1983, Townshend 1981a). Moreover there is considerable variation in bill length and

decurvature within sex classes (see Section 3.2). This led to the hope that any variation in feeding efficiency discovered might be related to bill morphology. Differences in the diet of male and female curlew have already been documented (Zwarts 1979, Townshend 1981a). Sex related differences in foraging have been related to bill morphology before (Selander 1966, Newton 1967, 1986, Puttick 1981), but few studies have looked at this relationship at the individual level. Recently bill morphology has been shown to influence intraspecific niche utilization in the African estrildid finch, *Pyrenestes ostrinus*, (Smith 1987) and to constrain feeding behaviour in Darwin's medium ground finch, *Geospiza fortis* (Grant *et al* 1976, Price 1987). Differences in bill phenotype have been shown to relate to individual feeding specialisations in oystercatcher, *Haematopus ostralegus*, but these are largely the result of environmental influence rather than genotype (Swennen *et al.* 1983). Gosler (1987) not only found a relationship between bill morphology and niche utilization in the great tit, *Parus major*, but was able to show that seasonal variation in bill shape was related to seasonality in food supplies.

The vast bulk of research on wintering waders has been carried out on estuaries, rather than rocky shores (but see Baker 1981, Marshall 1981, Whitfield 1985a). This is perhaps the result of the ease of observation of the birds on mudflats and the threat to estuaries already discussed. A large percentage of many wader populations, however, winter on rocky shores (Moser & Summers 1987). The results of the Winter Shorebird Count 1984-85 (Moser & Summers 1987) suggest that at least 5000 curlew utilise non-estuarine coasts in Britain. It is possible that rocky shores offer refuge in severe weather, when estuarine and terrestrial habitats become unsuitable for feeding. As Whitfield (1985a) points out, rocky shores are in much less danger of destruction than estuaries and could conceivably support a proportion of birds displaced by loss of estuaries: their ecology thus demands further study.

Additionally, the study site chosen appeared to offer a greater array and increased diversity of microhabitats to the birds than would an estuary. I reasoned that the greater the environmental complexity, the greater the chance of variation in feeding behaviour being evident (Van Valen 1965).

Interindividual differences in phenotype are a recurring theme throughout this thesis. In chapter 2 I document population size, migration patterns and mortality. Chapter 3 is concerned with the measurement of phenotypic variation in both morphology and behaviour as related to habitat utilization. In chapter 4 I describe the spacing and ranging behaviour of individual birds. Roosting behaviour and vigilance are examined in chapter 5. Flocking and vigilance may seem strange subsidiary subjects to choose, in view of the recent abundance of literature on these topics (see Barnard & Thompson 1985, or Chapter 5 for reviews). Most of these papers deal with feeding rather than roosting flocks. The large amount of time spent by curlew in communal roosts and the high level of disturbance at the study site (eliciting a high level of vigilance) encouraged me to investigate these behaviours.

1.1 THE STUDY SITE

Lying approximately 50km north-east of Edinburgh, Scotland, the study site comprised some 6km of the East Lothian coastline. (Fig.1.1). Curlew frequented both the littoral zone and the hinterland, up to 1km from the shore. Broadly speaking the site is divisible into two main regions, which I shall refer to as Scoughall and Tynninghame.

Scoughall

Scoughall (Fig.1.2) lies in the north, extending from Tantallon Castle ($56^{\circ} 03'N$ $02^{\circ} 38'W$) to Peffer Sands ($56^{\circ} 02'N$ $02^{\circ} 36'W$). Between Tantallon Castle and The Gegan, cliffs overlook a narrow band of rock which is largely devoid of fucoid seaweed and therefore somewhat unsuitable for curlew, as is the long stretch of sand comprising Seacliff Beach. The Great Car is a rocky islet,

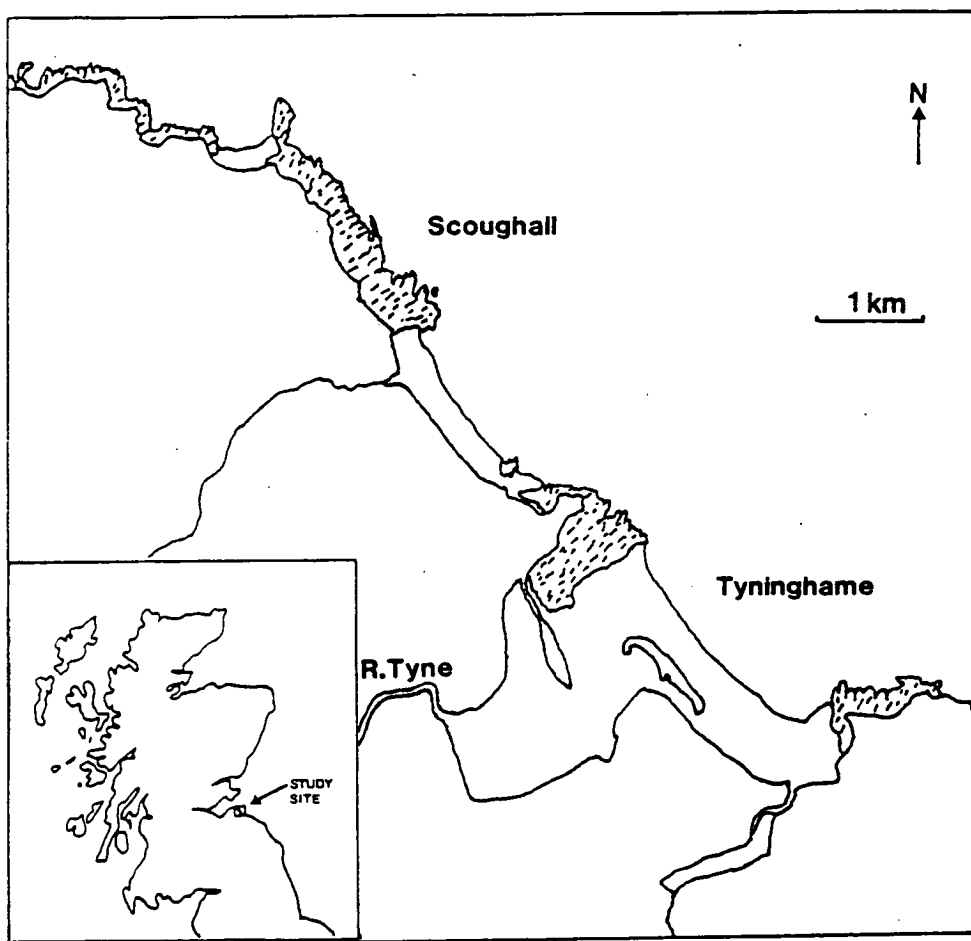


Fig. 1.1. The study site with inset showing location in Scotland.

isolated from the shore for 8 hours of every tidal cycle and is a favoured roost site for many of the resident waders over spring high tides. Between here and Seacliff Tower are found the Car Rocks, a broad area of flat rocks harbouring many shallow rock pools and sparsely covered with *Fucus serratus* and other seaweeds. Small numbers of curlew regularly feed in this area, but stealthy approach is difficult and few observations were made here. The intertidal zone between Seacliff Tower and Chapel Brae is the last area to be covered by spring high tides and is used extensively as a roost or pre-roost by many waders. Additionally it contains several rock pools of various depth. Many observations were taken from a hide constructed on the top of the cliffs at Chapel Brae. Feeding curlew were often observed on fucoid-covered rocky ridges or in shallow rock pools below Dump Beach. Sand-Strip is aptly named and both curlew and bar-tailed godwit, *Limosa lapponica*, often feed on marine polychaetes in this region. Scoughall Rocks hold large rock pools in which curlew and redshank, *Tringa totanus*, feed regularly. Curlew also use the lower littoral zone (of large rocks and boulders) as a pre-roost. Although curlew feed at Coastguard Rocks, visibility is seriously affected by the undulating terrain, making observation extremely difficult. Further description of the intertidal zone at Scoughall can be found in Marshall (1981) and Whitfield (1985a).

The hinterland here consists primarily of cereal crops, predominantly winter wheat and winter barley. These crops germinate in late November or early December and account for about 75% of the land area. Permanent pasture takes up a further 10% and the remainder consists of root crops, cabbages and mixed woodland. Curlew feed in most of the fields throughout the winter, providing that the vegetation is less than about 12cm in height. Roost Field is especially favoured and is often used as a roost site over spring high tides. The intensive cereal farming described commenced at the start of the study period in 1984; before then a more traditional mixed practice existed

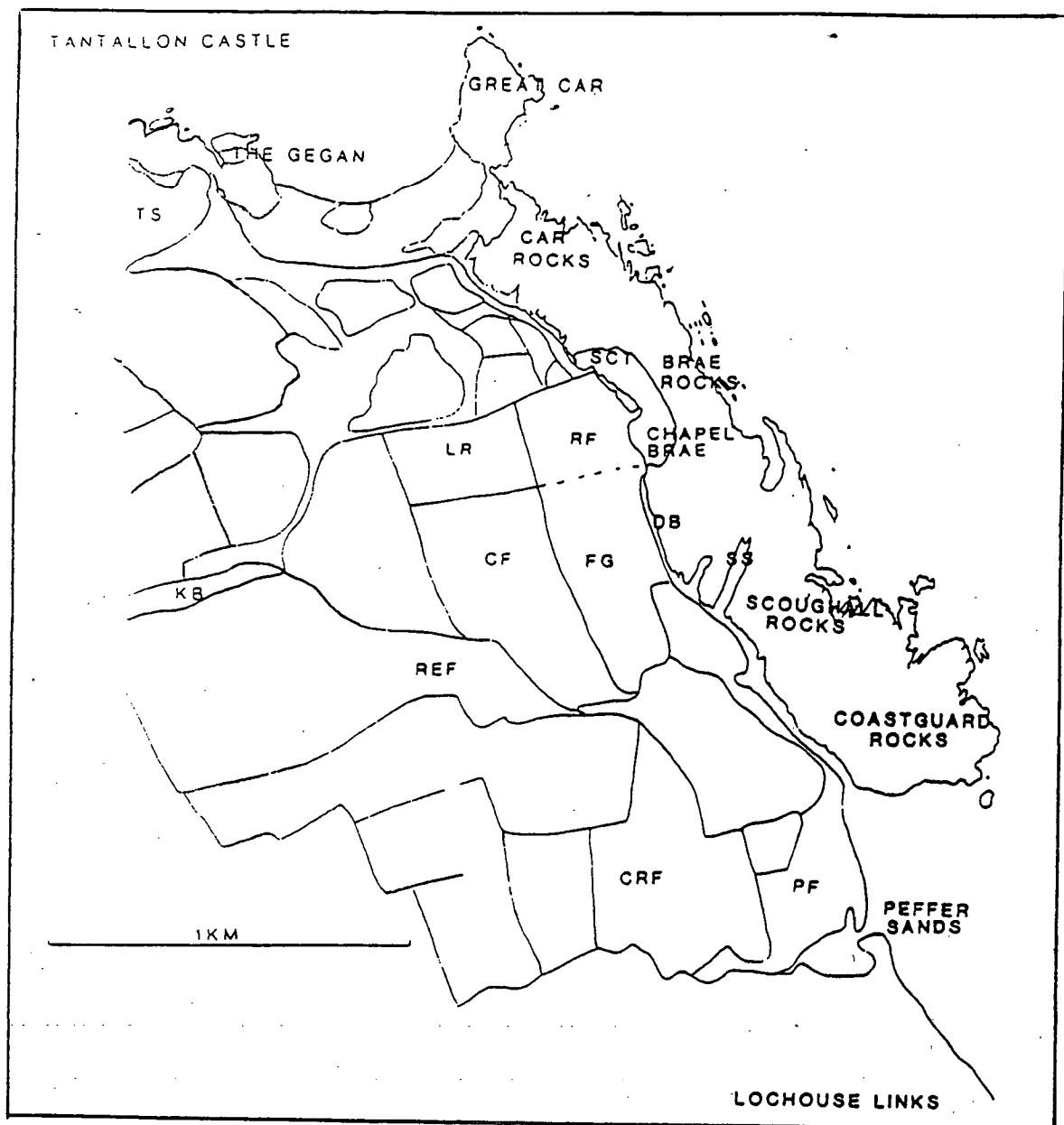


Fig 1.2. Scoughall showing major landmarks and habitats.

SCT = Seacliff Tower, DB = Dump Beach, SS = Sand Strip,

Preferred fields: TS = Tantallon Stubble, RF = Roost Field,

LR = Lower Roost, CF = Cabbage Field, FG = Field Gap,

REF = Reservoir Entrance Field, PF = Prefab Field,

KB = Knox Brook.

(D.P.Whitfield pers.comm.).

Scoughall and Tynninghame are separated by over 1km of sandy beach which is not utilised by the birds. A few curlew, however, feed or seek shelter in the the sand dunes backing the beach (Lochhouse Links). Unfortunately observations here were virtually impossible due to difficulties of access and depth of vegetation.

Tynninghame

In contrast to the rocky shoreline and arable hinterland described above, Tynninghame comprises the compact estuary mouth of the River Tyne and provides a range of different microhabitats (Fig.1.3). The northern limit is defined by St. Baldreds Cradle and the intertidal zone here is mainly flat rocks, holding pools and beds of fucoid seaweed. About 400m out from the shore there is a higher ridge (Estuary Mouth Rocks) commonly used as a pre-roost by curlew. Moving south towards Sandy Hirst (a sand spit colonised by sea buckthorn, *Hippophae rhamnoides*), mussel, *Mytilus edulis*, beds are found with increasing frequency. Approximately one quarter of the way along Sandy Hirst is another rocky area (referred to as Preroost). East of here the littoral zone is mainly estuarine mudflat interspersed with mussel beds. Running south from the base of Sandy Hirst to the southernmost limit of the study site (Moss House Point) is a broad band of saltmarsh over 1km long. Curlew (and other resident waders) feed regularly in all the areas described. The hinterland in this region is mostly mixed woodland and although curlew are beginning to utilise some fields within Tynninghame estate (since the birds were removed from the quarry list in 1982), few observations were made inland here.

1.2 GENERAL METHODS

Curlew are migratory and breed mainly in upland regions. Although a few non-breeders (predominantly 1st year birds [Bainbridge & Minton 1978]) are

Fig. 1.3. Tyninghame showing major landmarks and habitats.

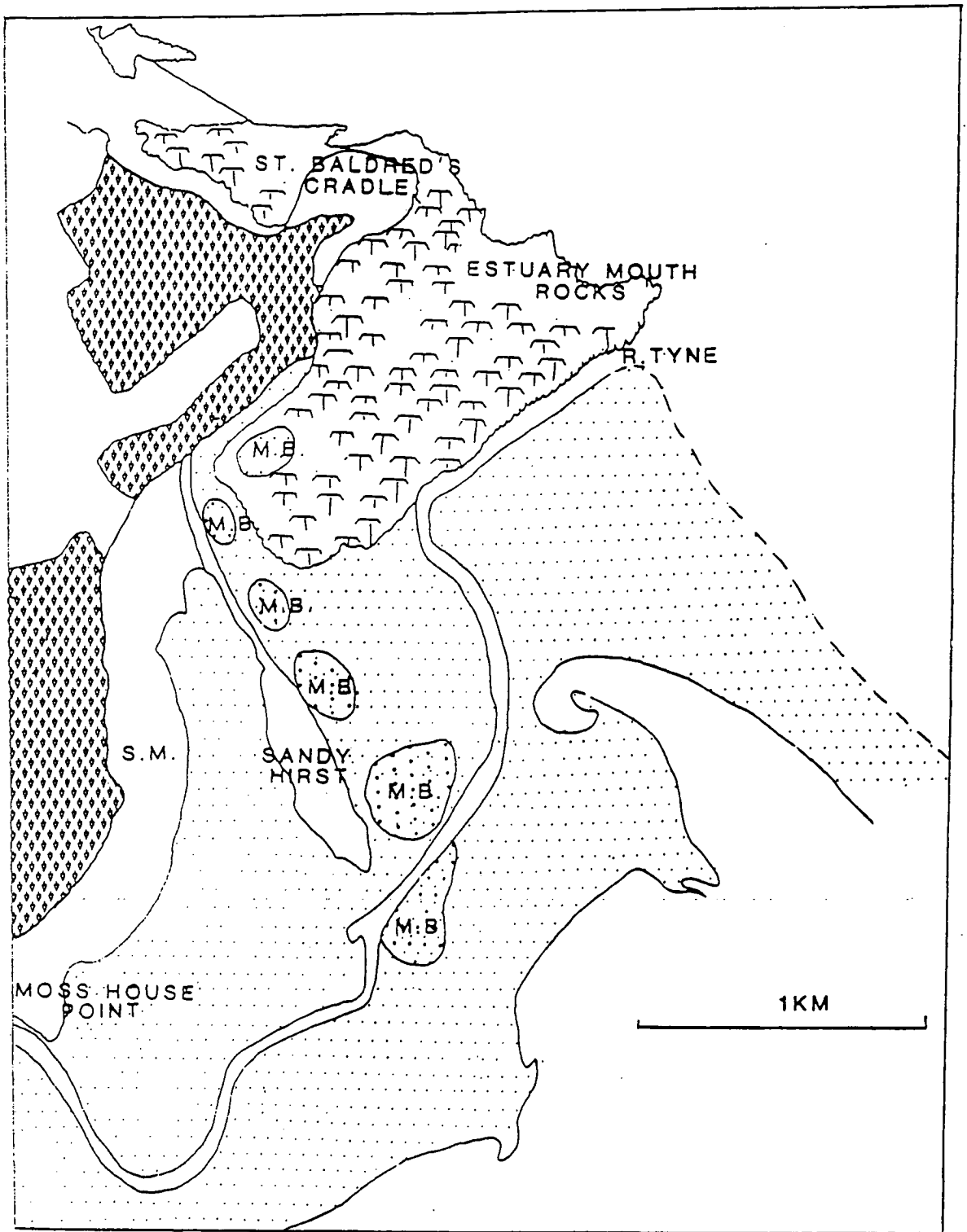
SM = Saltmarsh,

MB = Mussel bed,

Rocks = 

Coniferous woodland = 

Mudflats = 



present all year round, the main 'winter' season is between the second week of July and the first week of May. Seasonal migration is documented fully in chapter 2.

A pilot study was conducted in August 1983; the 'winter' of 1984-5 was mainly taken up in attempts to catch and colour mark birds, whilst the bulk of the data were collected in the 1985-6 and 1986-7 'winter' seasons.

Curlew are extremely shy and difficult to approach and for this reason it was necessary to use a car as a mobile hide wherever possible, especially when making observations on field-feeding birds. A static hide on Chapel Brae was used with success. When observing birds on the saltmarsh I had to approach on foot, through the bordering woods, about 2hr before high tide and wait for the incoming water to push birds towards me. Normally I found it easiest to locate birds by using 10x40 binoculars, whilst to collect observational data I used a 15-60x zoom telescope on a tripod or window mount. Under most circumstances a magnification of about 20x was sufficient for my needs, although the upper range was occasionally useful for reading colour rings at extreme range.

Two differing types of observation were made: scans (assigning an instantaneous activity to each flock member in turn) and running commentaries on the behaviour of focal animals recorded on to a dictaphone (Altmann 1974). Fuller details of these methods are to be found in chapters 5 and 3 respectively. Commentaries were transcribed on to an Apple II computer and subjected to 'real time' analysis using KEYBEHAVIOUR, KEYTIME II, and KEYTIME IV programmes (Deag 1983a, 1983b). The Edinburgh Regional Computing Centre (ERCC) provided two statistical packages: MINITAB (Ryan *et al* 1976) and SPSSX (Nie *et al* 1983). Unless otherwise stated, significance levels in tabulated results are given by: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Although many aspects of the behaviour of wintering waders are thought to be affected by the distribution and density of available food supplies (e.g. Goss-custard 1970b, Evans 1976, 1981, Pienkowski 1981, Myers 1984) it was decided before the start of the project not to attempt to sample prey availability. Adequate sampling is a difficult, time consuming procedure (especially for earthworms) (Waite 1983). Many waders appear to forage in an optimal manner, or at least in areas of greatest prey abundance (Evans 1976, 1979, Goss-custard 1977a & b, Zwarts & Drent 1981), therefore I felt that it would be more profitable to concentrate on documenting individual foraging techniques *per se* making the assumption that birds would tend to forage in the most profitable areas, within the particular set of constraints experienced (e.g. presence of conspecifics).

1.3 CATCHING METHODS

Catching curlew initially proved difficult. In order to catch large numbers of waders there are two standard techniques: mist-netting and cannon-netting. There was no suitable site for the former either at Scoughall or Tynningham. Access difficulties prevented any cannon-netting attempt at Tynningham and the rocky nature of the shore at Scoughall made it impossible to set nets at the major roost sites. This left one possibility; to set cannon-nets on Roost Field on spring series tides when moderate numbers of birds come in to roost. To deter birds from using the Great Car during a catching attempt several canes decorated with loosely flapping dustbin liners were set on the islet on the previous day. Attempts were made predominantly in April and August when numbers of birds were highest, but the autumn period was preferred as the field was then stubble, facilitating the camouflage of the nets. Two full-sized nets were used, roped and with projectiles as described by Clark (1983). The most successful deployment of nets was found to be a 'clap-net pair', *i.e.* having two nets set to fire towards each other simultaneously. Nets

were placed some 28m apart so that they would just overlap when in the fired position. Five decoys were made up using the methods described by Bainbridge (1976) and Clark (1983) and these were found to be effective in 'pulling' birds down.

A second catching method was used with some success. This was a modification of the 'Wilster' net described by Koopman & Hulscher (1979). Wilster nets were originally designed to catch golden plover, *Pluvialis apricaria*, in flight, for food. Basically a 20m x 4m 3-shelf gull mist net is strung between two bamboo poles and laid flat on the ground (Fig. 1.4). The bottom edge of the net is pegged to the ground. On the proximal (lee) side of the net a hinge mechanism is driven into the ground at the base of each pole, to which the poles are attached. Tension is applied by the taut steel cable running across the top of the poles, through the top edge of the net and pegged at the level of the hinges. The tension is adjusted (a task made easier by splicing rope on to the cable ends) until lifting one pole by hand simultaneously raises the other. An 8m length of steel cable is attached to the top of the pole nearer the firing position and pegged directly below the hinge. The release cable is attached to the mid-point of this cable (at the hinge level). Lift was achieved by placing a peg under the top of the pole proximal to the firing position, as opposed to digging a slanting trench for the pole as did Koopman and Hulscher. Decoys are placed on the windward side of the net and when a bird crosses the base line of the net as it glides in to land with the decoys, the release cable is pulled. This increases the pressure down the length of the pole towards the hinge, so that the entire net lifts to the vertical position, ensnares the target bird, then drops slowly down, completing an arc of 180°. When setting the net it is advisable to pay attention to the precise geometry of the layout. If the lift peg is not high enough, for instance, or the tops of the poles lie below the hinges, the net will try and describe an arc under the

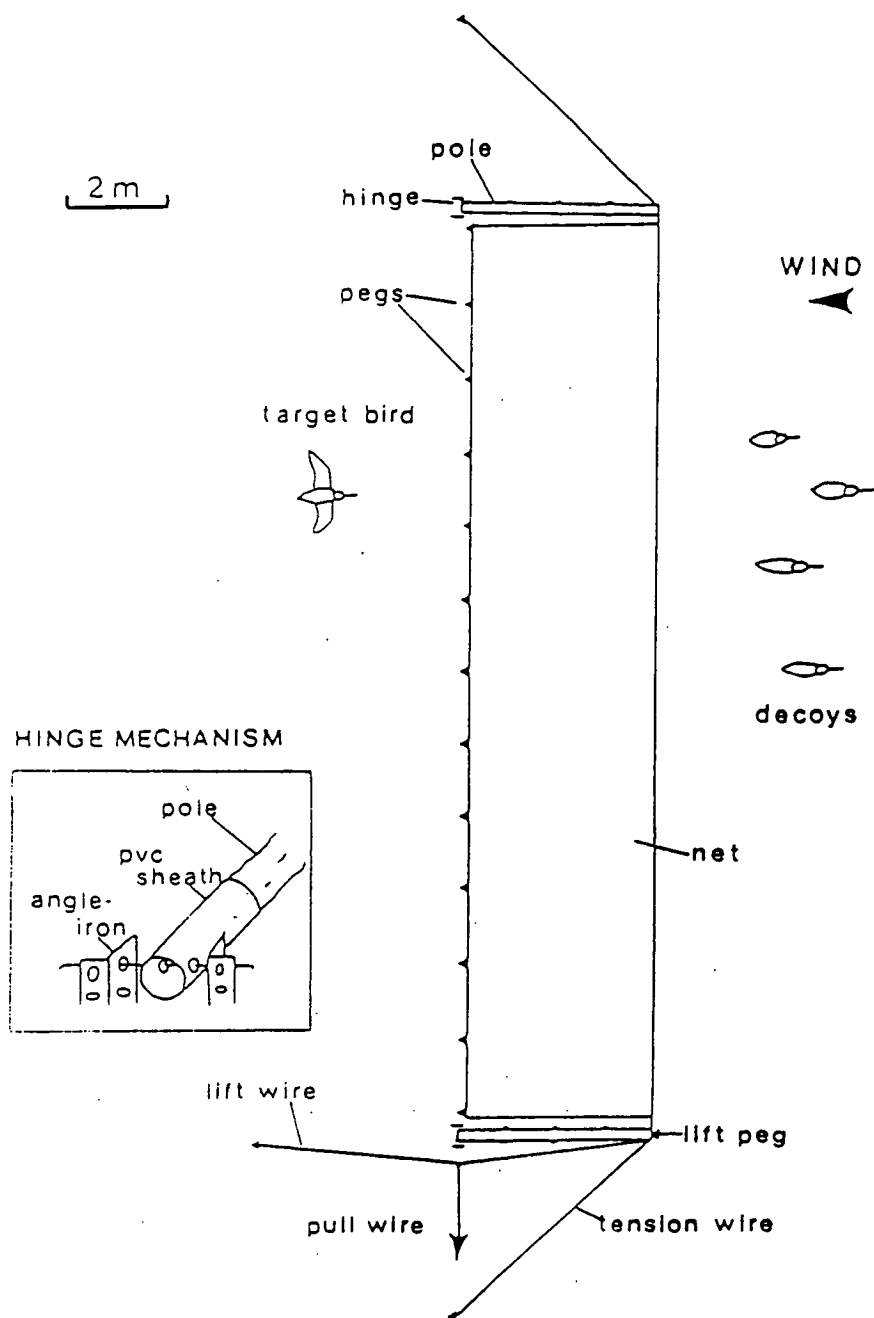


Fig 1.4. Plan view of Wilster net
with inset showing hinge mechanism.

ground (decreasing the chances of capture!). The disadvantage of only being able to catch one or two birds with one pull is offset by the rapidity with which the net can be reset (a matter of seconds) and the fact that the whole operation can be conducted by one person.

After capture all birds were ringed, aged, given an individual colour ring combination (section 1.4), and processed (measured and weighed, see section 3.2.2.). Birds were aged on the basis of plumage characteristics according to the method described by Prater *et al* (1977). Only two age classes were recognised; juveniles (1st year birds) and adults (more than one year old). The most useful criterion for determining age was found to be the notched appearance of the tertials of juveniles, caused by the differentially faster wear of the pale edge spots. Adult birds possess tertials with a grey-brown barring, which is not so subject to wear. A total of 140 birds were caught, comprising 130 new (unringed) birds, one control (ringed in Sweden) and nine retraps. The biggest single catch was 38 birds: this number could have been exceeded as birds were arriving in the catching area continuously, but capturing large numbers of curlew at one time can lead to problems with their health and safety. Curlew are notorious for suffering from severe myopathy (leg cramp). Symptoms include a contraction of the tendons in the back of the legs, causing the feet to adopt claw-like postures and preventing the bird from standing or taking off. There is no treatment as such for this condition. Stanyard (1979) considers myopathy to be a stress syndrome and attributes its incidence to the time the birds are left under the fired net before extraction. It is desirable, therefore, to operate extremely efficiently when catching. Special cages have been designed for keeping curlew between catching and ringing (Stanyard 1979), the main criterion being to give birds sufficient headroom when standing. I used a standard Wash Wader Ringing Group portable hide (approx. 2m x 1m x 1.5m high) for keeping birds prior to ringing. Fortunately, myopathy

posed few problems throughout this study. A few birds suffered from wing strain, manifesting itself in an inability to fly for up to 24hrs after capture. On the morning following a catch I made a habit of checking the study site thoroughly for birds suffering from either ailment.

1.4 COLOUR MARKING SCHEMES

Every 'new' bird caught was given a unique combination of colour rings so that I could identify individuals in the field. Two marking schemes were used. The first 20 birds were given permanent leg flags (Clark 1979), with strips of coloured 'Darvic' plastic stuck on to the projecting surface with 'Bartol' adhesive. The flags were placed above the tibio-tarsal (knee) joint and a colour ring was fixed immediately below each (Fig. 1.5). All colour rings were made with 100% overlap and an internal diameter of 9mm. Flags were read in the following order: 1) base colour of flag, 2) upper darvic strip, 3) lower darvic strip, 4) colour ring. The following 7 colours were used: white(W), lime(L), yellow(Y), orange(O), red(R), green(G), and black(N). The same combination was placed on each leg so that the combination of a roosting bird could always be read in full. Thus birds marked with the first scheme were known by a 4-letter code, *e.g.* YOWG, YWWR *etc.*

After the British Trust for Ornithology became concerned that hard plastic flags might contribute to egg cracking during incubation I switched to a system of soft flags. These were made by placing 3 standard colour rings on each leg, 1 on the tibio-tarsus and 2 on the tarso-metatarsus. Around each ring a 6cm length of coloured 'Scotch'lane marking' tape (made by 3M) was wrapped. By backing the tape on to itself and rolling the ring between the fingers (Fig. 1.6) a flag could be formed. After 3 years the majority of these flags are still in place. The same colours were used in this scheme and again the same combination was placed on each leg. This time the birds were known by a 3-letter combination, *e.g.* ROY, YNY *etc.* The two rings on the tarso-metatarsus were

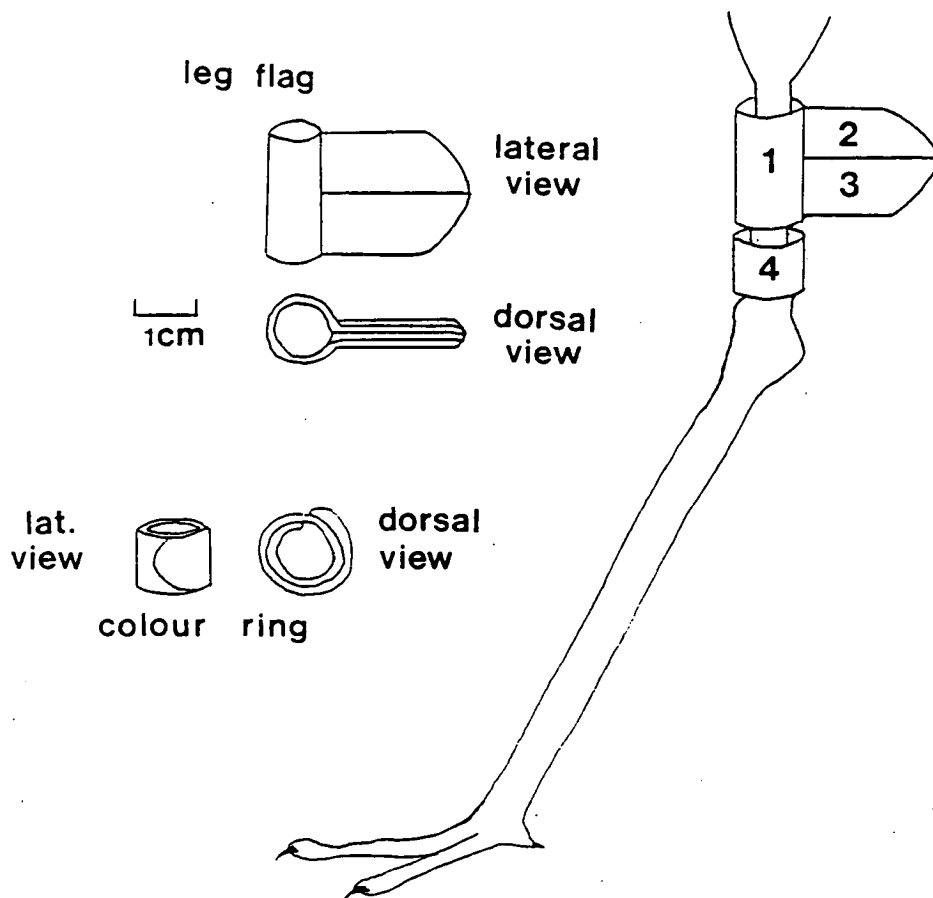


Fig. 1.5. First colour marking scheme.

Numbers indicate order of reading colours.

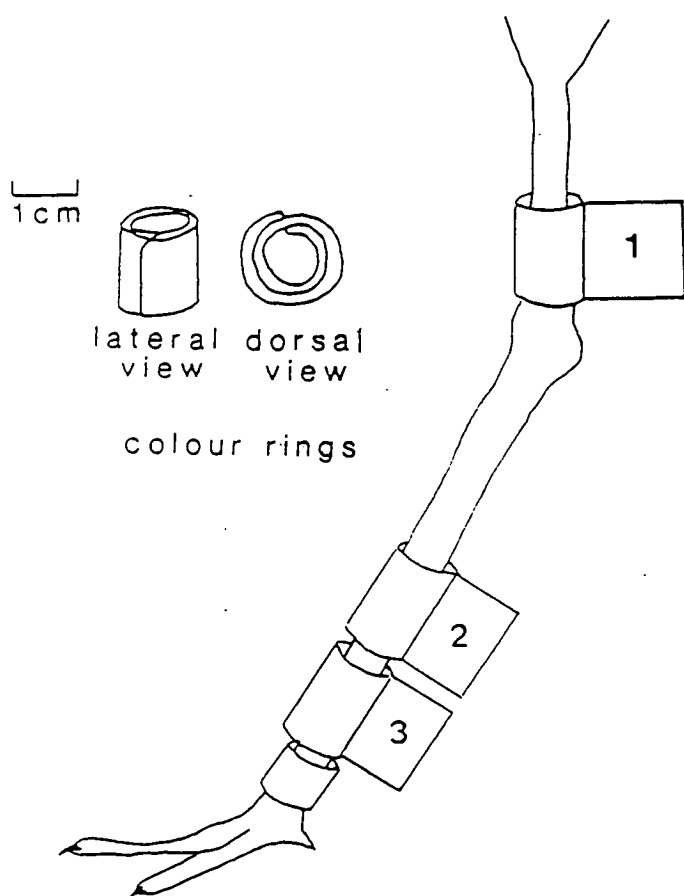


Fig. 1.6. Second colour marking scheme.

Numbers indicate order of reading colours.

never the same colour. I coded juveniles separately from adults, but made no attempt to code for each sex separately. Under ideal conditions the combinations of the second scheme could be read at a range of 800m, but more normally 400m was the limit at which combinations of both schemes could be reliably discerned.

CHAPTER 2.

THE STUDY POPULATION: MIGRATION AND MORTALITY.

*"Now the beach is deserted
Except for some kelp
And a piece of an old ship
That lies on the shore"*

BOB DYLAN 1975.

2.1 Introduction.

The curlew, *Numenius arquata*, is the largest wader of the Western Palearctic, with a wing span of up to one metre, but the most notable anatomical feature of the bird is its long decurved bill (up to 17cm in length) (Cramp & Simmons 1983). A full field description can be found in Hayman *et al* (1986). Two races are recognised: *N.a.arquata*, found in western and central Europe and *N.a.orientalis*, found in central Asia. The races represent either end of a continuous cline of increasing bill and tarsus length towards the east (Cramp & Simmons 1983). It was assumed that all the individuals in the study population were of the race *N.a.arquata*. Curlew are relatively long-lived birds; one British-ringed individual survived for at least 23 years in the wild (Spencer 1984) and a Swedish-ringed bird was recovered in its 32nd year (Boyd 1962). Curlew are normally migratory and individuals exhibit high fidelity to both wintering and breeding sites (Bainbridge & Minton 1978).

During the non-breeding season (July to April) curlew are found on estuarine mudflats, musselbeds and rocky shores where they use their bills to peck or probe in a diverse manner for a variety of intertidal invertebrate prey species (Burton 1974). Curlew also feed to some extent on arable fields close to the shore (Burton 1974, Townshend 1981b), or even on fields many kilometres inland (Elphick 1979). Preferred breeding habitat includes moist uplands, hummocky mosses, forest marshlands and, more recently, farmland (Cramp & Simmons 1983, Nethersole-Thompson & Nethersole-Thompson 1986).

In this chapter I document the number of curlew that used the study-site in the non-breeding season and describe the migration patterns of colour-marked birds, in terms of arrival and departure dates. I also attempt to assess mortality levels. Comparisons of migration patterns and mortality are made with previous studies.

2.2 COUNTS AND POPULATION ESTIMATES

2.2.1 Methods

I attempted to assess regularly the number of curlew utilizing Scoughall throughout the study period. Counts were made during the period approaching high tide, since over 50% of birds were obscured by boulders during low tide periods (pers.obs.). I conducted counts by driving a set route around the study site, commencing at the favoured areas of Scoughall Beach and Chapel Brae (Chapter 1), then continuing past the Great Car and visiting all the fields normally used by curlew. Counts were made as quickly as possible to minimize the risk of birds moving around the study site and being counted twice. This risk was further reduced by noting any colour-marked individuals seen and the size of the flock in which they occurred. Unfortunately it was not practicable to include Tynninghame in these standard counts, since this would have been too time-consuming and the problems of bird movement too great. I present data from counts made at Tynninghame by A.Clunas, M.Leven, R.Anderson and A.Buckham. These counts were not made regularly and not necessarily along a set route, however they do give an indication of population changes at Tynninghame.

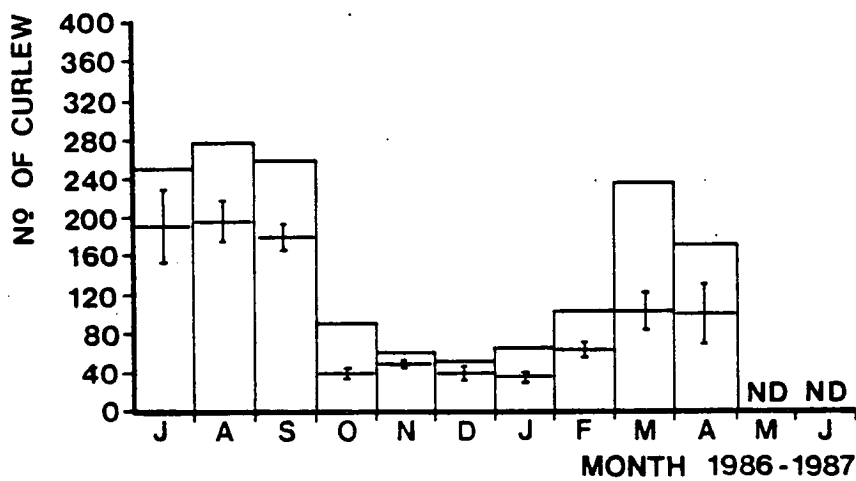
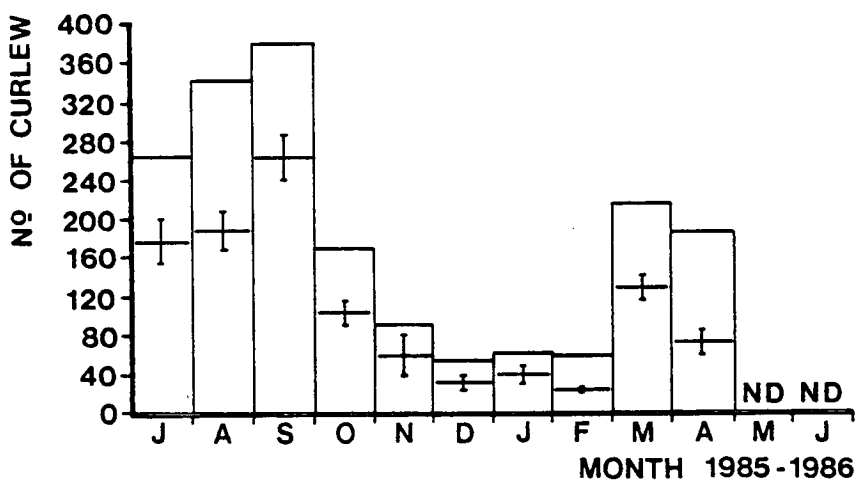
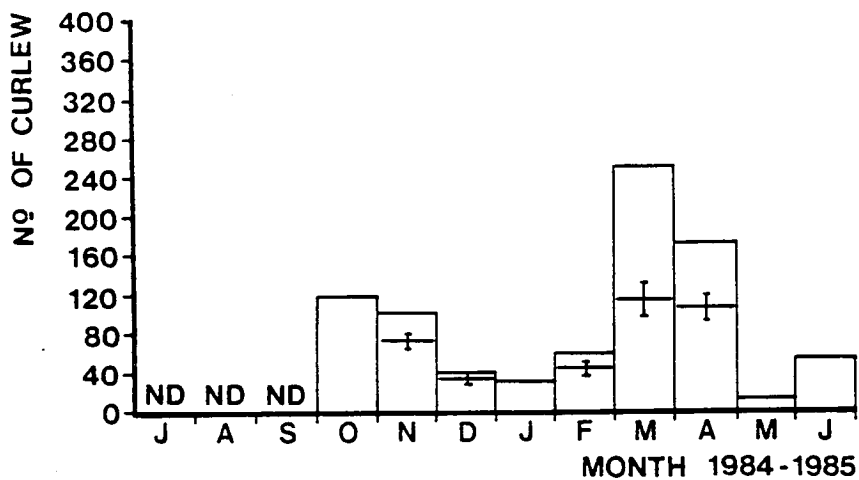
2.2.2 Results and Discussion

A) Scoughall

The numbers of curlew present at Scoughall vary considerably through the annual cycle (Fig.2.1). In the 'core' winter months (mid-November to mid-February) the wintering population is relatively stable, between 60 and 100 birds. In early March there is a large influx of birds, presumably migrants from the south-west (Bainbridge & Minton 1978). Birds begin to depart for their breeding grounds in this period, leaving a residual 'summering' population of juvenile birds in May and June. In July and August adults return from breeding and commence the process of moult. Numbers reach a peak in August and

Fig. 2.1 Monthly maximum counts of curlew at Scoughall for the 3 winters.

Inset bars give mean monthly counts + S.E. N.D. = no data available.



September, probably due to the arrival of birds of the year (Bainbridge & Minton 1978) and dwindle throughout October and November to the winter low as birds depart, presumably to wintering grounds in the south-west. This contrasts with the prior assumption that there is little post-moult movement (Cramp and Simmons 1983). Townshend (1981a) also found evidence of post-moult movement.

B) Tynninghame

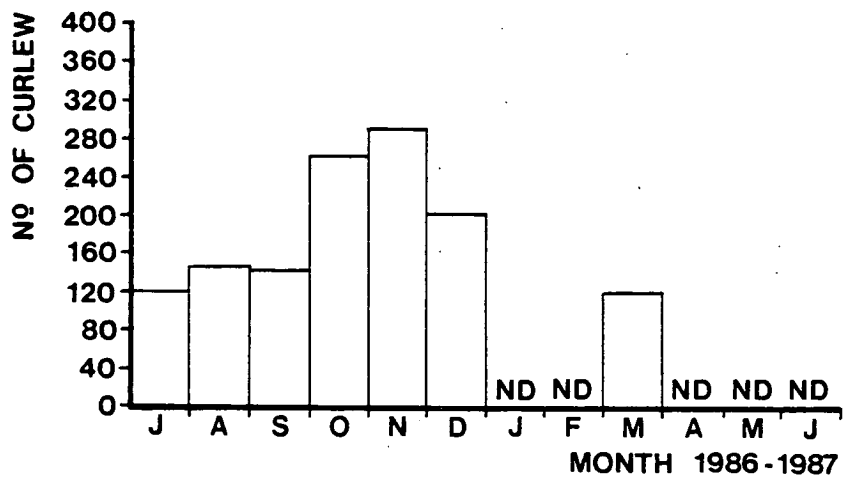
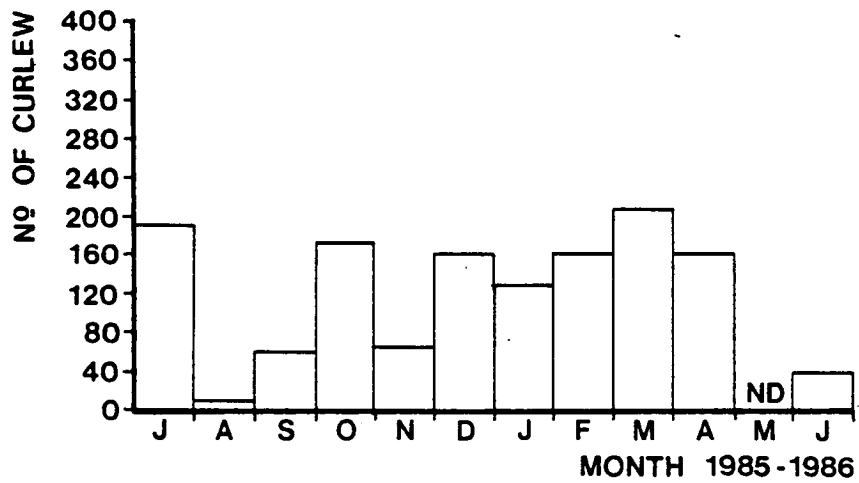
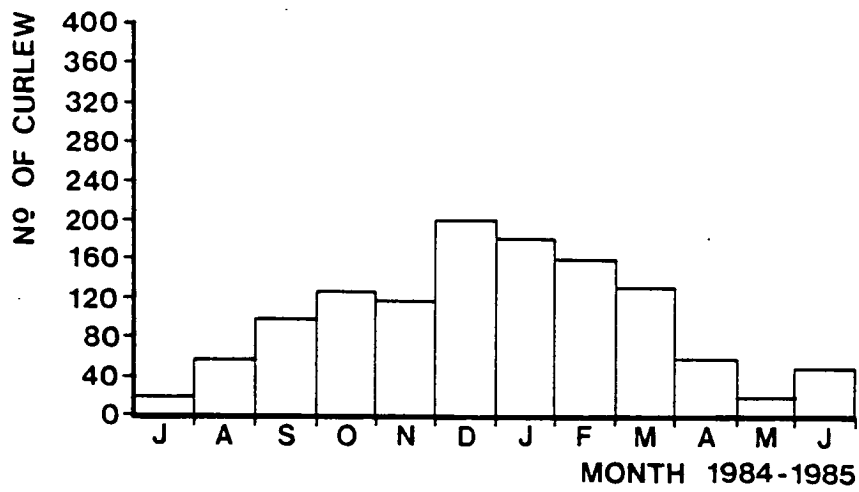
Although it is difficult to draw conclusions from irregular counts made by different people, the general pattern of variation in population at Tynninghame contrasts sharply with that at Scoughall (Fig. 2.2). Most obviously there is no peak during spring and autumn passage. This difference may be attributable to the levels of human-induced disturbance at Tynninghame. The estuary comprises part of the John Muir Country Park and is popular with the public, particularly in spring and autumn. Access to Scoughall, on the other hand, is mainly through private land and the beach attracts fewer visitors. Alternatively the rocky roosts at Chapel Brae and the Great Car may be safer from mammalian predators (especially foxes *Vulpes vulpes*) than the salt-marsh at Tynninghame. Any difference in predation risk between sites would be especially important during the moult period, when flight is somewhat impaired.

A second obvious difference in the pattern of population variation between sites is that there is no mid-winter low apparent at Tynninghame and if anything a tendency for numbers at Tynninghame to peak between November and January. This is possibly due to local movements of birds from nearby stretches of coast (particularly those individuals that habitually feed on fields), seeking shelter or alternative food sources in severe weather (chapter 3).

2.3 Occurrence of Individual Birds at the Study Site.

2.3.1. Introduction

Fig. 2.2 Monthly maximum counts of curlew at Tynninghame for the 3 winters. N.D. = no data available. Data supplied by A.Clunas, M.Leven, R.Anderson and A.Buckham.



At an early stage it became obvious that there were broad differences in the use of the study site by individual birds. Some were seen regularly throughout the winter and it was possible to predict with success in which area of the study site they could be located. Other birds were only ever seen in the 'passage' months and were clearly migrants. A third category of individuals were seen in winter, but only sporadically and unpredictably. These three groups were distinguished as follows.

2.3.2. Methods

Whenever a colour-marked bird was sighted its combination, location and activity were recorded. Birds were assigned to one of three categories on the basis of the frequency with which they were seen. The categories were as follows:

Residents; must have been sighted at least once each year in three out of the 'core' winter months (November to February).

Itinerants; seen sporadically throughout the winter, but absent for at least two of the 'core' months.

Migrants; seen only during the 'passage' months (March & April, July to October).

2.3.3. Results

Tables 2.1 to 2.4 document the attendance at the study site of individual birds of each category. Residents have been subdivided for ease into those birds which frequented Scoughall and those which normally frequented Tynninghame. Individual habitat selection is discussed in chapter 3.

2.4 Seasonal Migration of Curlew at the Study Site.

2.4.1. Introduction

Bainbridge and Minton (1978) conducted a detailed analysis of the recovery locations in Britain of over 900 curlew, ringed between 1909 and 1975. They discovered a marked trend for birds to migrate in a south-westerly

1985	1986
NDJFMAMJJASONDJFMAMJJASONDJFMA	
	NLO:S SSSSS
	WOR:SSSSS88S
	WYO:SSSSSSS
	WWR:SSSSSSSSS
	WWY:S SSSSSSSSSS
	WWL:S SSSSSSSSSS
	LWN:S S888S SSB
	LWR:S SSSSS SSSS
	OOR:S SS S SSSS
	OOW:S SS88SS8SS
	OYO:S SSB SS SSS
	OYW:S S8SS SSS
	LWO:S SSSSSSSSSS
	LWY:SSSSSS SSSSSSSSS
	LWL:SSSSSS SSS SSSSS
	ORO:SSS SSSSS SSSSSSSSSS
	YOL:SSS8SSSSS SSSSS SSS
	YLW:SS S SSS SS SSSSS
	YWL:SSS SSSS SS SSSSS
OWO:B S8S SS	SS8TSS 88S
RYN:B SSSS SSSS	S SSSSS
YNW:B S SS	T SSSS
YRW:B SSSSSSSS*	
YWN:S SSSS S SSS	SS8SSSSSS
YNI:SSS SSSSSSSSSS	S S88SSS
YOWG:SSS SSSSSSSS8S	SS SSSSSS
YLGG:SSSS SSSSSSSS	SSSSS
YWLR:S SSS SSS SSSSSS	SSSSSSSSS
OLY:S SSSS SSSSSSSSS	S8SSSS88
YLOG:S SS SS*	
YWRG:SSSSSS SSSSSSSS	SSSSSSSSS
YWOG:SS SS SSSSSSSS	S*
YWLG:SSSS8 SSSS SSSSS	SSSSSSSSS
YWWR:SS S SSSSSS SSSS*	
NDJFMAMJJASONDJFMAMJJASONDJFMA	
1985	1986

Table 2.1 Monthly attendance at the study site of individual birds classified as 'Resident-Scoughall'. Colons indicate month of capture. S= = seen at Scoughall, T = seen at Tynningname, B = seen at both sites, * = presumed dead.

	1985	1986
	NDJFMAMJJASON	NDJFMAMJJASON
		LNL:STTTTBSB
		NI.N:STT TTB
		WRL:BT TTSB
		WLR:BT TTTTBSB
		WWN:BT TTT TBT
	OOL:BS SB	SBTTT BSB
	OYL:BSBTB TSS	SSSTTTTBSB
	OWR:B SSB TTSS	SSSTBTBBSB
	RRY:B SSSBT TTBS	SSTTTT TTT
	ROY:S SSB TSS	S BT TTT B
	YNY:S SSS T TTBS	STTTT B
	YRO:B SSSST T SS	SSSST TBSB
	YYR:B SSSSTB TSS	S BT TTTBSB
YOWR:S	B SSBSTTTTTSB	SSBT TTT BT
	NDJFMAMJJASON	NDJFMAMJJASON
	1985	1986

Table 2.2 Monthly attendance at the study site of individual birds classified as 'Resident-Tynninghame'. Colons indicate month of capture. S = seen at Scoughall, T = seen at Tynninghame, B = seen at both sites, * = presumed dead.

1985				1986			
FMAMJJASONDJFMAMJJASONDJFMA				FMAMJJASONDJFMAMJJASONDJFMA			
				WRO:SS		SS	
				WON:S		TBT	
				WYL:S		BBB	
				OLW:S	S	BSB	
NWL:SSS				S	ST	S	
ONY:SSS				TSS	SS	BBB	
ORY:SS				S	S	S	
ORW:BS				S	S B	ST	
OLN:SS					SSS*		
OLO:SS					S*		
YLN:BS				S	BTT	S	
YLR:SS				T T	S*		
YLO:SS				SS*			
RON:B SSSS				T	SST	S	
ROW:B S				S	S	S	
RYS:S				S	S		
RYO:BSBS				S*			
RYW:S BS				SS	S BT	BB	
RWN:B						S	
RWR:S SSSST				SS	SSSTT	S	
YRN:S SSS				SS	S SS	BSB	
YRY:B				SS	B	BST	
YOY:B				TSS	S	B	
YYO:S					S		
YLNG:SSS SSS				S*			
YORG:S					S		
FMAMJJASONDJFMAMJJASONDJFMA				FMAMJJASONDJFMAMJJASONDJFMA			
1985				1986			

Table 2.4 Monthly attendance at the study site of individual birds classified as 'Migrants'. Colons indicate month of capture. S = seen at Scoughall, T = seen at Tynninghame, B = seen at both sites, * = presumed dead.

direction to their wintering grounds and a north-easterly direction to their breeding areas. Thus the majority of curlew that originate in Scotland winter in Ireland or on the west coast of England, although 23% of pulli ringed in Scotland winter within 100km of their natal site. Similarly birds which originate in Scandinavia tend to winter in Scotland. These observations indicate that birds seen at the study site in the non-breeding season could conceivably be from three populations:

- a) Scandinavian breeders/Scottish winterers
- b) Scottish breeders/Scottish winterers
- c) Scottish breeders/Irish (or west of England) winterers

Post-breeding adults undergo complete moult in August and September and are relatively sedentary during the replacement of their primary feathers (Bainbridge & Minton 1979). Thus birds may use a site (such as the Wash, south-east England) as a 'stopover' during the moulting process, before commencing or continuing their migration. Bainbridge and Minton (1978) also present evidence that the main influx of Scandinavian-breeding adult curlew to Britain occurs in late June and July, whilst juveniles arrive mainly in September. Spring passage to Scandinavia peaks in April and is complete by May. Evans and Pienkowski (1984) and Townshend (1981a) suggest that birds which depart from Teesmouth, north-east England, in March probably breed locally, whilst those that remain on the coast until April are probably Scandinavian breeders. Conditions are likely to be more amenable to early breeding in Britain than they are in Scandinavia (Pienkowski & Evans 1984). Birds that breed at more northerly latitudes tend to have a shorter breeding season. Townshend (1981a) recorded the month in which marked individuals disappeared from, or arrived back at their wintering site at Teesmouth. Most birds departed in March and returned in August. Evans and Pienkowski (1984) studied the spring departure of individually marked adult curlew from Teesmouth in 1982 and found that

most birds departed in the last two weeks of March and the first two weeks of April. In this section I present data on the direction and timing of the autumn and spring migration of individually marked curlew to and from the study-site and compare the results with earlier studies.

2.4.2. Methods

Data on the locations of birds seen outside the study site are based on reports submitted by members of the public. Every time I saw a marked bird at the study site I recorded the date and colour-combination. In addition I made regular visits to the traditional roost-sites at Scoughall Rocks and Chapel Brae during the spring migration period (March/April) in 1985, 1986 and 1987 and the autumn migration period (mid-June to September) in 1985 and 1986 to scan roosting flocks, recording every colour-marked bird that was visible. The date on which a given individual was last seen at the study site in spring was assumed to be the date on which that bird departed for the breeding grounds. Similarly the first day on which the bird was observed in the autumn was assumed to be the date on which it arrived back. Of course there will have been occasions when I failed to observe an individual after its supposed departure or before its true arrival, giving rise to error. It is possible to calculate the mean inter-sighting interval (in days) for each individual and derive a correction factor to give a more accurate estimation of the true dates of arrival/departure based on the probability of seeing a particular bird, however the work involved in such a procedure would be immense and the greater accuracy achieved probably would not justify the time investment. After regular checks (made every second day) of other areas of the study site I was convinced that my methods provided an acceptable estimation of the true dates involved.

2.4.3. Results

2.4.3.1. Sightings outside the study-site.

Sightings of colour-marked birds outside the study-site are shown in Fig.2.3.

I obtained three controls (i.e. birds seen, captured or ringed outside the study site) that lend support to the hypothesis that birds move in a north-easterly direction to the breeding grounds (Bainbridge & Minton 1978).

a) a bird (OWL) was captured bearing a Swedish ring; it had been marked as a breeding adult in Hullberget, Sweden, 59° 53'N, 16° 22'E, in 1985, and was seen at the same site in the summers of 1986 and '87. This individual was often observed at Tynningham during the winter.

b) YRY was sighted in May 1985 and August 1986 on the Ythan estuary, Aberdeenshire. It occurred at the study site on both spring^{and} autumn passage.

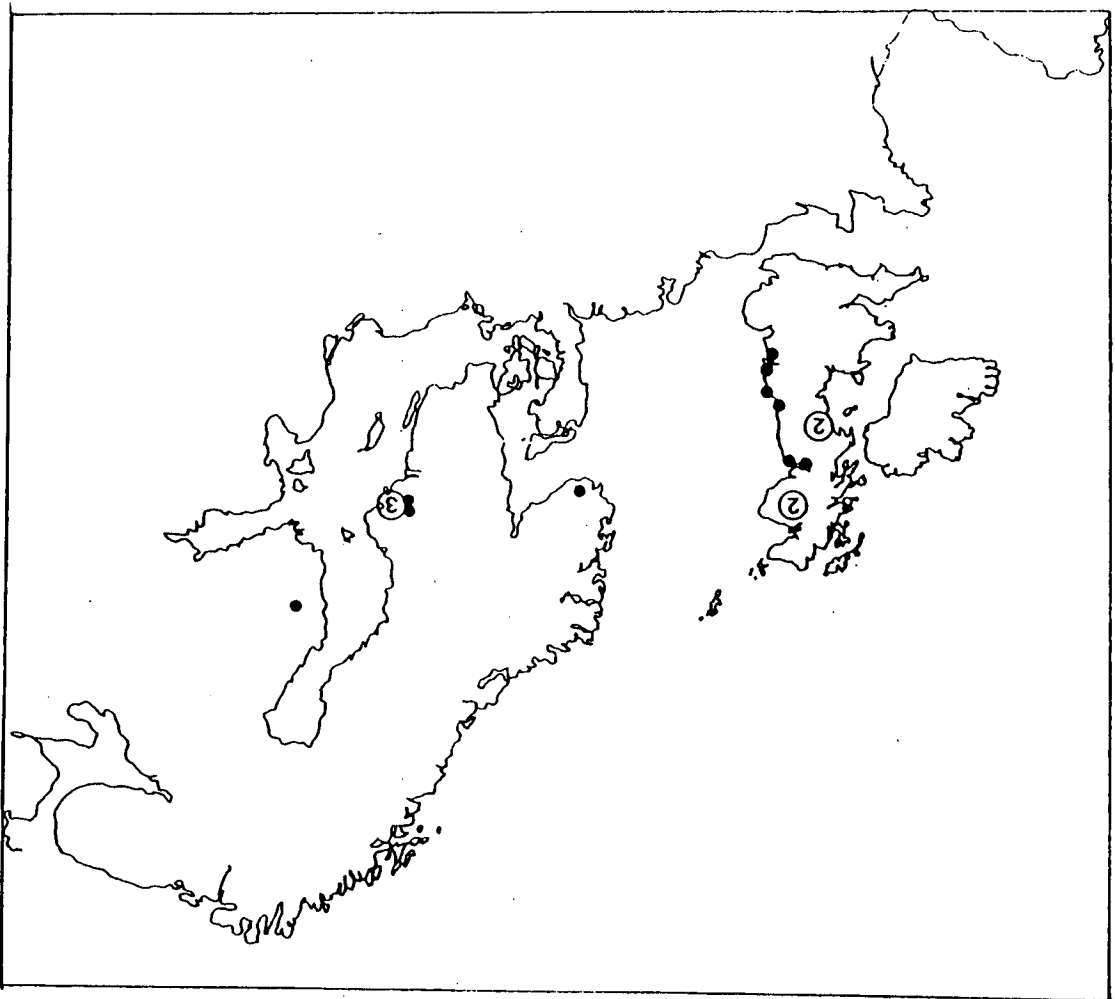
c) ORW was recorded on the Solway estuary, Cumbria, in March 1987. It was in a migratory flock of over 3000 birds and had presumably spent the winter either in the locale, or more probably in Ireland. The same individual was reported on the south Solway again, in February 1988. It was seen at Scoughall only in the passage months of March/April and August/September and was in heavy primary moult when captured in August 1985.

OWL was thus a Scandinavian breeder/Scottish winterer, YRY probably bred in Scotland but did not winter at the study site and ORW wintered to the south-west and probably bred in Scotland (or possibly Scandinavia).

Recently I received a report of a bird (OLN) found dead on breeding grounds in Finland in June 1987. This individual was seldom seen at the study site and only in the autumn passage months in 1985 and 1986. I have also recently received reports of sightings of two birds (WYW & WYR) on migration in central Sweden in April 1988. Both individuals were classified as itinerants at the study site in the winter 1986-7.

Other sightings outside the study site were less conclusive, and include one bird on the Humber estuary, one at Teesmouth and one (found dead) in the

Fig. 2.3 Sightings of birds outside the study site. Numbers indicate repeat sightings of an individual in different years.

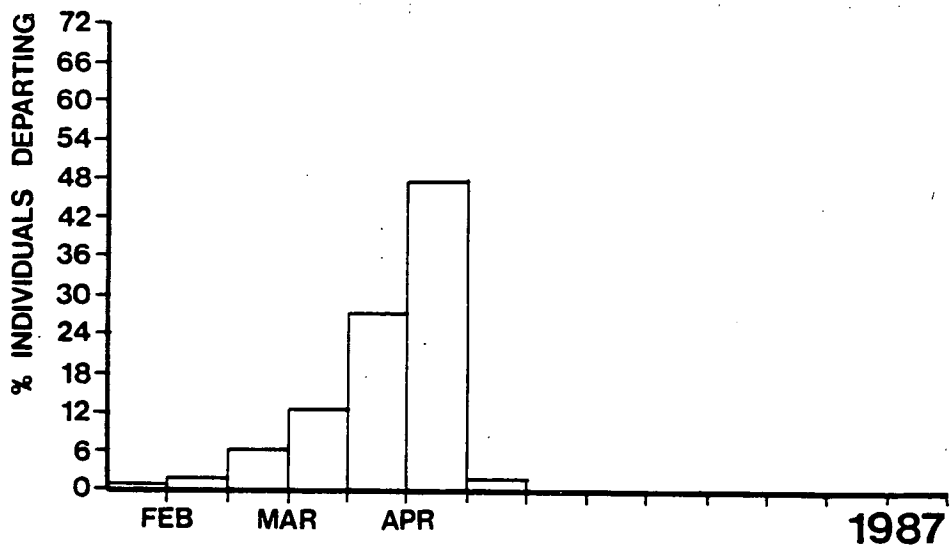
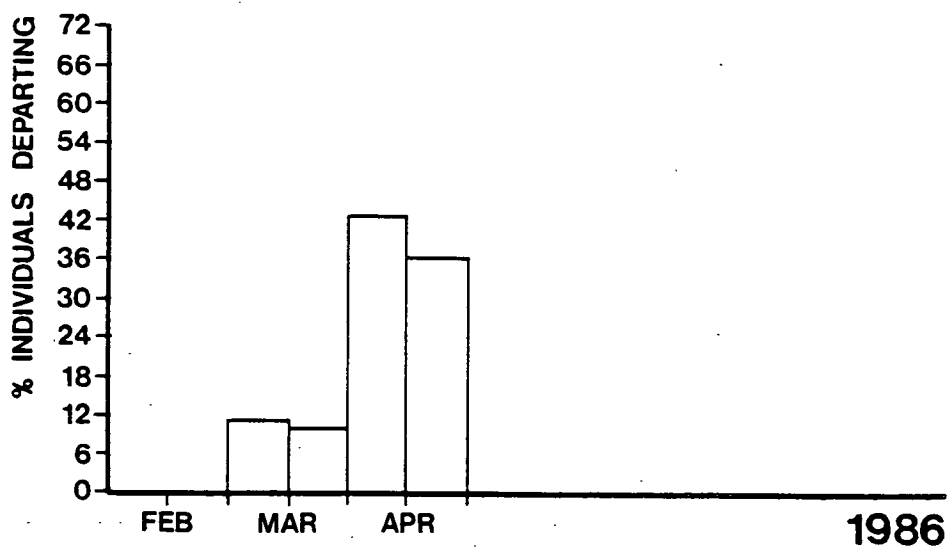
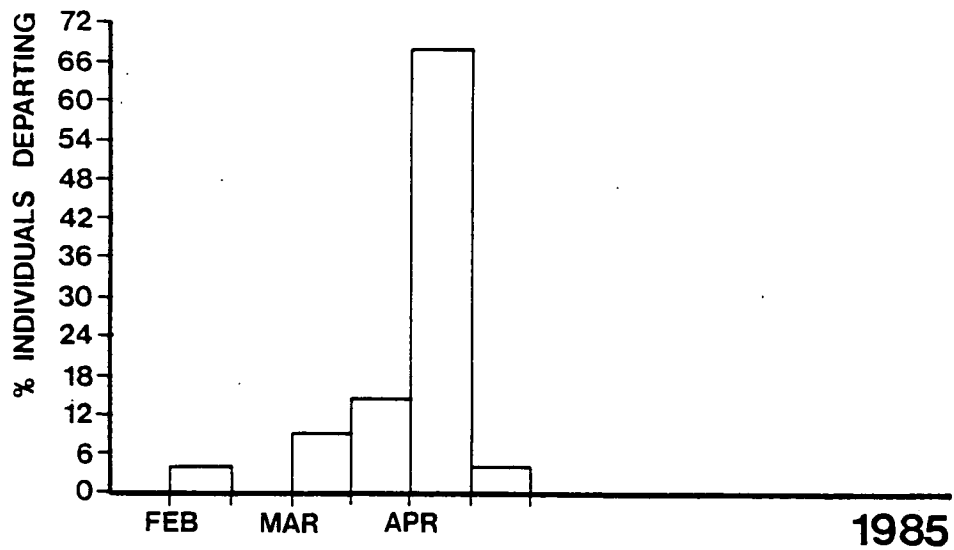


Borders region (all in spring migration periods). There was also one probable sighting of a bird on the Farne Islands in August 1985. These sightings indicate a southerly movement of some birds; possibly they are moving along the coast to Scandinavia, rather than flying directly over the North Sea.

2.4.3.2. Timing of migration: Spring Departure.

The percentage of individuals that departed in fortnightly periods each year is shown in histogram form in Fig. 2.4 and actual departure dates are summarised in Table 2.5. Birds begin to leave the study site in late February/early March, during which period migrants are still arriving (Fig. 2.1). In early April the frequency of departure increases, rising to a peak in the second and third weeks of the month. By the first week in May departure is complete. This departure pattern is about a week to a fortnight later than that found at Teesmouth in 1982 (Evans and Pienkowski 1984). Whether this difference is due to climatic or geographical variation is not known. A few juvenile (first year) birds remain throughout the summer. Although many juveniles spend their first summer at the study site, approximately 50% leave (Table 2.6). Whether their absence during the breeding season represents a true breeding attempt, or gaining of experience on the breeding grounds, or even just a local movement is a matter for conjecture. The age of the first breeding attempt is generally assumed to be two years (Cramp and Simmons 1983). There is a tendency for birds which depart early or late one spring to do the same the following year (Fig. 2.5 A & B). This observation could arise if birds which depart early are moving to different breeding grounds than those which depart later in the season. However this effect could also arise as a result of the increasing age of individuals; it is likely that older, more experienced birds would depart earlier than younger birds (particularly those in their first two years). The high correlation between departure dates two years apart (Fig. 2.5c) suggests perhaps, that age may not be so important in determining departure date. To test the effect of increasing age upon departure date I plotted the departure date of individuals relative to the mean departure date of all marked individuals in that year, in 1985 against 1987 (Fig. 2.151). A positive number means that the individual left before the mean departure date, a negative number after the mean. The curve indicates no change in the relative departure date, points to the right of the curve indicate birds which left relatively earlier in 1987 than 1985. It appears that there may be a tendency towards earlier departure with increasing age, however this was not significant when relative departure dates of individuals in the two years were compared (Wilcoxon matched pairs test, $W = 151.5$, ns). Resident birds appear to depart later than migrants (Fig. 2.6a) significantly so in 1986 (Table 2.5 Mann-Whitney U-test, $W = 1170.5$, $p < 0.001$). This is in accordance with the hypothesis that birds move in a north-easterly direction to breed. Scottish wintering birds will tend to breed in Scandinavia, whilst 'migrants' will have

Fig. 2.4 Percentage of marked individuals that departed from the study site in fortnightly periods in spring 1985,86 and 87.



ALL BIRDS			MIGRANTS			RESIDENTS		
	N	MEAN $\pm$ S.E.	N	MEAN $\pm$ S.E.		N	MEAN $\pm$ S.E.	
1985	DEPART	43 14APR $\pm$ 2.2	8	11APR $\pm$ 4.2		17	14APR $\pm$ 3.5	
	ARRIVE	35 02AUG $\pm$ 5.9	3	30JUL $\pm$ 7.9		16	04AUG $\pm$ 9.4	
	DURATION	35 109.6 $\pm$ 7.0	3	116.0 $\pm$ 3.8		16	114.2 $\pm$ 11.5	
1986	DEPART	80 06APR $\pm$ 1.5	16	29MAR $\pm$ 3.0***		37	10APR $\pm$ 2.0	
	ARRIVE	79 03AUG $\pm$ 3.4	16	23AUG $\pm$ 9.2 **		35	31JUL $\pm$ 5.1	
	DURATION	75 102.2 $\pm$ 4.0	13	153.8 $\pm$ 10.7		35	113.7 $\pm$ 5.9	
1987	DEPART	95 06APR $\pm$ 1.5	16	29MAR $\pm$ 5.1		43	08APR $\pm$ 1.6	
ALL MALES			ALL FEMALES					
	N	MEAN $\pm$ S.E.	N	MEAN $\pm$ S.E.				
1985	DEPART	27 13APR $\pm$ 3.0	16	17APR $\pm$ 2.9				
	ARRIVE	22 02AUG $\pm$ 7.1	13	02AUG $\pm$ 10.5				
	DURATION	22 113.2 $\pm$ 9.2	13	103.5 $\pm$ 10.4				
1986	DEPART	51 07APR $\pm$ 1.8	29	05APR $\pm$ 2.6				
	ARRIVE	50 09AUG $\pm$ 4.9	29	23JUL $\pm$ 2.4				
	DURATION	46 127.0 $\pm$ 6.0	29	109.5 $\pm$ 3.6				
1987	DEPART	51 05APR $\pm$ 2.2	44	08APR $\pm$ 2.1				
RES. MALES			RES FEMALES					
	N	MEAN $\pm$ S.E.	N	MEAN $\pm$ S.E.				
1985	DEPART	12 12APR $\pm$ 4.7	4	22APR $\pm$ 1.6				
	ARRIVE	11 11AUG $\pm$ 13.0	4	26JUL $\pm$ 4.0				
	DURATION	11 123.3 $\pm$ 15.9	4	95.3 $\pm$ 2.4				
1986	DEPART	28 11APR $\pm$ 1.9	8	09APR $\pm$ 4.5				
	ARRIVE	26 03AUG $\pm$ 6.6	8	20JUL $\pm$ 3.9				
	DURATION	26 116.0 $\pm$ 7.5	8	103.4 $\pm$ 7.1				
1987	DEPART	29 07APR $\pm$ 2.0	13	11APR $\pm$ 2.3				

Table 2.5 Mean dates ($\pm$ S.E. in days) of departure and arrival at the study site and duration of absence for a) all birds combined, b) migrants c) residents d) all males e) all females f) resident males g) resident females.

	REMAINED AT STUDY SITE	ABSENT FROM STUDY SITE	SWITCHED SITES OR DIED
1985	8	5	3
1986	0	5	0
TOTAL	8	10	3

Table 2.6 Number of juveniles that remained, at or moved away from, the study site in their first summer.

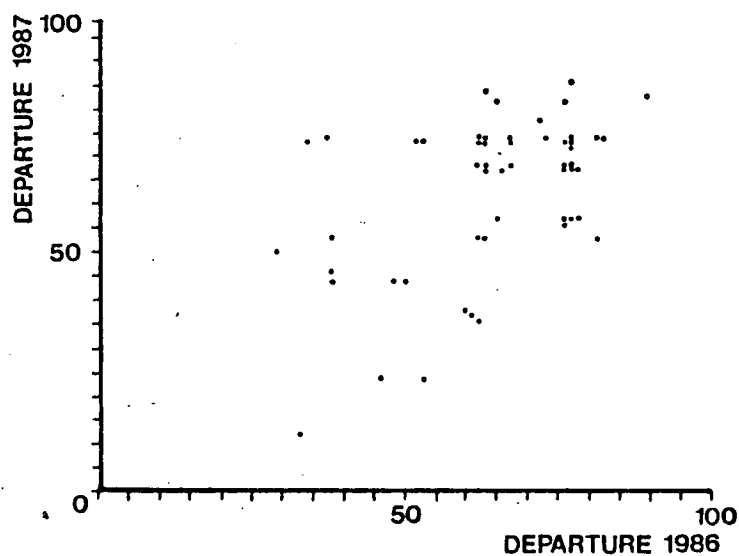
Fig. 2.5 Departure dates of individual birds in different years.

A) 1987 vs 1986, ($N = 72$, $r = 0.466$, $p < 0.001$)

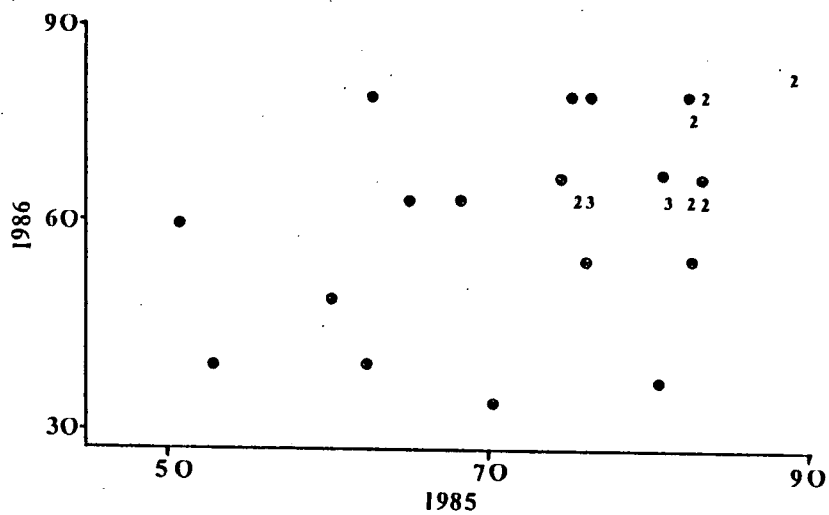
B) 1986 vs 1985, ($N = 34$, $r = 0.474$, $p < 0.01$)

C) 1987 vs 1985, ($N = 30$, $r = 0.717$, $p < 0.001$).

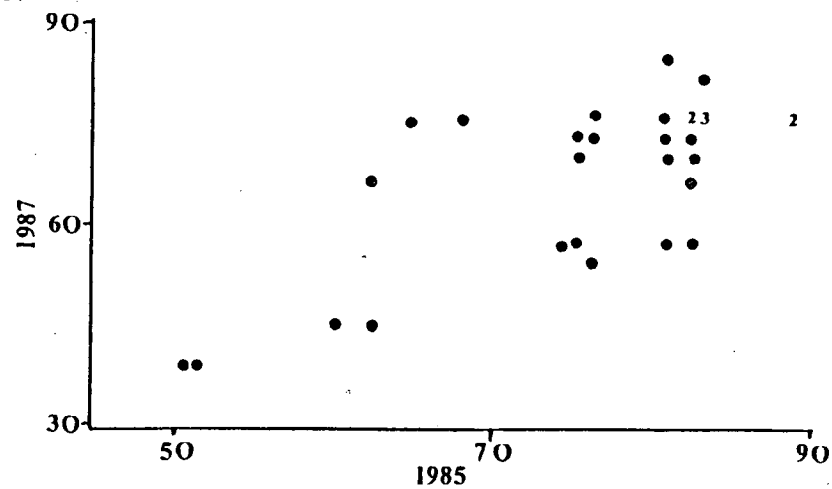
A)



B)



C)



wintered in the south-west and will tend to breed in Scotland. It is reasonable to suppose that conditions will be suitable for breeding earlier in Scotland than they will in Scandinavia. No difference was found in the departure dates of males and females (Fig. 2.7a Mann-Whitney U-test, $P > 0.05$). Sexes tend to arrive at much the same time in the vicinity of the breeding grounds, although males sometimes start defending a breeding territory before they are apparently paired (Nethersole-Thompson & Nethersole-Thompson 1986). In the spring of 1985 birds left significantly later than in both 1986 and 1987 (Table 2.5, Mann-Whitney U test, $W=3554.5$, $p < 0.001$). This apparent delay in departure date may be due to climatic factors. The weather experienced during the period December to April in 1984-5 was somewhat harsher than in either 1985-6 or 1986-7, with a more prolonged spell of sub-zero daily mean minimum air temperatures (Table 2.7). It is possible that these conditions caused a delay in the departure of birds, either if individuals found it harder to build up the necessary pre-migratory fat levels, or if birds wait for an environmental cue before migrating.

2.4.3.3. Timing of migration: Autumn Arrival.

The pattern of return of marked individuals to the study site after the breeding seasons of 1985 and 1986 is depicted in Fig.2.8 and summarised in Table 2.5. Return dates of birds are much less synchronised than departure dates; this is expected as there is pressure to arrive on the breeding grounds to initiate reproduction as soon as conditions become suitable both to make the most of a relatively short season and to maximise the chances of laying a second clutch should the first be predated. Such constraints do not apply to the return date. Termination of breeding will tend to vary between pairs, contributing to the variation in return date (Pienkowski & Evans 1984). Most birds return in July and the first half of August and then commence moult. Birds continue to arrive in small numbers until the end of November. I suspect

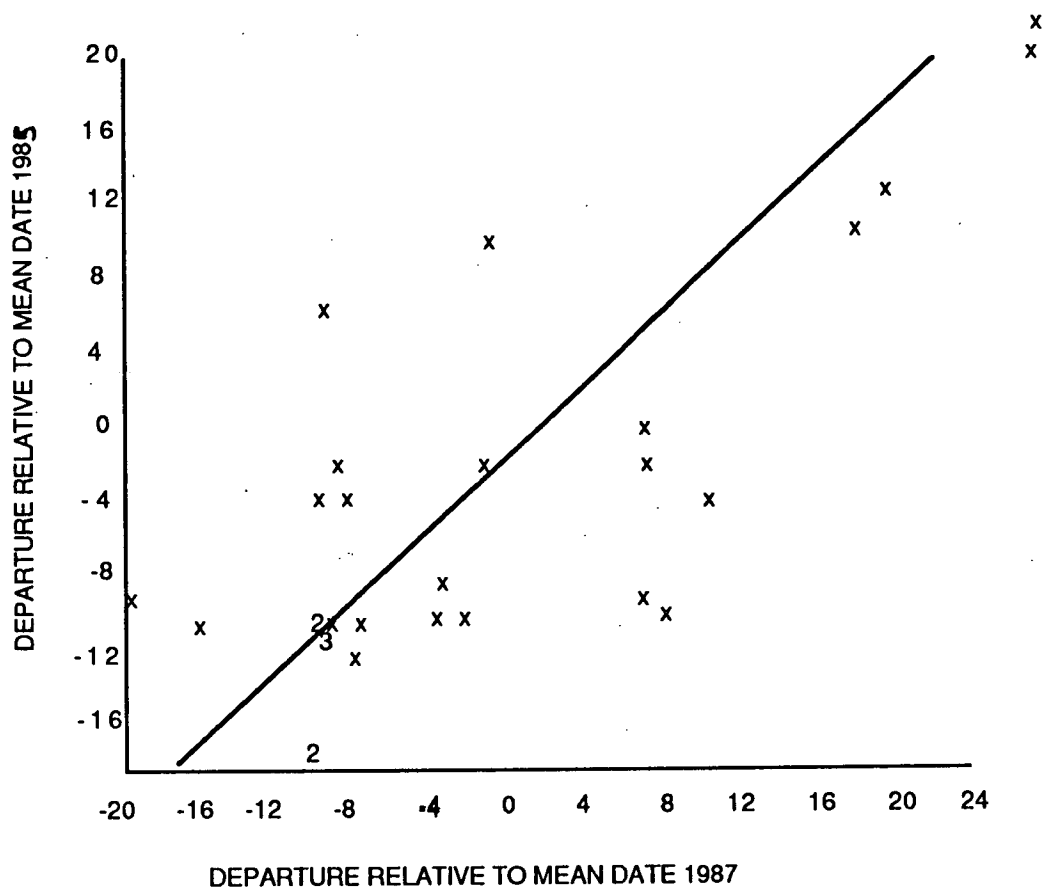


Fig. 2.151. Departure dates of individuals relative to the mean departure date of marked individuals that year in 1985 against 1987.

Fig. 2.6 a) Cumulative percentage of marked individuals departing from the study site in fortnightly periods in spring 1987. ---o--- = 'migrant' birds, --o----- = 'resident' birds.

Fig. 2.6 b) Cumulative percentage of marked individuals arriving at the study site in fortnightly periods in autumn 1986. ---o--- = 'migrant' birds, --o----- = 'resident' birds.

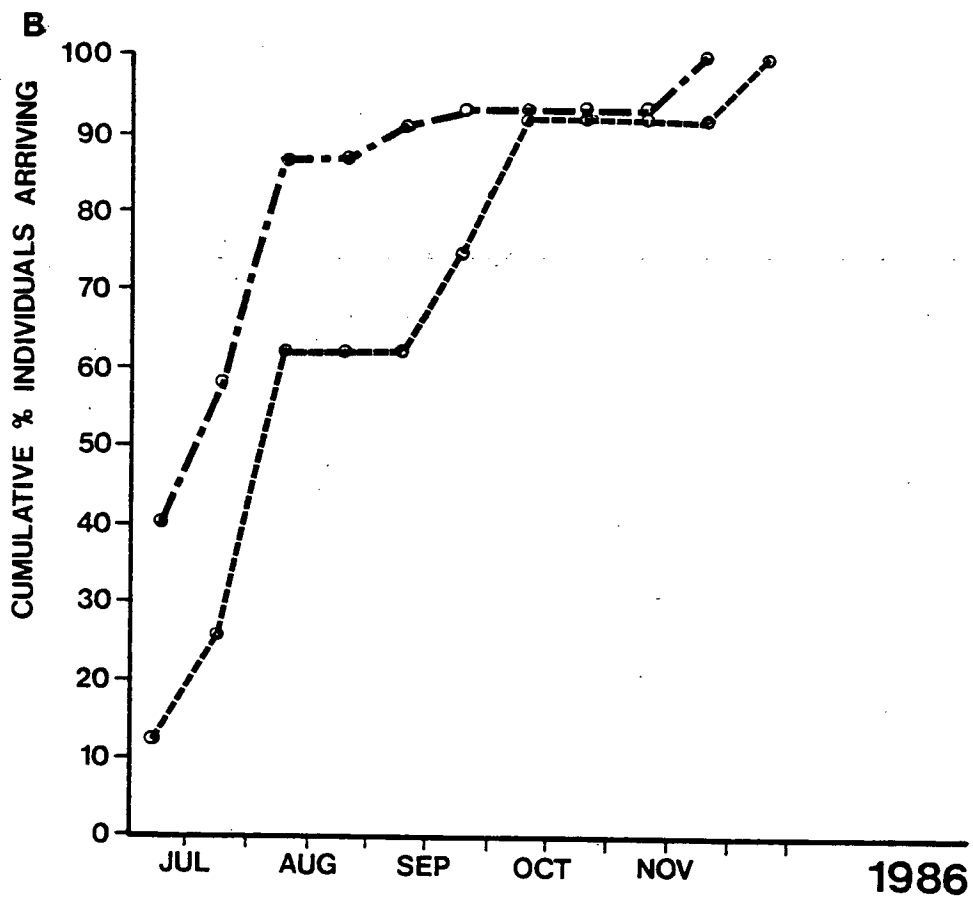
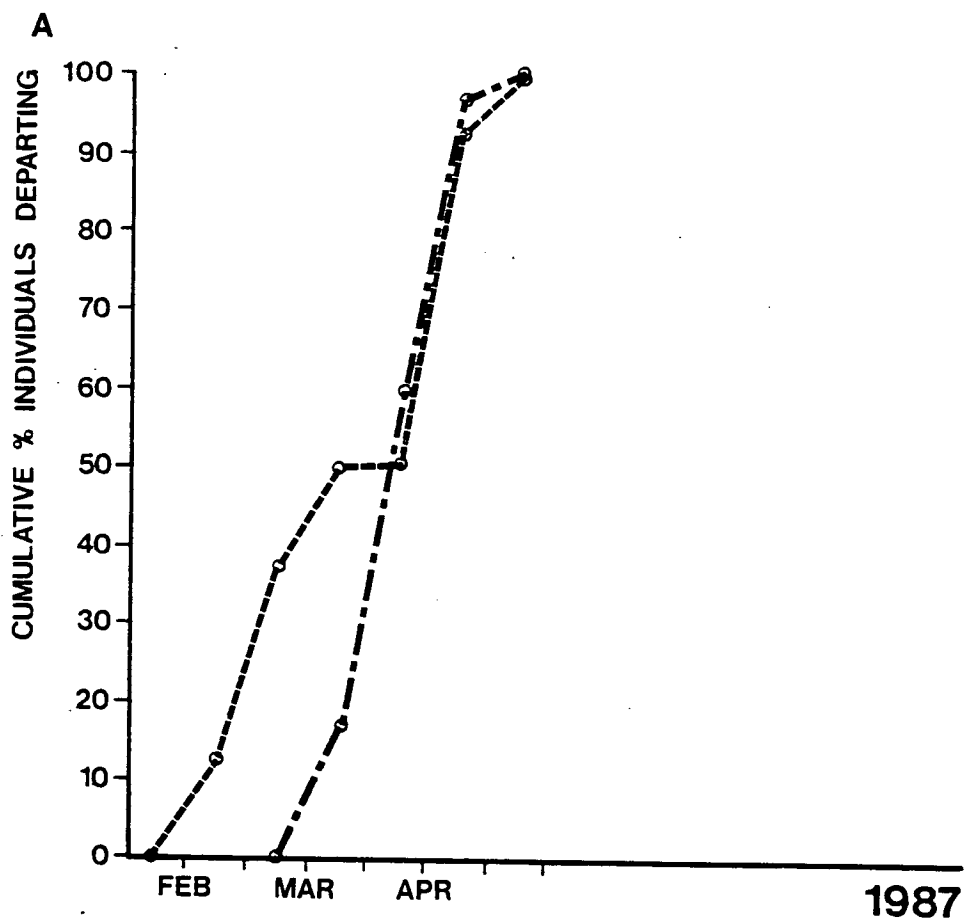
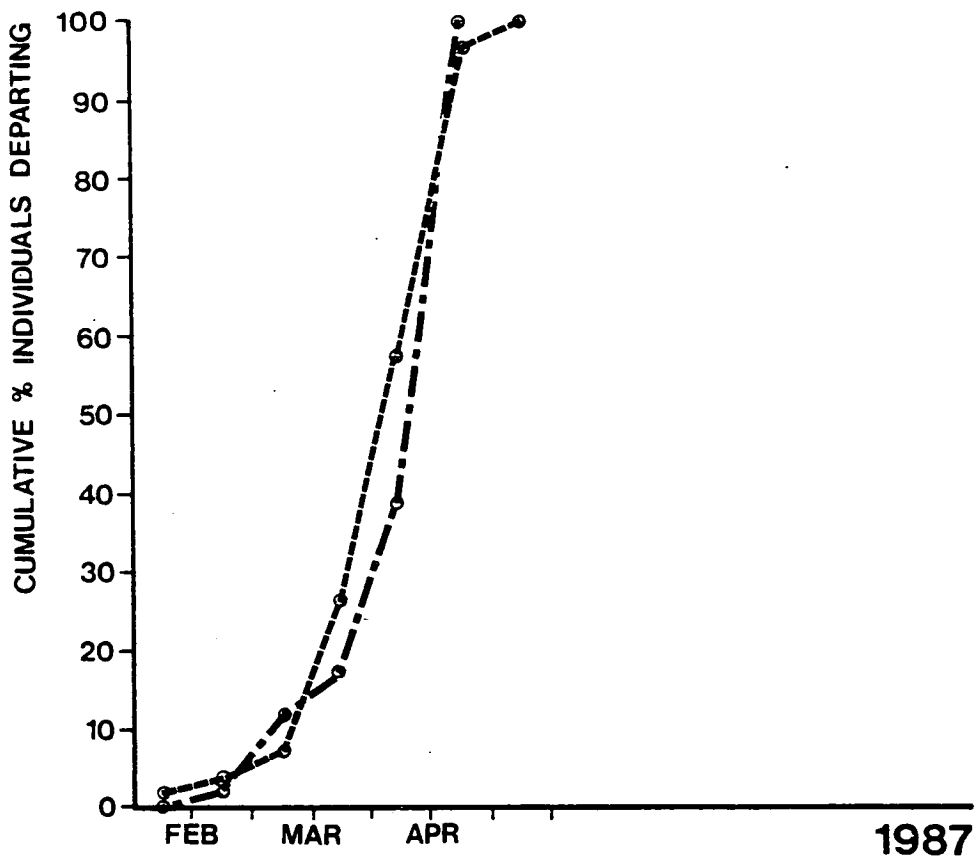


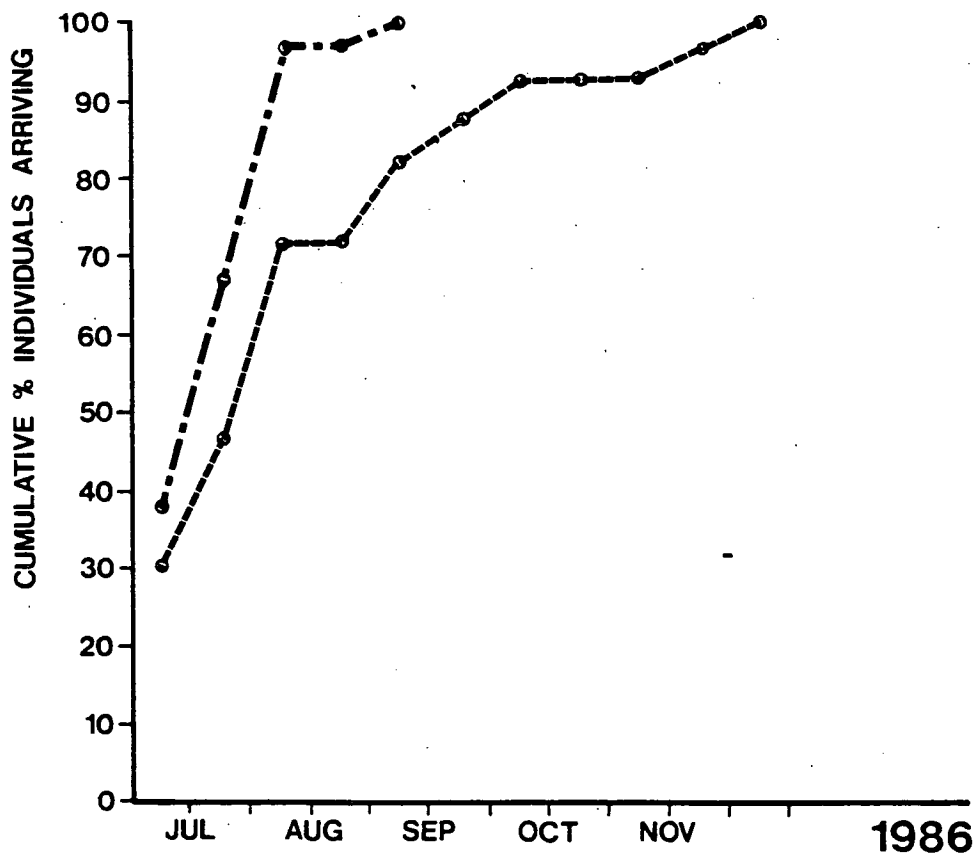
Fig. 2.7 a) Cumulative percentage of marked individuals departing from the study site in fortnightly periods in spring 1987. ---o--- = males, -·-·-o-·-·- = females.

Fig. 2.7 b) Cumulative percentage of marked individuals arriving at the study site in fortnightly periods in autumn 1986. ---o--- = males, -·-·-o-·-·- = females.

A.



B.



1 9 8 4 - 1 9 8 5				
MONTH	MEAN MAX TEMP °C	MEAN MIN TEMP °C	DAYS BELOW 0°C	DAYS SNOW+ ICE COVER
DEC	8.3	2.8	5	0
JAN	4.9	-0.3	17	6
FEB	6.2	-1.1	16	5
MAR	7.8	1.7	8	4
APR	11.2	2.5	5	0
-----			-----	-----
TOTAL			51	15
-----			-----	-----

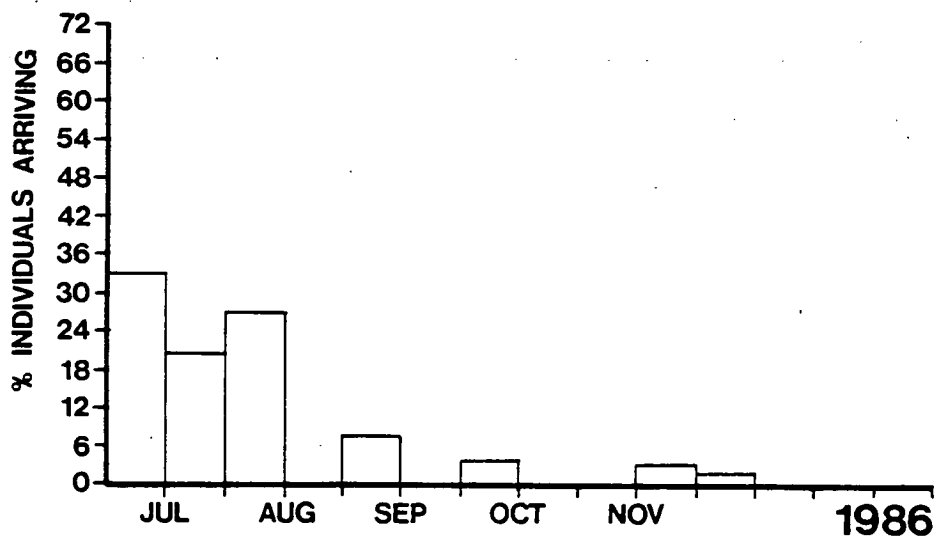
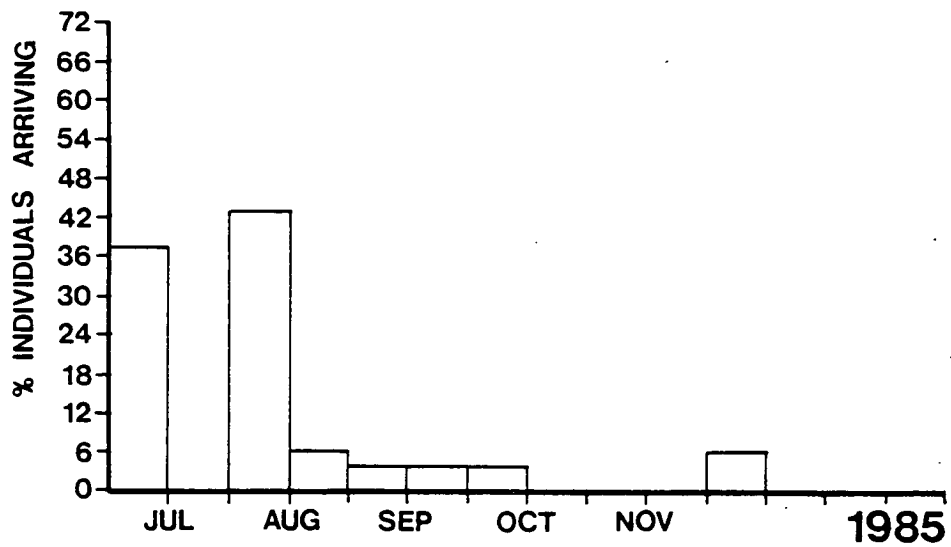
1 9 8 5 - 1 9 8 6				
MONTH	MEAN MAX TEMP °C	MEAN MIN TEMP °C	DAYS BELOW 0°C	DAYS SNOW+ ICE COVER
DEC	7.9	3.3	5	2
JAN	5.3	0.9	8	3
FEB	2.5	-0.6	17	6
MAR	7.8	1.6	3	0
APR	6.8	2.4	0	0
-----			-----	-----
TOTAL			33	11
-----			-----	-----

1 9 8 6 - 1 9 8 7				
MONTH	MEAN MAX TEMP °C	MEAN MIN TEMP °C	DAYS BELOW 0°C	DAYS SNOW+ ICE COVER
DEC	7.6	2.6	3	0
JAN	4.3	-0.4	15	13
FEB	6.4	1.2	10	5
MAR	7.3	1.2	8	2
APR	12.4	5.0	0	0
-----			-----	-----
TOTAL			36	20
-----			-----	-----

Table 2.7 Summary of climatic conditions in the three winters 1984-5, 1985-6 and 1986-7.



Fig. 2.8. Percentage of marked individuals that arrived at the study site in fortnightly periods during autumn 1985 and 86.



that these late arrivals are mainly birds which have undergone moult elsewhere, either close to the breeding grounds or at 'stop-over' sites such as the Wash (Bainbridge and Minton 1979).

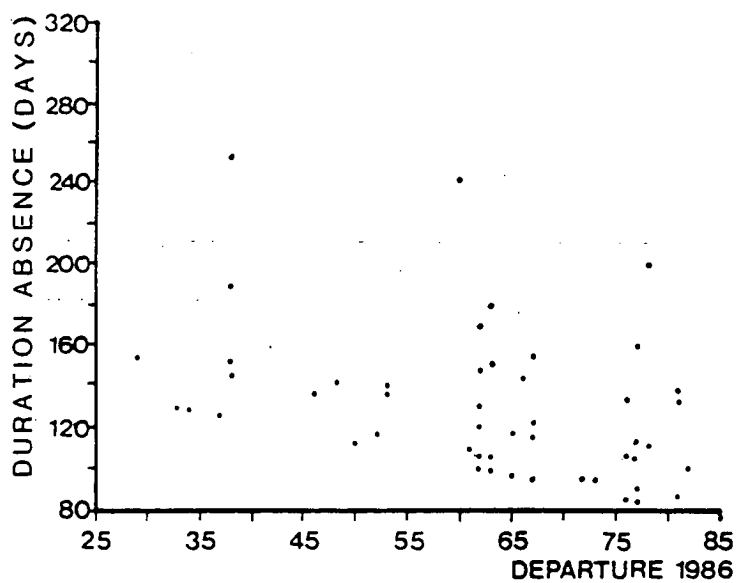
There appears to be a tendency for females to return before males, (Fig. 2.7b, Table 2.5) although the trend is not significant in either year (Mann-Whitney U-test $p > 0.05$) probably due to the small sample sizes of females. This is in agreement with the observation that females tend to leave the male to care for the brood before the pulli have fledged (Cramp and Simmons 1983). 'Residents' return to the study site before 'migrants' (Fig. 2.6b), a trend which was significant in 1986 (Mann-Whitney U Test, $W=772$, $p < 0.01$). This is again consistent with the hypothesis that 'resident' birds experience a shorter breeding season in Scandinavia than do 'migrants' in Scotland. Further evidence in support of this theory comes from the observation that birds which leave early in the spring tend to be absent for a longer period than those which leave late (Fig. 2.9 $r = -0.506$, $N = 49$, $p < 0.001$).

2.5 Annual Mortality.

2.5.1. Introduction.

Curlew have a relatively long life expectancy (Boyd 1962, Spencer 1984). Estimates of mortality vary. From analysis of ringing recoveries Boyd (1962) estimated annual mortality levels as: 1st year: 62%; 2nd year: 33% and 3rd year and older: 25.2%. Bainbridge and Minton (1978) arrived at figures of 53%, 37% and 26.4% for the same age classes, using a longer data series than did Boyd. Evans (1981) and Townshend (1981a) analysed the disappearance of colour-marked individuals from Teesmouth, north-east England. Evans estimated mortality amongst adults (2nd year and older) at between 18% and 25%. Townshend's estimate for the same age class (15% to 25%) is in accordance with that of Evans. Townshend's estimate of mortality amongst juveniles (12%) was remarkably low.

Fig. 2.9 Date of spring departure plotted against duration of absence of individual birds during the 1986 breeding season. $N=49$, $r = -0.506$, $p < 0.001$.



Until the winter of 1981-2 curlew were legally shot as quarry in Britain. Boyd (1962) discovered that 60% of ringed birds recovered in their first year and 65% of birds recovered as adults were deliberately killed by man. Bainbridge and Minton (1978) also state that the majority of recoveries of curlew were of birds which had been shot. In the winter of 1981-2 91 curlew (at least 30% of the wintering population) were killed by wildfowlers at Tynningham. Since this study commenced in autumn 1984, two years after the start of a government imposed ban on shooting curlew in Britain (they are still shot on the continent, particularly during migration) I decided to attempt to assess mortality levels to see if they had dropped.

2.5.2. Methods.

There are three methods that can be used to assess mortality:

- a) analysis of ringing recoveries (e.g. Boyd 1962, Bainbridge & Minton 1978);
- b) recording the disappearance of colour-marked individuals from the study-site (Townshend 1981a, Whitfield 1985b);
- c) making regular searches for corpses (Whitfield 1985b).

All three methods are prone to error. Method 'a' tends to overestimate mortality since wear and abrasion of rings will tend to exclude older birds from analysis. This method was unsuitable for my use due to the low number of recoveries reported. Method 'c' will tend to underestimate mortality because no matter how intensive the search regime, some corpses will inevitably be missed (Whitfield 1985^b). This approach is also very time consuming and therefore unsuitable unless looking at specific causes of mortality. Method 'c' also only permits estimation of mortality on the wintering grounds. I therefore restricted my assessment of mortality to method 'b'. Equating disappearance of marked individuals with mortality can lead to overestimation since some birds, especially juveniles, can switch sites between successive winters as

Townshend (1982) found for grey plover, *Pluvialis squatarola*. Also it is possible to miss a migrant bird that stays at the study-site for only a few days. My estimates of mortality must, therefore, be regarded as maxima. I used this method to make estimates for the two components of annual mortality: mortality that occurs on the wintering grounds and mortality on the migration routes/breeding grounds (Evans & Pienkowski 1984, Whitfield 1985). The two estimates can be added to give annual mortality. Winter mortality was taken as that occurring between 1st July and 1st March (the earliest normal departure date). The number of birds dying in this period is given by the number seen after 1st July, but last seen before 1st March in winter x, and failing to return in winter (x+1). The number dying in the breeding season is given by the number seen in winter x, last seen after 1st March, but not seen in winter (x+1). This procedure tends to underestimate the winter component of mortality since some birds may die at the study site after March 1st. Unfortunately insufficient birds were caught early in the 1984-5 winter to attempt to estimate mortality within this period. I have arrived at two estimates for each component of mortality in the 1985-6 season. The first is based solely on birds which were not seen in the winter (x+1), whilst the second takes into account individuals which were not seen in winter (x+1) (assumed dead at the time) but returned in winter (x+2).

2.5.3. Results.

Estimated mortality levels are shown in Table 2.8. In the summer of 1985 (the only period in which sufficient juveniles were marked to attempt a mortality estimate) mortality of juveniles appeared to be higher than that of adults, but this was not significant ($\chi^2 = 1.583$, $p > 0.1$). Juvenile mortality is normally higher than that in adults (Boyd 1962) and, additionally, juveniles tend to be more itinerant than adults and more likely to switch wintering sites. Although overall more adult males than adult females disappeared in the study

	ANNUAL														
	SUMMER 1985					WINTER 1985-6					MORTALITY 1985-6				
	N	A	B	%A	%B	N	A	B	%A	%B	1985-6	N	A	%A	
JUVENILES	17	4	2	23.5	11.8	2	0	0	0	0	11.8	5	0	0	
ADULTS	37	4	1	10.8	2.7	73	4	4	5.5	5.5	8.2	81	6	7.4	
AD MALE	23	3	0	13.0	0	47	4	4	8.5	8.5	8.5	50	5	10.0	
AD FEMALE	13	1	1	7.7	7.7	25	0	0	0	0	7.7	30	1	3.3	

Table 2.8 Mortality estimates. N = number of colour-marked birds from which each estimate is derived, A = number of marked birds that disappear in the relevant period, B = number that disappear corrected for birds which subsequently return. See text for methods of calculation.

period, the difference was not significant ($\chi^2 = 1.051$ $p > 0.1$) and there were no intersexual differences in mortality in any of the three periods assessed (χ^2 values = 1.58, 1.44 and 2.2, $p > 0.1$ for summer '85, winter '85-6 and summer '86 respectively). Estimated annual mortality in the period March 1st 1985 to March 1st 1986 for both adults and juveniles was lower than that calculated by either Boyd (1962) or Bainbridge and Minton (1978) and my estimate for adult mortality was less than that determined by Evans (1981) or Townshend (1981a). To test for significance I used Bainbridge and Minton's estimate of 53% for juveniles and Boyd's and Evans' estimates of approximately 25% for adults to produce the expected numbers of birds in each age class that would have died in my marked population (i.e. 9 juveniles and 19 adults). My estimate for annual adult mortality is significantly lower than those from earlier studies ($\chi^2 = 6.964$, $p < 0.01$), but my estimate for juvenile mortality does not differ significantly from that of Bainbridge and Minton. The difference in annual adult mortality estimates between this and the two previous studies based on ringing recoveries is even more marked considering that my 'adult' population included 17 known 2nd ^ayer birds and earlier studies have demonstrated that mortality amongst 2nd years is higher than amongst older birds. The lower annual mortality amongst adults described in this study could have arisen if the analysis of ringing recoveries (Boyd 1962, Bainbridge & Minton 1978) overestimates mortality to a greater extent than using the disappearance of colour-marked birds. It seems unlikely, however, that any discrepancy between methods should be so large. Much of the difference can probably be attributed to the removal of shooting pressure on British wintering grounds.

2.6. Proportion of juveniles in the the population.

2.6.1. Introduction and methods.

Mortality in the curlew is higher in the first year of life than in subsequent years (see preceding section). Thus I attempted to assess the age composition of the population. Unfortunately juveniles are only discernible from adults in the hand, therefore I could only attempt an assessment of age composition of the population through the number of juveniles caught. This is likely to lead to an overestimate since juvenile birds are more likely to be caught than adults (Pienkowski & Dick 1976, Goss-custard *et al* 1981a).

2.6.2. Results.

The proportion of juvenile birds caught varied between 3% and 30% over the three years (Table 2.9). Significantly more 1st year birds were caught in 1984-5 than in 1985-6 ($\chi^2 = 7.31$, $p < 0.01$), or 1986-7 ($\chi^2 = 6.83$, $p < 0.01$). This variation could reflect a decline in breeding success over the three years, but I think it is more likely to be the result of seasonal variation. Proportionately more juveniles were caught in the month of April than in all other months when catches were made (Table 2.9, $\chi^2 = 14.75$, $p < 0.001$). In the first year a large catch was made in April. As already stated, many juveniles remain at the study site throughout their first summer. During this period they tend to form aggregations along the coast. Since by April many adults have already departed for the breeding grounds (sections 2.2,2.4) it might be expected that the proportion of juveniles is highest at this time of year, despite the fact that mortality amongst juveniles is proportionately higher than amongst adults (Bainbridge and Minton 1978, section 2.5).

2.7. Summary.

The study-site supports a fairly stable wintering population of between 200 and 300 curlew, between 60 and 100 of which exploit food resources at Scoughall. Eighty-four colour-marked birds used the study site in winter, of which 55% were resident and seen regularly, whilst 45% were itinerant and seen only sporadically. Many curlew used the study-site as a 'stop over'

	JUVS	ADULTS	%JUVS
1984-5	18	43	29.5
1985-6	4	46	8.0
1986-7	1	29	3.3
APRIL			
ALL YEARS	17	37	31.5
REST OF			
YEAR	6	81	6.9

Table 2.9 Proportion of juveniles in catches by year and season.

during spring and autumn migration, when up to 400 birds congregate at Scoughall. Sightings of colour-marked birds outside the study-site broadly confirm Bainbridge and Minton's (1978) finding that curlew in this area tend to move in a south-westerly direction to their wintering grounds. The late departure date and shorter duration of absence of 'resident' birds compared to 'migrants' lends some support to the idea that Scoughall-wintering curlew tend to breed in Scandinavia, whilst those that winter in the south-west tend to breed in Scotland. Timing of migration agreed broadly with the findings of Bainbridge and Minton (1978) and Townshend (1981a). Estimates of annual mortality amongst adults were lower than those determined by two previous analyses of ringing recoveries (Boyd 1962, Bainbridge & Minton 1978) and also lower than those determined by Evans (1981) and Townshend (1981a) using disappearance of colour-marked birds. This discrepancy is probably the result of the removal of shooting pressure.

CHAPTER 3.
PHENOTYPIC VARIATION AND FEEDING SPECIALISATIONS.

*"He's eatin' bagels,
He's eatin' pizza,
He's eatin' chitlins"*

BOB DYLAN 1963.

3.1 Introduction.

Natural selection can act either to reduce or promote the degree of phenotypic variation within a population, depending upon the constraints and processes involved (Roughgarden 1972). Perhaps the traditional view of natural selection is of a single optimum phenotype conferring maximal fitness within a stable environment. Directional selection would act differentially upon one or other of the tails of the normal distribution of phenotypes, tending to push the modal phenotype in the direction of the optimum and at the same time reducing the range of phenotypic variation. Once the modal phenotype coincided with the optimum, directional selection would give way to stabilising selection, acting simultaneously on both the tails of the normal distribution and thus reducing the phenotypic range about the mode (Roughgarden 1972, Boag 1987). Van Valen (1965) produced a hypothesis (the 'niche variation hypothesis') whereby natural selection can promote phenotypic variation within a population inhabiting a stable environment. Fundamental to Van Valen's theory is the concept of 'niche width', which refers to the variety of resources that a population exploits (Roughgarden 1972) and was defined by Van Valen as: "the proportion of total multidimensional space of limiting resources used by a species or segment of a community". The niche width of any population has two components: within and between phenotype. For instance the population can consist of many similar individuals each exploiting a wide range of limiting resources (within phenotype) or diverse individuals each exploiting different subsets of the range of resources (between phenotype) (Van Valen & Grant 1970, Roughgarden 1972, Price 1987). If the major component of niche width is between phenotypes (i.e. if individuals within a population exploit differing subsets of the environment exploited by the population as a whole), Van Valen argued, then in effect there can be several optimum phenotypes and regimes of weak stabilising selection or disruptive selection can promote

phenotypic variability. Variability can only be maintained, however, if the following requirements are satisfied:

- 1) there is differential fitness between environmental subsets, i.e. phenotype 'a' is fitter than phenotype 'b' in subset 'A', whilst 'b' is fitter than 'a' in subset 'B'. It is however predicted that the fitness of 'a' in subset 'A' will not differ from that of 'b' in subset 'B';

- 2) the above difference is in part genetic;

- 3) there is an appropriate mechanism for the segregation of individuals between subsets 'A' and 'B', including choice.

If these conditions are fulfilled, then a varied environment can produce and maintain both polymorphism and continuous variation. Moreover, intrapopulation variation in niche exploitation can permit a greater population size and thus variability can be considered adaptive in itself (Van Valen 1965). There are two components of phenotype in which variation can be easily measured: morphology (normally genetically determined and relatively fixed) and behaviour (often plastic and modified by the environment).

Curlew would appear to exploit a broad niche (Ens 1979, Zwarts 1979, Townshend 1981b), to show large variation in bill length (Prater *et al* 1977, Townshend 1981a, Cramp & Simmons 1983) and to exhibit a wide range of foraging behaviour (Burton 1974, Ens 1979, Phillips 1980, Townshend 1981a). In this chapter I describe the results of detailed measurements of the above three variables (environment, morphology and behaviour) and analyse the relationship between them in order to assess the applicability of the niche variation hypothesis to curlew. I also cite recent evidence that appears to support the niche variation hypothesis.

3.2 Morphological variation.

3.2.1. Introduction.

Bill morphology is usually fixed (but see Swennen *et al* 1983, Gosler 1987) and highly heritable (Boag 1983, Gosler 1987). Moreover bill shape has been shown to be related to niche utilization (e.g. Selander 1966, Partridge 1974, Gosler 1987) and foraging efficiency (Partridge 1976b, Gosler 1987). Many of these studies, however, refer to interspecific or intersexual differences. The long term study of Darwin's medium ground finch by Grant and his co-workers has shown large, continuous variation in bill morphology, correlated with increasing environmental heterogeneity (Grant *et al* 1976). In times of food shortage beak morphology is subject to periods of intense ('bottleneck') directional selection (Boag & Grant 1981, Price *et al* 1984). However, given plentiful food, there is a tendency for disruptive selection to promote phenotypic variation in bill shape (Grant 1985, Price 1987). Smith (1987) documents a non sex-linked polymorphism in bill size in an African estrildid finch. This polymorphism is correlated with diet and differential niche utilization and postulated to be important in reducing intersexual competition. Smith is careful to point out, though, that this trophic divergence in his study species is not the result of increasing sexual dimorphism. This is an important point; curlew exhibit a high degree of sexual dimorphism, with females being considerably larger than males (Cramp & Simmons 1983). It has been suggested that intersexual differences, particularly in body size, could result from differing reproductive roles (Partridge & Green 1985). Since biometric measurements are normally highly correlated, variation in trophic apparatus may have evolved passively, simply as an isometric function of body size. In this section I document the degree of inter- and intrasexual variation in the biometric measurements of curlew, especially of bill morphology. Variation in bill morphology is compared to that in three related species of shorebird, all with long, curved bills and with that in two passerine species where bill morphology has been shown to be related to niche utilization. I also test

whether bill morphology in curlew is simply an isometric function of body size.

3.2.2. Methods.

3.2.2.1. Recording biometrics.

After capture all birds were ringed, colour-ringed, aged and had a standard set of biometrics recorded. To avoid individual differences in technique all measurements were taken by the same person.

Wing length: wing length was measured to the nearest millimetre with a 320mm stopped steel wing rule, using the maximum chord method (Svensson 1984, Evans 1986).

Tarsus and toe: to make this measurement the tibio-tarsal joint was bent at right-angles and held against the stop of a steel wing rule. The tarsus and foot were held flat against the face of the rule and the measurement taken (to the nearest millimetre) to the tip of the fleshy pad beneath the claw of the longest (middle) toe (Anderson 1975).

Mass: birds were weighed to the nearest 5g on a 1000g (or 1300g) 'Pesola' spring balance.

Bill length: bill length was taken to the nearest millimetre by placing the stop of a wing rule on the upper mandible at the edge of the feathering where the bill joins the skull. The face of the rule was held along the length of the bill and the measurement taken to the bill tip. In effect this meant that it was the chord of the bill from base to tip that was the measurement recorded (A-D in Fig.3.1).

Sexing birds: post-mortem examinations have shown that bill length is bimodally distributed with respect to sex, with females having longer bills (Prater *et al* 1977, Cramp & Simmons 1983). In fact there is almost no overlap in the bill lengths between sexes. Griffiths (1968) published a method of determining the population parameters of a bimodally distributed character, without having to resort to post-mortem analysis. I used this method to

ascertain the points above and below which I could reliably assign sex to an individual on the basis of bill length alone. The method involves converting the frequency distribution of the character into percentage cumulative frequencies (PCF) at the class boundaries. These are then plotted on arithmetic probability paper to give a sigmoid curve. The point of inflexion of this curve (P%) gives the proportion of the sample with the lower mean. A number of points on the lower region of the curve are then multiplied by $100/P$ and plotted on the same diagram. A sample of points from the upper region of the curve are multiplied by $100/(100-P)$ and plotted on the same diagram. This gives two linear curves, one either side of the sigmoid curve, representing the 'population' lines for each subset of the population. The point at which a population line crosses the 50% PCF level gives the mean of that subset and the difference between the points at which it crosses the 84% and 50% PCF levels gives the standard deviation.

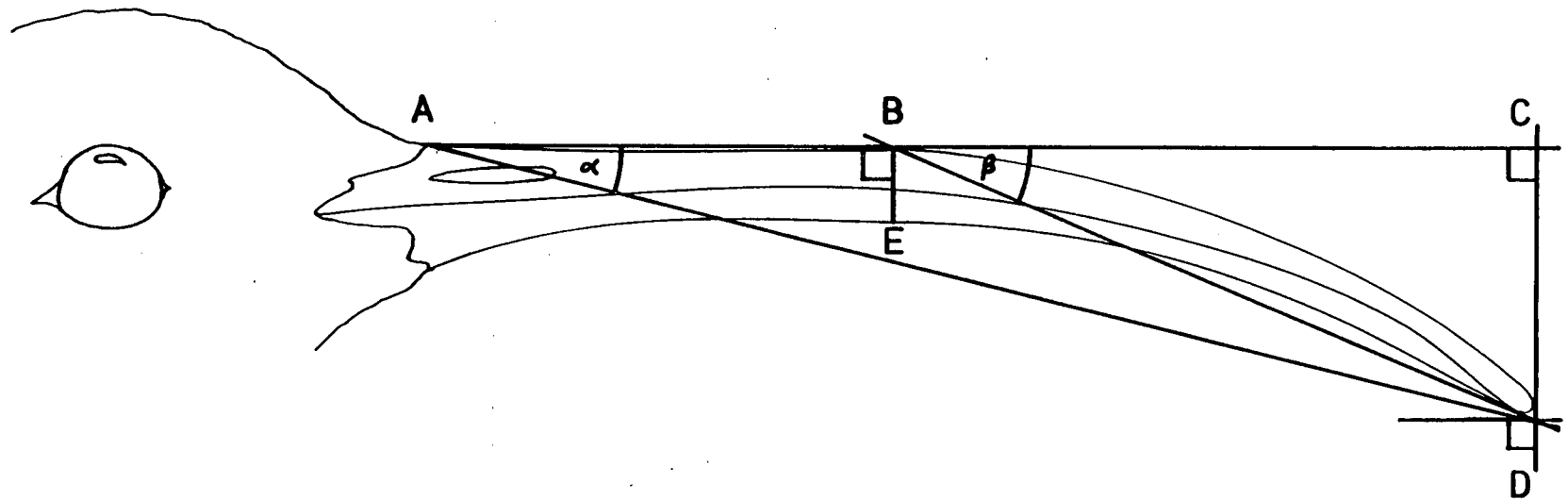
Bill decurvature: In order to measure bill decurvature I constructed a board (40cm x 30cm x 0.5cm thick), to which I stuck a sheet of graph paper (1mm squares). Two nails were driven into the centre of the board 4cm apart. The bird was held under the right arm, with the head controlled by the thumb of the right hand and the right forefinger placed underneath the lower mandible. The left hand held the board vertically behind the head and the bill was positioned so that it was touching the graph paper all along its length. The right forefinger was used to hold the upper mandible gently against the lower edge of the two nails. An assistant then took a 35mm photographic transparency of the lateral view of the head and bill. Photographs were taken using a flash unit and from a distance of about 1m, so that the head and bill filled the frame. At a later date the transparencies were projected onto a sheet of paper 50cm x 30cm. The image was traced onto the paper, together with the outline of a 1cm square of the graph paper on the board. All

measurements could thus be scaled down into real units. To make the required measurements (Fig. 3.1) I first drew a tangent to the straight base of the bill (line A-C). A perpendicular (C-D) was dropped to the bill tip. 'B' was the point of inflexion at which the bill dropped below the tangent. I measured (to the nearest millimetre) the length of the straight (AB) and curved (BC) portions of the bill and the depression (CD) from the tangent to the nearest millimetre. The percentage (X%) of the bill that was curved was calculated using: $X = BC/(AB+BC) \times 100\%$. The angles from the base of the bill (Alpha = CAD) and the point of inflexion (Beta = CBD) were measured to the nearest half-degree using a transparent protractor. The depth of the bill (BE) was measured perpendicular to the tangent at the point of inflexion, to the nearest 0.1mm. Gosler (1987) emphasized the importance of small differences in bill shape to great tits, in terms of niche utilization. To analyse bill shape he calculated 'bill index' as bill depth/bill length. I calculated the same index, multiplying the ratio by 100 to give values greater than one. This index I refer to as the 'taper index'. Curlews' bills are also highly decurved; to take this into account when analysing bill shape I divided the taper index by bill depression and multiplied the ratio by 10. This is referred to as the 'shape index'.

3.2.2.2 Testing for Isometry.

To test whether variations in biometric measurements were simply the result of isometric functions with body size, I followed the procedure described by Summers (in press). Summers points out that mass is theoretically a cubic function of linear measurement (e.g. wing or foot length), i.e. that mass should be proportional to the cube of a linear measurement. If the logarithm of mass is plotted against the logarithm of a linear measurement, the slope of the least-squares regression line will give the exponent to which the linear measurement has to be raised in order to make it directly proportional to mass. This gives the expectation that if a linear measurement is isometric with mass,

Fig. 3.1 Measurements taken from projected transparencies of the bills of curlew.



the slope of the least-squares regression on the log. plot should be equal to three. Least-squares regressions were calculated for all birds, regardless of sex, for the following measurements: wing length, tarsus and toe, bill length, bill depression, alpha, beta, taper index and shape index.

3.2.2.3. Comparisons with other species.

In order to compare the degree of variation in curlew biometrics with that in other species I calculated coefficients of variation for each measurement. The coefficient of variation (CV) is simply the ratio of standard deviation to the mean, expressed as a percentage and is directly comparable between species. Comparisons are made with published figures for great tits (Gosler 1987) and the seedcracker, *Pyrenestes ostrinus* (Smith 1987). CVs for other species have been calculated from figures presented by Mallory (1981) and Cramp & Simmons (1983).

3.2.3. Results.

3.2.3.1. Sexing birds in the hand.

As expected, bill length was bimodally distributed (Fig. 3.2), reflecting the sexual dimorphism exhibited by curlew. Using Griffith's (1968) method I determined the population lines for the bill length of each sex (Fig. 3.3). From the population lines I determined the parameters for each distribution of bill length. These were: male, mean = 113mm + 9.5mm (sd), females, mean = 142mm + 8.0mm (sd). This means that 95% of males will have a bill length less than 132mm (mean + 2S.D.) and 95% of females will have bills longer than 126mm (mean - 2S.D.). Therefore I took cut-off points for sexing birds as male <126mm, female >132mm. There remains the possibility that 5% of birds were incorrectly sexed. Of 131 birds measured 3 (2.3%) had bill lengths intermediate to the limits set and were therefore left undetermined. Of the rest 78 (59.5%) were sexed as males and 50 (38.2%) as females.

Fig. 3.2 Bimodal distribution of bill length (mm) in curlew. N=140.

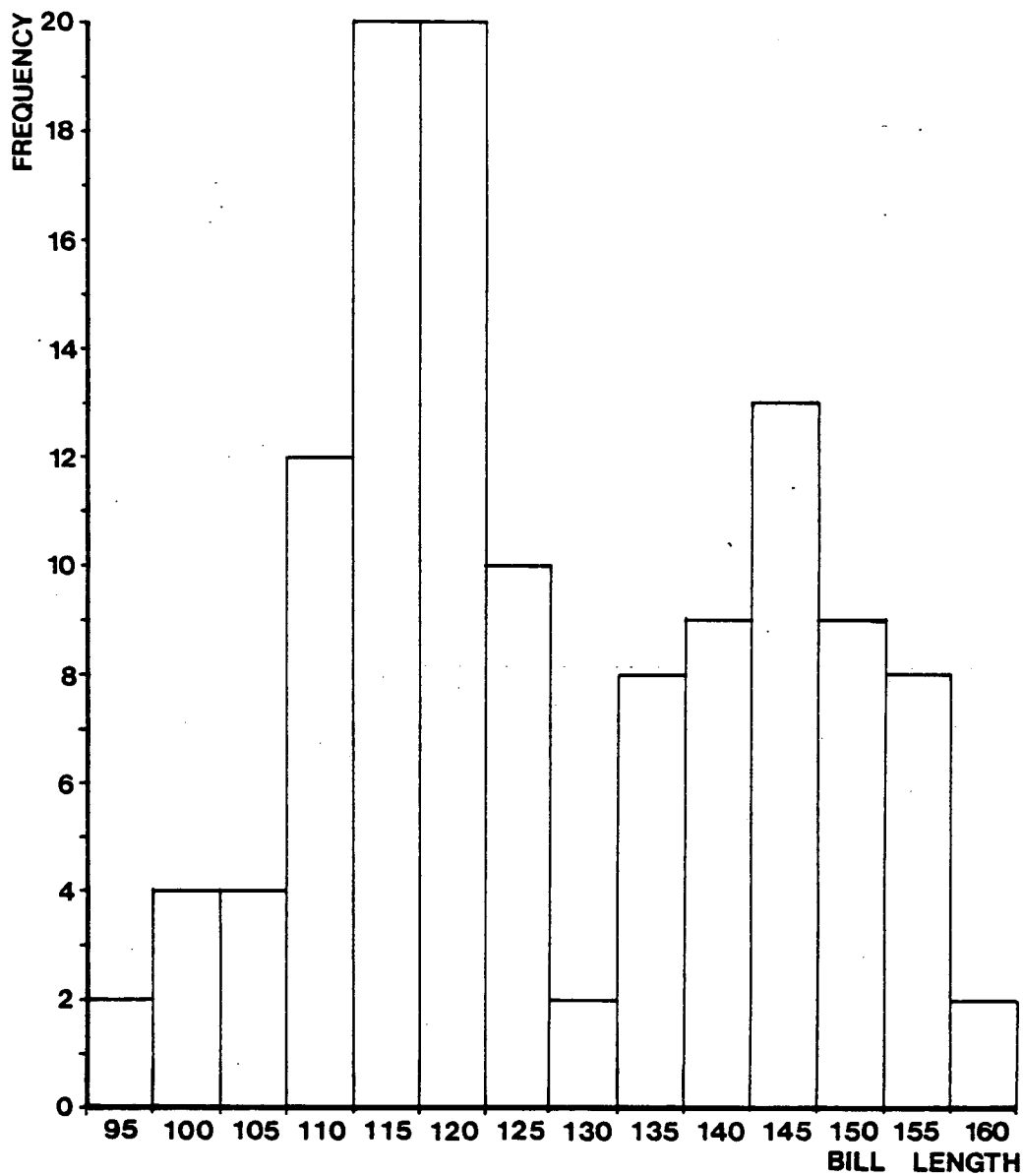
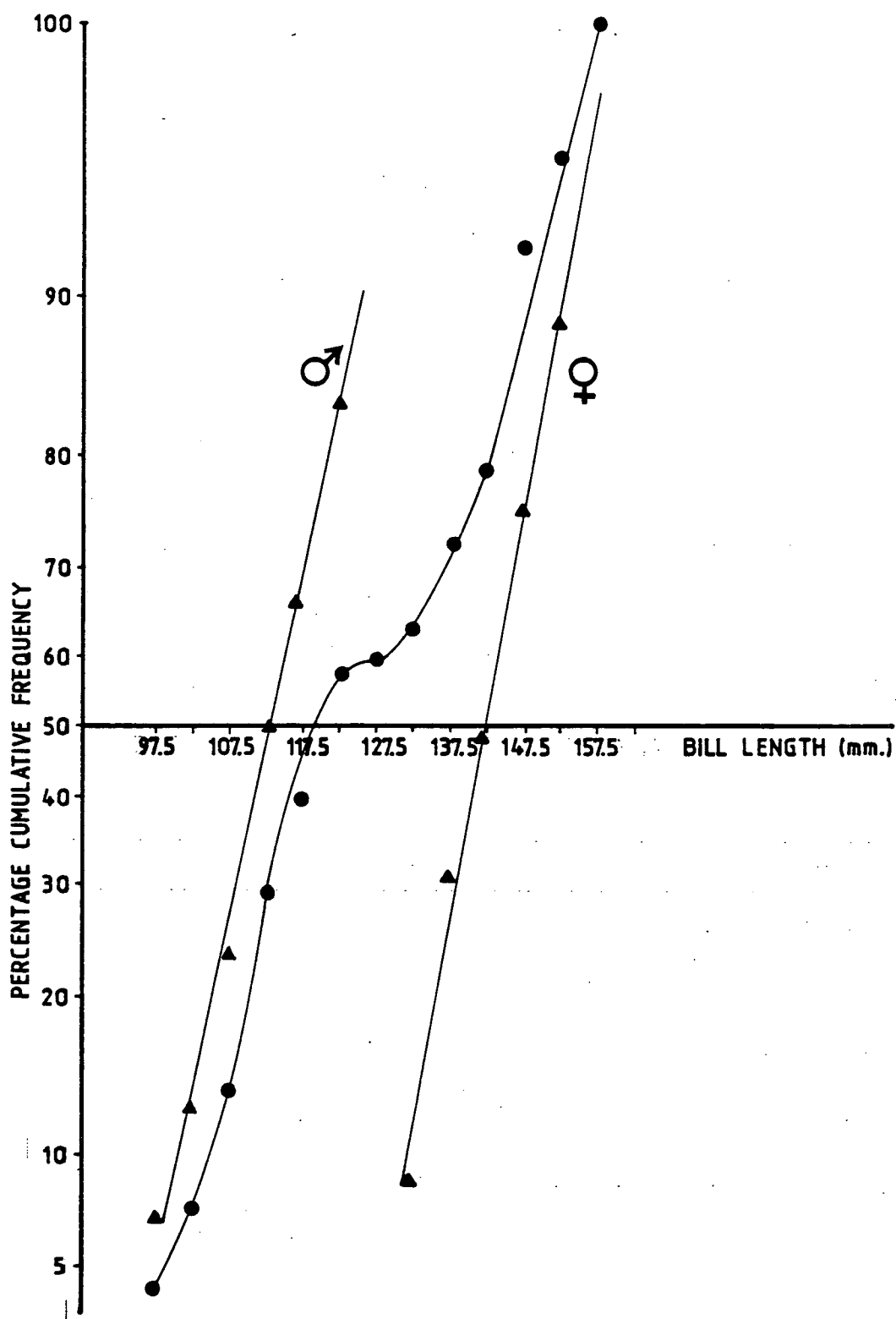


Fig. 3.3 Probability graph paper plot of bill length percentage cumulative frequency (after Griffiths 1965). Sigmoid curve = all birds. Left hand linear curve = population line for males. Right hand linear curve = population line for females. See text for methods and full explanation.



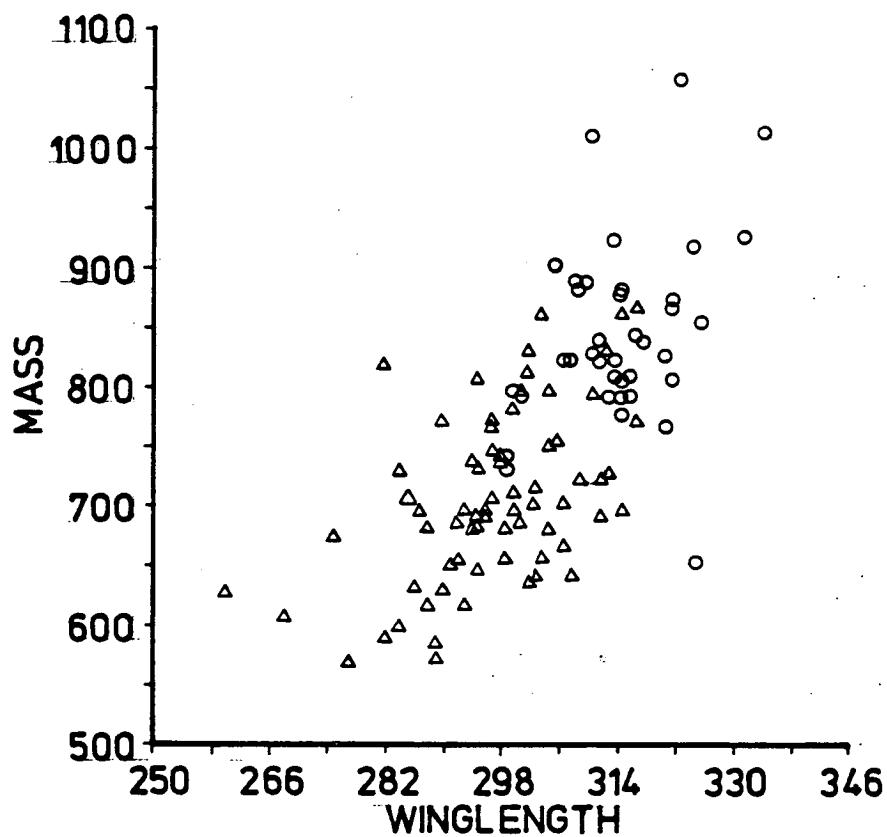
3.2.3.2. Biometrics.

All biometric measurements appeared to be normally distributed within sex classes. There were significant intrasexual positive correlations between wing length and mass and wing length and tarsus and toe (the latter in males only) (Fig. 3.4, Table 3.1) but not between wing length and any measure of bill morphology (Table 3.1, Fig. 3.5). Bill length is, however, correlated with wing length if both sexes are combined (Fig. 3.5). Biometric measurements recorded for each sex are summarised in Table 3.2. The ratios of male: female measurements (comparing means) are given in the final column. The ratios of male: female wing length, tarsus and toe and mass are fairly similar, but those for bill length and length of straight and decurved portions of the bill are somewhat lower, indicating that females may have disproportionately long and males disproportionately short bills. There is little intrasexual difference in the means of the % of the bill that is decurved, angle of decurvature or bill taper index. Males have a higher bill shape index, indicating that males have relatively straighter, thicker bills than females (Males were sexed on the basis of having short bills in the first place).

3.2.3.3. Testing for isometry.

If two objects of different size are geometrically similar they are said to be isometric; they have exactly the same shape and thus the linear dimensions of the larger are all greater by the same proportion than the smaller and the volume of the larger is greater by the cubic function of this proportion (Schmidt-Nielsen 1984). This concept is important; if female curlew were selected for large body size, for say egg-laying potential, then their bills may be proportionately longer simply due to isometry. However, if bill length is non-isometric it is possible that other selection pressures have been operating. I used Summer's (in press) method to check for isometric relationships with mass. Exponents derived from the slopes of the least-squares regression lines are shown in Table 3.3. Exponents for wing length and tarsus and toe are close to three, indicating that as expected mass is proportional to the cube of these linear measurements, i.e. there is an isometric relationship. The exponent for bill length is close to one, meaning that bill length is *directly* proportional to mass, i.e. that large birds tend to have disproportionately long and small birds disproportionately short bills, or that bill length is non-isometric with mass. Exponents for bill depression, angles of decurvature and bill taper index are small, indicating a very weak or no relationship with mass.

Fig. 3.4 Relationship between wing length (mm) and mass (g). Triangles = males ($r=0.511$, 69df, $p < 0.01^{**}$), circles = females ($r=0.346$, 38df, $p < 0.05^{*}$). Sexes combined: $r=0.689$, 111df, $p < 0.001^{***}$.



	MALES			FEMALES		
	r	df	p	r	df	p
WING vs TARSUS + TOE	0.369	71	**	0.132	36	NS
WING vs MASS	0.511	71	**	0.346	36	*
WING vs BILL LENGTH	0.057	71	NS	0.186	36	NS
WING vs DEPRESSION	-0.235	69	NS	0.125	36	NS
WING vs ALPHA	-0.185	69	NS	0.046	36	NS
WING VS DEPTH	-0.037	69	NS	0.049	36	NS
WING vs TAPER INDEX	-0.065	69	NS	-0.015	36	NS
WING vs SHAPE INDEX	0.058	69	NS	-0.095	36	NS

Table 3.1 Within-sex correlation coefficients of biometric measurements.

Fig. 3.5 Relationship between bill length (mm) and wing length (mm).
 Triangles = males ($r=0.057$, 71df, N.S.), circles = females ($r=0.186$, 38df, N.S.).
 Sexes combined: $r=0.707$, 111df, $p < 0.001^{***}$.

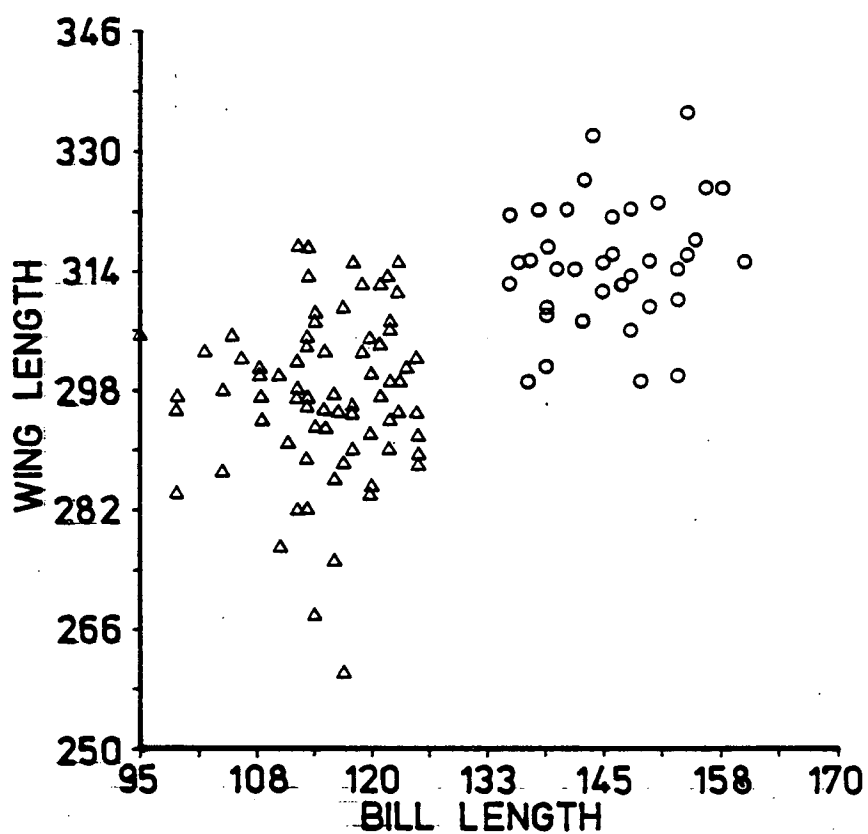


Table 3.2 Summary of biometric measurements within sex-classes. Ratio

M:F calculated by mean male/mean female measurement.

	M A L E S				F E M A L E S				RATIO
	N	RANGE	MEAN	SD	N	RANGE	MEAN	SD	M:F
MASS (g)	76	567-865	701.5	71.2	50	650-1055	839.7	71.2	0.84
WING LENGTH (mm)	73	260-317	297.2	10.9	38	299- 335	314.9	8.4	0.94
TARSUS + TOE (mm)	78	119-144	129.8	4.7	49	130- 151	138.5	4.2	0.94
BILL LENGTH (mm)	78	95-112	114.5	7.4	50	134- 160	145.5	7.0	0.79
LENGTH STRAIGHT (mm)	71	37- 71	54.2	7.9	49	47- 88	70.1	9.3	0.77
LENGTH DECURVED (mm)	71	36- 87	60.9	8.6	49	42- 106	76.7	10.8	0.79
% BILL DECURVED	71	40- 70	53.2	5.9	49	43- 66	52.5	5.2	1.01
BILL DEPTH (mm)	71	5.0-9.5	7.26	0.93	49	5.8-10.9	8.44	1.19	0.86
DEPRESSION (mm)	71	11- 29	20.2	3.0	49	14- 37	24.7	4.2	0.82
ALPHA (degrees)	71	8-14.5	11.1	1.3	49	7.5-14.5	10.5	1.3	1.05
BETA (degrees)	71	14- 24	18.8	2.2	49	14-22.5	18.3	2.3	1.03
TAPER INDEX	71	4.2-8.5	6.34	0.81	49	4.1-7.8	5.99	0.82	1.06
SHAPE INDEX (mm ⁻¹)	71	2.0-5.5	3.18	0.58	49	1.5-4.2	2.41	0.49	1.32

Table 3.3 Exponents from least-squares regression of biometric measurements on mass (after Summers In Press). See text for explanation.

CHARACTER	EXPONENT
WING LENGTH	2.66
TARSUS + TOE	2.71
BILL LENGTH	0.78
DEPRESSION	0.22
ANGLE ALPHA	-0.15
ANGLE BETA	-0.08
BILL DEPTH	0.45
TAPER INDEX	-0.06
SHAPE INDEX	-0.26

The exponent for bill shape index is negative indicating that small birds do indeed have shorter, straighter, stouter bills.

3.2.3.4. Variability in biometric measurements.

Within-sex coefficients of variation for biometric measurements of curlew are shown in Table 3.4 and compared with those for other species. CVs for wing length, tarsus and toe and mass are very similar across the range of species. CVs for bill length are remarkably similar for the shorebird species, exceeding that found in the great tit, but exceeded by that in the seedcracker. The highest CV shown in any species other than the curlew is the 12% in bill length in *P.ostrinus*. This degree of variation is also found in bill depth, angle of decurvature and taper index in both sexes of the curlew and exceeded by that found in the length of the straight and of the decurved portion of the bill and bill depression. The CV for bill shape index is remarkably high.

3.2.4. Summary and Discussion.

Three important points emerge from the above results:

1) bill length is non-isometric with mass. This means that the extreme sexual dimorphism in bill length shown by curlew is not simply a passive result of past selection for large body size in females and/or small body size in males. Large birds (in terms of mass) tend to have disproportionately long and small birds disproportionately short, bills. None of the measurements of bill morphology were found to be isometric with mass in contrast with other linear measurements of morphology;

2) the bills of small birds are not only disproportionately shorter, but they tend to be relatively straighter and thicker than the bills of large birds;

3) all bill measurements are highly variable, with bill shape index being by far the most variable character. Coefficients of variation of bill characters are, on the whole, greater than those shown in two other species whose bill morphology is known to influence niche utilization. It would be interesting to

Table 3.4 A comparison of within-sex coefficients of variation for six species of bird. * = tarsus + toe. 1= From Gosler 1987, 2= From Smith 1987, 3= From Mallory 1981 (race *hudsonicus*), 4= From Cramp & Simmons 1983 (race *hudsonicus* n=12,14), 5= From Cramp & Simmons 1983 (race *limosa*), 6= From Cramp & Simmons 1983 (race *lapponica*).

CHARACTER	CURLEW		GREAT TITS ¹		SEEDCRACKER ²		WHIMBRELS		BLACK-TAILED ⁵		BAR-TAILED ⁶	
									GODWIT		GODWIT	
	M	F	M	F	M	F	M	F	M	F	M	F
WING	3.7	2.7	1.9	2.0	3	3	2.1	1.6 ⁴	2.8	3.3	2.4	2.5
TARSUS	3.6*	3.1*	2.6	2.7	5	5	3.5	3.8 ⁴	6.0	5.4	3.9	4.9
MASS	10.1	8.5	4.6	5.3	8	8	*	*	*	*	*	*
BILL LENGTH	6.5	4.8	3.3	3.8	9	9	6.5	5.6 ³	6.6	6.7	4.1	5.6
BILL DEPTH	12.7	14.1	3.9	3.9	12	12	*	*	*	*	*	*
TAPER INDEX	12.7	13.7	4.6	5.2	*	*	*	*	*	*	*	*
SHAPE INDEX	18.2	20.8	*	*	*	*	*	*	*	*	*	*
LENGTH STRAIGHT	14.6	13.3	*	*	*	*	*	*	*	*	*	*
LENGTH CURVED	14.1	14.1	*	*	*	*	*	*	*	*	*	*
PERCENT CURVED	11.1	9.9	*	*	*	*	7.7	8.1 ³	*	*	*	*
DEPRESSION	15.0	17.1	*	*	*	*	*	*	*	*	*	*
ANGLE ALPHA	11.7	12.6	*	*	*	*	9.9	10.2 ³	*	*	*	*
ANGLE BETA	11.5	12.3	*	*	*	*	*	*	*	*	*	*
BILL WIDTH	*	*	*	8	11	11	*	*	*	*	*	8

know the degree of variation in the bill shape of the other shorebird species. Mallory (1981) found high degrees of variation in the percentage of the bill that is decurved and the angle of decurvature (α) in whimbrel, *Numenius phaeopus*, but she herself admits that her method of measurement (tracing projected silhouettes of museum specimens) is somewhat rough and ready.

From these results it is clear that there is considerable phenotypic variation in the trophic apparatus of the curlew. The greatest amount of variation is shown in bill shape index. It would thus seem profitable to examine habitat utilization in relation to bill shape. This I do in the next section.

3.3 Habitat utilization.

3.3.1. Introduction.

If the niche variation hypothesis is correct and a broad niche can indeed promote and support phenotypic variation through the action of disruptive selection, then the argument can be reversed. Given a large variation in phenotype we should predict a wide niche (Grant *et al* 1976). From the preceding section it is clear that curlew show extreme levels of morphological variation in their trophic apparatus, therefore it is reasonable to predict that the species should occupy a wide niche. Moreover because the niche variation hypothesis concerns the between-phenotype component of niche width, it is also reasonable to predict that individuals should specialise in the exploitation of different subsets of the environment exploited by the population as a whole.

There is already some evidence that curlew as a species occupy a wide niche. Males and females feeding on the intertidal zone showed little overlap in their diet (Zwarts 1979). Ens (1979) and Townshend (1981b) described birds feeding both on the intertidal zone and on fields and Elphick (1979) documented a flock of curlew feeding some 25km inland. These studies also emphasize that it is mainly males that feed on terrestrial habitats, whilst

females tend to restrict their foraging to the intertidal zone. Is this division purely a function of sex, or is it determined more by individual differences in bill morphology? Townshend (1981b) states that there is a correlation between bill length and the amount of time spent by an individual on fields. In fact this statement is based on a very small sample of birds of known bill length and the observation that the majority of field-feeders are male; he does not present a significant correlation between bill length *per se* and habitat use, so although an intriguing prospect, any relationship remains to be proven. In his study of the importance of field-feeding to curlew, Townshend (1981b) attributes the preponderance of males on fields to cold weather causing mobile intertidal invertebrates on which curlew feed to migrate vertically downwards in the substrate. He argues that under such conditions short-billed birds (primarily males) will be unable to meet their energetic requirements through foraging on the intertidal zone and will be forced on to fields to supplement their diets. The niche variation hypothesis predicts different phenotypes exploiting different subsets of the environment because each is best adapted to a particular subset. If this is correct field-feeding may be the optimal strategy for curlew of a particular phenotype and as such a preferred long-term behaviour pattern. Townshend's 'forced option' hypothesis also predicts an increase in curlew numbers feeding in fields in cold weather (provided the fields remain ice-free), whilst the niche variation hypothesis makes no prediction *per se* about the number of curlew field-feeding. It is reasonable to assume, however, that a specialist will remain in its preferred habitat as long as that habitat remains optimal. Therefore it might be expected that the number of curlew field-feeding would not fluctuate with temperature, providing that food availability does not drop to a level where it becomes unprofitable to feed.

In this section I describe the utilization of different microhabitats within the study site by both sexes and marked individual curlew. I attempt to relate

habitat use to bill morphology. Finally I assess the effect of temperature upon the number of curlew seen field-feeding and discuss the results in relation to the predictions of Townshend's 'forced option' hypothesis and the niche variation hypothesis.

3.3.2. Methods.

3.3.2.1. Sexing birds in the field.

In order to determine whether there was indeed an intersexual difference in use of habitat, I could not rely on sightings of colour marked birds since all birds were caught on field habitats, increasing the chances that marked birds would have a predisposition for field-feeding. Therefore I attempted to assign sex to birds in the field on the basis of estimated bill length. Firstly it was necessary to estimate the accuracy of this technique. To do this I regularly assigned sex to colour-marked birds on the basis of estimated bill length before I read their colour rings. This meant that some birds were sexed on more than one occasion, but each assignation of sex was an independent event so repeat observations were included in the analysis. I also recorded whether I was certain or uncertain about my decision for each individual. Sex as assigned in the field was compared at a later date to that assigned as a result of accurate measurement of bill length when the bird was in the hand.

3.3.2.2. Sex differences in habitat utilization.

I made regular scans through flocks of feeding curlew, assigning sex on the basis of estimated bill length to as many individuals as possible. I only assigned sex if the bill was in profile and I was certain about my decision. Comparisons were made between terrestrial and intertidal habitats.

3.3.2.3. Individual differences in habitat utilization.

From sightings of colour-marked birds:

Whenever I sighted a colour-marked bird I recorded the date, time, the bird's location and its activity (Table 3.5). If the bird was feeding I also

BEHAVIOURS RECORDED

FEEDING: actively pecking or probing at substrate

SWALLOWING:

LOOK UP: vigilant scan with bill horizontal or above
bird stationary

ALERT: as LOOK UP but with neck fully extended

ROOSTING: 'sleep' posture with bill tucked under scapular
feathers or pointing forward with neck hunched

PREENING: using bill or feet in plumage maintenance

Table 3.5 Behaviour types recorded when assessing habitat utilization.

MICROHABITATS RECORDED

FIELD

Germinated wheat	GWS	(includes winter barley)
Grass field	GFS	(permenant pasture)
Stubble	STUB	
Plough	PLGH	

INTERTIDAL ZONE

Fucus		(includes all living seaweeds)
Musselbed	MBED	
Sand		
Rock pool	RPOOL	
Rock		(includes boulders, pebbles)
Mudflat	MUD	
Saltmarsh	SM	

Table 3.6 Microhabitats recorded.

recorded the microhabitat in which the bird was found (Table 3.6).

From fixes of radiomarked birds:

In order to study the ranging behaviour of curlew I attached radio-transmitters to five birds. The construction, attachment and success of radio packages and the methods employed in fixing the location of tagged birds are described in section 4.2.2.3 and Appendix 1. Habitat selection as determined by radio fixes is not directly comparable with that determined by sightings of colour-marked birds for two reasons: firstly since I could only fix a bird's position to within 100m I could not hope to assess microhabitat selection although I could highlight specialisations in macrohabitat and secondly without the benefit of a mercury tilt switch incorporated into the transmitter as an activity sensor (Amlaner & Macdonald 1980) I could never be sure whether an individual was foraging or not. Many of the fixes placed birds on the traditional roost-sites at Chapel Brae, Great Car, Scoughall Rocks and Tynninghame estuary mouth; I placed these fixes in a separate category that was not analysed since it was likely that the individual was roosting at these times.

3.3.2.4. Diet.

Wintering curlew are known to take a wide range of prey species, including *Littorina* (Fenton 1953), crabs (Burton 1974, Barrett 1975), marine worms, especially *Arenicola marina*, *Lanice* and *Nereis diversicolor* (Goss-Custard & Jones 1976, Townshend 1981a) bivalves, notably *Macoma balthica*, *Mya arenaria* and *Cardium edule* (Goss-Custard & Jones 1976, Zwarts 1979, Zwarts & Wanink 1984). earthworms and insect larvae (Burton 1974). Much of the data presented in this section come from the focal animal samples described in section 3.4. I recorded every occasion on which I observed a bird swallowing and where possible I identified prey species. Due to the great variability in bill length in the curlew and because I was often taking observations from considerable distances I was not confident that I could

reliably estimate the size of individual prey items taken in relation to bill length, therefore I did not attempt to use this technique.

3.3.2.5. Effect of bill morphology on habitat selection.

Microhabitat utilization was assessed in terms of bill morphology using data from section 3.2.

3.3.2.6. Effect of meteorological conditions on field-feeding.

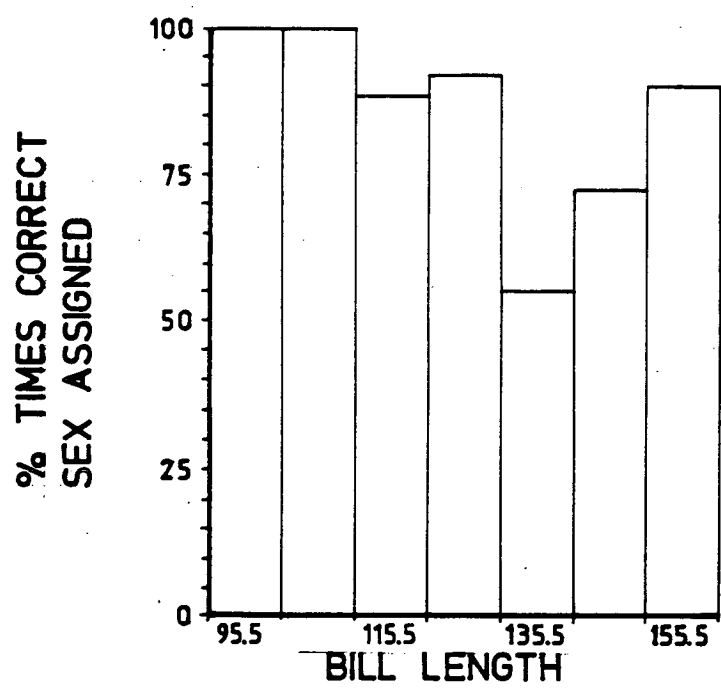
In order to assess the effect of meteorological conditions upon habitat selection I made regular counts of the numbers of curlew feeding in the fields at Scoughall by driving a set route. Meteorological data were obtained retrospectively from Dunbar weather station, situated approximately 3km east of Tynninghame. The two criteria used in analysis were minimum 24h air temperature in the period ending at 9AM on the day of observation and whether or not there was snow/ice cover on the day of observation. Minimum 24h temperature was considered a more appropriate measure than mid-day air temperature (as used by Townshend 1981b) since on a sunny winter's day the temperature can rise well above 0°C even though the ground remains frozen.

3.3.3. Results.

3.3.3.1. Accuracy of assignation of sex in the field.

I assigned sex on the basis of estimated bill length in the field on 290 occasions to individuals whose colour-ring combinations I was subsequently able to read. Results are shown in Fig. 3.6. I was able to correctly assign sex in males reliably, but less so in females (χ^2 , $p < 0.005$). This difference is almost certainly due to the fact that I tended to underestimate bill length due to fore-shortening if the bird was looking towards me. However, if an individual had a bill length less than the mean for males (113mm), or greater than the mean for females (142.5mm) the accuracy with which I could assign sex was acceptable (100% for males, 80% for females). When assigning sex I indicated whether I was 'certain' or 'uncertain' about my decision. 'Uncertain'

Fig. 3.6 Percentage of occasions that sex was correctly assigned on the basis of estimated bill length to individual birds in the field.



decisions occurred within the bill range 115–141mm. By refraining from assigning sex if I was 'uncertain' I was confident that I could predict sex with acceptable accuracy.

3.3.3.2. Sex differences in habitat selection.

Sample sizes for individual flock scans taken when determining sex-ratios in the two macrohabitats were small, therefore I combined all scans for each month over the three years (Table 3.7). It can be seen that it is predominantly males which are seen feeding in fields. Unfortunately (due to the small sample sizes) there are only two months for which I can directly compare the sex-ratio on each macrohabitat; February and March. In both these months there was a significantly higher proportion of males on the fields ($\chi^2 = 9.05$, $p < 0.01$ and $\chi^2 = 4.34$, $p < 0.05$ respectively).

3.3.3.3. Habitat utilization by individuals.

From sightings of colour-marked birds:

Different colour-marked curlew appeared to utilize the available habitats within the study-site in different ways. Generally there appeared to be three categories of birds; those which restricted their foraging activity largely to field habitats, those which foraged almost entirely within the intertidal zone and those which appeared to be catholic in their choice of feeding habitat (generalists). In reality these categories are probably points along a continuum of habitat utilization by individuals. In order to test how realistic these categories were, I first had to determine the minimum number of repeated sightings of an individual needed to assign that individual to one of the three classes with confidence. To achieve this I took the 18 marked individuals which I had observed foraging on more than 12 occasions during the study period and plotted the percentage frequency of field-feeding against the cumulative number of sightings for each individual (Fig. 3.7.). Although the percentage of occasions on which a given individual was observed

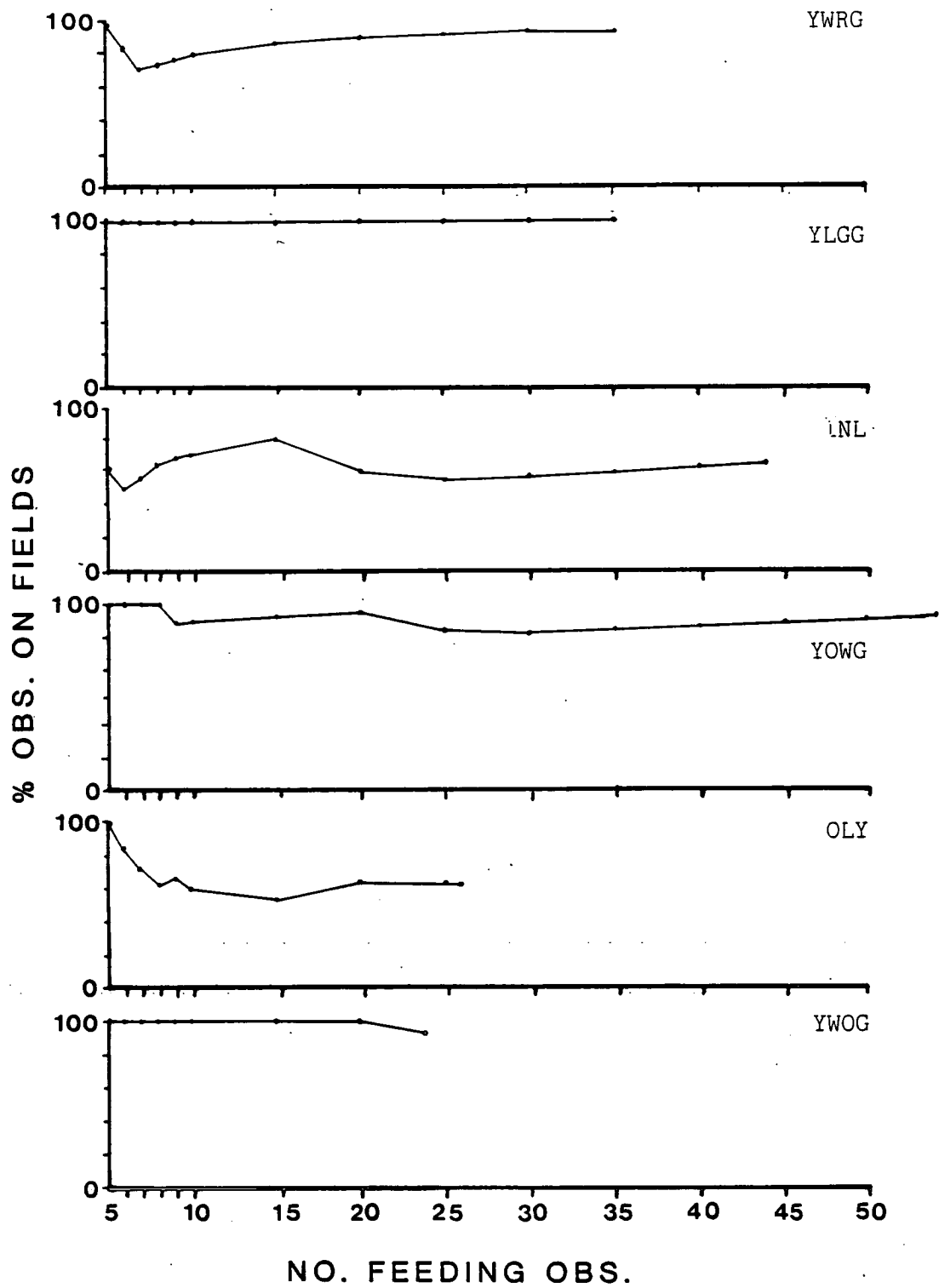
Table 3.7 Estimated sex-ratio of birds feeding on the fields and the intertidal zone for each month. Data for 3 winters combined.

	JAN	FEB	MAR	APR	JUL	AUG	SEP	NOV	DEC
No.									
F SCANS	9	15	11	1	0	0	0	12	3
I									
E M:F	52:11	106:15	90:38	3:1	-	-	-	196:43	43:0
L									
D %M	82.5	87.6	70.3	75.0	-	-	-	82.0	100.0

NO.									
I SCANS	-	5	24	11	1	1	2	2	-
T M:F	-	40:18	255:169	75:53	6:5	2:2	67:34	8:1	-
Z %M	-	68.9	60.0	58.6	54.5	50.0	66.3	88.9	-

N.B. I T Z = INTERTIDAL ZONE

Fig. 3.7 Percentage of occasions on which 18 marked individuals were observed feeding on fields as opposed to the intertidal zone, as a function of the number of times that individual was observed feeding.



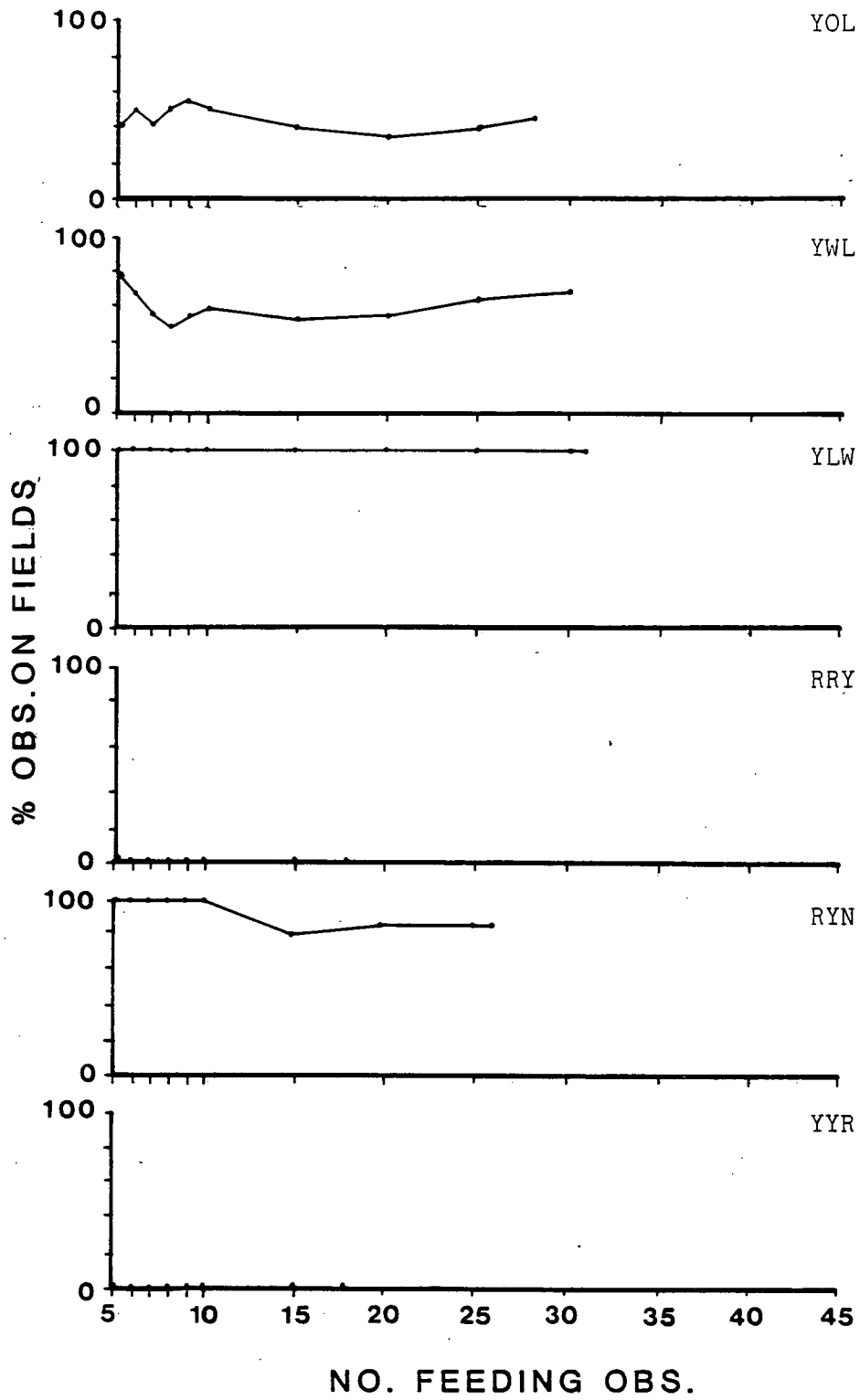


FIG. 3.7

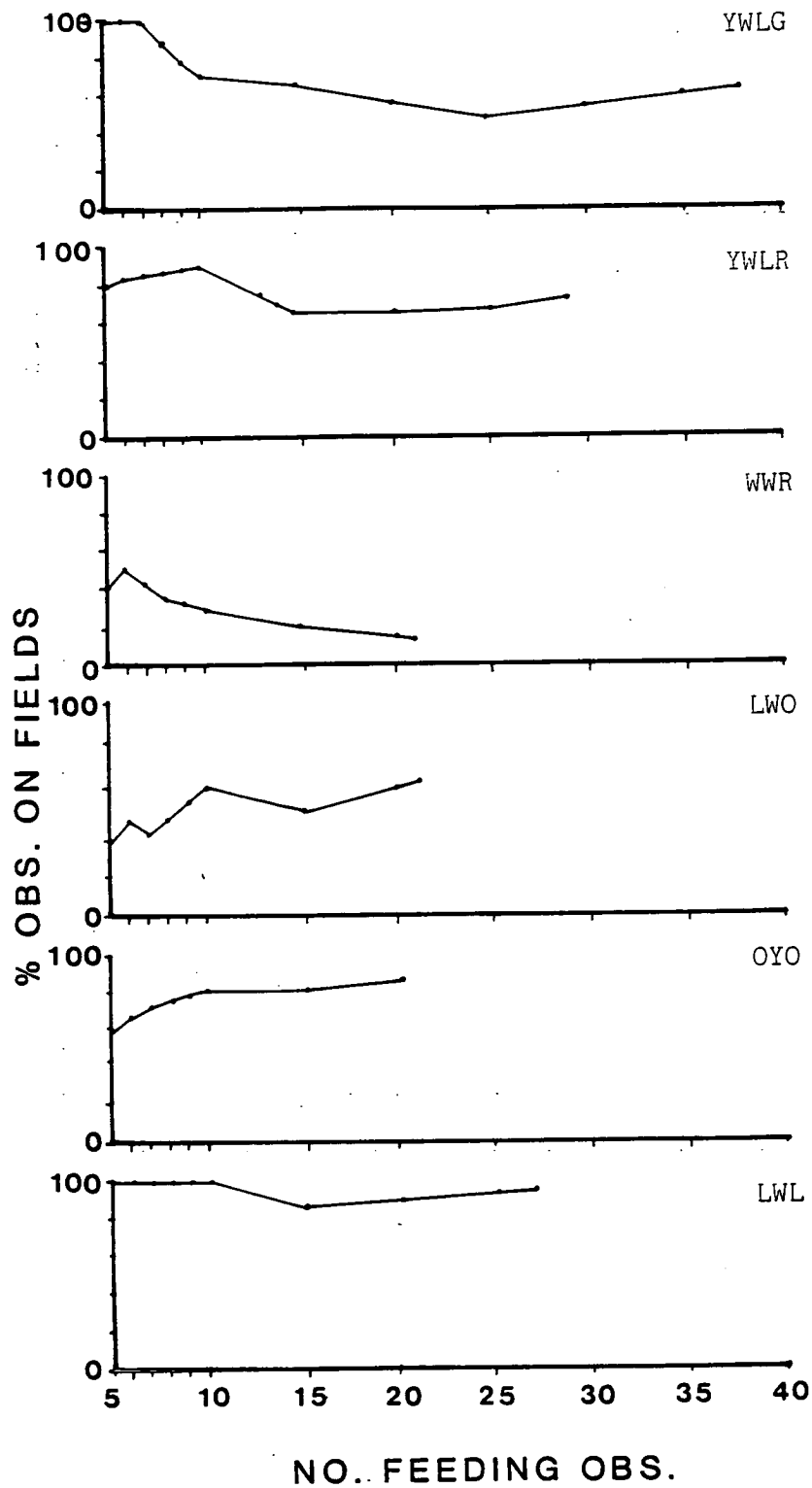


FIG. 3.7

field-feeding fluctuates wildly at sample-sizes below 10, the level of field-feeding was remarkably constant once 10 observations had been taken. I then plotted the frequency distribution of percentage use of fields for the 37 individuals for which I had 10 or more feeding observations over the three winters (Fig. 3.8). It can be seen that this histogram is trimodal, with peaks between 0 and 10%, 60 and 70% and 90 and 100%. On the basis of this histogram I decided to use the following cut-off points for placing an individual for which I had 10 or more foraging sightings:

- A) seen on field habitats on > 80% of occasions = field-feeder;
- B) seen on field habitats on < 20% of occasions = inter-tidal specialist;
- C) seen on field habitats between 20% and 80% occasions = generalist.

The 80% level was also used as a definition of specialisation in foraging type in sunfish (Werner *et al* 1981).

Using these cut-offs I identified 14 colour-marked birds that specialised in field-feeding, 12 which restricted their foraging largely to the intertidal zone and 11 which generalized in their choice of macrohabitat (Table 3.8). To test whether the differences in the use of macrohabitat between these 37 birds were significant I performed a χ^2 test of heterogeneity on the distribution of foraging sightings between intertidal and field habitats. Individuals did in fact differ significantly in their comparative use of each habitat ($\chi^2 = 448.218$, 36 d.f., $p < 0.001$).

Obviously, assigning a bird to one of the above three categories is an oversimplification of the situation, given that the macrohabitats described comprise many different microhabitats (Table 3.6). To determine whether individuals do in fact specialise in choice of available microhabitat I plotted the relative frequency of utilization of each microhabitat as a feeding resource by each of the 37 birds for which I had 10 or more feeding observations (Fig. 3.9). Unfortunately no data are available on the relative availability of each

Fig. 3.8 Trimodal distribution of the relative frequency with which individually marked birds were observed feeding on fields as opposed to the intertidal zone.

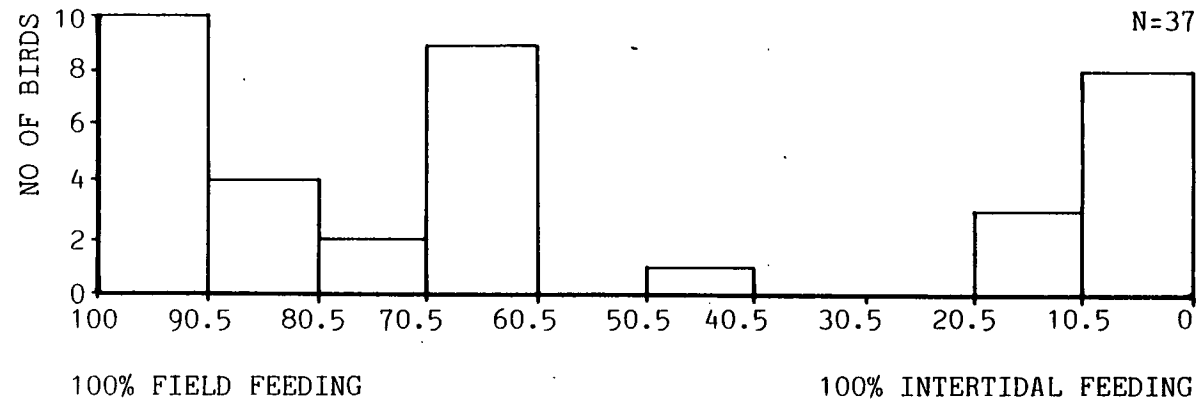


Table 3.8 Classification of individually marked birds as Field-feeding specialists (>80% of foraging observations made on fields), Intertidal zone specialists (>80% of foraging observations made on the intertidal zone) or Generalists (between 20% and 80% of foraging observations made on fields).

FIELD-FEEDERS

INTERTIDAL FEEDERS

GENERALISTS

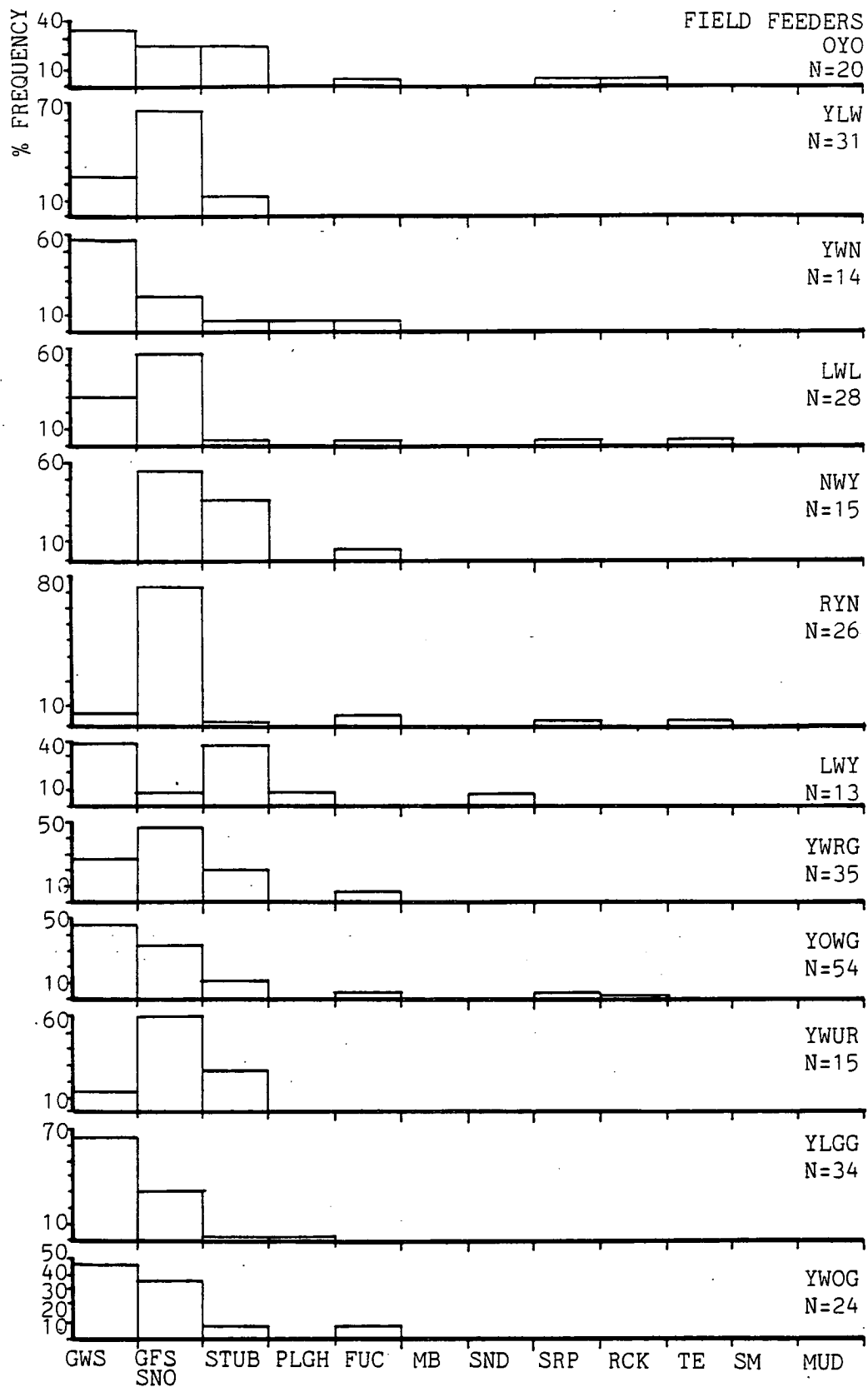
FIELD-FEEDERS			INTERTIDAL FEEDERS			GENERALISTS		
	No	% USE		No	% USE		No	% USE
BIRD	OBS	FIELDS	BIRD	OBS	FIELDS	BIRD	OBS	FIELDS
YWOG	24	91.7	YOWR	12	8.3	YWLR	29	72.4
YOWG	54	90.7	LNL	12	0	YWLK	38	63.2
YLGG	34	100.0	ROY	16	0	YOL	28	46.4
YWWR	15	100.0	RRY	18	0	YWL	30	70.0
YWRG	35	94.3	YOR	10	20.0	YNL	44	65.9
LWY	13	92.3	YON	12	0	OLY	34	61.5
NWY	15	93.3	YNY	12	0	ORO	17	64.7
RYN	26	84.6	YYR	21	0	OYW	10	70.0
LWL	28	89.3	OYL	18	16.7	WWL	13	69.2
YWN	14	92.9	OWL	12	0	WOW	10	70.0
YLW	31	100.0	WWR	21	14.3	WWY	11	72.7
OYO	20	85.0				LWO	21	61.9
WOR	16	87.5						
NLO	12	100.0						

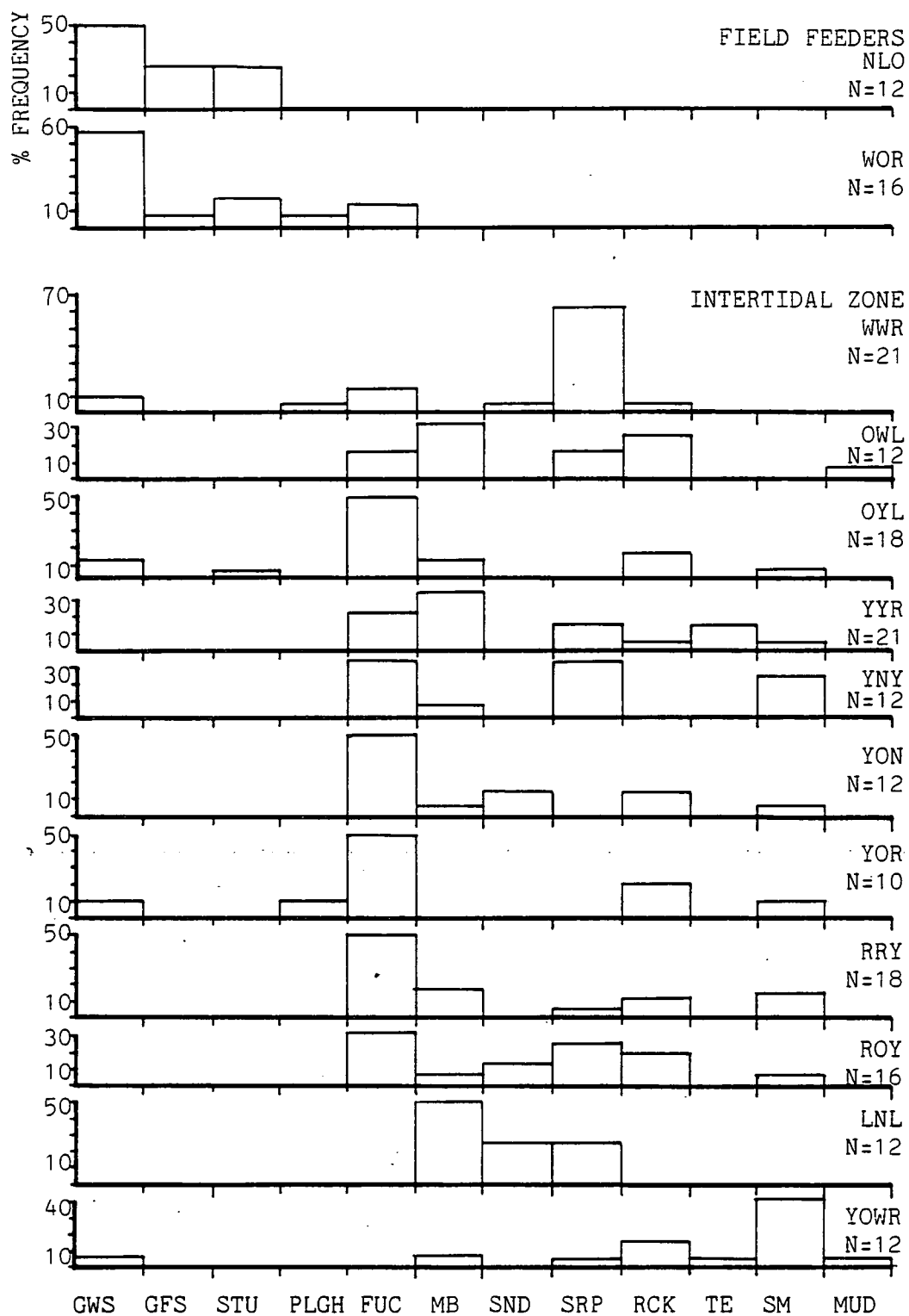
microhabitat, but comparisons between individuals are still valid since each microhabitat is theoretically equally available to all individuals. The data presented in Fig. 3.9 strongly suggest that not only do individual curlew specialise in choice of macrohabitat, but also in their choice of microhabitat. For instance amongst the field-feeders, birds YLW, LWL, NWY, RYN and YWWR foraged more frequently on grass fields/pasture than on germinated winter wheat, whilst YLGG, LWY, YWN and YOWG were seen more frequently on germinating crops than on pasture. Intertidal specialists also seem to exhibit some degree of fidelity to particular microhabitats: WWR spent most time foraging in rock pools, OWL and LNL were observed most often on musselbeds, whilst OYL restricted most of its foraging effort to *Fucus* and YOWR to saltmarsh. To test whether the differences between individuals were significant I performed a χ^2 test of heterogeneity upon the frequency of occurrence of the 14 field-feeding curlew on the three habitats GWS, GFS and STU. There were indeed significant differences between these individuals in their patterns of use of these microhabitats ($\chi^2 = 115.476$, 26 d.f. $p < 0.001$). A similar test was performed upon the distribution of sightings of the 12 intertidal specialists between the following microhabitats: FUC, MB, SND, RKP, RCK, TDE and SM. Again there were significant differences between individuals ($\chi^2 = 139.93$, 60 d.f., $p < 0.001$). In many ways saltmarsh more closely resembles a field-habitat than an intertidal habitat. Even if saltmarsh is excluded from analysis there are still significant differences between individuals in their use of microhabitats within the intertidal zone ($\chi^2 = 116.99$, 50 d.f., $p < 0.001$).

As determined from fixes of radio-marked birds:

The utilization of different macrohabitats by the five radio-marked curlew (when presumed to be feeding) is shown in Fig. 3.10. Four radio-marked birds appeared to be intertidal specialists, one a generalist (Table 3.9). Once again there are significant differences between individuals in their utilization of

Fig. 3.9 Relative frequency with which individually marked birds were observed feeding on different microhabitats. N = total number of feeding observations.





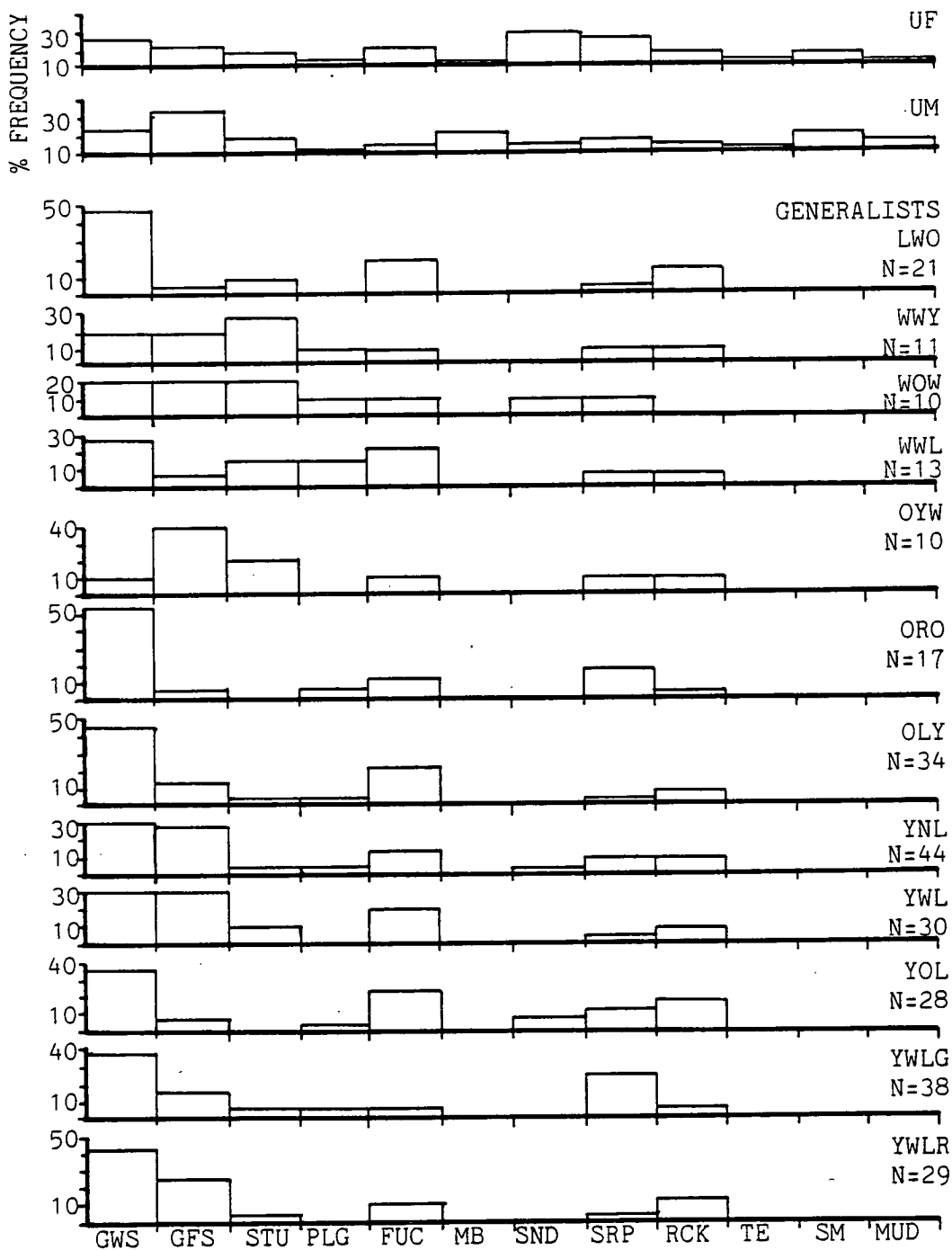
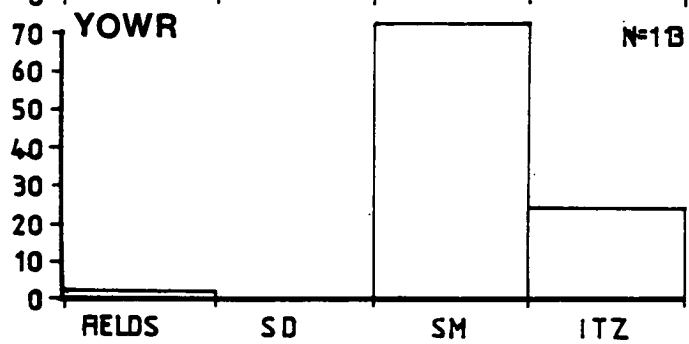
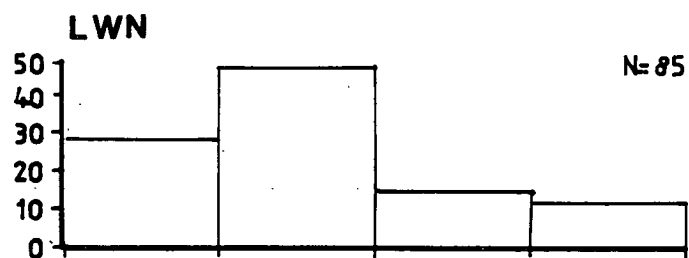
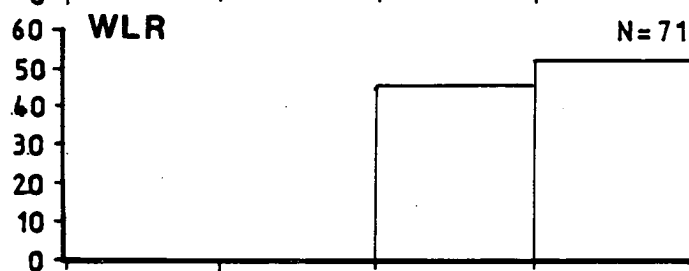
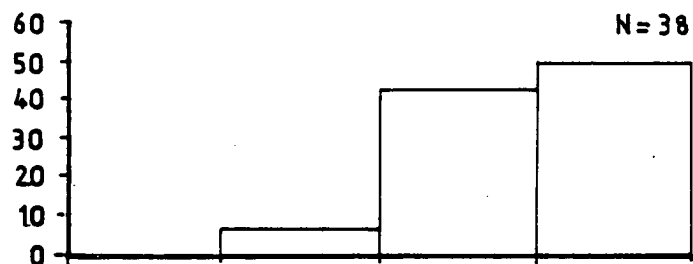
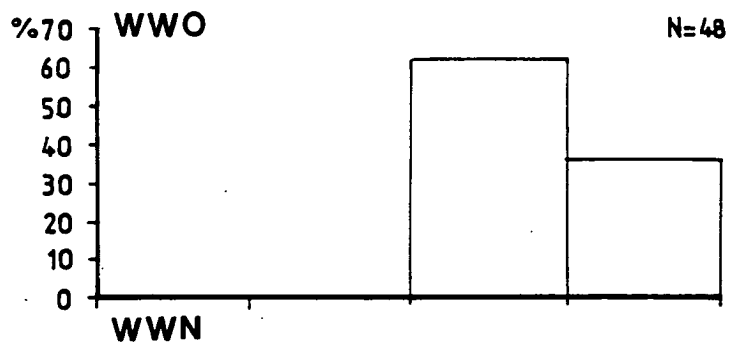


Fig. 3-9

Fig. 3.10 Relative frequency of use of macrohabitat by radio-marked birds.

S/D= Sand Dunes, SM= Saltmarsh, ITZ= Intertidal Zone. N= total number of radio-fixes.



BIRD	TOTAL No.	ROCK ROOSTS		INTERTIDAL ZONE		SALT MARSH		SAND DUNES		FIELDS		SPECIALISATION
	FIXES	FIXES	%USE	FIXES	%USE	FIXES	%USE	FIXES	%USE	FIXES	%USE	
WWO	48	22	45.8	10	20.8	16	33.3	0	0	0	0	INTERTIDAL ZONE
WWN	38	24	63.2	7	18.4	6	15.8	1	2.6	0	0	INTERTIDAL ZONE
WLR	71	43	60.6	15	21.1	13	18.3	0	0	0	0	INTERTIDAL ZONE
LWN	85	36	42.3	6	7.1	8	9.4	24	28.2	11	12.9	GENERALIST
YOWR	113	68	60.2	11	9.7	33	29.2	0	0	1	0.9	INTERTIDAL ZONE

Table 3.9 Classification of individually radio-tagged birds as Intertidal specialists (>80% of fixes when presumed foraging made on the intertidal zone) or Generalists (between 20% and 80% of fixes when presumed foraging made on the intertidal zone).

different macrohabitats (χ^2 test of heterogeneity, $\chi^2 = 111.32$, 12 d.f., $p < 0.001$). Three of the birds however, exhibit a similar choice of habitat (namely WWO, WWN and WLR (χ^2 test of heterogeneity, $\chi^2 = 4.70$, 6 d.f. N.S.). Use of radio-telemetry served to highlight the extensive use of two macrohabitats by some individuals which would not have been discovered using more traditional techniques; namely the fairly exclusive use of saltmarsh by YOWR and the use of sand dunes by LWN. Data on the use of saltmarsh by radio-marked birds have to be interpreted with caution as this area is used as a roost by up to 250 birds on high tides during neap series. YOWR however was seen actively foraging on this habitat on six occasions and the majority of the rest of the fixes were taken during low-water periods, therefore I am confident that this individual often used the saltmarsh as a feeding resource. The use of sand dunes by LWN was particularly interesting. Although access to this area was difficult I observed this bird feeding in the dunes on three occasions. I never observed more than six curlew using this relatively large area, possibly suggesting that it is not as profitable a food source as other macrohabitats.

3.3.3.4. Diet

The prey taken in each microhabitat is summarised in Table 3.10. Unfortunately I was only able to identify a small proportion (16%) of prey items taken. The major prey species eaten varied with microhabitat. Littorinids were the main prey taken from *Fucus*, rockpools and rocks. On sand and mud substrates prey consisted almost entirely of marine worms, whilst the diet on musselbeds and at the tide edge consisted of roughly equal proportions of marine worms and crabs. Small fish were occasionally taken from the tide edge. I was unable to identify the main prey taken from the saltmarsh. I witnessed two instances of opportunistic feeding; once I saw a bird consume a dead sand eel that it found on a musselbed and on another occasion I watched a bird eat 19 woodlice taken from a crevice in a dead log. On the fields it was

Table 3.10 Prey species taken by foraging curlew from different microhabitats.

	TIDE												TOTAL
	GWS	GFS	STUB	PLGH	FUCUS	MBED	SAND	RPOOL	ROCK	EDGE	MUD	SM	
UNIDENTIFIED	335	270	281	48	106	59	129	172	107	0	29	466	2002
EARTHWORM	32	71	15	1	*	*	*	*	*	*	*	*	119
GRAIN	*	*	6	*	*	*	*	*	*	*	*	*	6
INSECT LARVAE	*	*	*	1	*	*	*	*	*	*	*	*	1
LITTORINIDS	*	*	*	*	23	1	*	68	10	*	1	*	103
MARINE WORM	*	*	*	*	1	3	22	2	1	4	2	1	36
NEREIS	*	*	*	*	2	1	21	3	*	*	27	*	54
ARENICOLA	*	*	*	*	*	6	9	4	*	2	*	*	21
CRABS	*	*	*	*	3	9	2	9	1	4	1	*	29
FISH	*	*	*	*	*	*	*	1	*	3	*	*	*

TOTAL	367	341	302	50	135	79	183	259	119	13	60	467	2375

relatively easy to observe when a bird captured an earthworm and I am confident that unidentified prey taken from terrestrial habitats were either insect larvae or seeds. A significantly higher proportion of earthworms were taken from grass fields than either germinated wheat ($\chi^2 = 20.82$, $p < 0.001$) or stubble fields ($\chi^2 = 33.67$, $p < 0.001$). This is in accordance with the finding that earthworm densities are lowered by cultivation of the ground (Evans & Guild 1947, McLennan 1979).

It is clear from these results that individual curlew that specialise in foraging in different microhabitats will also have different diets.

3.3.3.5. Biometrics, Bill morphology and Habitat Selection.

I compared the biometrics of the 11 field-feeding specialists and the 11 intertidal specialists (identified in section 3.3.3.4.) for which I had measurements of bill morphology. The field-feeding group included 9 males, one female and one bird of indeterminate sex. The intertidal group included 8 males and 3 females. Mann-Whitney U-tests were performed on each biometric measurement taken, since the sample sizes were too small to determine whether the distribution of measurements in each class were normal. Results are summarised in Table 3.11. There were no apparent differences in wing length, tarsus and toe or mass, or in measures of bill length, depth or either angle of decurvature. Although there appeared to be differences in both bill depression and bill taper index between the groups, in neither case were these differences significant. Field-feeding specialists did, however, have significantly higher bill shape indices than intertidal specialists, i.e. field-feeders tend to have shorter, straighter, thicker bills than birds which forage mainly on the intertidal zone.

I then took all 37 birds for which I had seen feeding on more than 10 occasions and plotted the percentage of occasions on which an individual was observed field-feeding against each biometric measurement recorded. Bill

CHARACTER	N	W	P VALUE
WING LENGTH	11,9	118.5	0.85 NS
TARSUS + TOE	11,11	119.5	0.67 NS
MASS	11,11	131.0	0.79 NS
BILL LENGTH	11,11	115.5	0.49 NS
LENGTH STRAIGHT	11,11	111.5	0.34 NS
LENGTH BENT	11,11	111.0	0.32 NS
% BENT	11,11	129.5	0.87 NS
ANGLE ALPHA	11,11	125.5	0.97 NS
ANGLE BETA	11,11	121.5	0.77 NS
DEPRESSION	11,11	104.0	0.15 NS
BILL DEPTH	11,11	140.5	0.38 NS
TAPER INDEX	11,11	150.5	0.12 NS
SHAPE INDEX	11,11	162.5	0.02 *

Table 3.11 Results of comparison of bill morphology between field-feeding and intertidal specialists using Mann-Whitney U-test.

Linear regressions were performed for each biometric. Bill shape index was the only variable for which the regression was significant (Table 3.12, Fig. 3.11). Thus birds which were seen field-feeding on the largest percentage of occasions tended to have a large bill shape index.

3.3.3.6. Effect of temperature on field-feeding.

Fig. 3.12 shows the fluctuation in the numbers of curlew field-feeding at Scoughall between December and March 1986-7 and the fluctuation in minimum daily temperature over the same period. It is noticeable that troughs in the number of curlew field-feeding occur during periods of snow or ice cover. In fact there is a significant positive correlation between number of curlew seen field-feeding and minimum 24h temperature in both the winters 1985-6 and 1986-7 (Fig. 3.13 a & b). It could be argued that this is simply the result of there being an increased number of curlew at Scoughall in March (due to the arrival of migrants) when the weather is warmer. Multiple regression of date and temperature on the number of birds field-feeding suggests that this is not the case, since in both years temperature, but not date had a significant effect (Table 3.13). To try and avoid the problems of population fluctuation I expressed the number of curlew seen field-feeding as a percentage of the maximum number seen that month. There was still a positive correlation with temperature in both years (Fig. 3.14). Whilst this finding would seem to refute Townshend's 'forced option' hypothesis, it is not necessarily incompatible with the niche variation hypothesis for two reasons:

a) At low temperatures it may become no longer profitable for field-feeding specialists to feed on fields. This is certainly the case when snow or ice cover reduces prey availability to zero. Under such conditions specialists should either switch to foraging on the intertidal zone or cease to forage. There is evidence that at sub-zero temperatures they adopt both strategies (see below).

CHARACTER	DF	t-RATIO	p
WING LENGTH	35	-0.06	NS
TARSUS AND TOE	35	-0.73	NS
MASS	34	0.52	NS
BILL LENGTH	35	-1.43	NS
LENGTH STRAIGHT	31	-1.14	NS
LENGTH BENT	31	-1.76	NS
% BENT	31	-0.26	NS
ANGLE ALPHA	31	0.21	NS
ANGLE BETA	31	-0.12	NS
DEPRESSION	31	-1.75	NS
BILL DEPTH	31	0.31	NS
BILL SHAPE INDEX	31	2.48	<0.02*

Table 3.12 Results of linear regressions of the percentage of occasions on which an individual was observed field-feeding on biometric measurements.

Fig. 3.11 Relationship between bill shape index and the percentage of feeding observations that were made on field microhabitats. ($t=2.48$, 35df, $p < 0.02^*$).

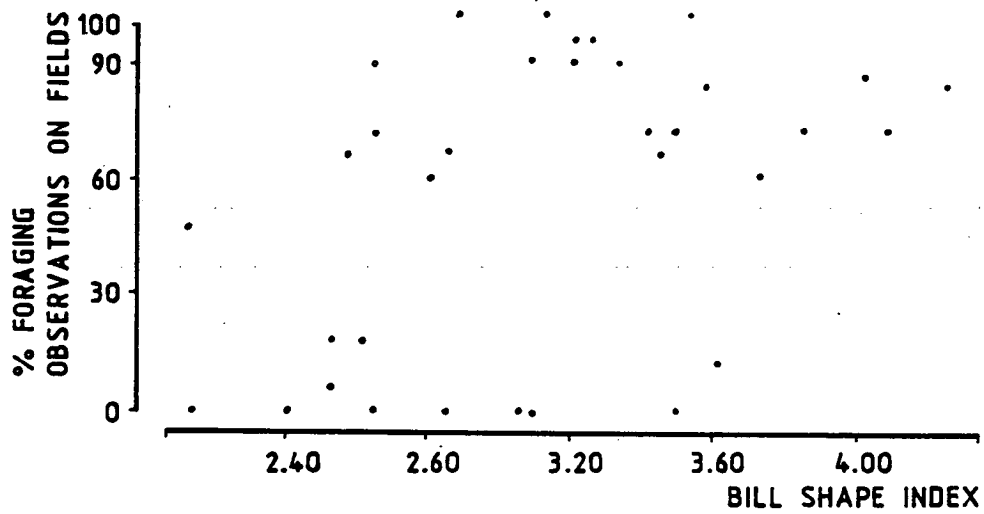


Fig. 3.12 Fluctuations in the number of curlew observed field-feeding at Scoughall (circles, unbroken line) and minimum temperature in 24h period ending at 9am on day of observation (squares, dashed line) in the winter 1986-7. Vertical bars indicate snow or ice cover.

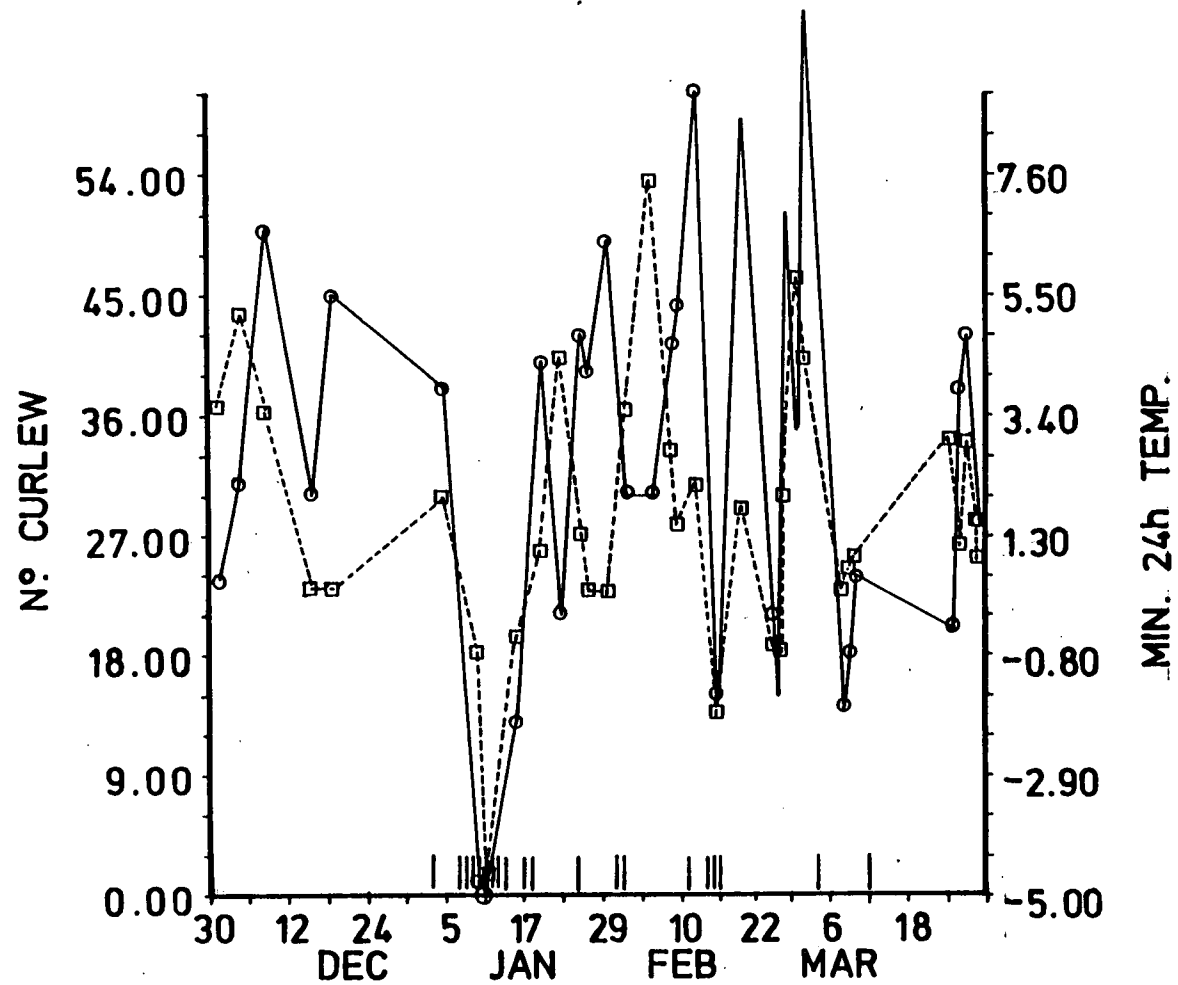
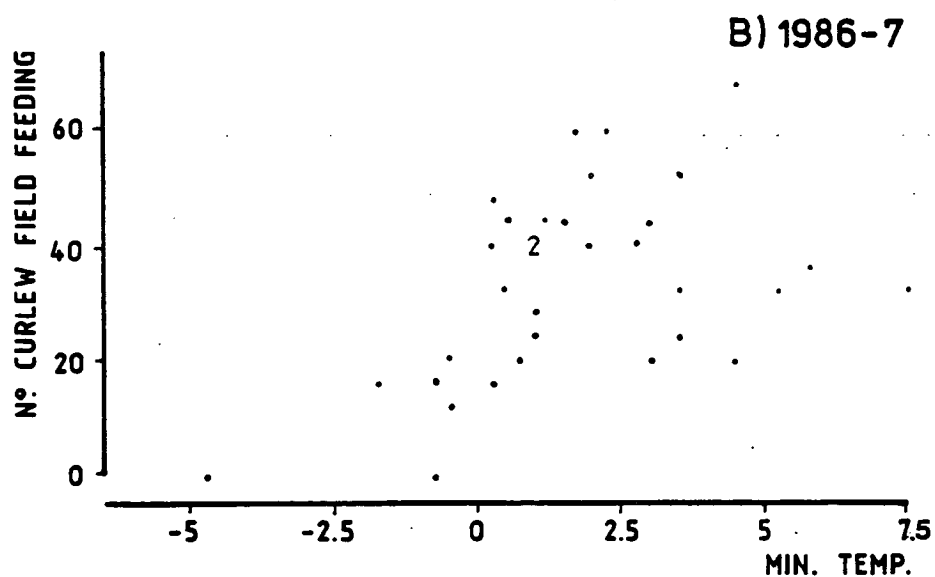
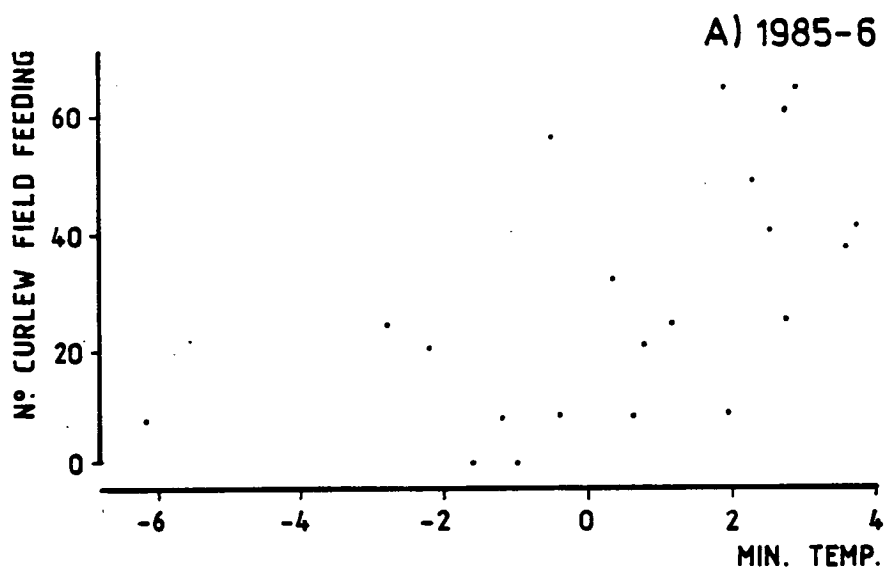


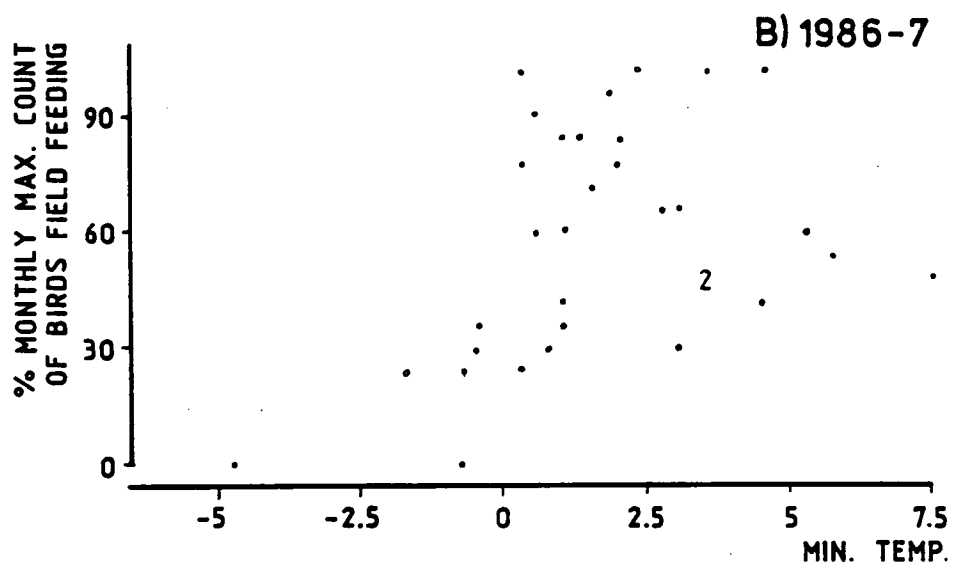
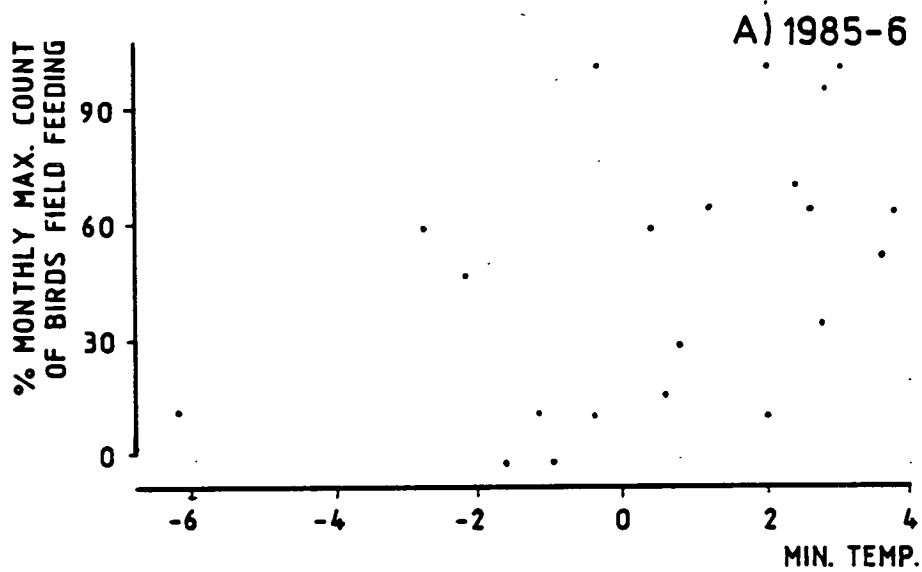
Fig. 3.13 Correlation between the number of curlew observed field-feeding at Scoughall and minimum temperature in 24h period ending at 9am on the day of observation a) In winter 1985-6 ($r=0.507$, 23df, $p < 0.01^{**}$) b) In winter 1986-7 ($r=0.440$, 31df, $p < 0.02^{*}$).



PREDICTOR	t-RATIO	P VALUE
Min. temp.	2.69	< 0.05 *
1986-7		
Date	-0.46	NS
Min. temp.	2.53	< 0.02 *
1985-6		
Date	-0.86	NS

Table 3.13 Results of multiple regression analysis of minimum temperature in 24h period preceding day of observation and date upon the number of curlew seen field-feeding at Scoughall in 1985-6 and 1986-7.

Fig. 3.14 Correlation between the number of curlew observed field feeding at Scoughall expressed as a percentage of the maximum number seen field-feeding in that month and minimum temperature in 24h period ending at 9am on day of observation a) In winter 1985-6 ($r=0.465$, 23df, $p < 0.05^*$), b) In winter 1986-7 ($r=0.386$, 31df, $p < 0.05^*$).



b) The fluctuation in numbers of curlew field-feeding is caused mainly by generalists switching between the intertidal zone and fields, presumably as a result of changes in the relative profitability of the two. *Nereis* availability certainly is depressed by low temperatures. Clark (1983) found that the availability of large and medium worms in the top 43mm of mud was severely reduced at temperatures below 6°C, although the abundance of small *Nereis* was virtually unaffected at temperatures above zero. However, McLennan (1979) found that both the number and biomass available of both earthworms and leatherjackets reached their lowest levels in January and February; the coldest months. Littorinids formed a large proportion of the diet of intertidal birds. The availability of such prey is unlikely to be affected nearly as much by low temperatures than that of either *Nereis* or earthworms, so it is possible that intertidal foraging becomes more profitable to generalists than foraging on fields during cold spells at this study-site. This situation is dissimilar to that found at Teesmouth by Townshend (1981b) where the vast majority of intertidal prey taken were marine worms. However, Townshend's supposition that the availability of earthworms on the surrounding fields will be unaffected by temperature is both speculative and unconvincing. At Scoughall generalists certainly abandon field-feeding during sub-zero temperatures (Fig. 3.15); this is in agreement with Townshend (1981b). However, Townshend predicts that a decreasing number of birds should feed on the intertidal zone as temperatures drop towards zero; at Scoughall generalists tended to feed most on the intertidal zone at temperatures between 0 and 3°C and 7 and 9°C, switching to fields at intermediate temperatures (Fig. 3.15). This supports the idea that generalists switch microhabitats in response to the relative availability of food (Townshend 1981a) but not the theory of forced movement of birds to fields as a result of an inability to reach prey on the intertidal zone at low temperatures (Townshend 1981b). In February 1986 many generalists switched from fields to the intertidal zone in a particularly cold spell (Fig. 3.16a). In cold weather there was a tendency for birds either to switch to the intertidal zone or to cease foraging altogether (Fig. 3.16) These movements are in the opposite direction to those found by Townshend (1981b).

There are several faults in both Townshend's methodology and the rationale behind his argument. First he took observations on just one of many accessible fields and often he could not locate specific birds either on the

Fig. 3.15 Frequency distribution of foraging observations of generalists in relation to temperature a) on fields (N=184) and b) on the intertidal zone (N=59).

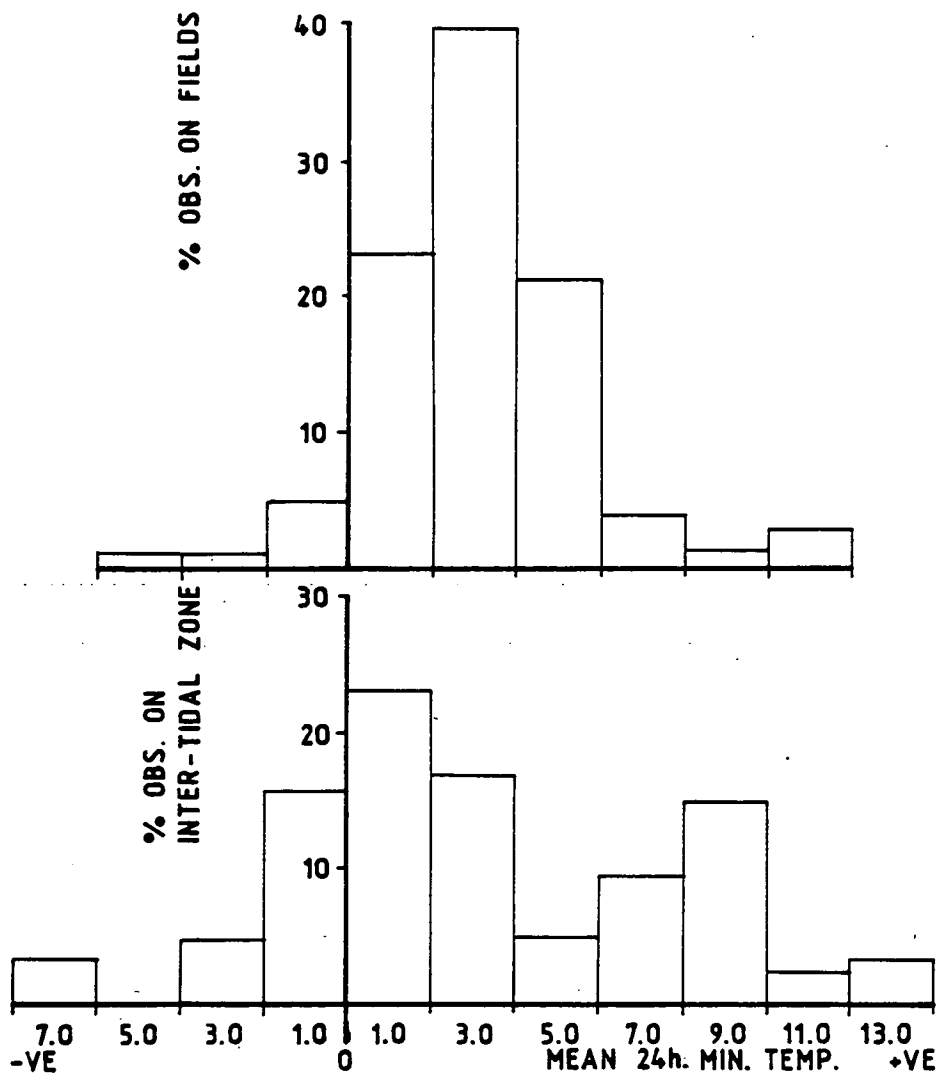
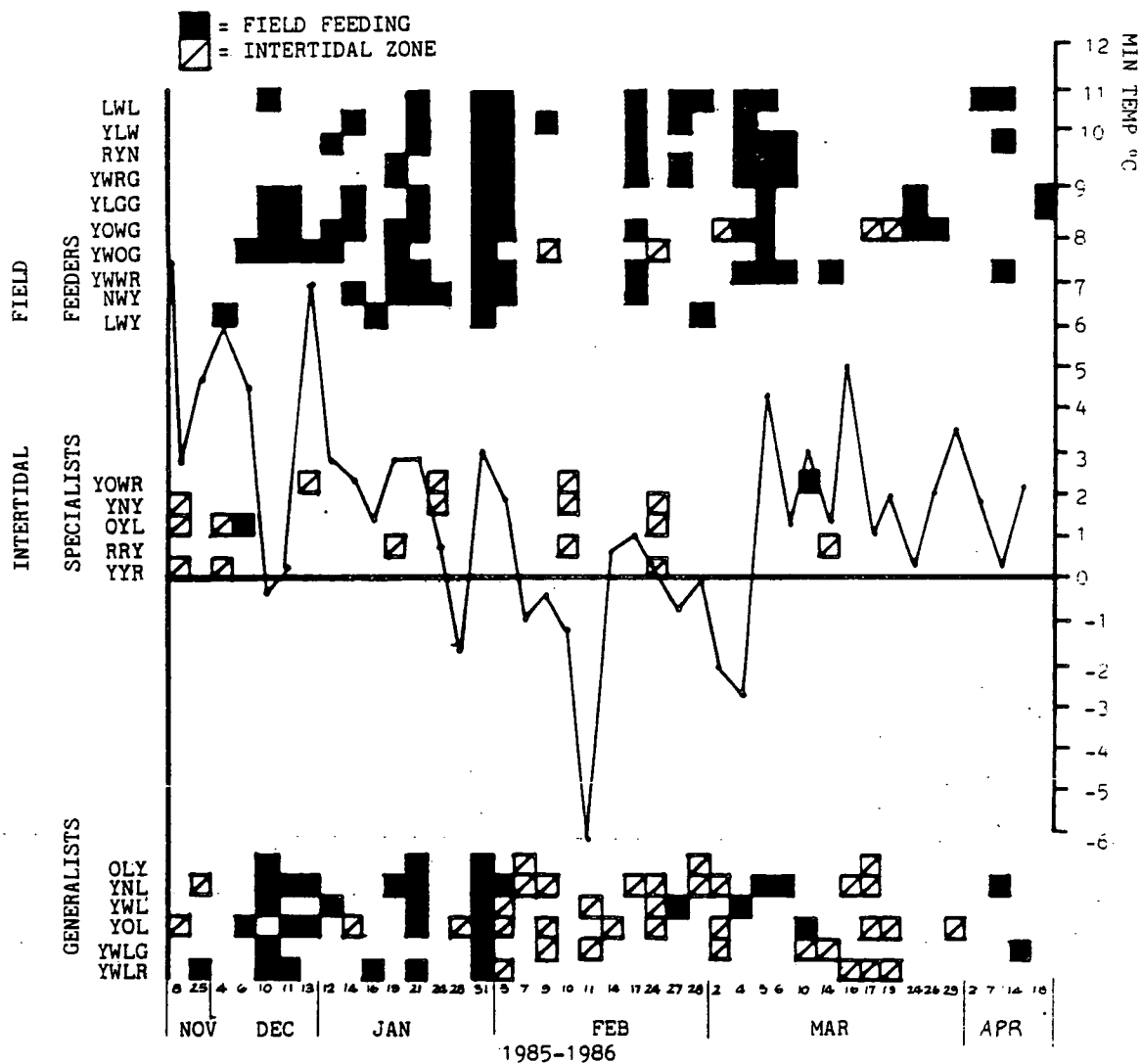
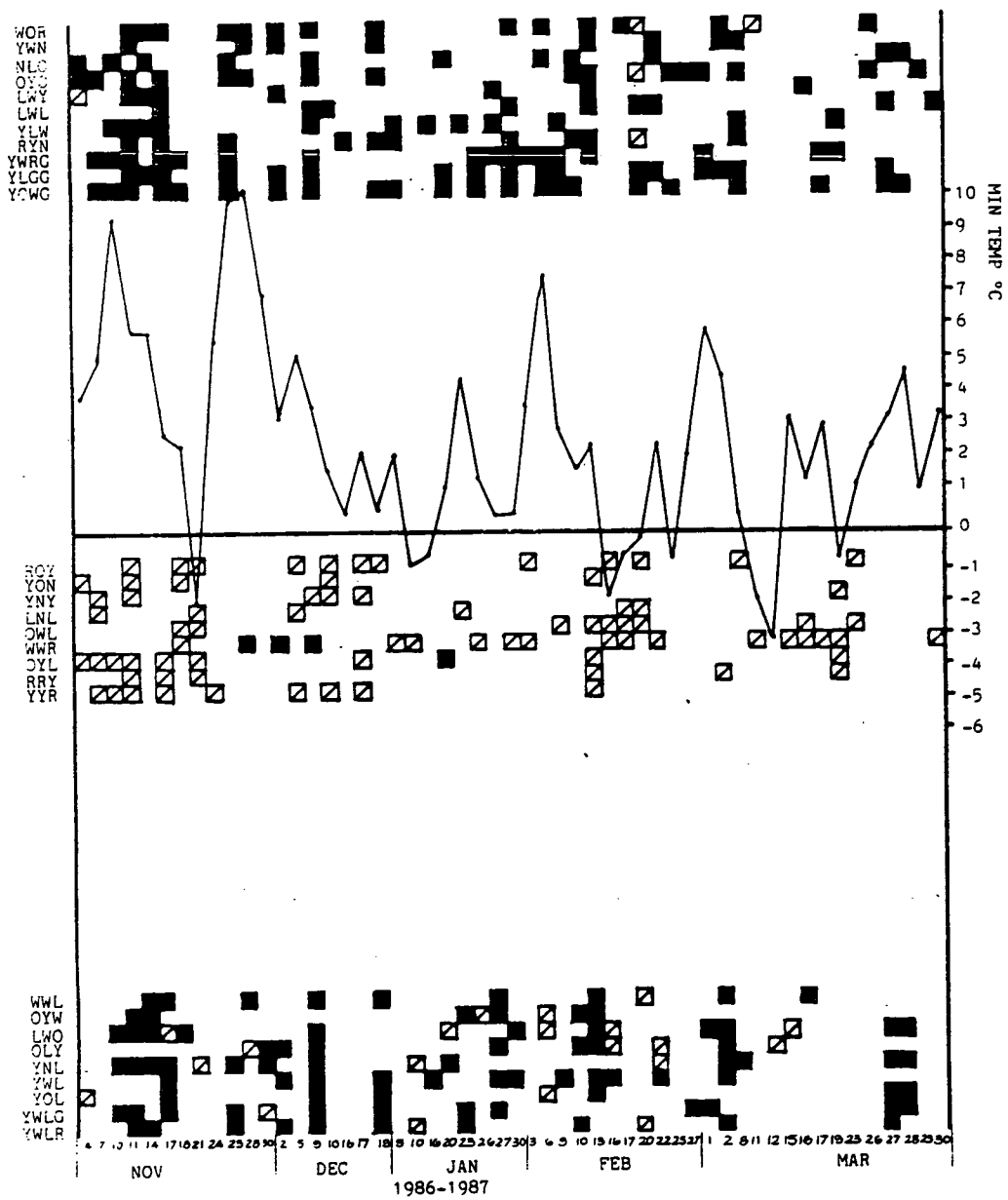


Fig. 3.16 Foraging observations of individually marked birds on fields (=) and the intertidal zone (= □). Curve shows minimum temperature in 24h period ending at 9am on day of observation. a) 1985-6, b) 1986-7.





mudflats or on this particular field. The evidence he presents that individual birds switched macrohabitat at low temperatures is equivocal given the low numbers of sightings he reports. Second, as already stated his use of midday air temperature is likely to be a less reliable indicator of ground condition or food availability than minimum 24h temperature preceding the day of observation. Third, Townshend presents results of observations of the capture rate of a single male and a single female which foraged close to each other on the mudflats. His conclusion that the capture rate of the male but not that of the female fell with temperature is not warranted given his sample sizes; no clear relationship is evident. When biomass intake rate was estimated the male appeared to obtain less than the female. Although he controls for the relative body size of the two individuals, Townshend never actually tests whether the male was still able to meet its daily energetic requirements through foraging on mudflats alone. Despite this he constructs the hypothesis that males must be forced on to fields to feed in order to obtain their daily calorific requirement in cold weather. This is all the more surprising given that the male from which the detailed intertidal observations were taken and on which this hypothesis is based, was never actually observed field-feeding.

3.3.3.7. Discussion.

In section 3.2 I documented the large degree of variation in bill morphology shown by curlew, the most variable character being bill-shape index. Given such large phenotypic variation I predicted that individual curlew should specialise in the exploitation of a subset of the environment exploited by the population as a whole. From the results presented in this section it is clear that ^{many} individuals do indeed specialise in the exploitation of particular macrohabitats. Further there are significant differences between individuals in their use of microhabitat within macrohabitat. These findings are in accordance with the prediction made from the niche variation hypothesis. As found in

previous studies there was a significantly higher proportion of males feeding on fields than on the intertidal zone. However, field feeding was not exclusively a male trait and several males were intertidal specialists; this, coupled with the finding that bill morphology is non-allometric with body size suggests that habitat partitioning is not simply a function of sex. Townshend (1981b) suggests that it is mainly short-billed birds (hence the predominance of males) that feed on fields. Although I found a tendency for field-feeding specialists to have short bills the difference between bill length of field-feeders and intertidal birds was not significant. Bill shape, however, as defined by 'bill shape index' did differ between the two groups of birds, field-feeders tending to have shorter, straighter, thicker bills than intertidal specialists. Moreover I found a significant positive correlation between bill shape index and the number of occasions on which a bird was seen field-feeding. Why bill shape is important in determining habitat selection is a question that can only be answered by detailed analysis of bill use in different habitats. I address this question in section 3.5.

The data I present on the use of field habitats would appear to refute Townshend's hypothesis that field-feeding is a forced option in adverse conditions, yet are not inconsistent with the niche variation hypothesis, that field-feeding is a specialist strategy for individuals of a given phenotype and as such a preferred behavioural pattern.

3.4. Individual variation in foraging behaviour.

3.4.1. Introduction.

Phenotypic variation is not restricted to morphology, but extends to behavioural traits. In fact behaviour is often considered the plastic component of phenotype. Having shown that individual curlew specialise in their exploitation of microhabitat and that habitat choice is related to bill morphology, it is reasonable to predict that there will also be individual variation

in foraging behaviour. This is important, since development of foraging skills may affect an individual's fitness and impose a cost to switching feeding specialisation (Partridge 1978, Partridge & Green 1985). Behavioural traits in foraging behaviour can be genetically inherited, passed to the next generation through cultural inheritance, or acquired through individual experience.

In this section I describe in detail bill use of birds foraging in different microhabitats. I use these data to assess whether there is significant variation in foraging behaviour and to discuss the possible adaptive reasons for curlew having a decurved bill. Variation in the broader aspects of foraging behaviour (ranging and spacing behaviour) is described in Chapter 4.

So far I have shown how curlew fulfil two of the requirements for promotion of phenotypic variation dictated by the niche variation hypothesis: they occupy a wide niche with a large between phenotype component and they show a great degree of variability in a highly heritable trait (bill morphology) which is related to niche utilization. In this section I investigate the third requirement, namely that there is differential fitness between phenotypes when in a given microhabitat. I realise a priori that fitness measures should refer to lifetime reproductive success but unfortunately such data are almost impossible to collect in a long-lived migratory species. However, winter survival must be considered an important component of the fitness of an individual. Given that, in the absence of shooting, starvation is the major cause of winter mortality amongst curlew at this study site (Whitfield 1985b, Whitfield *et al* in press) it is reasonable to assume that feeding efficiency is positively related to winter survival. Here I analyse the relative feeding efficiency of individual field-feeding specialists and generalists both when feeding on fields and when feeding on the intertidal zone. If specialisation increases fitness within a microhabitat (through experience or development of foraging skills) then field-feeders should have a higher foraging efficiency than generalists when

foraging on fields, but a lower foraging efficiency than generalists when on the intertidal zone.

3.4.2. Methods

All data described in this section were obtained from a series of focal-animal observations taken in the winters 1985-6 and 1986-7. A bird was chosen at random and observed for between one and six minutes. Observations of less than one minute duration were discarded. Prior to the start of each observation the following variables were recorded: date, time, location, colour-combination, sex (if unmarked), microhabitat (table 3.6), flock size (if in a flock) and distance to nearest conspecific neighbour (NND) in bird lengths. A bird was defined as belonging to a flock if it was within 30 bird-lengths (approximately 10m) of another flock member. The rationale behind this definition was that at a separation greater than this an individual did not always respond with the rest of the flock as a unit. For instance a 'satellite' bird (>30 bird-lengths from a flock) would often remain on the ground during some disturbance, whilst a nearby flock would more or less simultaneously take flight.

I then recorded a detailed commentary of the bird's feeding behaviour on to a running tape-recorder. I noted the following behaviours: every step, feeding motion (see below), swallow (recording prey species where possible) and vigilant scan (with the bill held at the horizontal or above). Fifty different types of feeding motion were identified: peck (where the tip of the bill just touches the ground) multiple peck (several pecks made in rapid succession without lifting the bill) and 48 different probe types. Each probe was divided into three components (after Mallory 1981):

- a) the depth to which the bill was inserted;
- b) the angle at which the bill was inserted;

c) the application of the bill after insertion.

Depth of insertion was divided into four categories:

- 1) tip only inserted (TIP);
- 2) up to half the bill inserted (0.5);
- 3) more than half the bill inserted (>.5);
- 4) all the bill inserted (ALL) (Fig. 3.17).

Angle of insertion was also divided into four categories:

- 1) vertical (V): the normal mode of insertion with the bill roughly perpendicular to the substrate;
- 2) horizontal (H): head and bill rotated laterally by up to 90° ;
- 3) upturned (U): head and bill rotated laterally more than 90° (Burton 1974, Piersma 1986);
- 4) stretch (St): bill inserted vertically but with neck extended so that the probe was made some distance in front of the feet (Davidson *et al* 1986) (Fig. 3.17).

Application of the bill after insertion was divided into three categories:

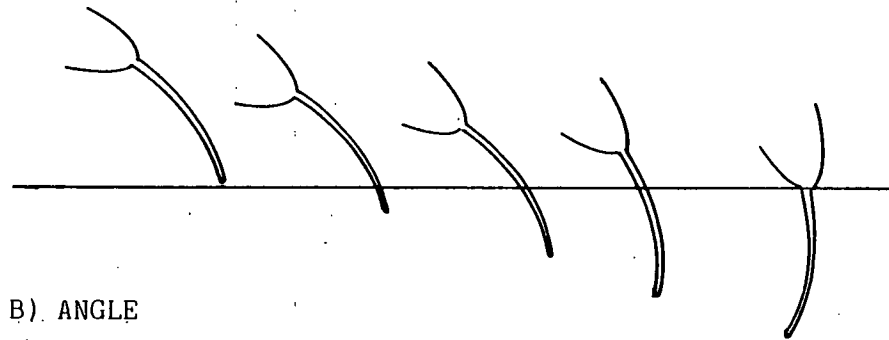
- 1) single (S): here the bill is simply inserted and withdrawn;
- 2) multiple (M): this category comprised complex probes (or rapid series of probes) where the bill was only partly withdrawn before reinsertion;
- 3) circle (C): here the bill is rotated around its long axis whilst still inserted in the substrate, by means of the bird walking in an arc around the axis of the bill (Burton 1974, Owens 1984). This motion was easily discernable in the field, with birds often rotating their bills by 180° or more.

Combination of the three components gave $4 \times 4 \times 3 = 48$ possible probe types (Table 3.14).

Fig. 3.17 Components of probe type recorded. a) depth, b) angle of insertion.

A) DEPTH

PECK TIP 0.5 0.75 ALL



B) ANGLE

VERTICAL HORIZONTAL UPTURNED STRETCH

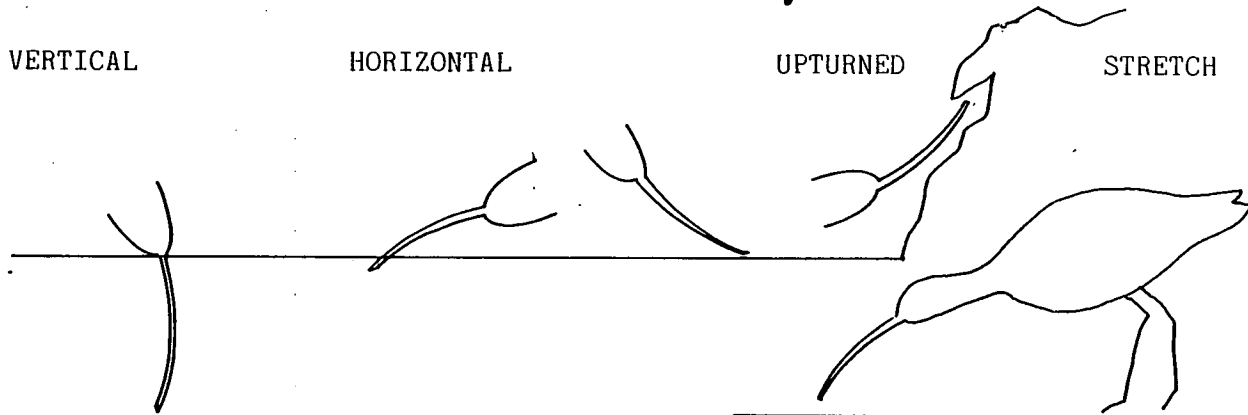


Table 3.14 Probe types recorded.

TIP-VERTICAL-----SINGLE	>.5-VERTICAL-----SINGLE
TIP-HORIZONTAL---SINGLE	>.5-HORIZONTAL---SINGLE
TIP-UPTURNED-----SINGLE	>.5-UPTURNED-----SINGLE
TIP-STRETCH-----SINGLE	>.5-STRETCH-----SINGLE
TIP-VERTICAL---MULTIPLE	>.5-VERTICAL---MULTIPLE
TIP-HORIZONTAL-MULTIPLE	>.5-HORIZONTAL-MULTIPLE
TIP-UPTURNED---MULTIPLE	>.5-UPTURNED---MULTIPLE
TIP-STRETCH---MULTIPLE	>.5-STRETCH---MULTIPLE
TIP-VERTICAL-----CIRCLE	>.5-VERTICAL-----CIRCLE
TIP-HORIZONTAL---CIRCLE	>.5-HORIZONTAL---CIRCLE
TIP-UPTURNED-----CIRCLE	>.5-UPTURNED-----CIRCLE
TIP-STRETCH-----CIRCLE	>.5-STRETCH-----CIRCLE
0.5-VERTICAL-----SINGLE	ALL-VERTICAL-----SINGLE
0.5-HORIZONTAL---SINGLE	ALL-HORIZONTAL---SINGLE
0.5-UPTURNED-----SINGLE	ALL-UPTURNED-----SINGLE
0.5-STRETCH-----SINGLE	ALL-STRETCH-----SINGLE
0.5-VERTICAL---MULTIPLE	ALL-VERTICAL---MULTIPLE
0.5-HORIZONTAL-MULTIPLE	ALL-HORIZONTAL-MULTIPLE
0.5-UPTURNED---MULTIPLE	ALL-UPTURNED---MULTIPLE
0.5-STRETCH---MULTIPLE	ALL-STRETCH---MULTIPLE
0.5-VERTICAL-----CIRCLE	ALL-VERTICAL-----CIRCLE
0.5-HORIZONTAL---CIRCLE	ALL-HORIZONTAL---CIRCLE
0.5-UPTURNED-----CIRCLE	ALL-UPTURNED-----CIRCLE
0.5-STRETCH-----CIRCLE	ALL-STRETCH-----CIRCLE

3.4.3. Results.

3.4.3.1. Bill use repertoire in different macrohabitats.

I plotted the frequency of occurrence of each probe type combining all observations for birds foraging on fields and on the intertidal zone (Fig. 3.18). It can be seen that there are apparent differences between bill use on each macrohabitat, with birds tending to utilize more of their bill length on the intertidal zone. The frequency of occurrence of bill manoeuvres involving horizontal or upturned angles of insertion is also greater on the intertidal zone. To clarify the situation I plotted the frequency of occurrence of each category of each of the three components of bill use (Fig. 3.19). Note that frequencies were calculated from the total number of probes that occurred on each microhabitat inclusive of PECK and M.PECK, therefore the sum of the percentages of occurrence of categories for each component is not necessarily 100%. There were significant differences in the frequency of occurrence of each category of the depth component of bill use between the two macrohabitats (χ^2 test of heterogeneity, $\chi^2=2288$, 3df, $p < 0.001$). The differences between macrohabitats in the repertoires of angle of insertion and application were also significant (χ^2 test of heterogeneity, $\chi^2=1826$, 3df, $p < 0.001$ and $\chi^2=310$, 2df, $p < 0.001$ respectively).

3.4.3.2. Bill use repertoire in different microhabitats.

The frequency of occurrence of PECK and M.PECK in each microhabitat is shown in Fig.3.20. It can be seen that pecking occurs more frequently on field microhabitats than on the intertidal zone. PECKs seldom and M.PECKs never resulted in prey capture, as indicated by the shaded columns. For ease of analysis I plotted only the frequency of occurrence of each category of each component of bill use for every microhabitat, combining data from observations on all birds (Fig. 3.21). Although the pattern of bill use amongst the four field microhabitats (GWS, GFS, PLOUGH and STUBBLE) comprised mainly single,

Fig. 3.18 Relative frequency of occurrence of probe types on fields (N=12605, from 420 observations) and the intertidal zone (N=10007 from 341 observations).

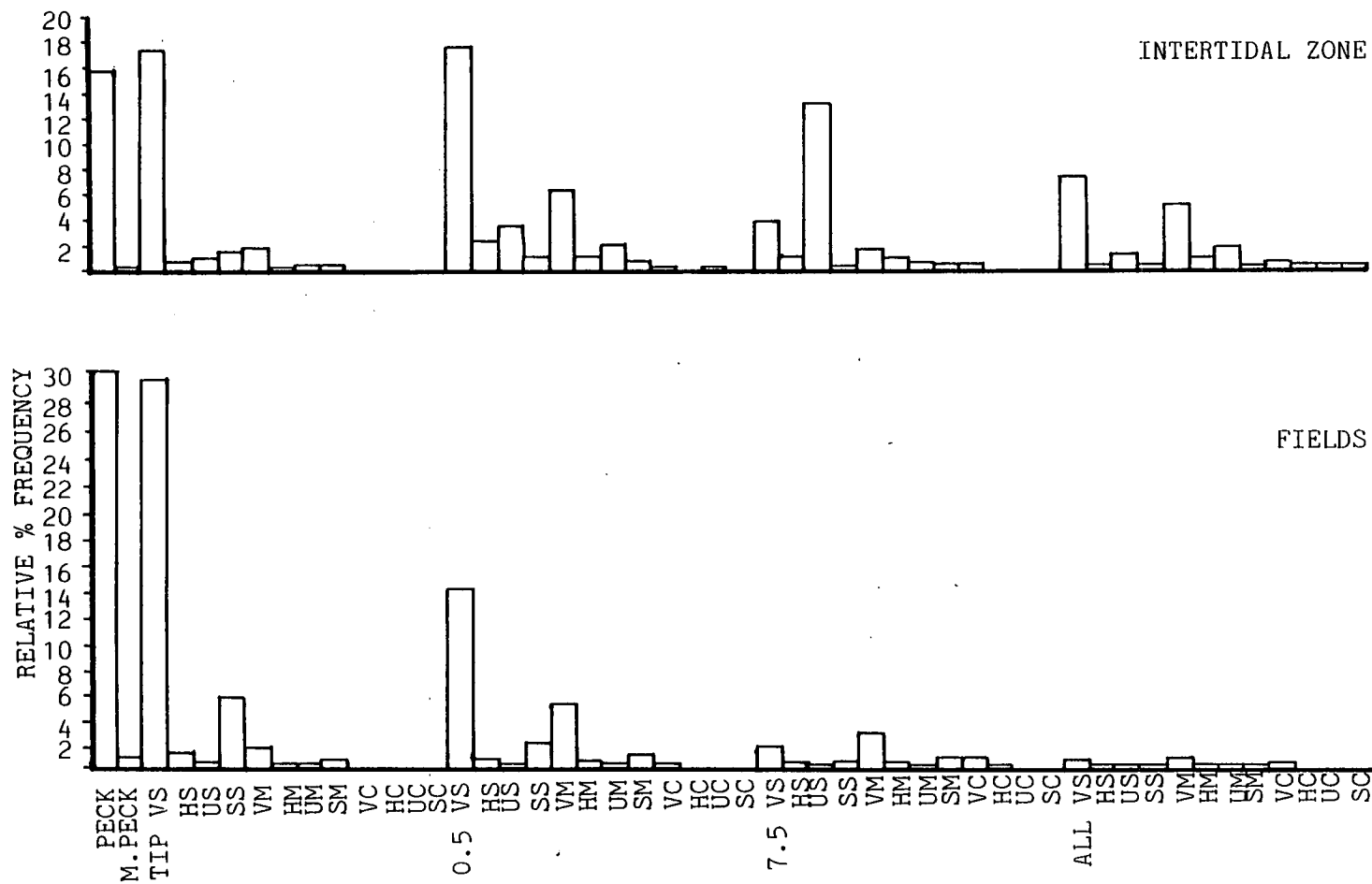


Fig. 3.19 Relative frequency of occurrence of each category of each component of bill use on fields (N=12605 from 420 observations) and the intertidal zone (N=10007 from 341 observations).

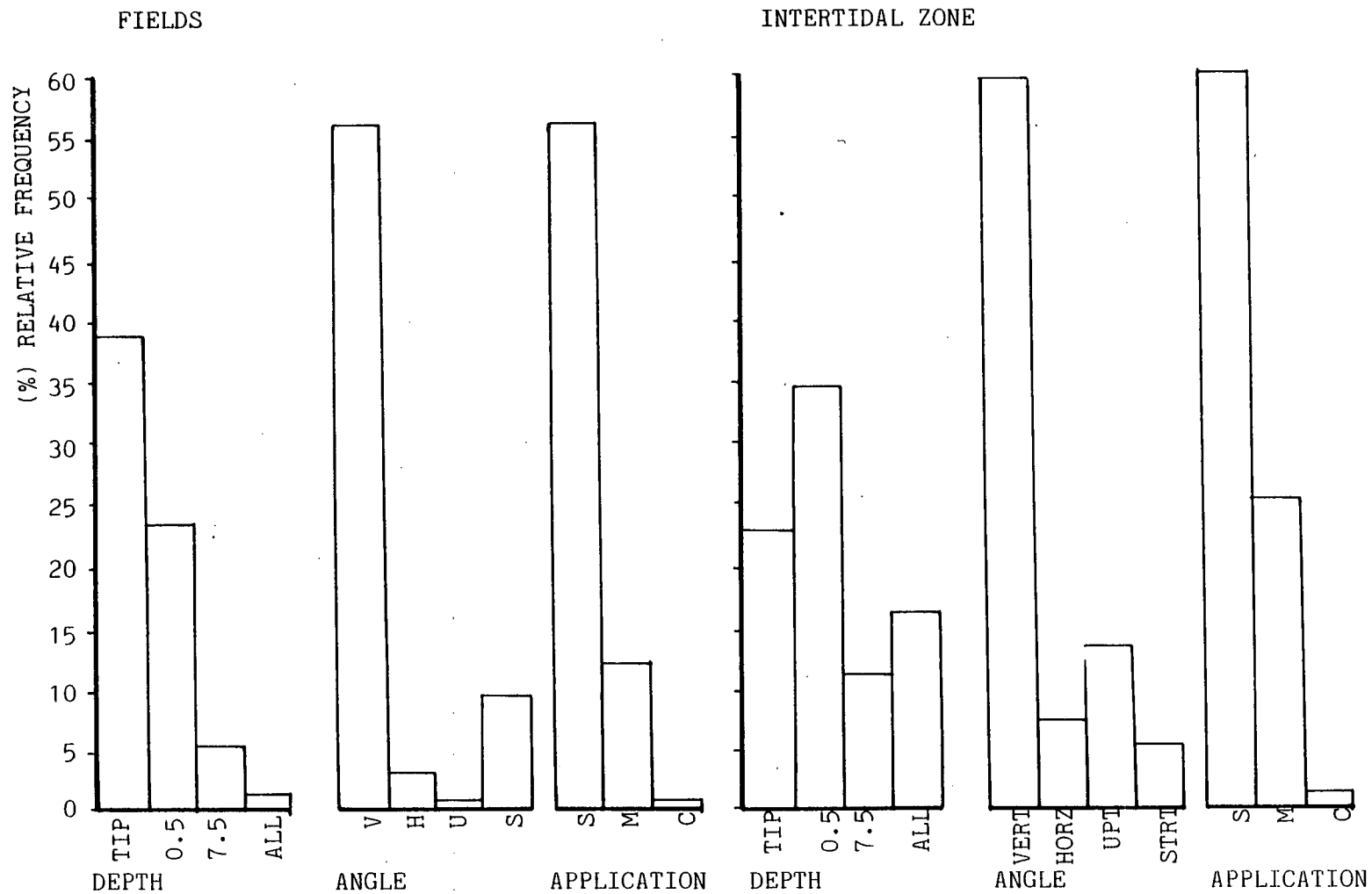
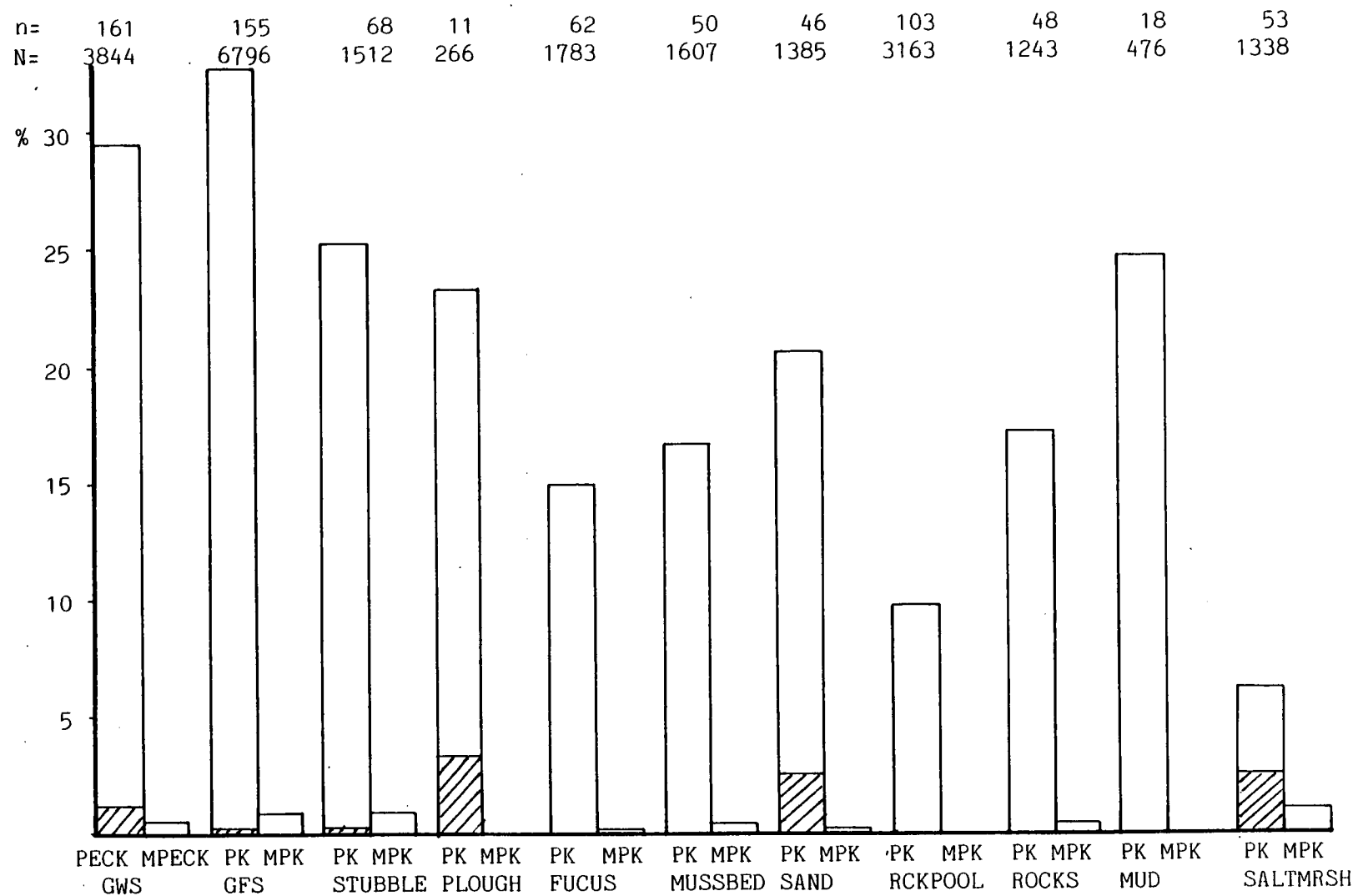


Fig. 3.20 Relative frequency of occurrence of PECK and M.PECK on each microhabitat (open bars) and percentage of PECKs that resulted in a swallow (shaded bars). N= total number of feeding motions observed. n= number of observations made.



shallow, vertical probes (Fig. 3.21), there were no significant differences in the frequency of occurrence of each category of all three components of bill use between the habitat types (χ^2 test of heterogeneity: depth; $\chi^2=328$, 9df, $p < 0.001$, angle; $\chi^2=84$, 9df $p < 0.001$, application; $\chi^2=14$, 2df $p < 0.005$).

Greater differences were apparent in bill use between the six microhabitats identified on the intertidal zone (Fig. 3.21). On ROCKS, FUCUS and ROCKPOOLS probes tended to be shallow with a high occurrence of horizontal and upturned angles of insertion, reflecting birds picking out littorinids and shore crabs from under boulders, within crevices and amongst *Fucus*. On SAND, MUSSELBEDS and MUD probes tended to be deeper and vertical, with a higher occurrence of circling applications on MUD. Once again there were significant differences in the frequency of occurrence of each category of each component between these six microhabitats (χ^2 test of heterogeneity: depth; $\chi^2=442$, 15df, $p < 0.001$, angle; $\chi^2=642$, 15df, $p < 0.001$, application; $\chi^2=298$, 10df $p < 0.001$). Bill use repertoire on SALTMARSH was largely restricted to relatively deep, vertical, multiple probes.

3.4.3.3. Relative success of different probe types.

In Fig. 3.22 I show the percentage of each category of each component of probe type which resulted in prey capture, for every microhabitat. From a comparison with Fig. 3.21 it is clear that the least common probe types are the most successful. For instance the use of CIRCLE is infrequent on all microhabitats except MUD (Fig. 3.21) yet when CIRCLE is used it is often successful (Fig. 3.22). Interpretation of these data is difficult since by definition the sample sizes of rare events are small (only two instances of UPTURNED bill use were seen in over 1500 probes observed on STUBBLE, both of which were successful). It is more useful, perhaps, to look at the contribution to the diet as a whole made by each category of each component of probe type. To do this I plotted the percentage of the total number of swallows observed on each

Fig. 3.21 Occurrence of different probe types in each microhabitat. Relative frequency of occurrence of each category of each component of bill use by microhabitat a) depth, b) angle of insertion, c) application. N = total number of feeding motions observed.

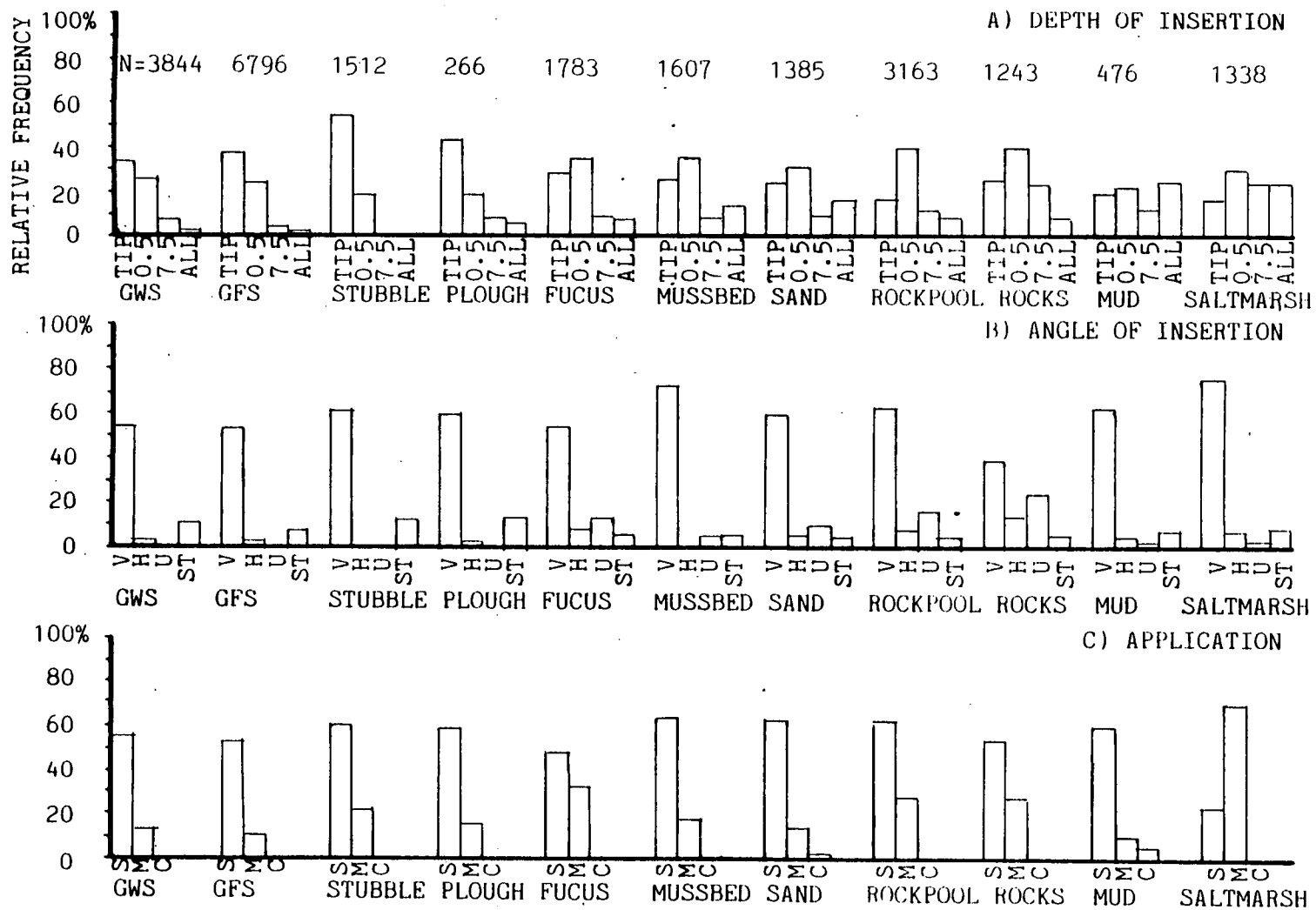
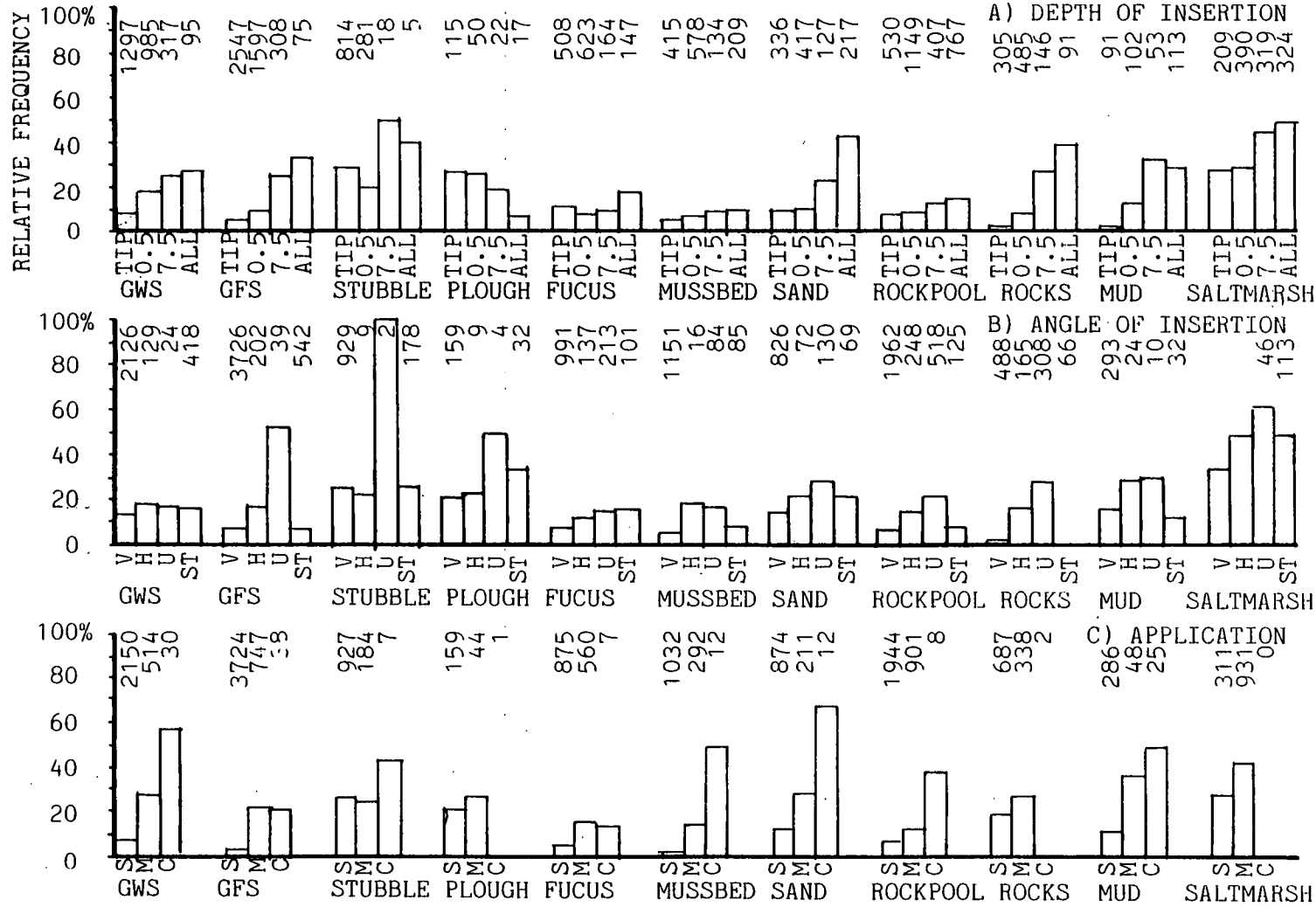


Fig. 3.22 Success of different probe types in each microhabitat. Percentage of each category of each component of probe type that resulted in a swallow. a) depth, b) angle of insertion, c) application. Numbers indicate total number of probes involving each category observed on each microhabitat.



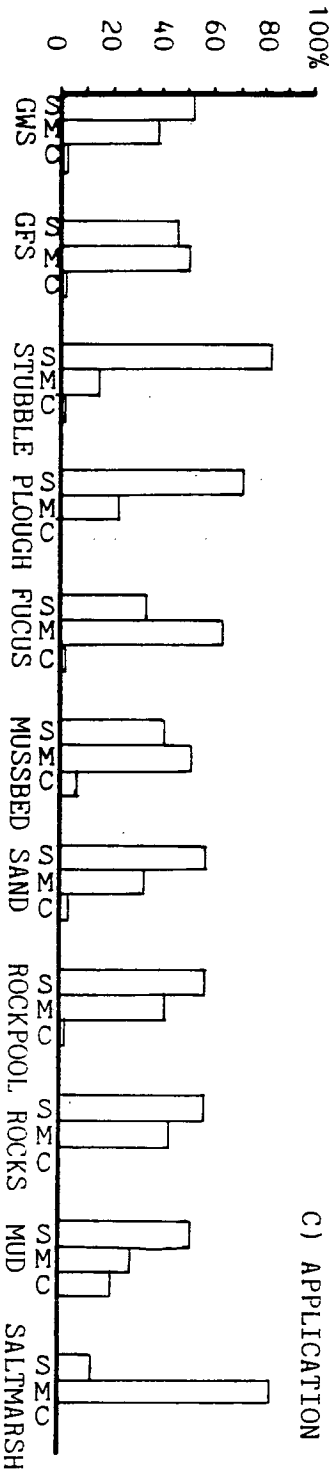
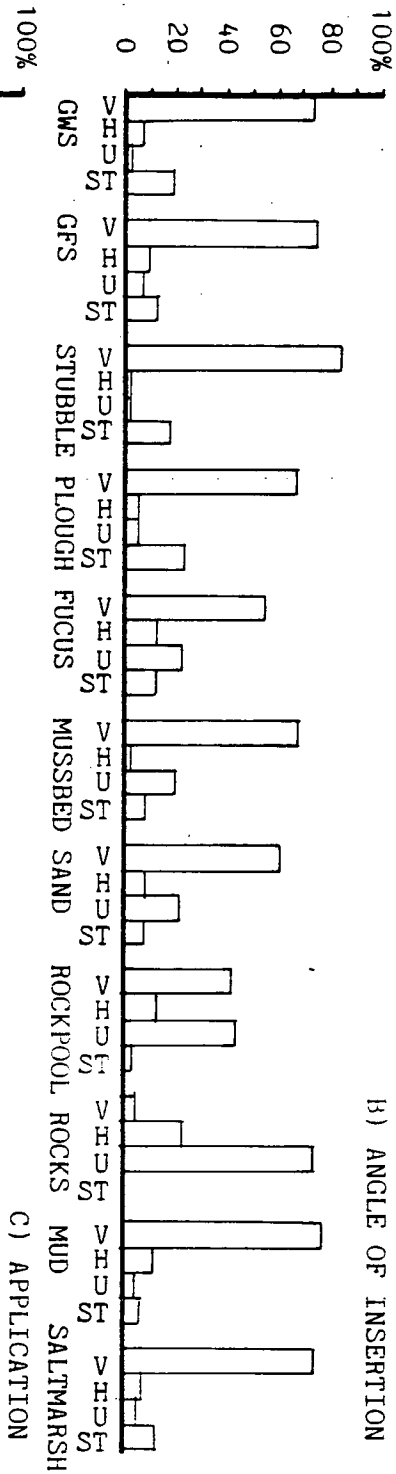
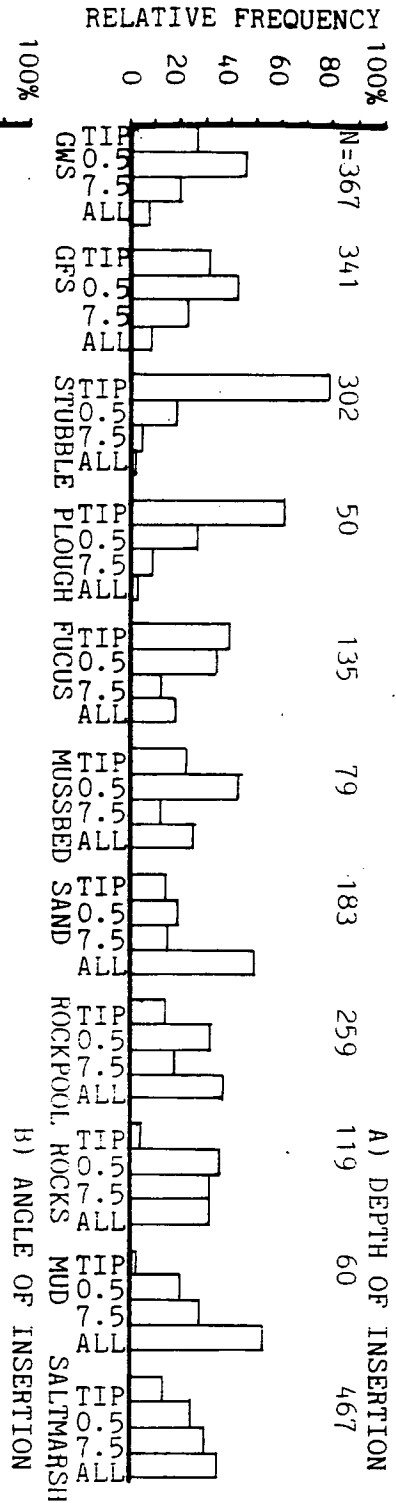
microhabitat that were preceded by each category of bill use (Fig. 3.23). Considering the component of depth of insertion it is clear that the majority of prey taken on fields are captured by shallow probes (less than half the bill length) whilst on the intertidal zone, particularly on sand or mudflats, many prey are captured by deep probes involving more than half, or indeed all the bill. If the angle of insertion is considered next, most prey on fields are captured by vertical probes, although some are taken by probes involving 'stretch'. Very few prey are captured on fields by probes where the bill is inserted horizontally or upturned. In contrast on the intertidal zone a much higher proportion of successful probes involved horizontal or upturned angles of insertion. This is particularly marked in the case of rockpool and rock microhabitats where 42% and 72% of captures respectively are made with the bill upturned. The majority of prey captures on SALTMARSH were made with deep, vertical, multiple probes.

3.4.3.4. Relative foraging success of field-feeding specialists in preferred and non-preferred environments.

The swallow rate (swallows/min.) of field-feeding specialists was compared to that of generalists when the birds were foraging on fields, using the Wilcoxon matched-pairs signed-ranks test. Application of this test controlled for variation in season, microhabitat, climatic conditions and food availability. Field-feeding specialists had a significantly higher swallow rate than generalists when both were feeding on fields ($T=242$, $N=50$, $p<0.005$). Unfortunately the sample size of intertidal specialists feeding on fields was too small to permit a comparison of swallow rate.

The swallow rate of field-feeding specialists was then compared to that of generalists when feeding on the same microhabitat on the intertidal zone, again using the Wilcoxon matched-pairs signed-ranks test. Although the sample size was extremely small, generalists had a significantly higher swallow rate than

Fig. 3.23 Relative contribution to diet of different probe types in each microhabitat. Percentage of swallows that were preceded by each category of each component of probe type for each microhabitat. a) depth component, b) angle of insertion, c) application. N= number of swallows observed on each microhabitat.



field-feeders ($T=0$, $N=5$, $p < 0.05$). Again comparisons could not be made with intertidal specialists due to the small number of matched-pair observations.

3.4.4. Discussion.

In the first part of this section I have shown that there are significant differences in the bill use repertoire of curlew foraging on different microhabitats. Since individual birds specialise in exploitation of specific microhabitats, it follows that different individual curlew will employ different patterns of bill use whilst foraging. This supports the prediction from the niche variation hypothesis, that a broad niche with a large between phenotype component will promote phenotypic variation both in morphology and behaviour. Habitat selection appears to be influenced to some extent by bill morphology, however the differences in bill use between microhabitats may reflect the development of foraging skills specific to a given habitat type. Acquisition of foraging skill will tend to enhance the degree of specialisation by, for instance, increasing the cost of switching between microhabitats (Partridge 1978, Partridge & Green 1985). It is interesting that the least common probe types were usually the most successful in any given microhabitat. This may reflect the need for the development of foraging skills or the acquisition of experience for the effective exploitation of different microhabitats. The majority of the diet of curlew foraging on field microhabitats was obtained by the use of relatively simple, shallow, vertical probes, whilst on the intertidal zone a greater proportion of prey are captured by deeper probes, often with the bill orientated horizontally or upturned. These results are analysed and discussed more fully in relation to bill morphology in section 3.5.

In the second part of this section I attempted to test a further prediction from the niche variation hypothesis; that field-feeders should have a higher swallow rate than generalists when both are foraging on fields, but a lower

swallow rate than generalists when foraging on the same intertidal microhabitat. The results obtained support this prediction. If the assumption that when two birds are foraging on the same microhabitat (particularly on fields) then they are taking approximately the same prey type and size is correct, then it would appear that specialisation pays, at least in the short-term, by increasing an individuals intake rate when foraging on its preferred habitat-type (see also Partridge & Green 1987).

3.5. Why do curlew have decurved bills?

3.5.1. Introduction.

The adaptive function of the remarkable trophic apparatus of the curlew has puzzled researchers for some time. Hale (1980) and Owens (1984) argue that the decurved bill of the curlew is primarily a result of selection on the breeding grounds and an adaptation for reaching and probing for insects in long vegetation, or berries amongst heather. Davidson *et al* (1986) point out that this is unlikely, since several species of Charadrii of differing bill form (including godwits, which have straight or slightly upturned bills) exploit similar prey arrays in similar habitats and cite evidence that the the major selective force on bill morphology occurs on the wintering grounds. Bicak (1983) produces evidence from his study of long-billed curlew, *Numenius americanus*, that would also seem to refute the breeding ground hypothesis. He showed that although the density of available insect prey was positively correlated with grass height, birds spent a significantly higher proportion of their time foraging in short grass and also had a significantly higher capture rate in shorter vegetation. In the present study curlew were never observed feeding in vegetation longer than about 10cm.

Owens (1984) also suggests that decurvature could be an exaptation (secondary benefit of adaptation to another function) to feeding on mudflats. He presents the hypothesis that rotating the bill around its longitudinal axis

whilst inserted (circling) causes the bill tip to describe an arc beneath the surface, thus increasing the chances of intercepting a worm burrow. Davidson *et al* (1986) dismiss this idea with the unsupported statement that: 'common curlews seldom pivot around the probe site with the bill deeply inserted'. Burton (1974) describes curlew circling in this manner, but suggests that turning normally takes place with a relatively short length of the bill inserted. The assertion of Davidson *et al* that such a motion is unlikely to increase the element of surprise to the prey animal (as suggested by Owens 1984) is probably correct, since the targeted worm would almost certainly detect the initial nearby insertion of the bill and react by retreating down its burrow; furthermore the bill tip will end up closer to the feet of the foraging bird than if the bill were straight.

Davidson *et al* (1986) propose three further advantages of decurvature for birds foraging on mudflats. The first of these is that a decurved bill permits vertical insertion of the bill tip further in front of the feet than does a straight bill. Whilst this is true, the same effect could be achieved by elongation of the neck. Moreover there is no evidence to support the idea that such a motion is advantageous (in fact Mallory (1981) found that there was no difference in the efficiency of model straight and decurved bills at capturing insects on the breeding grounds). The second advantage of decurvature proposed by Davidson *et al* (1986) is that it allows for lengthening of the bill, without a corresponding lengthening of the legs. Long legs, they argue, are disadvantageous for birds foraging on open mudflats as they increase the detrimental effects of buffeting in strong winds. Whilst it is clear that strong winds can have an adverse affect on the foraging success of birds, no data are presented on the comparative intraspecific effect of buffeting on long and short-legged birds. From section 3.2 it is clear that neither bill length nor bill decurvature are isometric with tarsus and toe length, invalidating this

hypothesis. The third possible advantage of decurvature proposed by Davidson and his colleagues is that a decurved bill aids vertical withdrawal of worms from the substrate without breakage. They present a comparison of efficiency of worm-withdrawal between curlew and bar-tailed godwit. Whilst their argument that breakage of worms can be costly is convincing, the figure they present to illustrate the way in which the risk of breakage is actually reduced (Fig. 1, p63) is not. Much depends upon the relative size of the bill, neck and legs and the distance of the feet from the probe (the last variable changes without explanation in the course of the diagram). In any case, the angle between the bill tip and the worm will change throughout withdrawal in both species and the decurved bill of the curlew will not (as stated) permit a vertical grip to be maintained throughout withdrawal. This hypothesis should be tested with models in the laboratory. Although the data presented suggest that bar-tailed godwit break more worms than curlew there is, in fact, no significant difference between the species in any of the months for which comparisons can be made (NOV. $\chi^2=3.057$ N.S., DEC. $\chi^2=0.973$ N.S., JAN. $\chi^2=0.014$ N.S., FEB. $\chi^2=0.382$ N.S.). Moreover if curlew were, in fact, more likely than godwit to extract worms without breakage, this would not necessarily be due to the difference in bill morphology between the species, there are two alternative hypotheses:

- 1) godwit might feed in substrates of different penetrability to curlew, increasing the likelihood of worm breakage;

- 2) godwit may take smaller worms than curlew. It is conceivable that small thin worms might be more prone to breakage than are large worms.

In any case, if the selection pressure exerted through breakage of worms is large enough to promote the evolution of bill decurvature in curlew, it is not clear why bar-tailed godwit should not also have evolved a decurved bill, particularly since marine worms constitute a much larger percentage of the diet

of bar-tailed godwit than of curlew (Cramp & Simmons 1983).

It has been suggested that the decurved bills of whimbrel (Mallory 1981) and Eastern curlew, *Numenius madagascariensis*, (Piersma 1986) are adapted to the shape of the burrows of the crab species which form a major part of the diets of these birds on the wintering grounds. However, evidence for this is circumstantial and this theory is not applicable to Eurasian curlew, which have a catholic diet (Fig. 3.10).

Davidson *et al* (1986) conclude that decurvature in the curlew is an adaptation for probing along complex pathways in mudflats, but also suggest that a decurved bill could be used to search the complex three-dimensional structure of a rocky shore and amongst the matted grass roots on fields.

In this section I present the results of detailed observations of curlew foraging behaviour in order to assess the applicability of some of these hypotheses.

3.5.2. Methods.

The data presented in this section were collected during the focal-animal observations described in section 3.4. Here I analyse the relative frequency of successful probe types (*i.e.* probes that precede a swallow) that involve the use of bill decurvature. I assume that the decurvature of the bill is used mainly in probe types that include either horizontal or upturned angles of insertion and in probes that involve circling. It seems intuitively obvious that when making probes that include these components a bird is actively using the decurvature of its bill. I acknowledge that decurvature might be used in an unknown way when making vertical probes or stretching.

3.5.3. Results.

A significantly higher proportion of successful probes were made with the bill horizontal on the intertidal zone than on fields ($\chi^2=23.61$, 1df, $p < 0.001$). Similarly significantly more successful probes were made with the bill upturned

on the intertidal zone than on fields ($\chi^2=398.1$, 1df, $p < 0.001$). The proportion of captures involving circling was not significantly different between the two microhabitats ($\chi^2=1.518$, N.S.). Overall, the proportion of probes involving components that used decurvature was higher on the intertidal zone than on the fields ($\chi^2=192.48$, $p < 0.001$). Single applications dominate on field habitats, whilst multiple applications are more common on the intertidal zone. Circling only appears to be an important method of prey capture on musselbeds and mudflats, accounting for 8% and 20% of prey respectively. The frequency of circling is positively correlated with depth of insertion (Fig. 3.24 $r=0.992$, 2df, $p < 0.01$).

The proportion of successful probes in each microhabitat that involve decurvature (horizontal insertion + upturned insertion + circling) is depicted in Fig. 3.25. Only a small proportion of successful probes involve use of decurvature on field habitats or saltmarsh (range 2.31%–17.6%). In contrast on each intertidal microhabitat more than 30% of captures involved the use of decurvature. Most dramatically 56% of captures in rockpools and 95% of captures amongst rocks were made with probes that made active use of the decurvature. The proportion of captures that used decurvature amongst rocks is significantly greater than that in rockpools ($\chi^2=10.69$, 1df, $p < 0.005$) and therefore in all other microhabitats. If the microhabitats rocks, rockpools and *Fucus* are combined and considered as primarily rocky shore habitats and compared with mud, sand and musselbeds (considered as estuarine habitats) then a significantly greater proportion of successful probes involve the use of decurvature on rocky-shores (70%) than on estuaries (33%) ($\chi^2=33.35$, $p < 0.001$).

3.5.4. Discussion.

These results clearly suggest that most prey are captured on fields by use of shallow, vertical, single probes, whilst the majority of probes on the

Fig. 3.24 Correlation between depth of insertion and the percentage of successful probes that involved circling. Points are means for all 11 microhabitats. Vertical bars indicate ± 1 S.E. ($r=0.992$, 2df, $p < 0.01^{**}$).

% OCCURRENCE OF SUCCESSFUL PROBES
IN ALL MICROHABITATS PRECEDED BY
CIRCLE

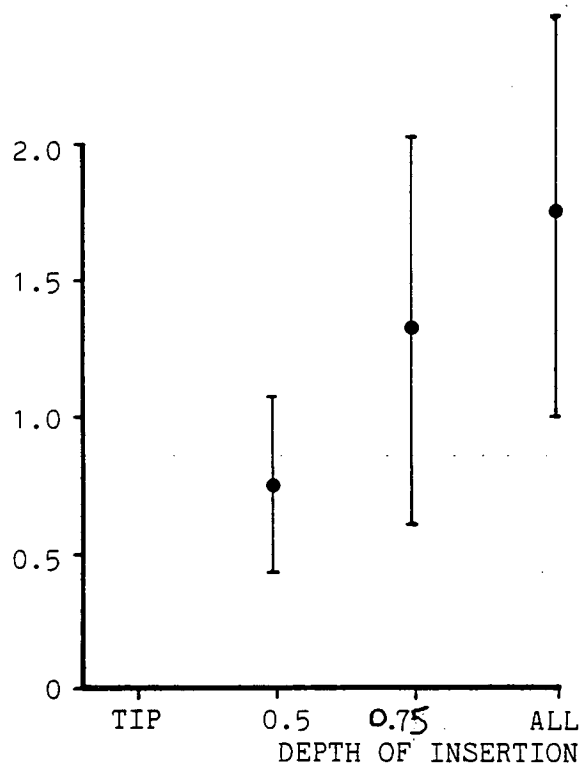
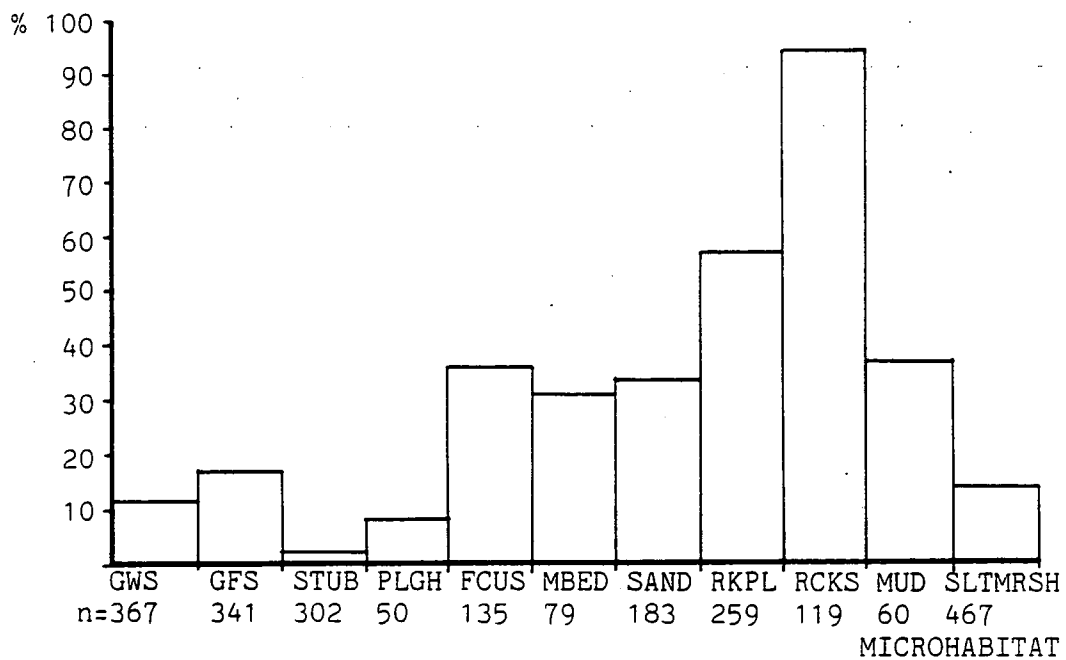


Fig. 3.25 Relative frequency of occurrence of succesful probes that involved components that utilized decurvature (horizontal + upturned + circle) for each microhabitat. N= total number of feeding motions observed.



intertidal zone are deep and complex, many involving use of bill decurvature. This supports the earlier finding, that birds which specialise on field microhabitats tend to have short, straight bills whilst those which specialise on intertidal habitats have long, decurved bills. These findings constitute further evidence against the hypothesis that selection for decurvature occurs primarily on the breeding grounds (Hale 1980, Owens 1984), but support the notion of Davidson *et al* (1986) that the decurved bill evolved on the intertidal zone on the wintering grounds. However, Davidson and his co-workers suggested that the primary selection occurred on mudflats; the data presented in Fig.3.23 suggests that decurvature is more advantageous on rocky-shores. Nevertheless, a high proportion of successful probes also involve decurvature on estuarine habitats. Particularly striking is the finding that 20% of successful probes on mudflats involved the use of circling manoeuvres. Curlew showed an increasing tendency to circle with deeper probes, in contrast to the suggestions of Burton (1974) and Davidson *et al* (1986). It is still not clear what the function of circling is; it may be a device to increase the chances of detection of buried prey (Owens 1984).

Little has been said about the possible disadvantages of decurvature. Perhaps less vertical pressure can be exerted on a decurved bill than on a straight bill. It is interesting to note that there is an indication that birds which feed on firm field substrates have relatively stouter bills than birds which feed on softer intertidal substrates. A more detailed study of niche utilization, in terms of substrate penetrability, in relation to bill morphology would be of great value, particularly at a time when tidal barrage schemes threaten to substantially alter the flow regimes of a number of British estuaries. Such schemes may have profound effects upon the distribution of sediment types (Goss-Custard 1987).

In conclusion it seems that decurvature is an adaptation to probing along complex pathways on the intertidal zone (as suggested by Davidson *et al* 1986), but seems to be particularly beneficial when foraging on rocky-shores.

3.6. Summary and discussion.

In this chapter I set out to test the applicability of the niche variation hypothesis to curlew foraging on the wintering grounds. The hypothesis as proposed by Van Valen (1965) suggests that a broad niche with a large between-phenotype component can promote variability in both morphology and behaviour. Firstly I documented an extremely high degree of variation in bill morphology, especially in bill shape. This led to two predictions:

1) that curlew should occupy a wide niche with individuals specialising in the exploitation of a subset of the environment exploited by the population as a whole;

2) the foraging behaviour of curlew will vary according to the microhabitat(s) that they exploit.

Data collected in the course of this study show that curlew fulfil both of these predictions. Individuals do specialise in the exploitation of specific habitats and their foraging behaviour varies accordingly. Van Valen (1965) suggested three conditions which must be met if variability is to be maintained:

1) There is differential fitness between environmental subsets for a given individual. I was unable to provide evidence to test this directly, but the finding that field-feeding specialists have a higher swallow rate than generalists when on fields but a lower swallow rate than generalists when on the intertidal zone suggests that specialisation may pay in the short term at least.

2) The above difference is in part genetic. I was able to show that habitat selection is influenced by bill shape; a highly heritable trait.

3) There is an appropriate mechanism for the segregation of individuals between environmental subsets, including choice. The existence of specialisations suggests that such a mechanism must be operating.

Thus my findings seem to support the operation of the niche variation hypothesis. More data are needed on the relative success rates (preferably measures of net intake rates) of specialists when foraging in non-preferred microhabitats. It would be interesting to obtain data on the variation in bill morphology in areas where available habitat type is more restricted (a narrower niche should result in a reduced degree of phenotypic variation), but of course it would be extremely difficult to find such a population that was reproductively isolated.

There is an alternative explanation for the existence of individual variation in habitat use and foraging behaviour; that one strategy is actually more successful than others and birds compete for the opportunity to employ it (*e.g.* Goss-Custard 1985). Townshend (1981b) believed that short-billed birds (males) were forced to switch to field habitats when falling temperatures depressed the availability of intertidal invertebrate prey. This hypothesis implies that intertidal zone habitats are preferred. Townshend's hypothesis predicts that the number of curlew field-feeding should increase during cold spells as a result of birds switching from foraging on the intertidal zone. I found that birds moved in the opposite direction during cold weather and that the number of curlew field-feeding was positively correlated with temperature. I was able to show that selection of field habitats was influenced by bill shape (field-feeders having relatively short, thick, straight bills) and not bill length *per se*. The differences in foraging behaviour between birds exploiting different microhabitats may enhance the degree of specialisation if they reflect the skill needed to capture prey efficiently or experience of a particular microhabitat.

Finally my detailed observations of probe types would seem to suggest that selection for bill decurvature occurred predominantly on intertidal zone habitat types rather than on grassland. Decurvature was used to a greater degree on rocky-shore microhabitats than on mudflats. I conclude that Davidson *et al* (1986) were correct to suggest that decurvature is an adaptation for probing along complex pathways, but that in the Eurasian curlew it may be more important on rocky shores rather than mudflats.

CHAPTER 4.
RANGING AND SPACING BEHAVIOUR.

*"Well, the moral of the story,
The moral of this song,
Is simply that one should never be
Where one does not belong."*

BOB DYLAN, 1968.

4.1 Introduction.

Waders exhibit a remarkable range of both inter- and intraspecific variation in site-fidelity, spacing and ranging behaviour (Evans 1981, Myers 1984, Goss-Custard 1985). At the interspecific level, one end of the spectrum is occupied by knot *Calidris canutus*, which form vast itinerant flocks of up to tens of thousands of individuals (e.g. Symonds et al 1984), whilst at the other end are found species such as the grey plover *Pluvialis squatarola*, which forage solitarily and can return year after year to the same small, defended territory (Townshend 1981a). Myers (1984) reviews the site-fidelity and spacing behaviour of many species of shorebird, but emphasizes the point that we should attempt not to be over reductionist when describing these behaviours since the bewildering array of phenotypes observed actually comprises a continuum. This becomes more obvious when looking at intraspecific variation in these behaviours. Sanderling, *Calidris alba*, for instance, generally show high site-fidelity, but some individuals can abruptly switch foraging location both within and between lagoon systems within a winter (Myers & McCaffery 1980). Turnstone, *Arenaria interpres*, also show considerable inter-individual variation in site-fidelity (Whitfield 1985a). Intraspecific variation has also been documented in spacing and territorial behaviour in sanderling and several other species (Myers et al 1979), redshank, *Tringa totanus*, (Mullin 1984), curlew (Ens 1979, Townshend 1979) and grey plover (Townshend 1979). This variation is not just restricted to individual birds, but extends to given individuals altering their behaviour with time (Dugan 1982, Townshend 1981a). Several authors have related variations in site-fidelity, ranging and spacing behaviour to variations in food supply, specifically absolute food availability (e.g. Goss-Custard et al 1977, Myers et al 1979) and the temporal stability (predictability) of food supplies (Evans 1981, Whitfield 1985a).

A cost/benefit approach has often been employed to elucidate variation in wader ranging and spacing behaviour (Townshend *et al* 1984). The benefits accruing to an individual through joining a foraging flock have been much discussed (review in Barnard & Thompson 1985) and are usually considered in terms of a reduction in the risk of being killed by a predator, rather than possible foraging benefits (Goss-Custard 1985). There are several reasons for this:

- 1) there is generally an absence of evidence that flocking enhances foraging rates, indeed in many cases flocking has been shown to depress intake rates (Goss-Custard 1980 and see below);

- 2) there is evidence that predation, particularly by raptors (Page & Whitacre 1975, Kus pers.comm., Whitfield 1985b, Whitfield *et al* in press) but also by mammals. (Townshend 1984) is a major source of mortality amongst wintering waders;

- 3) territorial birds and individuals feeding solitarily quickly form compact flocks on appearance of a raptor (Myers 1984, Whitfield 1987);

- 4) the cost of being killed by a raptor is absolute and irreversible, whilst the costs of a reduction in intake rate are not necessarily absolute, nor long-term.

The precise mechanisms by which the reduction in predation risk is brought about include the dilution effect, increased chances of predator detection, predator confusion and deterrence and are fully discussed in Barnard & Thompson (1985).

Many studies have shown that the time spent by an individual in vigilance decreases as flock size increases, permitting birds to spend more time foraging (*e.g.* Abramson 1979 for curlew, Fleischer 1983 for turnstone). This has often been interpreted as a benefit of flocking, but the decreased vigilance has seldom been reliably correlated with an increase in ingestion rate (Myers 1984

but see Metcalfe & Furness 1984). Moreover the vigilance/flock size function almost always reaches an asymptote at flock sizes in the region of 30 birds, yet flock sizes in excess of several hundred birds are not uncommon; this suggests that there may be other benefits to joining a flock.

Foraging rate may be seen to increase with flock size either through social facilitation (Myers 1984) or because of the fact that bird density tends to be higher in areas of high prey availability (Myers *et al* 1979, Goss-Custard *et al* 1977, Rands & Barkham 1981) *i.e.* larger flocks will tend to form at better feeding sites (Waite 1983). It seems unlikely that flocking in waders could have a direct benefit for foraging efficiency as a result of increased efficiency at finding patchy food resources, cooperative hunting or avoidance of duplication of search effort (Myers 1984, Goss-Custard 1985). Indeed the main cost of joining a flock is often seen as a reduction in foraging efficiency through interference, defined by Goss-Custard (1980) as: 'the immediate and reversible reduction in intake rate associated with increasing bird density'.

Interference has been documented in redshank (Goss-Custard 1970a), curlew (Zwarts 1978, cited in Goss-Custard 1980) and oystercatcher (Goss-Custard & Durell 1987a). There are several mechanisms by which the presence of conspecifics could bring about an immediate reduction in the intake rate of a foraging bird (Goss-Custard 1980):

- 1) an increase in aggression and/or food stealing (*e.g.* in oystercatcher Goss-Custard & Durell 1987b);

- 2) distraction of visually hunting birds (possibly occurs in redshank, Goss-Custard 1976);

- 3) depletion of the available fraction of the prey (possibly important in bar-tailed godwit, Smith 1975, cited in Goss-Custard 1980);

- 4) depression of prey availability caused by an increase in the frequency of escape responses of invertebrate prey (Goss-Custard 1970b);

5) birds being forced by high densities of conspecifics to use poorer feeding areas (Goss-Custard 1980).

Interference can encourage birds to spread out or even to defend feeding territories (Goss-Custard 1985). Cost/benefit approaches have also been applied to the problem of when wintering shorebirds should defend territories and to where and how large the territory should be (Myers *et al* 1979, Townshend *et al* 1984). It is generally accepted that the primary benefit of territorial defence is a net energetic gain either in the short or long term (Townshend *et al* 1984). Exclusion of conspecifics from a territory will remove the detrimental effects of interference and defence of an area may also help prevent long term depletion of prey (Dugan 1982). Such depletion can be severe (Evans *et al* 1979), but seems unlikely to be of substantial importance in either redshank (Goss-Custard *et al* 1984) or curlew (Ens 1984). Costs of territoriality include energetic output in defence and possibly an increased risk of predation, since, by definition, territorial birds feed solitarily and predation risk is reduced in flocks as already discussed. Theory suggests that defence should only occur if the costs involved in exclusion of conspecifics are outweighed by the increased energy supply secured. Measurement of net energetic gain in the field is extremely difficult, so this theory has never been adequately tested. Ens (1979) suggested that curlew that held territories had greater masses than those which did not, possibly indicating that there is a benefit to territoriality although there is a cause/effect problem here. Both Phillips (1980) and Baber (1988) were able to show that curlew that defended territories had higher swallow rates than those that did not.

The spacing/ranging strategy adopted by an individual would seem to be a trade-off between the need to maximise net energetic gain and the need to avoid predation (and thus may vary seasonally), since both the energetic requirements of waders and the risk of predation vary throughout the year

(Whitfield 1985a). Seasonal variation in the trade-off between feeding and vigilance has been documented in turnstone (Metcalf & Furness 1984). The situation is further complicated by individual differences in foraging and competitive ability (Ens & Goss-custard 1984, Goss-Custard 1986). In this chapter I attempt to assess the extent of variation in the ranging and spacing behaviour of curlew and discuss the possible importance of interference, predation and phenotype in determining individual strategies.

4.2. Ranging behaviour.

4.2.1. Introduction.

Curlew are known to be generally faithful to their wintering site (Bainbridge & Minton 1978) and to specific low-water feeding sites both within and between winters (Townshend 1981a). Individuals are often highly territorial; here I use Kaufmann's (1983) definition of territoriality, which specifies that a territory holder has priority of access to resources within a geographically defined area and that priority of access is achieved through dominance as a result of social interaction. Some individual curlew defend the same area throughout a winter (or even successive winters) whilst some become territorial for short periods and others may switch territories within a season or even within a tidal cycle (Ens 1979, 1984, Townshend 1981a, Baber 1988). Territorial behaviour is characterised by hunched runs or short flights at intruders, accompanied by the characteristic 'bubbling' call (Cramp & Simmons 1983). This behaviour normally results in the intruder quickly retreating beyond the territory boundary or flying off. Boundary disputes involve two adjacent territory holders conducting parallel walks along the common edge of the two territories. Often one bird lunges at the other with its bill, although prolonged fighting is uncommon. Frequently one or both birds pick up sticks, *Fucus* strands or other debris from the substrate. Such disputes can last in excess of 10min (Ens 1979, Phillips 1980, Townshend 1981a, Baber 1988, pers. obs.).

Some individuals exhibit behaviour intermediate between full territoriality and non-aggression (Townshend 1981a, Baber 1988, pers. obs.). The area utilized by territorial, intermediate and non-aggressive birds foraging on the intertidal zone is usually small (Ens 1979, Townshend 1981a, Baber 1988). Little is known about the ranging behaviour of birds foraging on field habitats, but from my preliminary observations it appeared that field-feeders were ranging over a far wider area than birds feeding on the intertidal zone. In this section I attempt to measure the feeding ranges of individual birds that specialised on different macrohabitats in order to test this observation.

4.2.2. Methods.

4.2.2.1. Definition and computation of feeding range.

'Home range' can be a confusing concept due mainly to the many disparate definitions used by previous authors, but is generally considered to refer to the area over which an animal usually travels in pursuit of its routine activities, but does not actively defend (Jewell 1966). Estimates of home range of an individual can vary considerably according to exactly how the behaviour is defined. For instance if I had decided to include roosting behaviour as part of the routine daily activity of curlew (which undeniably it is) my estimates of home range would have been considerably smaller and less meaningful than if I omitted roosting behaviour. This is because most birds habitually used the same, relatively small area as a communal roost. I wished to compare the area utilized by different individuals whilst they were in the process of actively harvesting food resources. Moreover, I wanted to make comparisons between 'free-ranging' individuals and birds that were obviously actively defending territories. I decided therefore to abandon the term 'home range' and I refer instead to an individual's 'feeding range'. This I defined as the area utilized by a foraging individual over the two winters 1985-6 and 1986-7. In computing feeding ranges I used only coordinates from sightings of actively foraging

birds.

Range estimations can also vary considerably according to the computational method employed. Since some curlew appeared to have several 'activity centres', and the distribution of coordinates obviously differed from normal I chose to use Anderson's (1982) non-parametric technique. Range estimations using this strong technique are based upon the probability of finding an animal at a particular location on a plane and are derived from the bivariate probability density function or Utilization Distribution (UD) (*N.B.* UD refers to the utilization of space, not other resources). It is possible to draw a series of equal-height contours around the UD, each representing a minimum area probability (MAP). Range is defined as the area under the UD enclosed by a given contour. I chose to work at the 0.9 probability level (MAP 0.9) (*cf* Whitfield 1985a). This means that the individual in question spent 90% of its foraging time in the area specified. Working at the 90% level will tend to eliminate spurious sightings (caused for instance by disturbance or mis-reading a colour-ring combination). For an assessment of Anderson's technique and a comparison with less powerful parametric estimations see Schoener (1981) and Wilkinson & Bradbury (1985).

4.2.2.2. Plotting bird's locations from sightings.

Whenever a colour-marked bird was sighted in the course of making counts or taking feeding observations (chapter 3) I recorded the following information: date, time, colour-combination, activity (see Table 3.5) and the microhabitat in which the bird was found (see Table 3.6). I also noted the location of the bird as precisely as possible and later assigned each sighting an eight figure map reference (O/S National Grid 10m reference). This was relatively easy for birds seen on the intertidal zone at Scoughall, since there were many delineating features (rockstrips, pools etc.) that could be used as reference points. At Tynninghame the task was more difficult because of the

extent and nature of the intertidal zone. I attempted to increase the accuracy of locations by taking a series of colour-print photographs (16cm x 10cm) from fixed points along the shore. These were mounted on a plastic folder and taken into the field. I took observations from the same points as I had taken the photographs (to minimise parallax error) and the position of any bird seen was marked on a tracing paper overlay of the photograph of the relevant area. By using a combination of aerial photographs (taken by the Scottish Office from a height of 5000 feet) and an Ordnance Survey 1:25,000 map of the area I could then find the eight figure co-ordinates for each sighting. I could thus define the location of any bird on the intertidal zone to within 10m. I was unable to plot the location of birds on fields so precisely due to the lack of delineating features in these habitats. Instead I mentally divided each field into four quarters and found the co-ordinates for the mid-point of each quarter. This meant that for birds seen on fields the accuracy of each sighting is no better than to the nearest 100m. However, it was noticeable that birds tended to utilize the same regions within a particular field. This meant that any calculation of the area used by an individual would tend to be an underestimate. Any bias introduced by the inconsistency in methodology in a comparison of ranging behaviour would thus favour the null hypothesis (i.e. that there was no difference in ranging behaviour between birds using different habitats). In order to ensure independence of sightings I rejected from analysis any sighting taken within one hour of a previous location. This was probably an unnecessarily conservative criterion, since as a rule of thumb the minimum inter-sample time should be potentially great enough to allow the focal animal to move between any two points within the study area (Whitfield 1985a), in the case of curlew 10min would probably have been adequate. Because of the difficulties experienced in obtaining repeated sightings of individuals foraging and the relatively large sample size required in order to estimate feeding range,

I have combined sightings for each individual over both winters. Obviously this is not completely satisfactory as there may be annual variation in an individual's use of the study site. Like Townshend (1981a) however, I found that birds did tend to show high fidelity to feeding sites between years and my methods should serve to highlight inter-individual variability in ranging behaviour.

4.2.2.3. Reception and plotting locations of radio-marked birds.

For details of construction and attachment of transmitters to birds see section 3.3.2.3 and appendix 1. In order to locate radio-tagged birds I used an LA12 receiver (marketed by AVM Instrument Co. Ltd.) and a three-element Yagi antenna. Headphones were essential for clarity of reception in the field. I made regular 'sweeps' for radio-marked birds throughout the 1986-7 season. This involved stopping at standard points (usually with a clear field of view, away from trees and as high as possible) tuning the receiver to the desired frequency and slowly swinging the Yagi antenna through 360° , with the elements perpendicular to the ground. If no signal was picked up I tried another rotation with the antenna elements horizontal to the ground (this tends to be more successful at picking up flying birds). If there was still no signal received I made several more sweeps, adjusting the fine-tuning of the receiver for each. The operating frequency of transmitters is inclined to 'drift', firstly due to an initial small but sharp drop in the voltage of the lithium copper-oxide cell (Kenward *et al* 1982), and secondly due to cold weather (Macdonald & Amlaner 1980).

In order to obtain really accurate locations of radio-marked birds it is normal to triangulate from two or even three receivers (e.g. Forbes & Warner 1974). Such a procedure however is very labour intensive. I found that I could get an excellent fix on the direction of a signal, by swinging the antenna slowly back and forth in an arc through the signal, until I had ascertained the point of

peak reception. I could also, after some experience, estimate range on the basis of signal strength. On the basis of these two factors, and given the habitat distribution at the study site I was confident that I could fix the position of a radio-marked bird to within 100m. This was verified by over 40 visual sightings of birds whose position I had previously fixed by radio-telemetry. The technique is prone to several sources of error. Macdonald and Amlaner (1980) divide the sources of error that can affect radio-location into three types:

1) System errors: Errors inherent in the equipment, for instance in the directionality of the receiving antenna should the elements become twisted.

2) Movement error: Errors arising from the movement of the focal animal between taking two fixes for triangulation. Since I was working with only one fix per location these sources were irrelevant.

3) Topographical errors: These error-types arise from topographical features disturbing transmission and include; reflection (from cliffs, hills etc.) transmission along metal fences and attenuation of the signal by heavy vegetation (especially trees).

With care and experience these errors can be minimized.

4.2.3. Results.

4.2.3.1. Estimates of individual feeding ranges as determined from sightings of colour-marked birds.

The accuracy of any estimation of ranging behaviour is dependent upon the number of sightings of the individual concerned (Wilkinson & Bradbury 1985). In order to assess the number of coordinates required for an accurate estimate it is usual to plot estimated range against the number of sightings and determine the point at which the range estimate stabilizes (Whitfield 1985a). For most subjects at least 20 observations are required. I therefore plotted cumulative feeding range estimates for the 17 individual curlew for

which I had more than 20 observations (Fig.4.1). From these plots it became apparent that the number of observations required for a stable estimate of feeding range varied with the habitat utilization of the individual. Estimates for field-feeders generally stabilized at about 25 sightings, whilst those for generalists did not stabilize below 30 sightings. Although estimates for some birds did not appear to reach a stable value, most had ^{passed} ~~pas~~ the characteristic initial large peak in range estimation. Estimates for intertidal zone specialists became stable very rapidly, at about 12 sightings, therefore I calculated feeding ranges for a further four intertidal birds for which I had 13 or more observations. Feeding range estimates are summarised in Table 4.1.

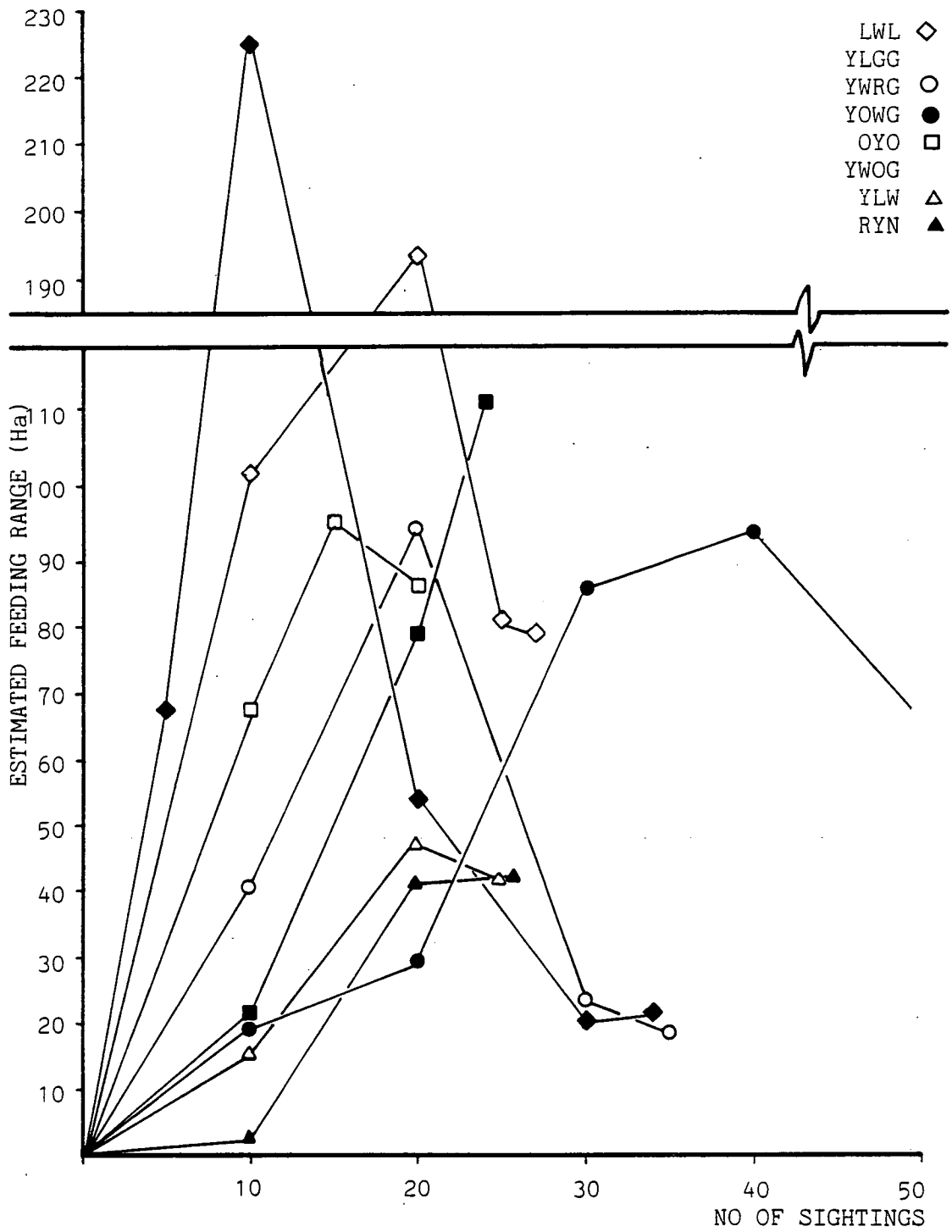
Both field feeders and generalists had larger feeding ranges than birds which specialised on the intertidal zone (Mann-Whitney U-test, $W=83.5$, $p=0.003$ and $W=21.0$, $p=0.003$ respectively). Generalists appeared to feed over a greater area than field-feeders, although this is not significant (Mann-Whitney U-test $W=48.0$, $p=0.072$). The mean feeding ranges of field-feeders, intertidal specialists and generalists are shown in Fig. 4.2. An example of the feeding coordinates of one field-feeder, one intertidal specialist and one generalist are shown in Fig. 4.3. Territory sizes were calculated for five birds, using sightings taken when the individual was observed actively defending an area. Results are shown in Table 4.2.

4.2.3.2. Ranging behaviour of radio-marked birds.

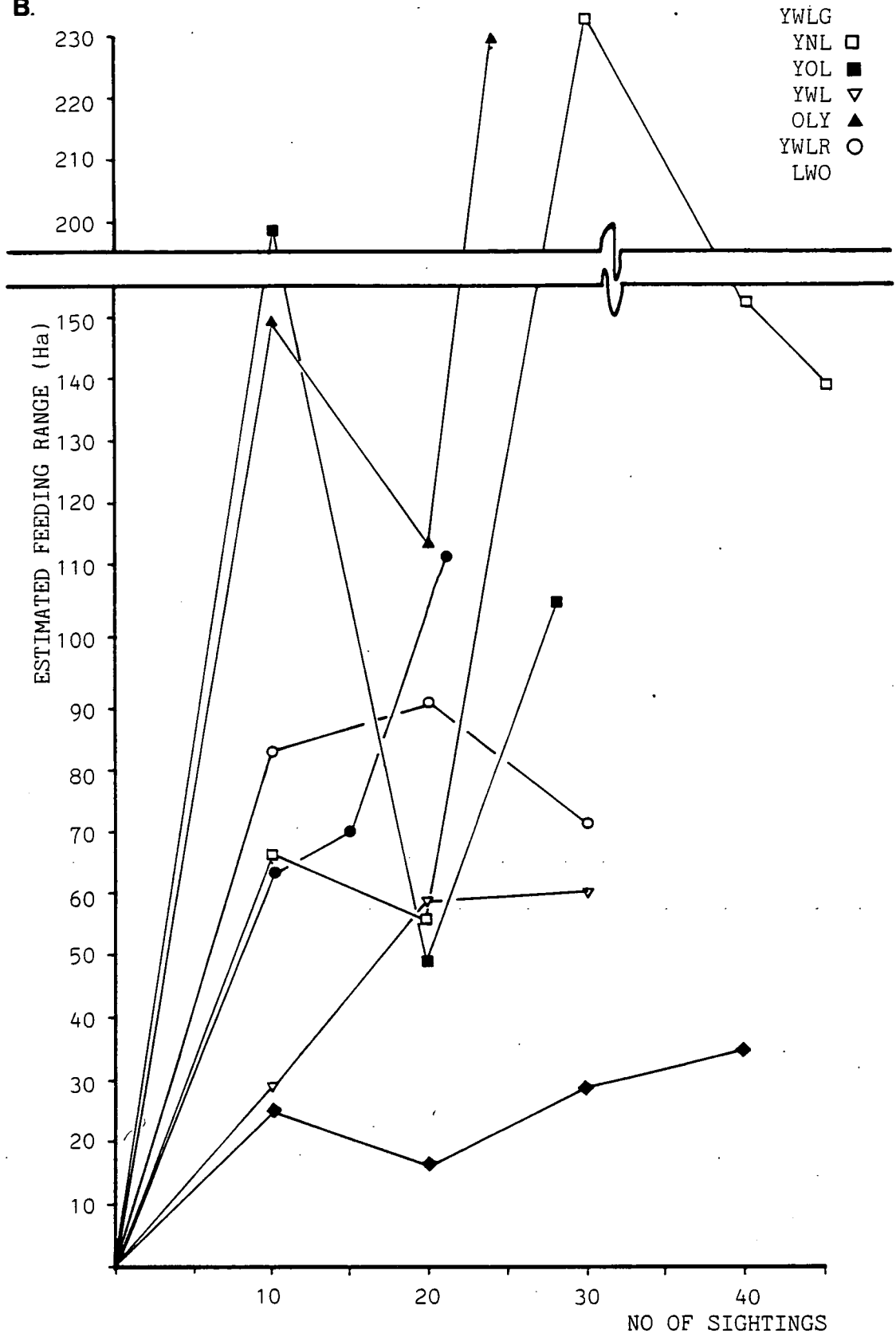
I followed the procedure outlined in section 4.2.3.1. to determine the point at which estimations of ranging behaviour of the five radio-marked birds stabilized (Fig. 4.4). All estimations appeared reasonably stable above 30 observations, apart from the remarkable change in the estimation for LWN between 70 and 85 sightings. This was due to a spate of fixes in the Chapel Brae area and Coastguard region in April, when I suspect the bird was joining pre-migratory communal roosts. As was the case when determining habitat

Fig. 4.1. Feeding range estimates for individual birds against cumulative number of sightings for each individual. A) Field-feeders, B) Generalists, C) Intertidal zone specialists.

A.



B.



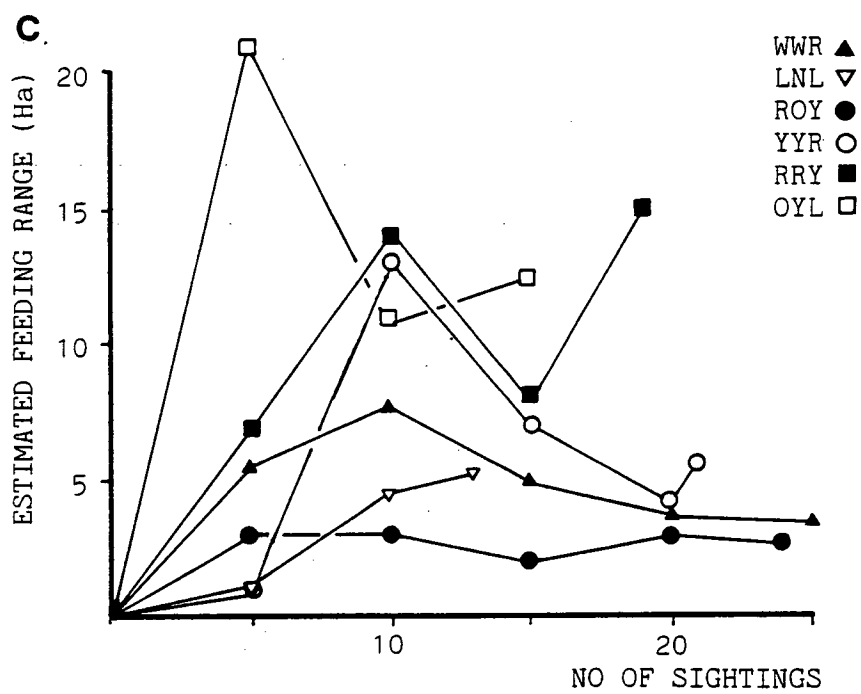


Table 4.1. Estimated feeding ranges of individual curlew.

FIELD-FEEDERS			INTERTIDAL ZONE			GENERALISTS		
	No	RANGE		No	RANGE		No	RANGE
BIRD	OBS	(Ha)	BIRD	OBS	(Ha)	BIRD	OBS	(Ha)
YOWG	54	72.1	WWR	21	3.4	YWLG	38	35.0
YLW	23	42.3	LNL	13	5.3	YOL	28	104.7
RYN	26	42.4	ROY	18	2.8	YWL	31	82.5
YWOG	24	110.7	OYL	15	13.0	YNL	45	139.8
YLGG	34	22.1	YYR	21	5.7	OLY	24	230.4
YWRG	36	15.1	RRY	18	15.1	LWO	21	111.7
LWL	27	78.9				YWLR	30	72.4
OYO	21	86.7						

Fig. 4.2. Mean feeding range estimates for macrohabitat specialists and generalists. Bars = $\pm$ 1S.E. N = No. individuals of each category of specialisation for which feeding range estimates were calculated.

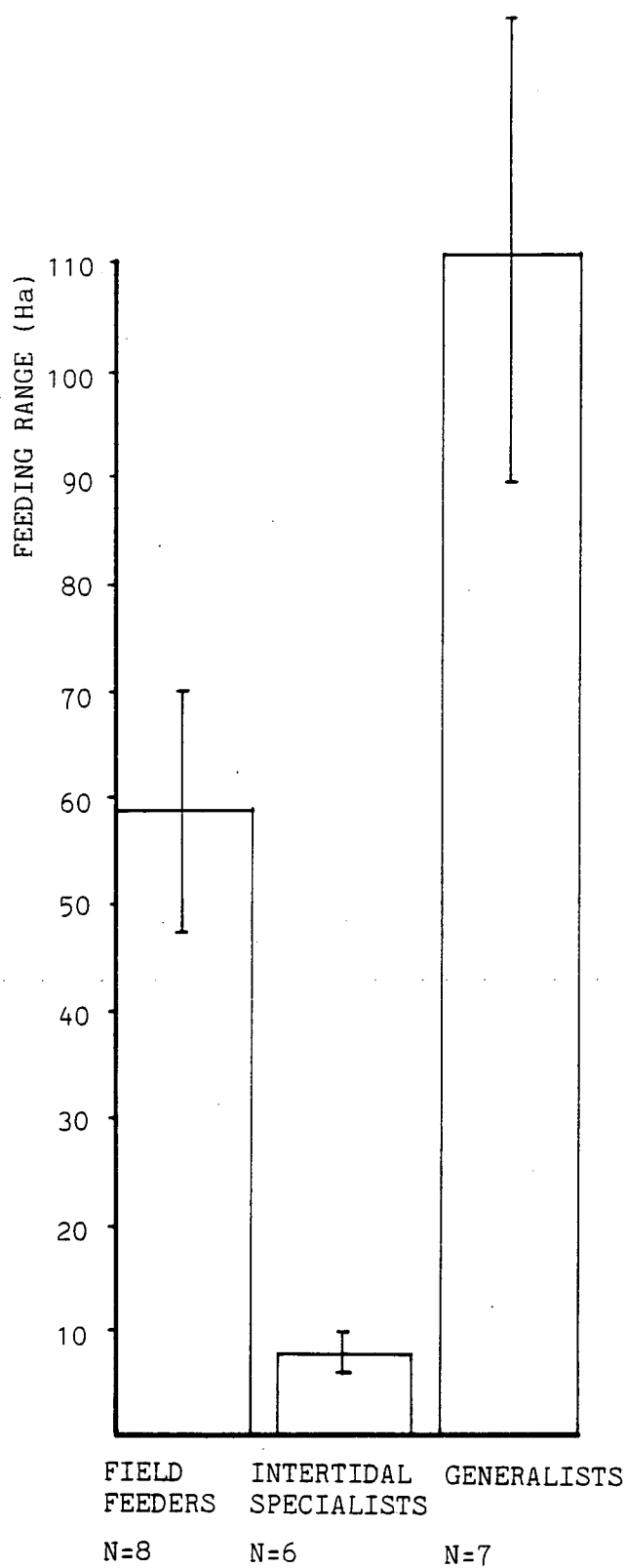
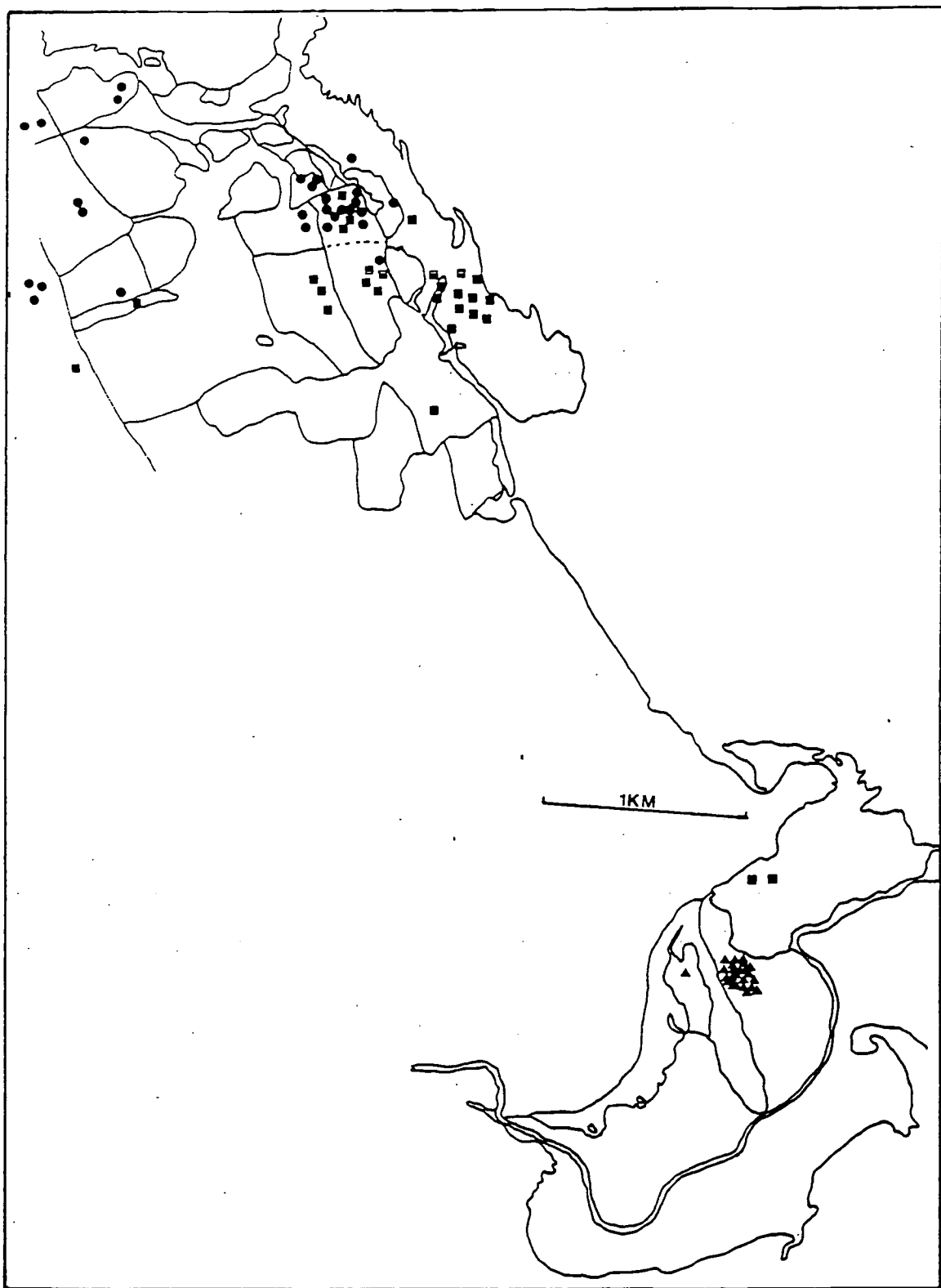


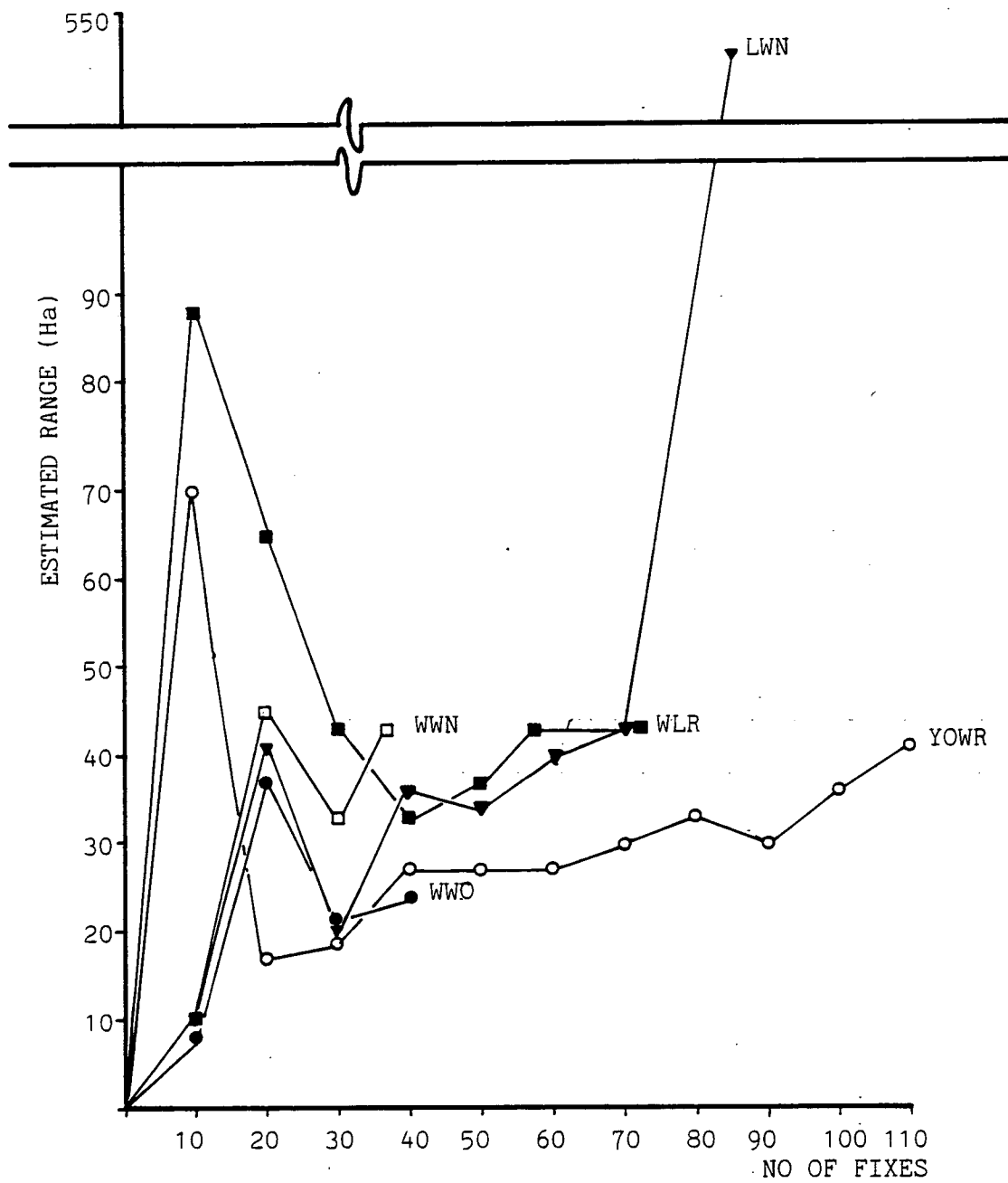
Fig. 4.3. Examples of feeding range coordinates for a field-feeder (YWRG - circles) an intertidal zone specialist (ROY - triangles) and a generalist (YOL - squares).



BIRD	ESTIMATED	
	No	TERRITORY
	OBS	SIZE (Ha)
*WWR	18	1.4
*ROY	17	1.9
LNL	13	5.3
OYL	12	3.6
RRY	14	2.9

Table 4.2. Estimated territory sizes of individual curlew. * indicates birds which defended long-term territories.

Fig. 4.4. Range estimates for radio-tagged birds against the cumulative number of fixes for each individual.



selection of radio-marked birds, estimations of the ranging behaviour of tagged curlew were not directly comparable with those of untagged birds because I could not be sure of the activity of a bird for a given fix, i.e. I could not be sure that I was measuring feeding range. In Table 4.3 I present two estimates of the ranging behaviour of each of the five radio-marked birds. The first of these is based on the distribution of all fixes, regardless of behaviour and the second is based on the distribution of coordinates omitting those fixes which placed the bird at one of the traditional rocky roost sites (on the basis that it was extremely unlikely that birds would be feeding at these locations).

Range estimations that exclude fixes from traditional roost sites for the four radio-tagged birds that foraged predominantly in the intertidal zone (YOWR, WWO, WLR and WWN) are significantly greater than those for untagged intertidal specialists (Mann-Whitney U-test $W=34.0$, $p=0.014$). This could have been due to two factors:

A) The distribution of coordinates still included some where the bird was roosting. This was especially likely to have been a factor for fixes which placed birds on the saltmarsh.

B) Birds were actually ranging further than I could determine by visual observation alone. Often colour-marked birds would abandon feeding sites at low water (*c.f.* Townshend 1981a) and I would not be able to relocate them.

There is evidence for the effect of both these possibilities making interpretation of the results very difficult. The range estimation for the radio-marked generalist LWN which excludes fixes at known roost sites is within the range of estimations for untagged generalists.

4.2.4. Discussion.

From these results it is clear that curlew which specialise in field-feeding or use fields as part of a generalist strategy, range over a far greater area in search of food than do intertidal specialists. Generalists, as might be expected

BIRD	INCLUDING ROOST-SITES		EXCLUDING ROOST-SITES	
	No	ESTIMATED	No	ESTIMATED
	FIXES	RANGE (Ha)	FIXES	RANGE (Ha)
WVO	49	24.0	25	72.0
WWN	37	42.8	16	97.3
WLR	71	42.7	28	58.1
LWN	85	545.0	53	36.6
YOWR	110	39.4	47	54.8

Table 4.3. Estimated ranges of radio-tagged curlew.

given the range of microhabitats which they exploit, tended to have the largest feeding ranges of all, although they were not significantly different from those of field-feeders. Field-feeders, then, can be said to exhibit less feeding-site fidelity than intertidal zone specialists. There are two possible reasons for this:

1) Evans (1981) relates itinerancy to lack of temporal stability in food supplies. If the food supply on the intertidal zone is more stable and predictable than that on field habitats, then intertidal zone specialists should show greater feeding-site fidelity than field-feeders and accordingly have smaller feeding ranges.

2) Myers *et al* (cited in Myers 1984) relate increasing itinerancy^a with increasing risk of predation. In fact sanderling doubled their home range sizes when a merlin, *Falco columbarius*, was present at the study site. Four possibilities are put forward to explain this observation: a) increased "spooking" of flocks; b) an adaptive response by sanderling to lower their predation risk by decreasing the probability that they will be at any particular location at a given moment; c) since sanderling abandon territories on the appearance of a raptor home ranges may be expected to increase, moreover movements of non-territorial birds will be freed from the restrictions imposed by territoriality; d) increased flock size may increase the effects of local prey depletion.

Unfortunately I have insufficient data to test between these two hypotheses; it would be worthwhile pursuing this subject further. I can however offer anecdotal evidence for the operation of both theories.

Whitfield (1985a) demonstrated that the supply of *Littorina* sp. at Scoughall is fairly constant throughout the winter. Long-term defence of feeding territories by wintering shorebirds usually occurs when the food supply is intermediate, stable and predictable (Myers *et al* 1979). The existence of territoriality at the study-site may indicate that these requirements are fulfilled. Estimated territory sizes were slightly larger than those calculated by Ens

(1979) for curlew feeding on mudflats (0.5–0.8ha). Waite (1983) amply demonstrates the lack of predictability of food supplies on arable habitats.

Mortality in curlew due to raptor predation at the study-site was virtually non-existent (Whitfield 1985b). I did however observe six unsuccessful raptor attacks (four by sparrowhawks, *Accipiter nisus*, one by a merlin) on flocks on fields, and only one by a sparrowhawk on birds on the intertidal zone. I have also witnessed an unsuccessful attack by a Montagus harrier, *Circus pygargus*, on curlew in a field on the Wash. Peregrine falcons, *Falco peregrinus*, are known to take adult curlew (Ratcliffe 1980). Little is known about the effects of mammalian predation, although foxes, *Vulpes vulpes*, may be important (Townshend 1984). Until 1982 the major source of mortality amongst curlew was shooting (see chapter 2). Most birds would probably have been killed as they left the intertidal zone to fly inland. There is then a possibility that risk of predation may be greater to field-feeders than to birds which feed on the intertidal zone. If predation is causal in increasing the feeding range of field-feeders it is not clear through which of the possibilities proposed by Myers *et al* the increase is mediated.

4.3. Spacing behaviour.

4.3.1. Introduction.

In the introduction to this chapter I stressed the considerable degree of intraspecific variation in spacing behaviour shown by waders. There is evidence that curlew conform to this pattern: Ens (1979), Phillips (1980), Townshend (1981a) and Baber (1988) describe curlew defending exclusive territories or feeding solitarily on the intertidal zone, whilst Elphick (1979) and Townshend (1981b) document curlew feeding in flocks on fields. Goss-Custard (1970b) documents curlew feeding in small ^{discrete}~~disparate~~ flocks on the intertidal zone. In this section I attempt to measure the degree of variation in spacing behaviour of curlew and relate this to macrohabitat use. I also discuss the

possible importance of predation and interference in shaping spacing behaviour.

4.3.2. Methods.

The data used in this analysis were collected during the feeding observations described in section 3.4. Before the start of each focal animal sample I recorded microhabitat, flock size and estimated nearest-neighbour distance (NND) in bird lengths. During each observation I recorded swallow rate (swallows/min) and the proportion of time spent in vigilance. Precise methods and definitions can be found in section 3.4.2. In chapter 3 I discovered that birds behaved in a different manner when feeding on saltmarsh than when feeding on either the intertidal zone or fields, therefore I have excluded saltmarsh habitats from this analysis.

4.3.3. Results.

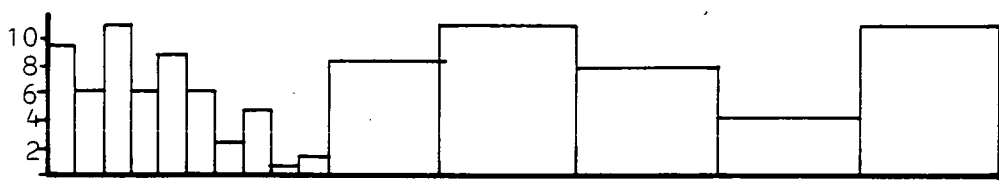
4.3.3.1. Spacing behaviour.

The percentage ^efrequencies of occurrence of different flock sizes on the two major macrohabitats are shown in Fig. 4.5. Perhaps the most striking difference between the habitats is the predominance of individuals feeding solitarily on the intertidal zone. The proportion of observations taken on solitary feeders on the intertidal zone (245 out of 341) is significantly higher than on fields (40 out of 420) ($\chi^2 = 305.5$, $p < 0.001$). Flock size on fields (excluding solitary birds) was significantly greater than on the intertidal zone (Mann Whitney U-test, $W=100438.0$, $p < 0.0001$).

The distribution of NNDs on the two macrohabitats is shown in Fig. 4.6. Estimated NNDs are significantly smaller on fields than on the intertidal zone (Mann Whitney U-test, $W=83920.0$, $p < 0.0001$). If flock sizes greater than one are considered, NND is negatively correlated with flock size on fields ((Fig. 4.7). Note that flock sizes of one have been excluded from this analysis since by definition solitary birds have a NND of >30 bird lengths; also, because of their skewed nature the data have been log-transformed. Application of the same

Fig. 4.5. The relative frequency of occurrence of different flock sizes on a) fields, b) the intertidal zone.

A.



B.

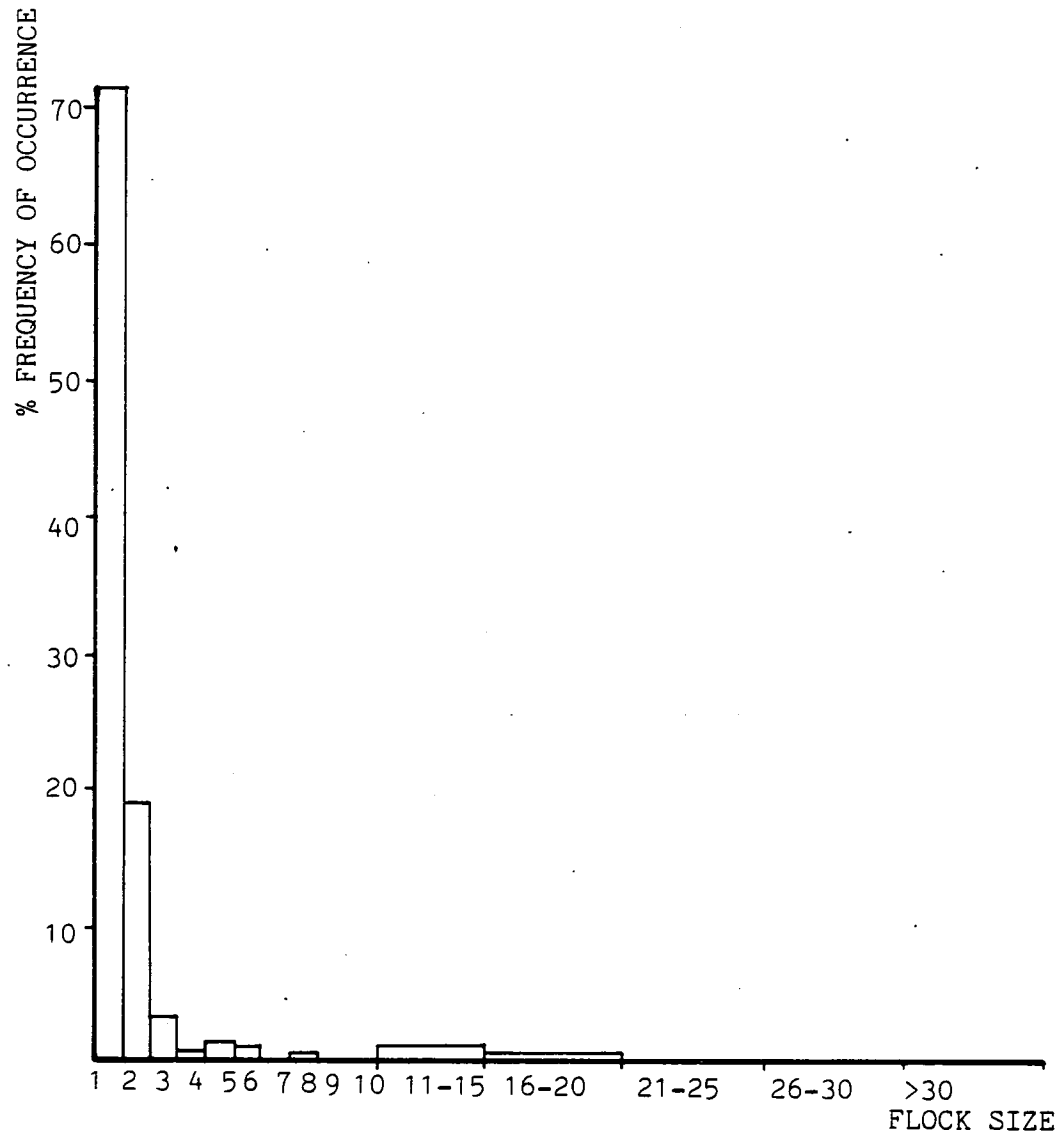
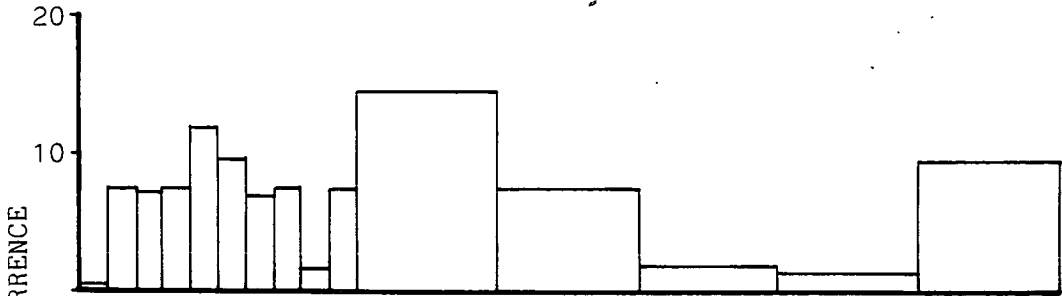


Fig. 4.6. Distribution of NNDs on a) fields, b) the intertidal zone.

A.



B.

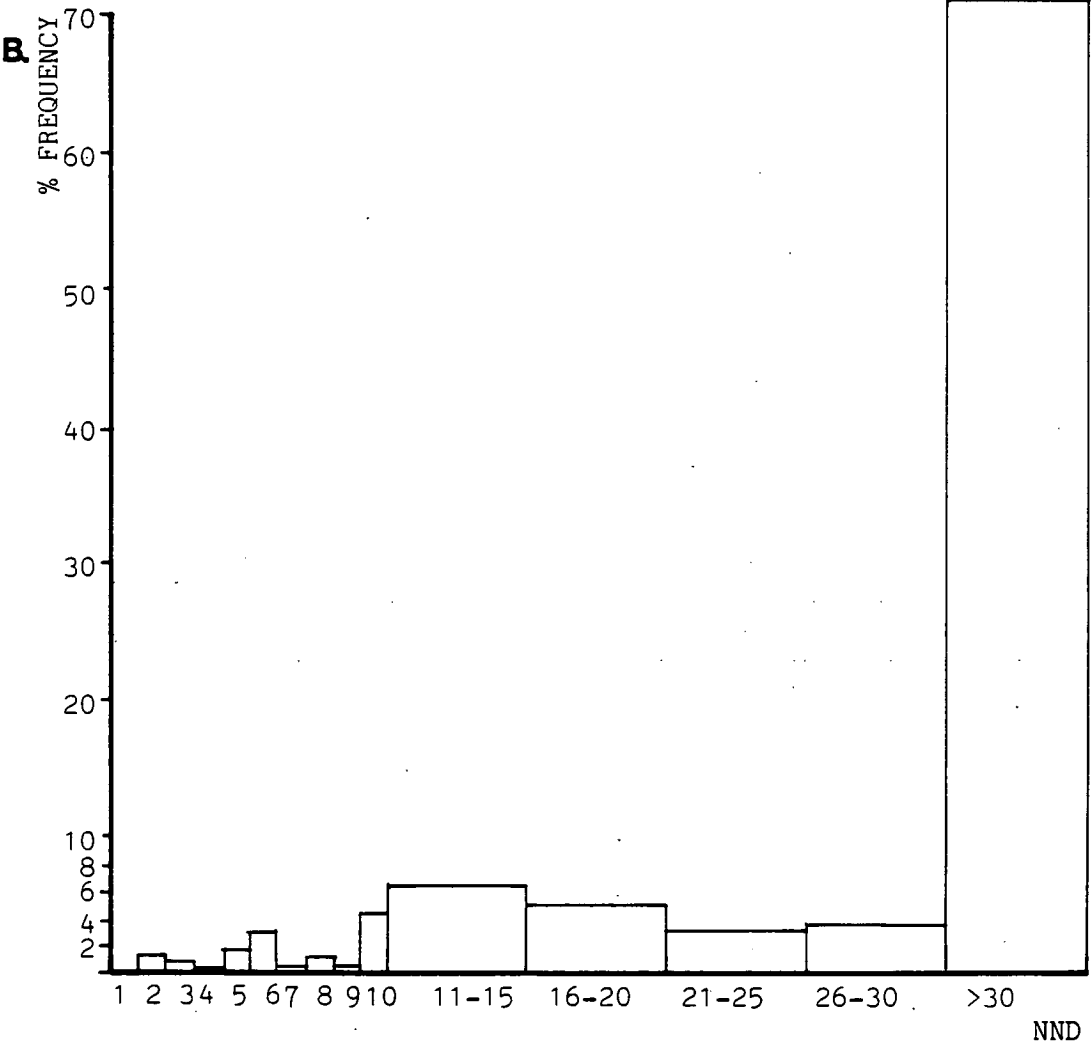


Fig. 4.7. Log(10) flock size against log(10) NND for birds feeding on fields in flock sizes >1 , ($N= 387$, $r= -0.1556$, $p< 0.002$).

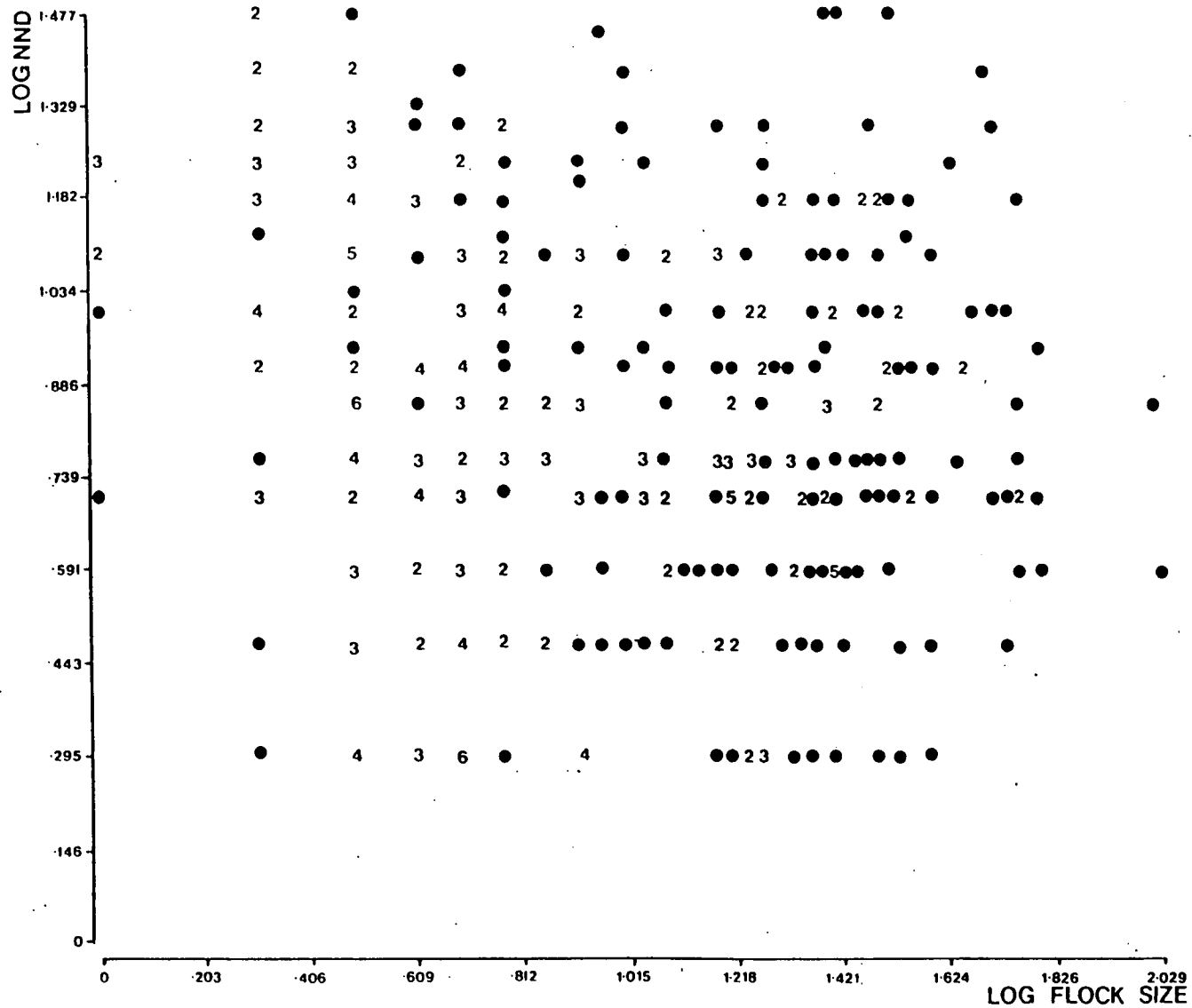
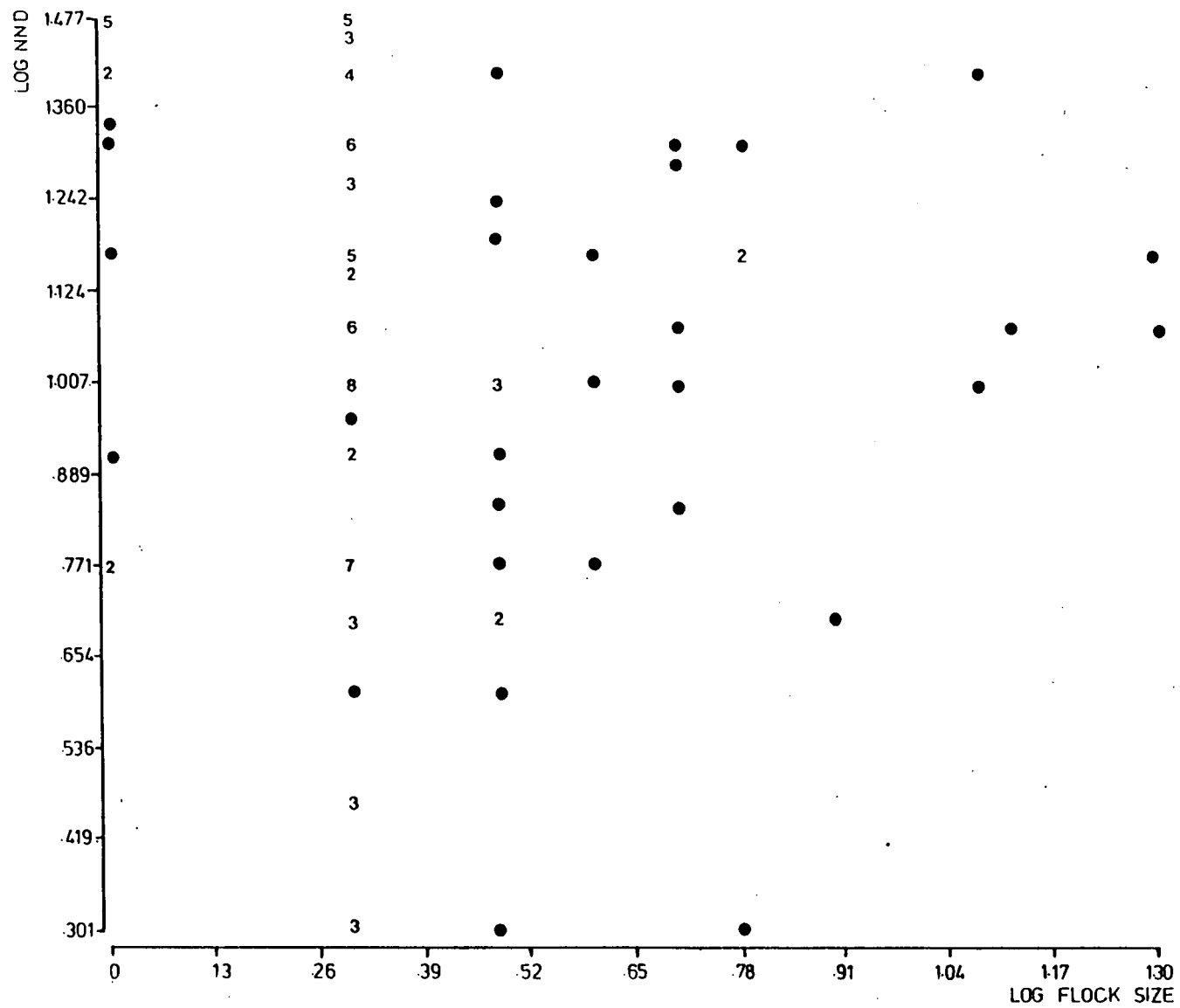


Fig. 4.8. Log(10) flock size against log(10) NND for birds feeding on the intertidal zone in flock sizes >1 , ($N= 107$, $r= -0.130$, $p> 0.05$, N.S.).



analysis to birds feeding on the intertidal zone revealed no correlation between NND and flock size (Fig. 4.8). Flocking and spacing behaviour observed on each microhabitat are summarised in Table 4.4.

4.3.3.2. Effect of flock size on vigilance and swallow rate.

The proportion of time spent in vigilance as a function of flock size on field habitats is shown in Fig. 4.9, and on the intertidal zone in Fig. 4.10. In both cases vigilance decreases with increasing flock size. The relationship between flock size and swallow rate on fields is shown in Fig. 4.11 and on the intertidal zone in Fig. 4.12. In both cases the data has been log-transformed since it was highly skewed to the left. On fields there was a positive correlation between flock size and swallow rate, but on the intertidal zone the correlation was negative.

4.3.4. Discussion.

As with foraging and ranging behaviour there are major differences in spacing behaviour between birds foraging on fields and birds foraging on the intertidal zone. Field-feeders tend to form large, compact flocks, whilst birds on the intertidal zone feed either solitarily or in small loose flocks (*cf* Goss-Custard 1970b, Elphick 1979, Townshend 1981a). The spacing behaviour on the intertidal zone can be partly explained by the high incidence of territoriality on this macrohabitat (Ens 1979, Townshend 1981a, pers.obs.). Territorial birds by definition maintain exclusive use of an area, moreover the presence of territories will place restrictions on the movements and spacing behaviour of non-territorial individuals (Myers 1984, Goss-Custard 1985). It is clear from Fig 4.12, however, that curlew feeding on the intertidal zone suffer from interference *i.e.* an immediate reduction in their intake rate due to the presence of conspecifics (Goss-Custard 1980). This may well be a major factor in shaping the spacing behaviour of curlew on the intertidal zone, particularly since long-term depletion of food resources seems unlikely to be significant in

% OBS FOR FLOCK SIZES GREATER THAN ONE								
SINGLE			F L O C K S I Z E			N N D		
HABITAT	N	BIRD	N	RANGE	MEAN $\pm$ S.D.	RANGE	MEAN $\pm$ S.D.	
GWS	161	11.8	142	2-104	13.1 $\pm$ 13.1	2-30	8.7 $\pm$ 6.2	
GFS	155	8.4	142	2- 62	16.7 $\pm$ 16.4	1-30	8.8 $\pm$ 5.9	
STUB	68	7.4	63	2- 6	18.3 $\pm$ 16.6	2-30	8.3 $\pm$ 6.6	
PLGH	11	27.3	8	4- 24	10.3 $\pm$ 7.5	2-13	7.0 $\pm$ 3.3	
FUCUS	62	52.3	29	2- 20	3.8 $\pm$ 3.9	2-30	16.4 $\pm$ 17.4	
MBED	50	86.0	7	2- 11	3.6 $\pm$ 3.8	3-25	9.5 $\pm$ 7.9	
SAND	46	84.8	7	2- 3	2.2 $\pm$ 0.4	2-30	28.7 $\pm$ 29.2	
RPOOL	103	72.8	28	2- 6	2.7 $\pm$ 1.2	2-30	12.3 $\pm$ 8.5	
ROCK	48	54.2	22	2- 20	3.9 $\pm$ 4.4	2-30	13.3 $\pm$ 6.9	
MUD	18	94.4	1	2	2.0	4	4.0	
SM	53	5.7	50	2- 40	12.5 $\pm$ 11.1	1-30	12.0 $\pm$ 14.3	
FIELDS	420	9.7	371	2-104	15.0 $\pm$ 15.0	1-30	8.7 $\pm$ 6.0	
ALL ITZ	341	71.8	96	2- 20	3.3 $\pm$ 3.2	2-30	14.9 $\pm$ 14.6	

N.B. ALL ITZ = ALL INTERTIDAL ZONE MICROHABITATS EXCEPT SM

Table 4.4. Summary of flocking and spacing behaviour by microhabitat.

Fig. 4.9. Proportion of time spent in vigilance by individuals as a function of flock size for birds feeding on fields (N= 420).

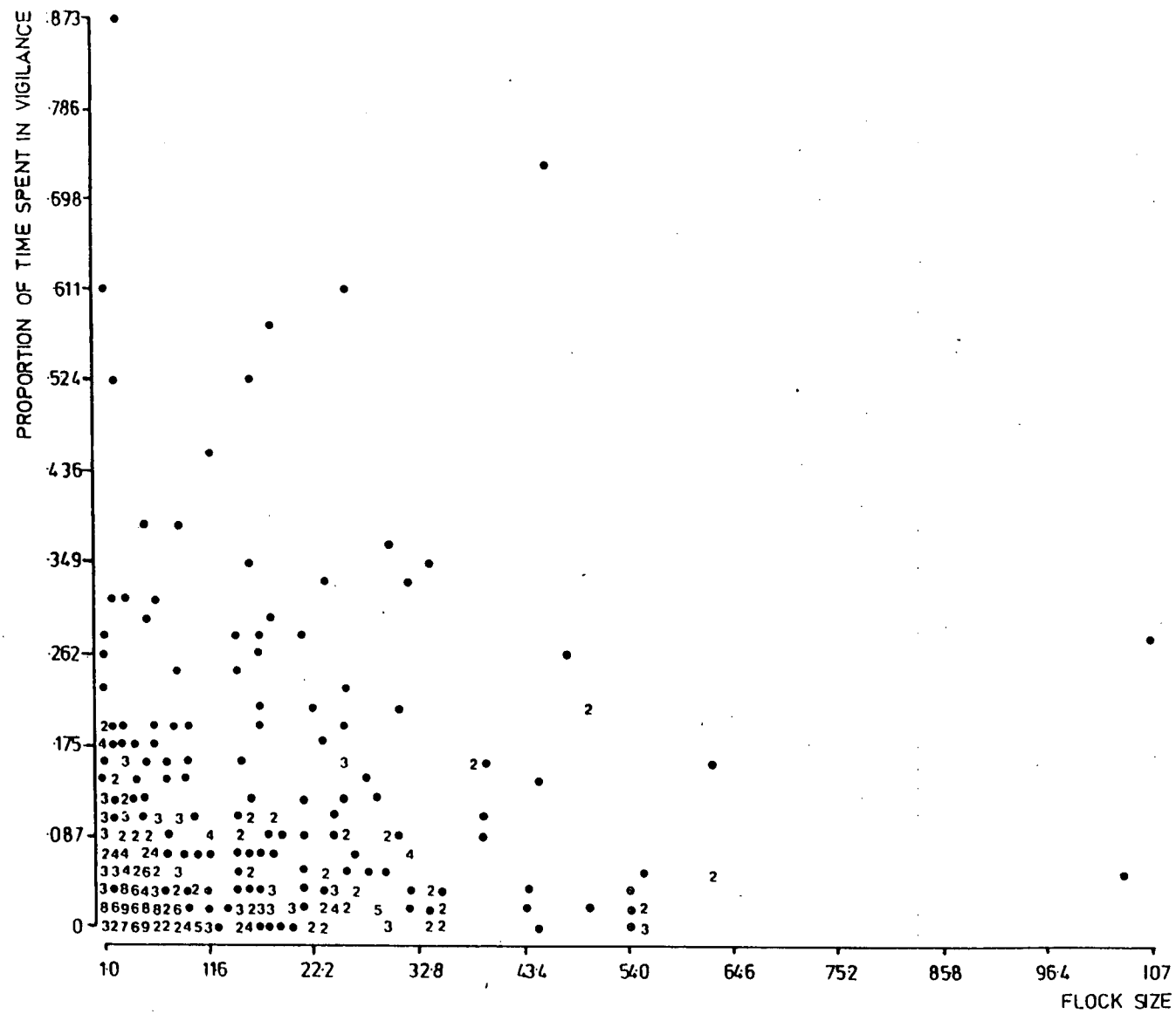


Fig. 4.10. Proportion of time spent in vigilance by individuals as a function of flock size for birds feeding on the intertidal zone (N= 341).

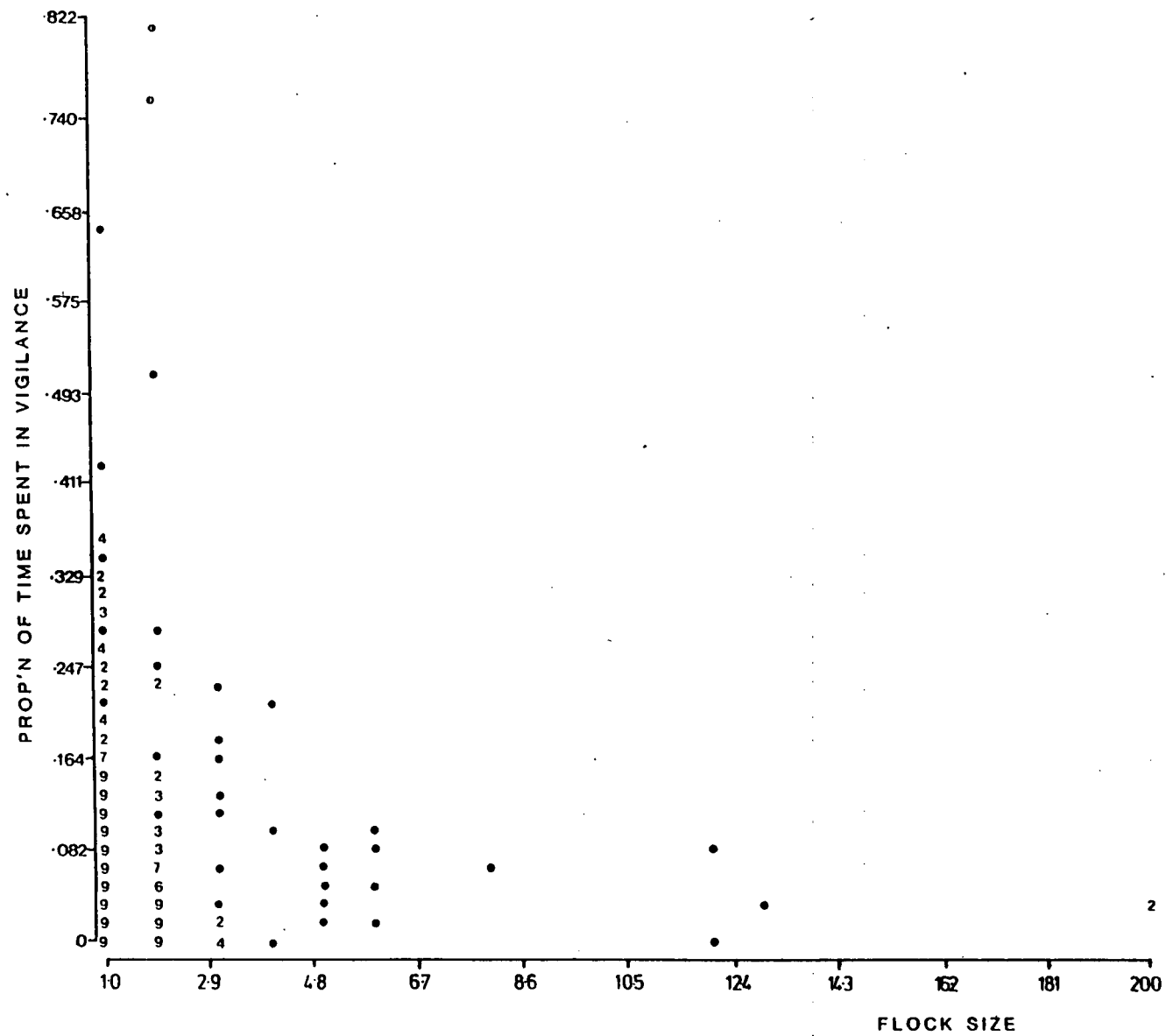


Fig. 4.11. Log(10) flock size against log(10) swallow rate on fields (N= 420, $r = 0.1713$, $p < 0.001$, $y = 0.226 + 0.091x$).

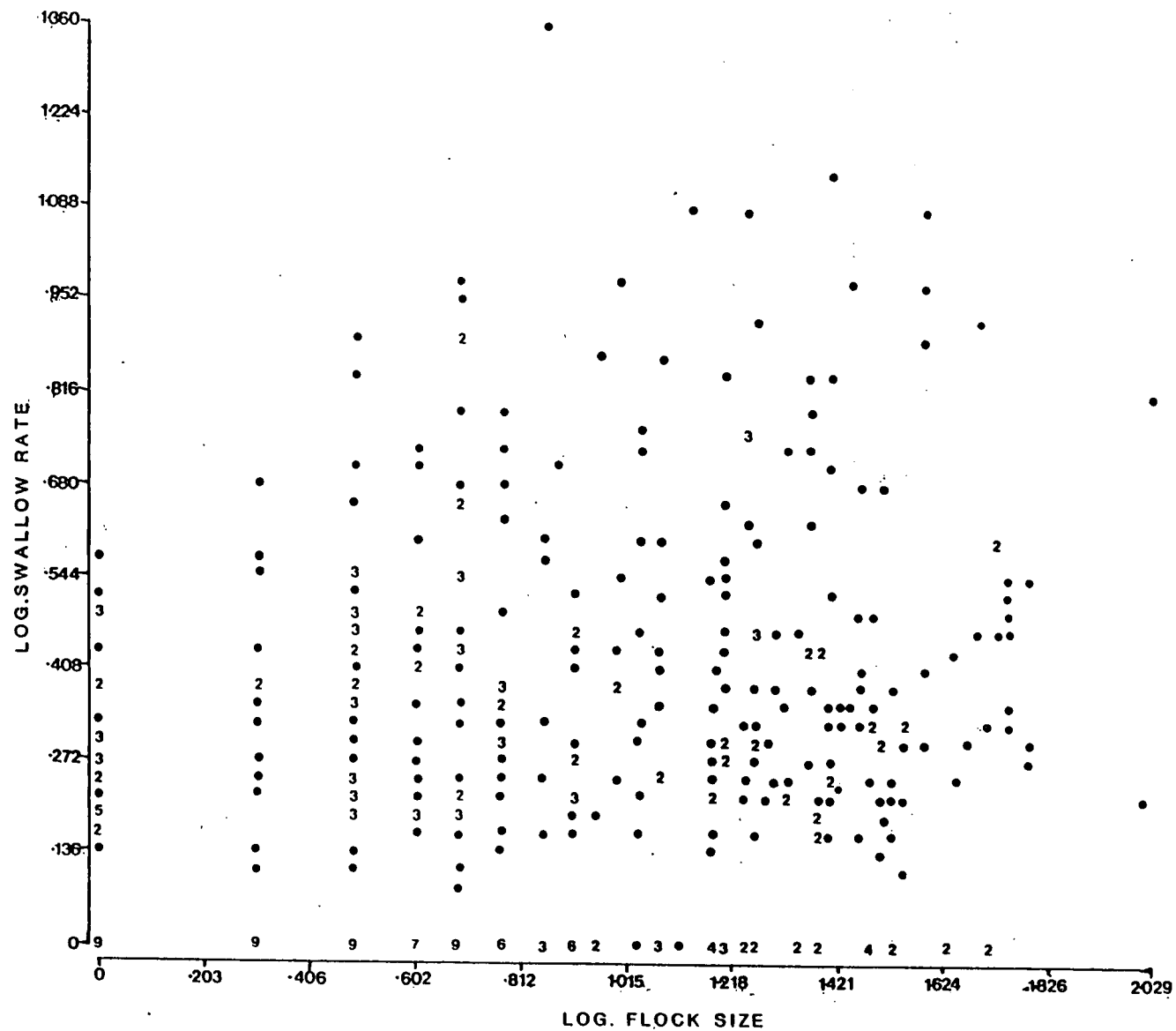
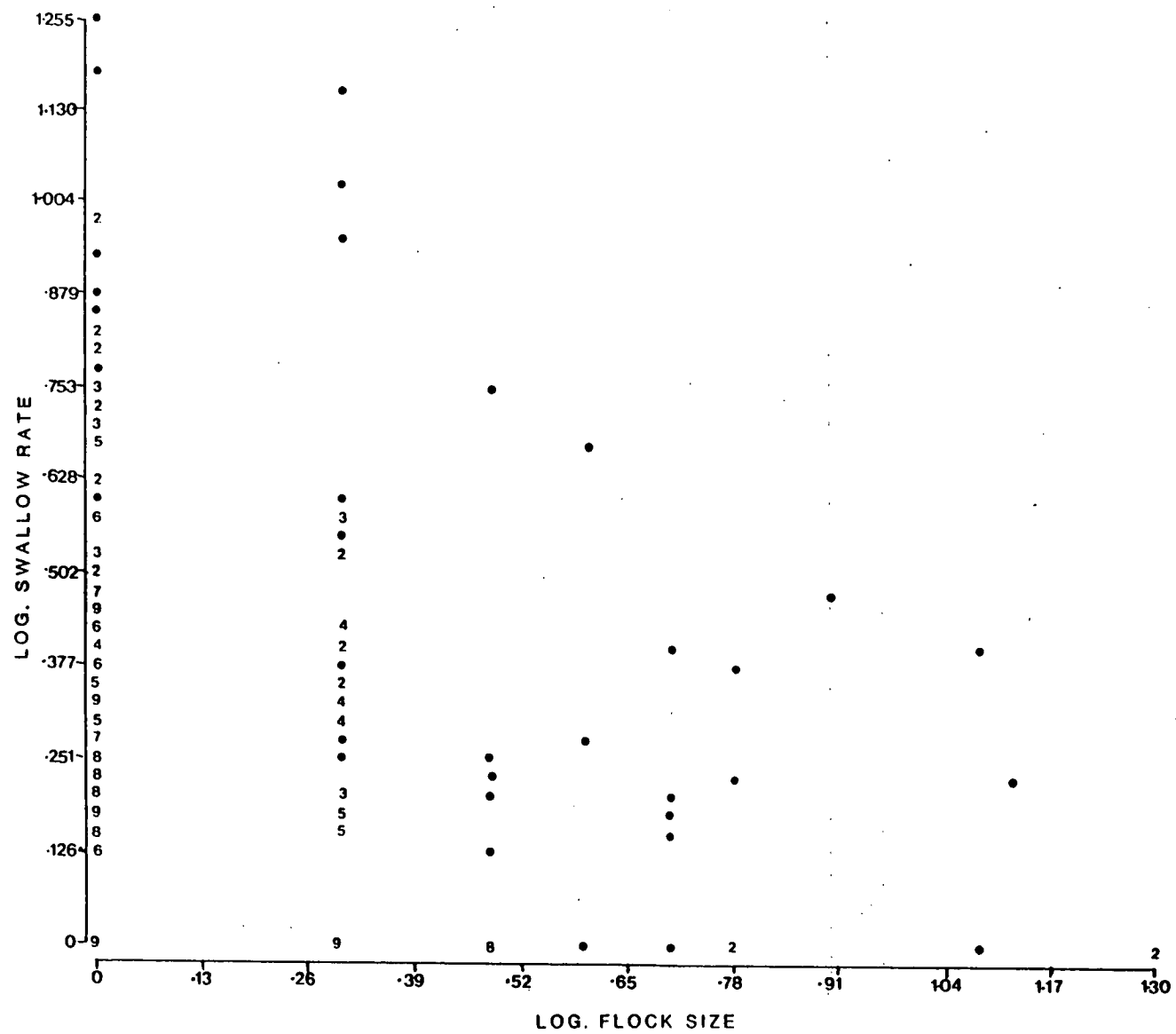


Fig. 4.12. Log(10) flock size against log(10) swallow rate on the intertidal zone (N= 341, $r = -0.0941$, $p < 0.05$, $y = 0.263 - 0.107x$).



this species (Ens 1984). In contrast, on fields I observed only one incidence of territoriality in three winters of observation and this occurred in exceptional weather conditions (Appendix 2). Curlew also appear to be unaffected by interference when foraging on fields, rather swallow rate increases with flock size (Fig. 4.11) in a manner similar to that described by Abramson (1979). This may be an effect of the flock size/vigilance function (Fig 4.9) which is also very similar to that described by Abramson. Certainly the proportion of time spent by individuals in vigilance decreases as flock size increases, indicating that predation risk may be an important factor in determining spacing behaviour on fields (as discussed in section 4.2.4.). However this does not necessarily imply that the increase in the proportion of time spent feeding was the cause of the increase in swallow rate; larger flocks may be simply more likely to form where prey availability is high (Waite 1981).

4.4. Summary.

In this chapter I have documented fundamental differences in the ranging and spacing behaviour between curlew feeding on fields and on the intertidal zone. On fields foraging birds form large, dense flocks and range over a wide area. In contrast, on the intertidal zone curlew normally forage solitarily, but occasionally form small loose flocks. Here they restrict their foraging to extremely small areas which are often exclusively defended. When feeding on the intertidal zone curlew are subject to interference, a fact which may be of major importance in determining the ranging/spacing behaviour of individuals on this macrohabitat. Interference is not a problem to birds foraging on fields and it seems possible that predation risk is the major determinant of ranging/spacing behaviour on this macrohabitat.

Since, in chapter 3, I have shown that bill morphology influences macrohabitat choice, phenotype will also influence to some extent the ranging/spacing behaviour strategy adopted by an individual.

CHAPTER 5.
ROOSTING BEHAVIOUR AND VIGILANCE.

*"So sleep with one eye open when you slumber
Every little sound just might be thunder,
Thunder from the barrel of his gun."*

BOB DYLAN 1972.

5.1. Introduction.

Perhaps one of the most spectacular and exciting aspects of the behavioural ecology of some birds is the formation of large communal roosts of up to several million individuals. There has been much debate amongst researchers over the past fifteen years as to the probable function of such assemblages, but surprisingly little data have been collected that support any one of the three main hypotheses as to why birds should gather in this manner.

The first of these theories is known as the 'Information Centre Hypothesis' (ICH) and originated when Ward (1965) observed some black-faced dioch, *Quelea quelea*, following 'more purposeful' birds out from the roost. Ward & Zahavi (1973) developed the idea of the ICH as follows: they argue that individuals of species which habitually feed in flocks on ephemeral food supplies will have differential foraging success on a given day. Individuals which have fared badly would benefit from 'information transfer' as to the whereabouts of good food supplies from birds which have fared well. Circumstantial evidence for the operation of the ICH in the wild has been collected by Krebs (1974) on colonial nesting great blue herons, *Ardea herodias*, and Loman & Tamm (1980) on ravens, *Corvus corax*, (but not crows, *Corvus cornix*,) gathering at carrion. De Groot (1981) demonstrated that captive naive *Quelea* can learn the whereabouts of food and water resources from experienced birds. Bayer (1982) attacked the ICH, pointing out that many birds need to locate new feeding sites only infrequently, but Ward & Zahavi cover this point by suggesting that even if information transfer is rare it may still be an 'insurance policy' against severe conditions. Bayer also argued that synchronous departure from a roost does not necessitate 'following'; moreover, even if birds do follow each other out from a roost, the following need not continue all the way to the feeding site. There is also a theoretical problem

with the ICH (Weatherhead 1983): it is difficult to envisage how information transfer could have evolved unless individuals are both givers and receivers of information at some time (barring group- or kin selection arguments) yet evidence is mounting that some birds are habitually better at foraging than others.

The second theory to explain why birds gather together in roosting flocks is that the risk of predation to an individual is lowered as a result of flock membership. There is much evidence to suggest that this is a contributory reason why birds form feeding flocks (review in Barnard & Thompson 1985) but roosting flocks have been less well studied. Gadgil (1972) argues that since many communal roosts comprise two or more species that do not form mixed feeding flocks, predation must be important. Broom *et al* (1976) suggest that the formation of large prerost gatherings of pied wagtails, *Motacilla alba yarrelli*, may afford protection from predation whilst the birds perform maintenance activities such as preening. Lazarus (1979) demonstrates that *Quelea* in flocks can detect an approaching goshawk, *Accipiter gentilis*, faster than single birds and moreover, as flock size increases the escape response elicited by an approaching predator decreases in intensity. I believe that this is an important point and it will be discussed further later. Zahavi (1971) describes how white wagtails, *M.a.alba*, are harder to catch when they are roosting communally than when they roost alone, but suggests that since assemblages of birds tend to attract more predators, the anti-predator function of roosts is a secondary adaptation necessitated by this consequence.

Finally, it is possible that birds roost communally because they benefit from a superior microclimate within the roost than outside and thus expend less energy in thermoregulation during periods when they are unable to feed. Gyllin *et al* (1977) and Yomtov *et al* (1979) discovered that the temperature within jackdaw, *Corvus monedula*, and starling, *Sturnus vulgaris*, roosts

respectively was higher than that of the surroundings. In neither study was the potential energy saving granted by the higher temperatures considered sufficient to offset that expended in often long flights to the roost; however in neither study were the effects of wind-chill considered. Peach *et al* (1987) document regular 'huddling' (roosting in body contact with one or more neighbours) in at least 45% of starlings at a communal roost at temperatures below 0°C. Brenner (1985) shows that such behaviour can halve the metabolic requirements of the individual, thus prolonging survival time in adverse conditions. Chaplin (1982) demonstrates that communal roosting in common bush tits, *Psaltriparus minimus*, can dramatically reduce nocturnal maintenance costs and Shaw (1979) found that dippers, *Cinclus cinclus*, roost in greater numbers as the temperature falls and particularly as the wind speed increases. Swingland (1977) describes how rooks, *Corvus frugilegus*, prefer to roost high in trees for safety from ground predators, except in windy conditions when they move downwards to benefit from superior microclimate. Fleming (1981) suggests that pied wagtails do not gain an advantage in terms of microclimate from the presence of conspecifics but that the nature of the roost site itself may provide a significant amount of shelter.

The failure of researchers to arrive at a common synthesis of the function of communal roosts is perhaps not surprising for two reasons:

- 1) a failure to acknowledge that roosting is not simply a default activity when birds are unable to feed. Sleeping may have a function in itself and birds often perform maintenance activities such as preening during roost periods. As Whitlock (1979) points out, roosting is an energetic activity; the lower critical temperature of the oystercatcher, for instance, is 21°C and at environmental temperatures below this birds have to expend metabolic energy simply to maintain normothermia. Surely the primary function of roosts is roosting *per se* and birds roost communally to increase their fitness whilst involved in this

activity. The argument should be about the mechanisms by which fitness is increased in such gatherings and these will vary between species. There have been an enormous range of species studied and it seems clear that the situation of between 20 and 40 dippers huddling under a bridge in mid-winter in Scotland is entirely different from that of a gathering of 8 million starlings in Israel;

2) whilst most researchers concede that a roost may have several functions, much energy has been directed to identifying the primary function, *i.e.* the major selection pressure shaping the behaviour. As Weatherhead (1983) points out, different individuals may join a gathering as a result of different selection pressures and gain from different benefits afforded by flock membership. Specifically he suggests that birds at the centre of red-winged blackbird, *Agelaius phoeniceus*, roosts might gain primarily from the reduced predation risk, whilst birds at the edge of the flock gain primarily from information transfer from the central birds. This 'Two Stage Hypothesis' is particularly attractive since it circumvents the problem inherent in the ICH, that birds must at some stage be both givers and receivers of information. In this case, although central birds may suffer from continually giving away the location of good food resources, they gain from the reduction in predation risk associated by having followers at the flock periphery.

The Two Stage Hypothesis highlights the important point, that different positions within a flock may afford different benefits to individuals and that flock infra-structure may be important. This idea had already been put forward by Yomtov (1977) who suggested that starlings occupying low positions within a roost suffered as a result of the soiling of their plumage from the deposition of droppings from birds in higher positions. Swingland (1977) showed that adult rooks preferentially adopt higher roost positions (which are safer from ground predators) than juveniles, except in adverse weather conditions, when

adult birds move down the tree to benefit from the superior microclimate, at the same time displacing juveniles to other trees. As a result juveniles suffer a reduction in their fitness through an acceleration of the loss of their energy reserves.

There is also circumstantial evidence that birds on the edge of a flock are more at risk from predation than birds in the centre. Jennings & Evans (1980) demonstrated that starlings in edge positions are more vigilant than birds in the centre. Kus (pers.comm.) found that juvenile dunlin are usually found on flock peripheries and are more at risk from predation by merlins, *Falco columbarius*, than are the centrally located adults. Weatherhead & Hoysak (1984) show that it is the dominant adult red-winged blackbirds that occupy central positions within a roost, probably benefiting from a reduced predation risk and possibly a superior microclimate, whilst the subordinate juveniles occupy positions on the flock periphery and may benefit from information transfer.

Communal roosting is a common behaviour pattern for many species of wader (Furness 1973a, Swennen 1984). Waders often fly several miles to a particular roost locality, possibly indicating that choice of site is important (Furness 1973b). Swennen (1984) has demonstrated variation in 'bird quality' and mortality between roost sites. Whitlock (1979) investigated the microclimate within wader roosts and predicted potential savings in energy expenditure of up to 20% in oystercatchers as a result of the shelter provided by conspecifics and topographical features of the roost. Furness & Galbraith (1980) showed that the distribution of colour-marked waders within a roosting flock was non random. In recent reviews Myers (1984) and Ydenberg & Prins (1984) both emphasize the ecological importance of roosts and highlight the need for further research in this area.

The ecological significance of roosting is an enormous subject, however I enjoyed the opportunity to collect some data on vigilance behaviour of roosting curlew. In this chapter I investigate the effect of flock size and position within a flock upon the vigilance of curlew. I also examine if and how birds can regulate their vigilance levels and whether different individuals tend to adopt different positions within a roosting flock.

5.2. Effect of flock size and position within flock on vigilance.

5.2.1. Methods.

In my assessment of vigilance and flock infra-structure I used two types of data collection:

a) flock scans. These were achieved by taking each bird of a roosting flock in turn, starting with the front-most (windward) individual, and assigning it an instantaneous activity. Three activities were identified for the purpose of flock scans: ROOST (bill positioned along the back or under the scapulae); LOOK UP (bill horizontal and forward facing, bird alert); and PREEN. Flock scans were only repeated after a minimum interval of 10min to insure independence, since this period exceeded the normal maximum duration of a LOOK UP, ALERT or PREEN bout and the flock size frequently changed in this time span. At least 5min were allowed to elapse after any disturbance before a flock scan was taken;

b) flock maps. These were used to examine flock infra-structure. I developed a shorthand method of designating the relative position of each flock member. This was based on the observation that when viewing a roosting flock through a telescope, birds appear to be arranged in lines running away from the observer. The windward bird was usually solitary and was taken as the reference point; its colour-rings were read or it was left unidentified (U) and its activity (see flock scans above) was noted. The lateral distance to the first line of birds (in bird-lengths) was then estimated. The distance of the first

bird (A) in this line towards (positive) or away from (negative) the observer relative to the windward bird was then estimated in bird lengths and bird (A) was identified and its activity noted. The distance between bird (A) and the next bird in that line was then estimated in bird-lengths and the bird identified and its activity recorded and so on down the line. Bird (A) was then taken as the reference point for locating the next line. In effect I was imagining a grid with squares of one bird-length superimposed on the flock (Fig. 5.1). A computer programme was written to convert the data into a plan representation of the flock. Individual birds or birds in given activities could be highlighted on the plan to assess relative positions (Fig. 5.2). Additionally a statistical package was written in order to calculate the average distribution of flocks, average distribution of birds in a given activity state or distance between any six specified birds. The prevailing winds at Chapel Brae (from where the data were collected) were northerly, meaning that I invariably observed flocks from the side, with the windward bird to my left. Thus, when I refer to *lateral* position I mean the position of a bird front to back along the flock length, and flock *depth* refers to flock width. Unfortunately maps tend to be slightly elongated because:

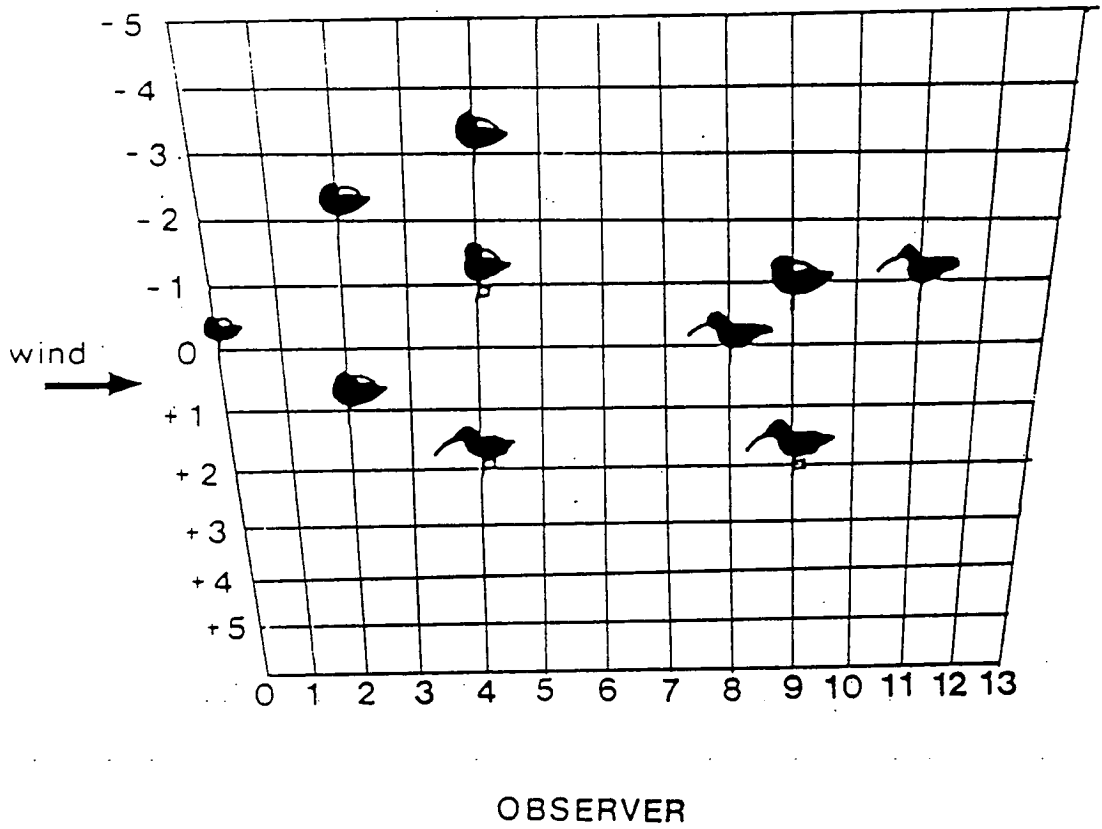
- a) of foreshortening effects in the field,
- b) the printer producing the maps can only work in rectangles, not squares. One bird-length in depth is equivalent to one space along a line of the printer whilst one bird-length laterally is equivalent to one line down the printer and these are not equal,
- c) at Chapel Brae where the data were collected roosts tended to form along long ridges of rock and were therefore naturally elongated.

Flock maps were always taken from the same position to standardise these effects. To ensure independence of observations only one map was taken of a flock per day. Flock map data were not taken within 5min of a

Fig. 5.1. Illustration of shorthand method of collecting FLOCKMAP data. The windward bird is always taken as the initial reference point; in this case it is unmarked and at roost and so designated UR. The lateral distance to the next line (L) of birds is then estimated in bird-lengths (BL); in this case 2, and the distance from the observer to the first bird in that line, relative to the windward bird is also estimated; in this case +1BL. The bird is unmarked and at roost. The distance from the observer to the next bird in the same line is then estimated (3BL) and this bird is also unmarked and at roost. The lateral distance to the next line of birds is 2BL and the distance from the observer to the first bird in that line is then estimated relative to the first bird of the preceding line. This bird is marked and in the LOOKUP posture. This procedure is repeated throughout the flock, thus the following shorthand notation describes the identification, activity and relative position of each flock member:

Ur;L2+1Ur,3Ur;L2+1ROYlu,3YNYr,2Ur;L4-2Ulu;L1+2WOWlu,3Ur;L2-3Ulu.

Semicolons indicate new lines, commas separate birds within a line. U = unmarked, L = start of new line, r = roost, lu = look up, ROY, YNY & WOW represent individual colour combinations.



OBSERVER

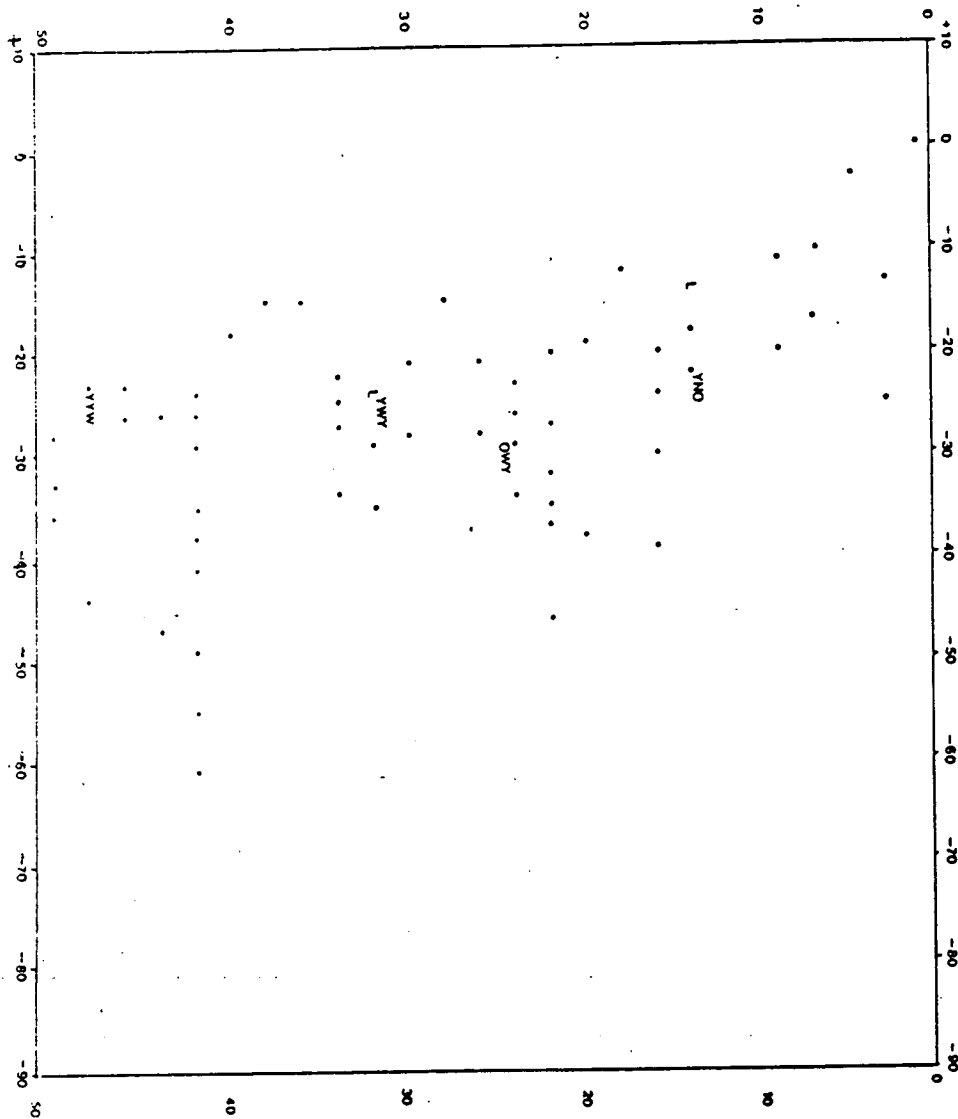


Fig. 5.2. Example of plan view of a roosting flock obtained by running the FLOCKMAP programme on data collected from curlew at Chapel Brae. Dots = roosting birds, L = bird in LOOK UP posture, letters identify known individuals. All distances in bird-lengths relative to windward (top left) bird.

disturbance and if a disturbance occurred during collection of flock map data the data were discarded.

In any assessment of ^{the effect of} position in the flock upon vigilance and position adopted by individual birds I first had to define the position of any bird within the flock. To do this I adopted two methods:

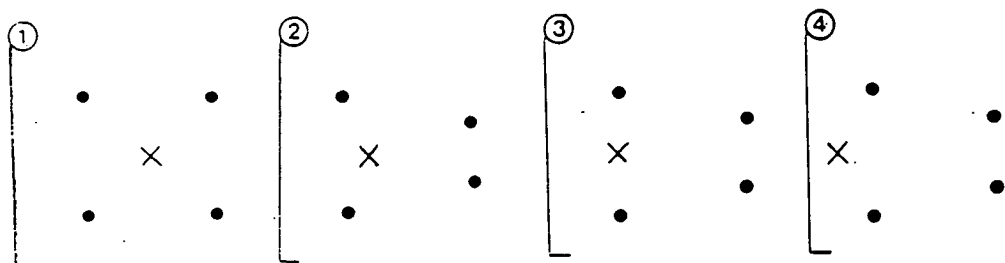
1) position laterally within the flock; I divided the flockmap along its length into three sections, front, middle and back. This was achieved by dividing the total length of the flock in bird lengths by four and assuming that the first quarter of this distance comprised the front of the flock, the last quarter the back and the remainder the middle.

2) edge or centre positions; these were harder to define. Fig. 5.3a shows four flocks of five birds. In the first diagram the bird marked X is clearly in a central position and in the last diagram it is clearly in an edge position, but what about the intermediate diagrams? I chose an arbitrary but standard method to determine whether a bird was in a central position or on the edge. This involved drawing an arc of 160° and radius of five bird-lengths on tracing paper. The centre of the circle from which the segment defined by this arc was taken was placed on the bird whose position I wished to determine, the base of the segment parallel to the longitudinal axis of the flock (Fig. 5.3b). If the segment did not encompass any other bird the individual concerned was defined as being on the flock edge, if one or more birds were within the segment the individual was taken as being in the flock centre. I chose not to use an arc of 180° since this would have placed all birds in a 'line ahead' formation in the flock centre; intuitively individuals in such an array would be on the flock edge.

Fig. 5.3a. Four hypothetical flocks of five birds showing difficulty in assigning position to bird X. In flock (1) X is clearly in the centre whilst in flock (4) it is clearly on the edge. The position in flocks (2) & (3) is less clear.

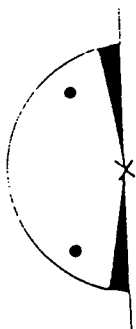
Fig. 5.3b. Method of assigning position to birds in FLOCKMAPS. An arc of 160° and 5BL ^{radius} ~~in diameter~~ is drawn on a transparent overlay and the centre of the circle from which this arc was derived is placed on the bird in question so that the base is parallel to the axis of the flock. In flock (1) the arc encloses one or more flock members, therefore bird X is defined as being in the centre. In flock (2) the arc doesn't encircle any birds, therefore X is defined as being on the edge.

A

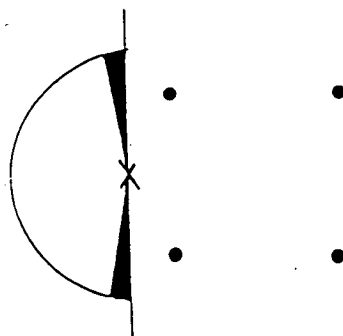


B.

①



②



5.2.2. Results.

5.2.2.1. Relationship between flock size and vigilance.

This relationship is shown in two ways in Fig. 5.4. The histogram indicates the mean percentage of birds in any flock scan in LOOK UP postures. This can be seen to fall rapidly with flock size, but to reach an asymptote at a flock size of about 40 birds. The curve indicates the mean number of birds in LOOK UP postures and can be seen to increase steadily with flock size. Since the biggest change occurs in the range of flock sizes 1-20 birds, and sample sizes in the category 1-10 birds are biased towards the lower flock sizes, I plotted flock sizes between 1 & 20 birds individually (Fig. 5.5).

5.2.2.2. Effect of position on vigilance.

A significantly higher proportion of birds in edge positions were in LOOK UP positions than birds in central positions (Table 5.1. $\chi^2 = 8.10$, $p < 0.005$, Fig. 5.6). There was no indication that the lateral position of a bird within a flock affected vigilance levels (Table 5.2. Front vs. Middle: $\chi^2 = 2.02$, N.S., Back vs Middle: $\chi^2 = 2.73$, N.S., Front vs Back: $\chi^2 = 0.006$, N.S.).

5.2.2.3. Position of individual birds.

Although it appeared that individual birds were consistently adopting a similar position laterally within a flock (Table 5.3.) sample sizes were small and no significant differences between individuals were found (χ^2 test of heterogeneity, $\chi^2 = 48.15$, 42 d.f., N.S.). However, birds did consistently tend to adopt edge or centre positions (Table 5.4.) and significant differences between birds were found (χ^2 test of heterogeneity, $\chi^2 = 36.39$, 21 d.f., $p < 0.05$).

5.2.3. Discussion.

The finding that birds on the edge of a flock are more vigilant than those at the centre is neither particularly novel nor surprising. It does, however, reinforce the idea that different positions within a roosting flock afford differential benefits (Weatherhead 1983). Therefore it is interesting to find that

Fig. 5.4. Relationship between vigilance and flock size for roosting flocks. Histograms show mean percentage ($\pm$ S.E.) of birds in LOOK UP positions for each flock size. Circles show mean number ($\pm$ S.E.) of birds in LOOK UP positions for each flock size. Numbers indicate number of scans made.

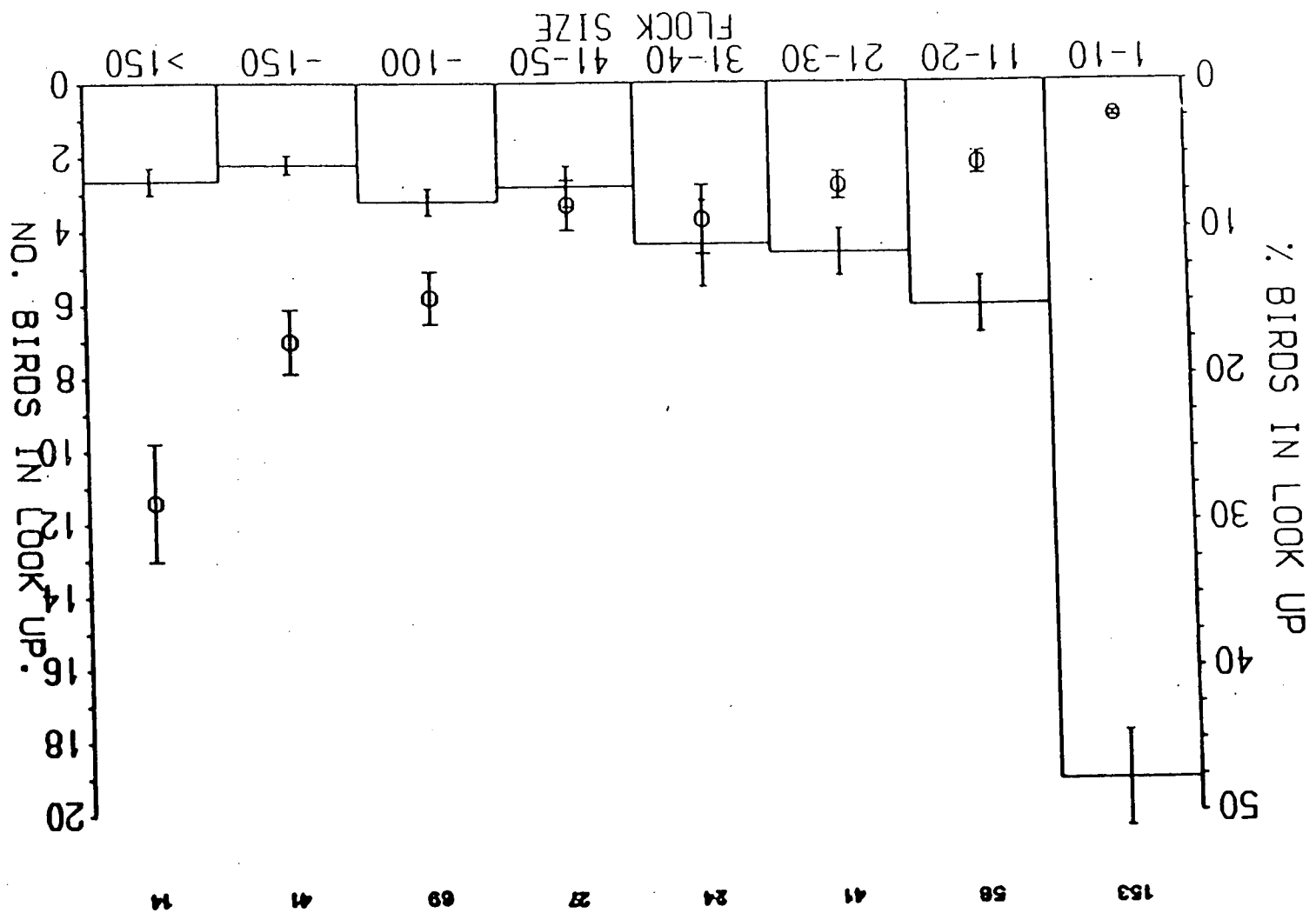


Fig. 5.5. Relationship between vigilance and flock size for roosting flocks.

As for Fig. 5.4, but for every flock size between 1 & 20 birds.

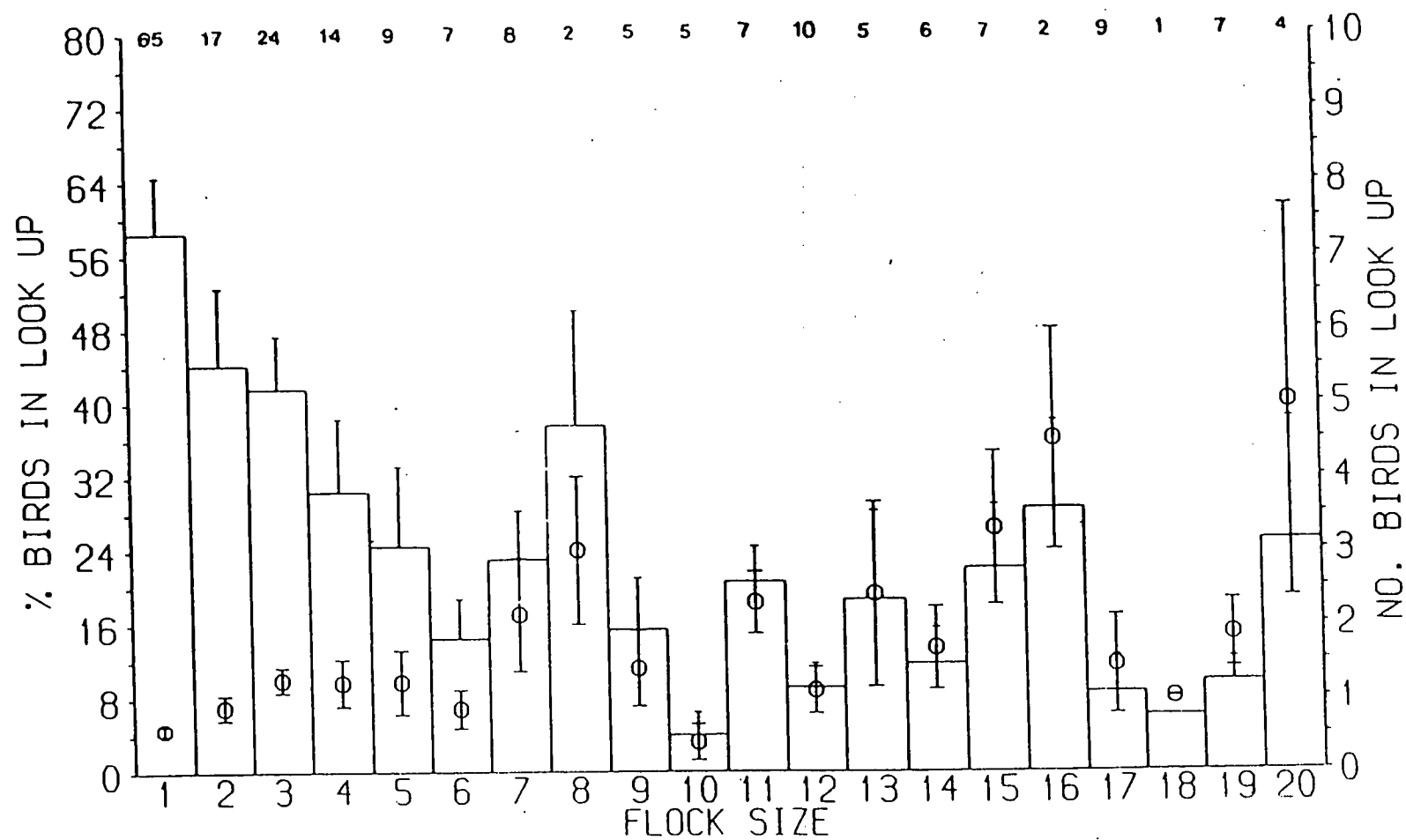
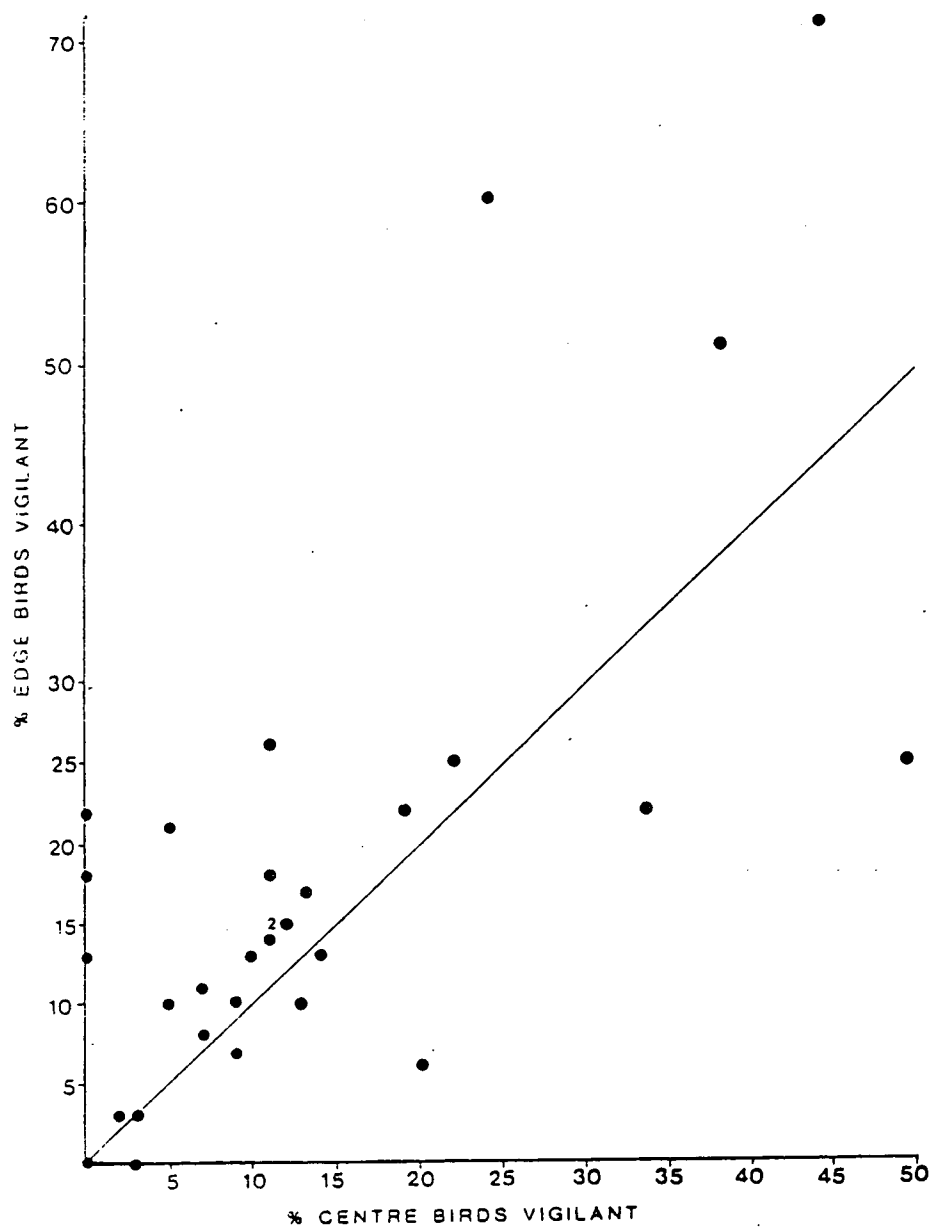


Fig. 5.6. Percentage of edge birds that are vigilant plotted against the percentage of centre birds that are vigilant in the same flock. The curve shows the null hypothesis; that is that there is no difference between the proportion of edge and centre birds that are vigilant.



FLOCK SIZE	ON EDGE		IN CENTRE	
	No. BIRDS	% IN LOOK UP	No. BIRDS	% IN LOOK UP
64	27	22	37	19
106	48	15	58	12
121	38	3	83	2
206	40	25	166	22
63	41	10	22	5
173	60	10	113	9
166	72	18	94	11
33	18	6	15	20
45	30	17	15	13
120	28	7	92	9
53	35	14	18	11
180	39	13	141	10
69	31	0	38	3
220	89	15	131	11
103	45	13	58	14
106	32	3	74	3
101	31	10	70	13
155	47	11	108	7
120	54	15	66	11
80	35	51	45	38
141	79	8	62	7
65	38	26	27	11
146	61	21	85	5
7	4	0	3	0
24	18	22	6	0
18	11	18	7	0
27	10	60	17	24
16	7	71	9	44
24	18	22	6	33
18	16	25	2	50
20	15	13	5	0

Table 5.1. Effect of edge/centre position upon vigilance in roosting flocks.

FLOCK SIZE	FRONT		MIDDLE		BACK	
	No. BIRDS	% IN LOOK UP	No. BIRDS	% IN LOOK UP	No. BIRDS	% IN LOOK UP
64	13	0	40	33	11	9
106	26	0	66	3	14	7
121	24	4	69	0	28	7
206	21	14	110	24	75	24
63	14	0	41	7	8	25
173	29	14	81	12	63	11
166	50	16	91	11	25	20
33	8	0	19	16	6	17
45	14	29	25	4	6	33
120	40	13	63	8	17	0
53	12	33	34	3	7	0
180	15	13	95	10	70	11
69	15	0	46	2	8	0
220	44	9	123	56	53	21
103	18	28	58	16	27	0
106	18	17	58	19	30	3
101	25	4	69	13	7	14
155	15	13	106	6	34	15
120	21	19	78	13	21	5
80	19	53	29	52	32	31
141	26	4	85	5	30	23
65	26	19	21	14	18	28
146	7	43	67	12	72	8
7	2	0	4	0	1	0
24	5	20	14	14	5	20
18	10	30	4	25	4	25
27	7	42	13	39	7	29
16	1	100	8	50	7	57
24	10	20	10	30	4	25
18	2	0	12	8	4	25
20	3	0	12	8	5	20

Table 5.2. Effect of lateral (front to back) position upon vigilance in roosting flocks.

BIRD	No FLOCKS	FRONT	MIDDLE	BACK
OWY	4	1	3	0
ROY	5	0	4	1
RWY	6	1	4	1
YRY	4	1	2	1
YYR	6	2	4	0
YOW	6	1	4	1
YNO	4	1	2	1
YRO	4	1	3	0
YYW	10	0	7	3
ORO	4	1	1	2
OWL	4	1	3	0
YON	4	1	2	1
ONL	5	0	2	3
OOW	4	2	1	1
ORN	5	1	4	0
YOR	4	0	1	3
WWY	5	1	4	0
OON	4	1	3	0
YOWR	4	0	4	0
NLY	4	0	4	0
OYR	4	0	2	2
OOL	5	1	3	1

Table 5.3. Lateral (front to back) positions adopted by individual birds in roosting flocks.

BIRD	No FLOCKS	ON EDGE	IN CENTRE
OWY	4	1	3
ROY	5	4	1
RWY	6	1	5
YRY	4	1	3
YYR	6	1	5
YOW	6	4	2
YNO	4	0	4
YRO	4	2	2
YYW	10	2	8
ORO	4	2	2
OWL	4	1	3
YON	4	2	2
ONL	5	3	2
OOW	4	2	2
ORN	5	1	4
YOR	4	3	1
WWY	5	2	3
OON	4	2	2
YOWR	4	1	3
NLY	4	0	4
OYR	4	4	0
OOL	5	0	5

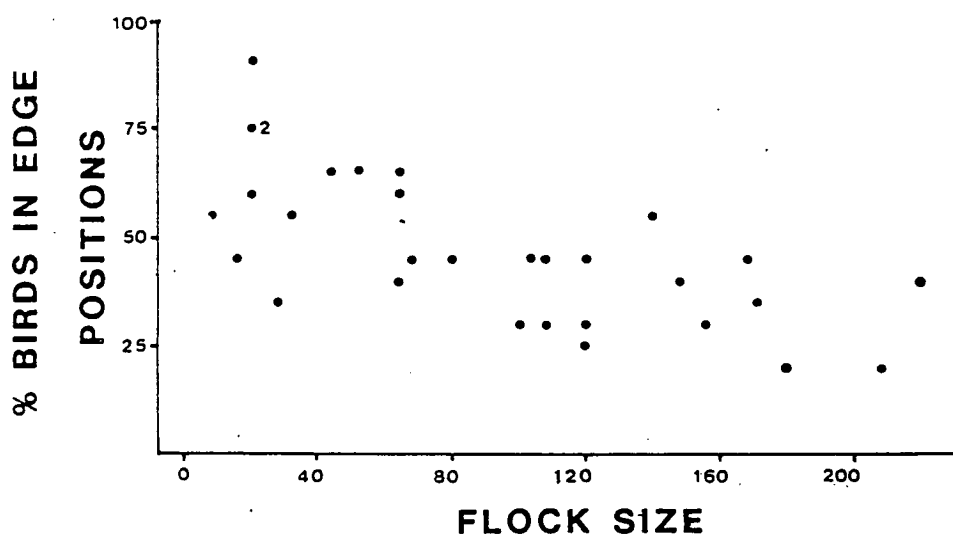
Table 54. Edge/centre positions adopted by individual birds in roosting flocks.

certain individuals preferentially adopt central positions whilst other birds are regularly found on the edge of the flock. It would be interesting to see if the sample size were increased whether individuals do also regularly adopt the same lateral position within a flock. During flock formation aggression involving supplants was common; this may be a mechanism by which preferred positions are taken up, although no data were collected on this.

The flock-size/vigilance function described for roosting curlew is similar to that found in feeding flocks of many species of bird (Barnard & Thompson 1985) especially curlew (Abramson 1979). To some extent this reduction in the proportion of birds vigilant with increasing flock size can be explained by the 'Edge Effect' (Inglis & Lazarus 1981) namely that the larger the flock size the smaller the percentage of birds found in vulnerable edge positions. This is certainly the case in curlew (Fig.5.7) although this effect does not appear to be large enough to explain the dramatic drop in vigilance levels with flock size. The flock size/vigilance function permits individuals in larger flocks to spend less time in vigilance and more time sleeping or in maintenance activities. It also implies that there must be some cost to vigilance; this could be unknown effects of loss of sleep (Lendrem 1983) or an increase in heat loss due to the greater surface area exposed when head and neck are extended. One criticism that has often been put forward in response to the use of the flock size/vigilance function as an explanation of why birds should flock is that the function almost always reaches an asymptote at flock sizes of 30 birds; thereafter no matter how large a flock gets, an individual will spend more or less the same proportion of its time in vigilance. However, it should be remembered that the absolute number of birds vigilant at any given time continues to increase with flock size; this has two possible benefits:

- 1) it is conceivable that the chances of $(x+1)$ vigilant birds detecting an approaching predator are greater than the chances of (x) birds;

Fig.5.7. Relationship between percentage of birds in edge positions and flock size ($r = -0.698$, 29 d.f., $p < 0.001$).



2) the risk of no birds in the flock being vigilant at a given time will also decrease with increasing flock size.

Both the magnitude of the reduction in vigilance with flock size and the lack of variation in the proportion of vigilant birds in the flock after the asymptote has been reached are impressive (Fig. 5.4.). It would appear as if individual birds are regulating their vigilance levels. If so how? This is investigated in the following section.

5.3. Regulation of vigilance.

5.3.1. Introduction.

As explained above the magnitude and regularity of the flock size/vigilance function suggest that birds are regulating their vigilance levels in some manner. Elgar *et al* (1983) describe how house sparrows, *Passer domesticus*, lower their vigilance levels according to the number of conspecifics visible (and not total flock size). However, the situation may not be that simple: if all birds in a flock scan independently of others and reduce scan frequency and/or duration in larger flocks there will exist situations where no birds in the flock are vigilant. Random, independent scanning has been invoked as a mechanism whereby if the vigilance level of the flock as a whole is unpredictable a predator is unsure of when to attack. Surely, though it would be preferable if at least one flock member was vigilant at any given time? This could be achieved if either:

a) there was a coordinated vigilance 'sharing' system, with some birds acting as 'sentinels' or;

b) individuals regulated their own vigilance dependent upon the vigilance levels of other birds within the flock.

Hypothesis (b) is perhaps the more attractive since it avoids problems with group/kin selection arguments, but it depends upon the ability of birds to assess the vigilance level of the flock. Inglis & Isaacson (1978) were able to

demonstrate that dark-bellied brent geese, *Branta bernicla bernicla*, could assess the proportion of decoy birds in alert postures. Incoming ^{el}skjens would only land if a high enough percentage of decoys were in 'head down' postures and the decoy flock thus appeared unalarmed. I therefore developed the hypothesis that a roosting curlew should assess the number of vigilant birds within the flock. If this is lower than expected for that flock size then the individual should perform a vigilant scan. Scans must be of finite duration, otherwise the same flock members would be constantly vigilant throughout a roosting period; since no other bird should initiate a vigilant scan whilst there is already a vigilant bird, vigilant birds have no other way of terminating a scan. This hypothesis raises a further question: how can sleeping birds assess the vigilance level of the flock? Close observation of a sleeping curlew reveals rapid bouts of eye opening and closure (peeking) similar to that described in herring gulls, *Larus argentatus*, by Amlaner & McFarland (1981). Lendrem (1983,1984) describes similar behaviour in mallard, *Anas platyrhynchos*, and barbary doves, *Streptopelia risoria*, however he suggests that peeking is: "directly analogous to head cocks" (LOOK UPS). I believe that this is unlikely in curlew; it is difficult to see how two such different behaviours could perform the same function, or that a rapid 'peek' could be as efficient at detecting a predator as a prolonged LOOK UP scan. Moreover Amlaner & McFarland (1981) were able to show that sleeping herring gulls had a higher arousal threshold than birds with their heads up. This was supported by the observations of Ball *et al* (1984) although roosting and resting gulls in their study did not differ in take off distance from an approaching predator. It seems more likely that peeking behaviour permits assessment of the behaviour of other flock members rather than detection of approaching predators. In this section I measure the peeking behaviour of curlew in relation to flock size and position within the flock and describe an experiment I performed to test the hypothesis that birds

in flocks assess the vigilant behaviour of other flock members and adjust their behaviour accordingly.

5.3.2. Methods.

5.3.2.1. Examination of peeking behaviour.

Roosting birds were chosen from a flock and observed for between 30s and 2min. During this period their activity was noted on to a running tape-recorder, so that duration of every period of eye opening (peek) and closure (roost) could be measured. If the bird changed from the roost posture to a LOOKUP or PREEN posture during the observation the data was discarded from analysis. Whenever possible I endeavoured to take alternate observations from individuals that were obviously on the edge of the flock and birds that were obviously in the centre, for matched pairs analysis. Flock size was noted after each observation. Tapes were later subjected to 'real time' analysis using Keytime II as described in section 1.2.

5.3.2.2. Experimental analysis of regulation of vigilance.

Experiments were conducted upon roosting flocks which formed in Roost Field over spring high tides. Four decoys were made up (section 1.2) in LOOK UP postures. At least 3h before predicted high tide the decoys were positioned on the field, head to wind, in the configuration shown in Fig.5.8. Decoys were always placed in the same position in order to control for distance to cover. Once live birds had landed with the decoys (within 30 bird-lengths) flock scans were taken as described in section 5.2.1.

5.3.3. Results.

5.3.3.1. Peeking behaviour.

Roosting curlew peeked at a mean rate of 9.45 peeks/min (S.E. + 0.46, n = 119, range = 0.5–21.3). The proportion of time spent by an individual in peeking declined with increasing flock size (Fig. 5.9.). Edge birds spent a higher proportion of their time peeking than central birds (Wilcoxon matched-pairs

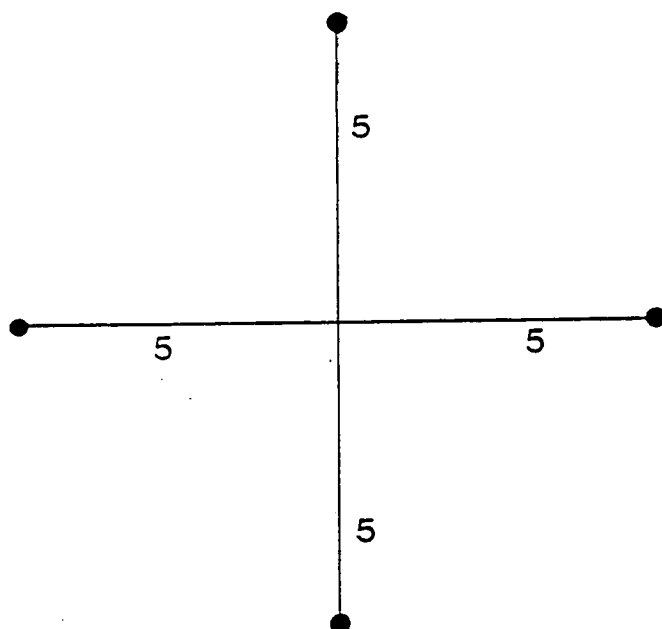
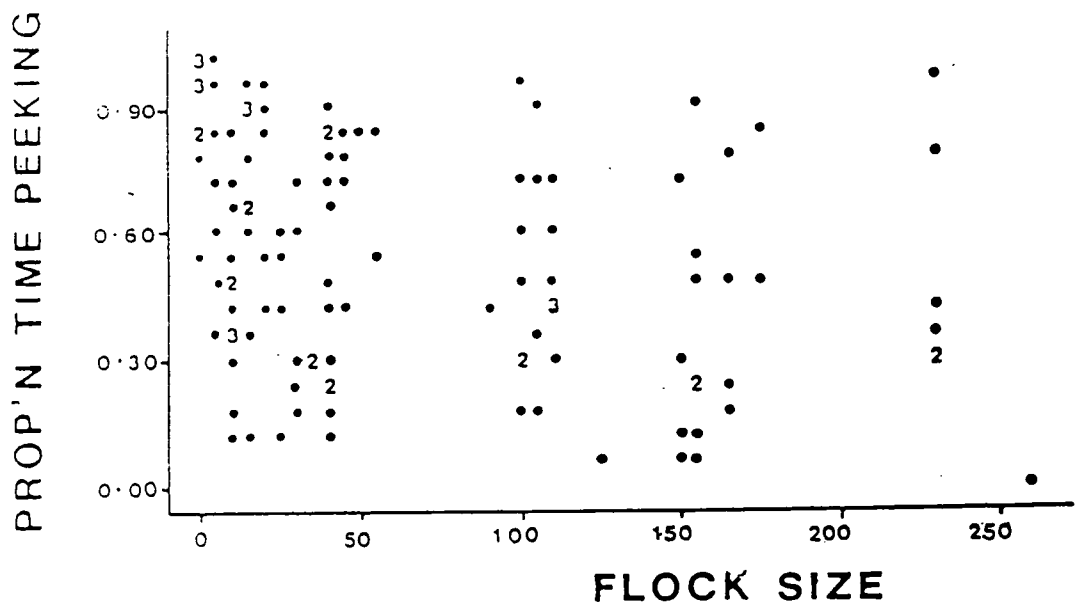


Fig.5.8. Configuration of decoys in vigilance experiment. Distances in bird-lengths.

Fig. 5.9. Relationship between proportion of time spent peeking and flock size ($r = -0.295$, 117 d.f., $p < 0.05$).



signed ranks test, $T_s = 5$, $n = 23$, $p < 0.005$).

5.3.3.2. Regulation of vigilance.

The proportion of live birds in LOOK UP postures in decoy flocks of different sizes was tested against expected values obtained from the flock scan data collected in section 5.2.2. This was done in two ways: a) flock sizes of birds in decoy flocks were taken as the number of live birds (real flock size) e.g. the situation of 4 decoys + 2 live birds was compared with the natural situation of 2 live birds. A lower proportion of vigilant live birds in the decoy flocks would suggest that the live birds are treating the decoys as live birds. However, this comparison does not distinguish whether live birds are assessing flock vigilance or just flock size, for instance if a single live bird with 4 decoys perceives that it is in a flock of 5 birds it should lower its vigilance according to either hypothesis.

b) flock sizes of birds in decoy flocks were taken as the number of live birds + the number of decoys (apparent flock size) e.g. the situation of 4 decoys and 2 live birds was compared with the natural situation of 6 live birds. A lower proportion of vigilant live birds in the decoy flock in this case can only be explained if the live birds are assessing the number of vigilant birds in the flock (and treating the decoys not only as real birds, but as vigilant real birds).

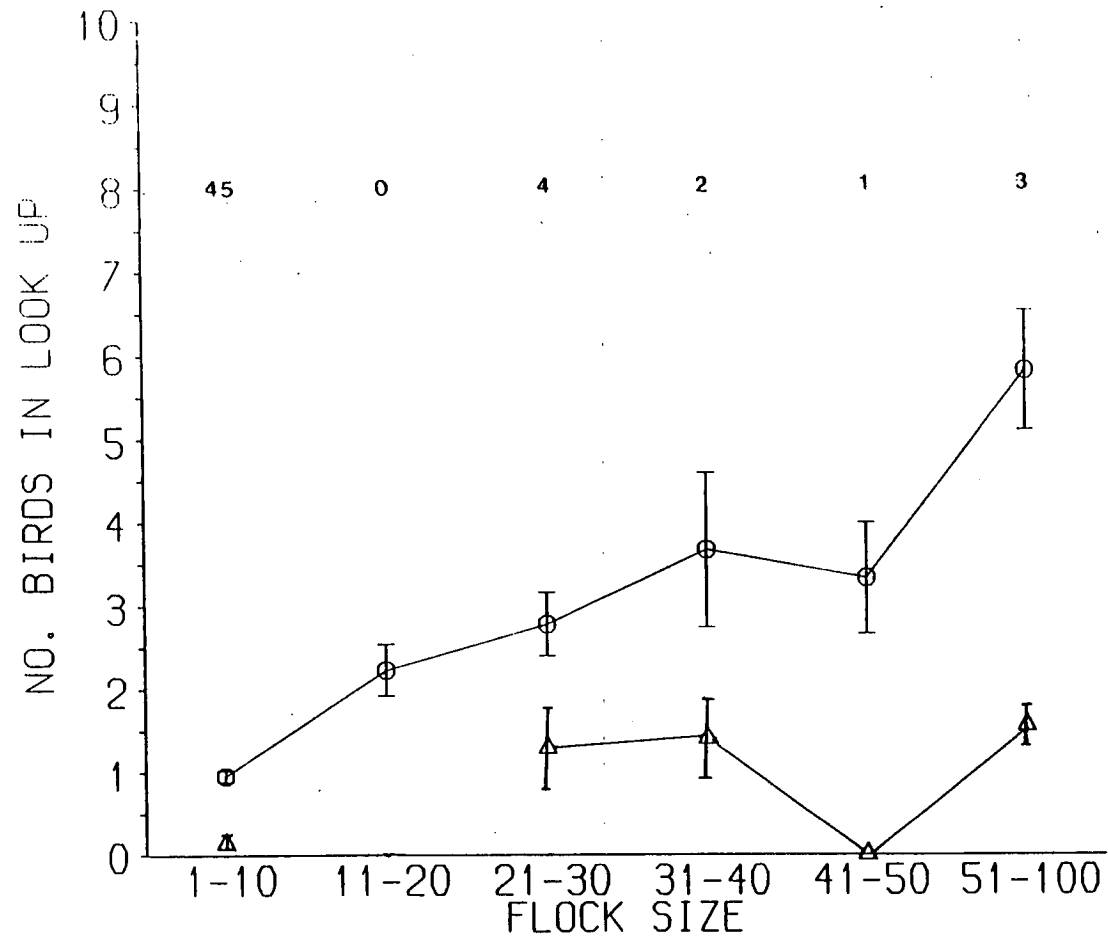
A comparison of the proportion of live vigilant birds in decoy flocks with the proportion of vigilant birds in natural flocks using real flock size reveals that live birds are indeed less vigilant when decoys are present (Table 5.5, Fig. 5.10.). This is significant only for flock sizes of 5, 9, 1–10 and 51–100; although the trend is the same for all flock sizes sample sizes are generally too small to reveal significance.

If apparent rather than real flock size is used, the proportion of live birds vigilant in the decoy flocks is significantly less than in natural flocks of equivalent size for flock sizes 5–10, 11–20, 41–50 and 51–100 (Table 5.6, Fig.

Table 5.5. Comparison of vigilance levels in natural and decoy flocks, taking flock size of decoy flocks as the number of live birds (REAL flock size).

FLOCK SIZE	WITHOUT DECOYS			WITH DECOYS			x ²	P
	No. SCANS	No. BIRDS	No. LOOKUP	No. SCANS	No. BIRDS	No. LOOKUP		
1	65	65	38	5	5	1	1.00	NS
2	17	34	15	6	12	1	2.81	NS
3	24	72	30	6	18	3	2.03	NS
4	14	56	17	2	8	1	0.69	NS
5	9	45	11	5	25	0	5.68	*
6	7	42	6	7	42	1	3.31	NS
7	8	56	17	4	28	0	7.84	**
8	2	16	7	NO DATA AVAILABLE				
9	5	45	7	10	90	0	12.74	***
1-10	153	515	146	45	2288	7	44.71	***
11-20	58	882	131	NO DATA AVAILABLE				
21-30	41	1013	114	4	96	5	2.60	NS
31-40	24	826	88	2	72	3	2.63	NS
41-50	27	1231	90	1	46	0	3.35	NS
51-100	69	4976	412	3	157	5	4.71	*

Fig. 5.10. Results of decoy experiment. Circles show mean number ($\pm$ S.E.) of birds in LOOK UP positions in natural flocks (from Fig. 5.4). Triangles show mean number ($\pm$ S.E.) of live birds in LOOK UP positions in decoy flocks. Flock size for decoy flocks is taken here as the number of live birds (REAL flock size). Numbers indicate the number of scans of decoy flocks taken in each flock size category.



5.11). Again the small sample sizes are probably responsible for the lack of significance in other flock sizes, since the trend is the same for all flock sizes.

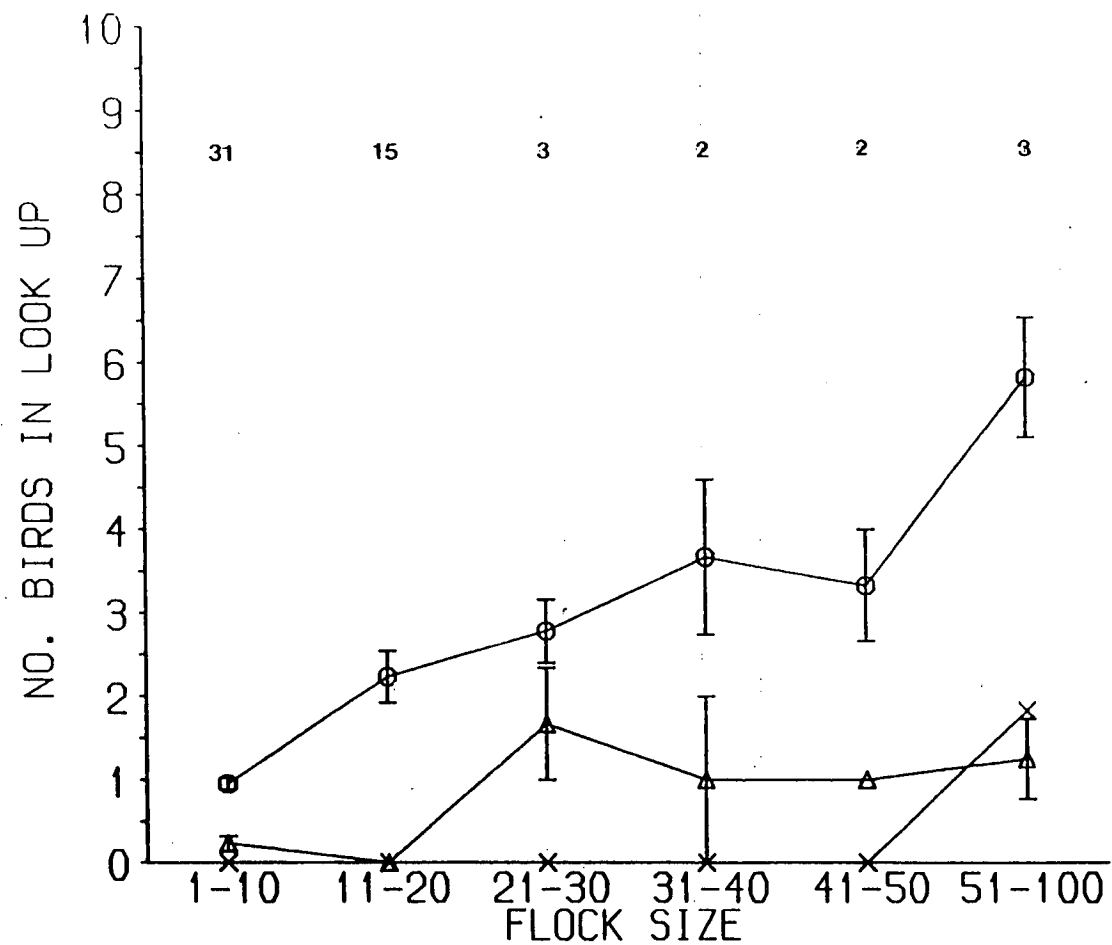
5.3.4. Discussion.

The peek rate of curlew is almost identical to that found in herring gulls (9.3 peeks/min, Amlaner & McFarland 1981) and within the range of that found in mallard (1-24 peeks/min, Lendrem 1983). The observation that the proportion of time spent peeking declines with increasing flock size was also reported in barbary doves (Lendrem 1984). Coupled with the finding that edge birds spend more time peeking than central birds, peeking behaviour seems to be similar to LOOK UP behaviour and the function of peeking could be interpreted as vigilance against attack (Lendrem 1983). There is, however, an alternative hypothesis consistent with the idea that birds peek in order to assess the vigilance level of the flock. In a large flock more birds are vigilant at any given time than in a smaller flock, therefore birds need to peek less often. In any flock an edge bird probably incurs a greater risk of predation than a centre bird and would therefore have to assess the vigilant state of its conspecifics more frequently. The results of the decoy experiment first of all indicate that decoys are accepted as real birds. From the second analysis it is clear that the vigilance level of live birds is depressed by the presence of the four decoys in LOOK UP postures, compared with a natural flock of equivalent size. This supports the hypothesis that curlew can assess the vigilance level of their roosting flock. Inglis & Isaacson (1978) showed that brent geese can assess the vigilance levels of decoys arranged to mimic a feeding flock, and base their decision on whether to land accordingly. It could be argued that such a system of vigilance regulation is open to 'cheating', i.e. certain birds having abnormally long periods of eye closure. However, such individuals would probably be slowest to react to an approaching predator; if this is the case they would certainly be most at risk from raptor predation and therefore

Table 5.6. Comparison of vigilance levels in natural and decoy flocks, taking flock size of decoy flocks as the number of live birds + the number of decoys (APPARENT flock size).

FLOCK SIZE	WITHOUT DECOYS			WITH DECOYS			x ²	P
	No. SCANS	No. BIRDS	No. LOOKUP	No. SCANS	No. BIRDS	No. LOOKUP		
5	9	45	11	5	5	1	0.03	NS
6	7	42	6	6	12	1	0.23	NS
7	8	56	17	6	18	3	0.79	NS
8	2	16	6	2	8	1	0.95	NS
9	5	45	7	5	25	0	3.70	NS
1-10	153	515	146	31	110	7	16.32	***
11-20	58	882	131	15	125	1	16.11	***
21-30	41	1031	114	3	69	5	0.88	NS
31-40	24	826	88	2	62	2	3.03	NS
41-50	27	1231	90	2	83	1	4.12	*
51-100	69	4976	412	3	157	5	4.71	*

Fig. 5.11. Results of decoy experiment. Circles show mean number ($\pm$ S.E.) of birds in LOOK UP positions in natural flocks (from Fig. 5.4). Triangles show mean number ($\pm$ S.E.) of live birds in LOOK UP positions in decoy flocks. Flock size for decoy flocks is taken here as the number of live birds + the number of decoys (APPARENT flock size). Crosses show the predicted number of live birds in LOOK UP positions in decoy flocks (mean number in natural flocks - 4). Numbers indicate number of scans of decoy flocks taken in each flock size category.



selected against. If the vigilance assessment hypothesis is indeed correct it would be expected that the situation when no birds in a flock are vigilant at a given time would seldom if ever arise. In Fig. 5.12 I show the percentage of flock scans in which all birds were roosting (i.e. none vigilant) as a function of flock size. Clearly at flock sizes above 10 birds it is very rare to find no birds vigilant. In flock sizes between 1 and 10 birds this situation does arise. This may imply that there is some unknown cost to being vigilant for prolonged periods of time. It would be interesting to perform a control experiment to test if decoys in ROOST positions promote the vigilance levels of live birds. There is another possible function of peeking; that it permits roosting birds to watch conspecifics for any sign of alarm or initiation of an escape response. The asymptotic nature of the flock size/vigilance function could be explained by a vigilance regulation mechanism such as I have described, if birds only assess the vigilance levels of near neighbours, or if there is an upper limit to the number of birds that an individual can assess.

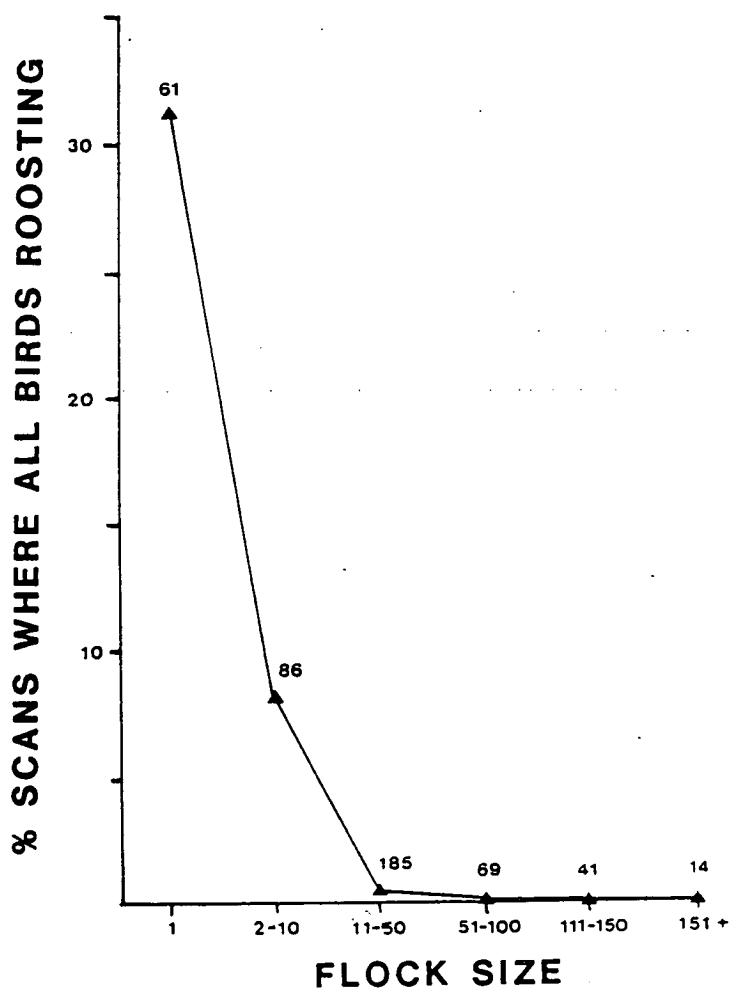
5.4. Discussion of communal roosting.

Until recently researchers have argued in favour of one of three possible primary functions of communal roosts:

- 1) the Information Centre Hypothesis (e.g. Ward & Zahavi 1973);
- 2) antipredator functions (e.g. Gadgil 1972);
- 3) superior microclimate (e.g. Chaplin 1982).

However, comparisons were made across widely different genera and interpretation of data often appeared clouded by preconception. For instance synchronous departure of groups of birds from a roost has often been interpreted as 'following behaviour' and invoked by advocates of the ICH as support for the idea of information transfer. It has never been demonstrated in the wild, however, that less successful birds follow more successful to better feeding grounds. An equally plausible hypothesis for synchronous departure is

Fig. 5.12. Percentage of flock scans in which all birds were at roost as a function of flock size. Numbers indicate sample sizes for each category.



that of predator evasion; individuals leaving a group are particularly vulnerable, all the more so if an assemblage of birds attracts many predators. An important step forward was made when Weatherhead (1983) proposed his 'Two Stage' hypothesis, i.e. that different individuals join a roost for different adaptive reasons and that different positions within a flock afford different benefits.

In this chapter I argue that the primary function of roosting is roosting *per se*, implying that roosting is positively beneficial and not simply a default activity. Those birds which roost communally do so to increase their fitness whilst roosting and the three primary functions suggested for communal roosts are simply mechanisms which help birds to do this. Which of the three is most important will depend not only on the species but on the individual or even on the time of year. I have shown that the relationship between flock size and vigilance in roosting curlew is similar to that in feeding flocks. In feeding flocks it is generally agreed that there is a trade-off between the time spent in feeding and the time spent in vigilance (Metcalf & Furness 1984) and that one benefit afforded by membership of larger flocks is a higher proportion of time available for feeding. The flock size/vigilance function for roosting flocks implies that there must be a cost to vigilance in this situation. The same argument used for feeding flocks can be applied to roosting flocks; membership of a larger flock requires less time to be spent in vigilance and thus permits more time to be spent roosting. Benefits could be in terms of reduced heat loss due to the smaller surface area presented by a bird in the roost posture, or in terms of an increased time spent sleeping. The relationship between the proportion of time spent pecking and flock size lends support to the latter argument (Lendrem 1984).

In a larger flock more individuals are vigilant at a given time; this may improve the predator detection efficiency of the flock as a unit. Furthermore,

the vigilance regulation system that I have hypothesised would ensure that there is always at least one bird vigilant in flocks greater than 10 birds. Lazarus (1979) describes how, in *Quelea*, the escape response elicited by a predator decreases with increasing flock size. I believe that this may be important in waders; taking flight at every disturbance must be very expensive. It would be interesting and fairly straightforward to test whether the escape response of waders in roosting flocks does decline with flock size.

So far I have discussed the ways in which the fitness of a roosting bird can be increased by flock membership as a result of a reduction in the risk of predation and an increase in time available for roosting due to vigilance regulation. I believe that curlew could also increase their fitness as a result of enjoying a superior microclimate within a roosting flock, particularly in severe conditions. Whitlock (1979) predicted total potential savings in energy expenditure of 20% in oystercatchers seeking 'total' shelter (i.e. that afforded by topographical features of the roost site + that afforded by the presence of conspecifics). Whitlock performed experiments on flocks of model birds. I would like to see these repeated in a natural situation, although this would comprise a study in itself.

I do not wish to appear to dismiss the ICH out of hand, but I believe it is unlikely to be of major importance to curlew for several reasons:

- 1) birds exhibit a high level of fidelity both between and within winters not only to the study site but to specific areas within the study site (chapter 3) therefore it is reasonable to suppose that individuals have considerable experience of the location of good food resources;

- 2) even in severe conditions when the food supply becomes patchy (particularly on field habitats) it is still predictable, since snow and ice melt occurs first near streams. On the one occasion when I observed a small snow-free patch one curlew gained exclusive use of the area through territorial

behaviour;

3) birds exploit a relatively small area and rarely travel far from the main roost-sites. If a bird was foraging with little success it could easily sample other areas within the study site or use local enhancement (Waite 1981) to locate good feeding areas;

4) individuals adopt specialist feeding strategies (chapter 3) related to their bill morphology and if they switch macrohabitats their feeding efficiency is reduced. Therefore to gain from the ICH they must recognise and follow birds which specialise in the same manner as themselves;

5) many individuals that feed on the intertidal zone are territorial and maintain exclusive use of their feeding area (chapter 4).

In conclusion it is becoming clear that roosting may be an important adaptive behavioural strategy and a subject requiring further study.

CHAPTER 6.
SUMMARY AND GENERAL DISCUSSION.

*"The ocean wild like an organ played,
The seaweed's wove its strands,
The crashin' waves like cymbals clashed
Against the rocks and sands.
Lay down your weary tune, lay down,
Lay down the song you strum,
And rest yourself 'neath the strength of strings
No voice can hope to hum."*

BOB DYLAN, 1964.

Research in to the behavioural ecology of waders has proliferated over the past 20 years or so for two reasons:

First, the relationship between waders and their intertidal invertebrate food is one of the easiest predator/prey interactions to study. Prey availability can be relatively easily determined and the foraging behaviour of the birds can be measured without difficulty. Comparative studies between different species of wader can help our understanding of the evolution of different morphologies and behaviour patterns.

Second, because the threat to estuaries is ever increasing it is important to understand the ecology of this ecosystem as fully as possible so that effective conservation measures can be implemented.

It is becoming increasingly apparent that different subsets of a population of waders behave in different manners and that the concept of an "average bird" is of very limited use. For instance Puttick (1981) described different foraging patterns in male and female curlew sandpipers, *Calidris ferruginea*, whilst Groves (1978) and Goss-Custard & Durell (1983,1987a) documented age related differences in turnstone and oystercatchers respectively. Further, it has been discovered that individuals can differ dramatically in foraging ability (e.g. oystercatchers, Goss-Custard & Durell 1983, Goss-Custard & Sutherland 1984, Goss-Custard 1986; and turnstone, Whitfield 1985a) and in spacing behaviour (Myers 1984). These findings may have implications for the population dynamics of a species. In consequence interindividual differences are a recurring theme throughout this thesis.

In chapter 3 I show that curlew have a very highly variable bill morphology. The degree of variation is comparable to or greater than that found in a seed cracker (Smith 1987), Darwin's medium ground finch (Grant *et al* 1986, Price 1987) and great tits (Gosler 1987). In all three of these species bill morphology has been shown to be related to niche utilisation. I also show

how curlew occupy a broad niche with a large between-phenotype component. Individual birds specialise in the exploitation not only of macrohabitat but of microhabitat and their diet varies accordingly. The microhabitat which a specific individual exploits would appear to be a function of that individual's bill morphology; birds with a high bill-shape index (relatively short, thick, straight bills) tend to specialise in field habitats, whilst birds with a low bill-shape index (relatively long, slim, decurved bills) tend to specialise on the intertidal zone. The bill-use repertoire of birds also varies according to the microhabitat which an individual exploits. On field habitats the majority of prey are captured by shallow, straight probes, whilst on the intertidal zone deep, complex probes, often with the bill held horizontally or upturned, are most successful in capturing prey.

The finding that field-specialists have a higher swallow rate than generalists when feeding on fields, but a lower swallow rate than generalists when feeding on the intertidal zone suggests that specialisation pays, at least in the short term, and that there may be a cost to switching specialisations.

These results are important for two reasons:-

- 1) They help shed some light upon the evolution of the trophic apparatus and foraging behaviour of the curlew. As argued in section 3.5 it would appear that the decurved bill is an adaptation to probing along complex pathways on a rocky shore, rather than on estuarine mudflats (Davidson *et al* 1986) or in long vegetation on the breeding grounds (Hale 1980, Owens 1984). In chapter 3 I describe how curlew meet the predictions of the niche variation hypothesis (van Valen 1965). This implies that the variation in bill morphology and foraging behaviour that I have documented in this species has evolved as a result of disruptive selection acting upon individuals specialising in the exploitation of subsets of the environment exploited by the population as a whole. This argument contrasts with that put forward by Townshend (1981b)

who suggested that short-billed birds (predominantly males) are forced to forage on fields during cold weather when intertidal prey migrate vertically downwards out of reach:

2) They have important implications for conservation; since females tend to have lower bill-shape indices than males and to feed on the intertidal zone, loss of estuarine habitats will have a greater adverse effect on females than on males. Such a differential effect of loss of habitat on the sexes may profoundly alter the population dynamics of the species.

From the results of chapter 4 it is clear that curlew show great variation in spacing behaviour. On fields they form moderately sized, relatively dense flocks, whilst on the intertidal zone they normally feed solitarily and often gain exclusive use of an area through territorial behaviour. This difference in spacing behaviour between individuals is probably the result of feeding interference between conspecifics on the intertidal zone (Goss-Custard & Durell 1987a+b) and also has implications for conservation measures; it is conceivable that rocky shores could support a proportion of birds displaced from estuaries. The number of individuals likely to be accommodated in this way would, however, probably be small because birds on the intertidal zone tend to feed in a dispersed manner and the presence of conspecifics tends to depress intake rate. Additionally curlew on estuarine mudflats feed in different manners to those on rocky shores and possibly differ in bill morphology, although my sample sizes were too small to test this.

Areas for further research on the topics so far discussed include:

1) collection of a larger data set on microhabitat specialisations, particularly within the intertidal zone, in relation to bill morphology,

2) collection of a larger data set on the relative success rates of specialists when foraging in preferred and non-preferred microhabitats, with a view to measuring any cost of switching feeding technique;

3) an assessment of bill morphology and habitat selection in relation to substrate penetrability. In Chapter 3 I suggest that birds with a higher bill-shape index may be better adapted to field habitats because a short, straight, thick bill may be more useful for penetrating firmer substrates. If this is the case, birds of differing bill shapes may feed in different areas of an estuary. Any change in the rate or nature of sediment deposition (as may result from a tidal barrage scheme or encroachment of cord grass, Goss-Custard 1987) may differentially affect birds of different bill morphologies. This should be the subject of further investigation, not just on curlew but also on other species, since it is known that the sexes segregate in terms of foraging substrate in bar-tailed godwit and dunlin (Smith 1975, Clark 1983).

Finally I investigated the vigilance behaviour of birds in roosting flocks. In chapter 5 I was able to show that birds assess the alertness of other flock members and adjust their own vigilance level accordingly. One advantage of roosting communally seems to be that individuals in larger flocks are able to spend more time in roost postures and have more prolonged periods of eye closure. I discussed other possible benefits of communal roosting including increased chances of predator detection, reduction in the intensity of the escape response, the Information Centre hypothesis and energy savings as a result of a superior microclimate. In view of the work of Whitlock (1979) and Swennen (1984) I believe that the ecological importance of roosting and roost-sites to waders should be the subject of further research. Traditional roost-sites are just as much under threat from industrial development as are feeding areas, yet almost nothing is known about the effects loss of such sites may have upon the birds. Moreover, once the characters that contribute to roost-site quality were documented, it is conceivable that artificial sites of high quality could be created to replace those lost.

In conclusion it is obvious that individual curlew utilise their environment in very different manners. In order to increase our understanding of the evolutionary ecology of wading birds and our ability to protect them, future research should be directed towards the identification and measurement of individual differences.

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APPENDIX 1.

RADIO-TELEMETRY: DESIGN, CONSTRUCTION AND SUCCESS OF TRANSMITTERS.

A1.1. Introduction.

Radio-telemetry involves attaching a miniture radio-transmitter to a free ranging animal and is now a fairly standard technique for locating or tracking wild animals. Simple transmitter designs provide information on the location of the individual and have been used extensively in studies of ranging behaviour. More complicated designs of transmitter have been used to permit remote data collection on activity, body temperature, heart/respiration rate, urination rate and so on. For reviews see Amlaner & Macdonald (1980) and Kenward (1987).

A1.2. Circuit design and components.

Transmitters had to be built from scratch for financial reasons. The circuit was designed around the following specifications:

- 1) the required range was 3km plus;
- 2) the desired package life was six months plus;
- 3) the finished transmitter/battery pack must not exceed the accepted safe mass limit of 5% of the body mass of the animal to be marked (Macdonald & Amlaner 1980). Working from the weight of the lightest bird caught, this gave an upper limit of 28g.

The requirements for long life and reasonably long range dictated the use of a relatively large, energy-dense battery, therefore, in order to conserve weight I decided to keep to the simplest circuit design possible, i.e. that first published by Cochran & Lord (1963) and updated by Kenward et al (1982) and Wilkinson & Bradbury (1985). The Cochran circuit I used is shown in Fig.A1.1 and the components listed in Table A1.1. Basically, the circuit works in the following manner; current flows through the resistor 'R1' and charges the capacitor 'C2', building up a potential difference (PD) across C2. When this PD reaches a sufficiently high value C2 will suddenly discharge, sending a pulse of

Fig. A1.1. Circuit diagram for construction of Cochran transmitter. C= capacitor, R= resistor, L= coil. See Table A1.1 for component specification.

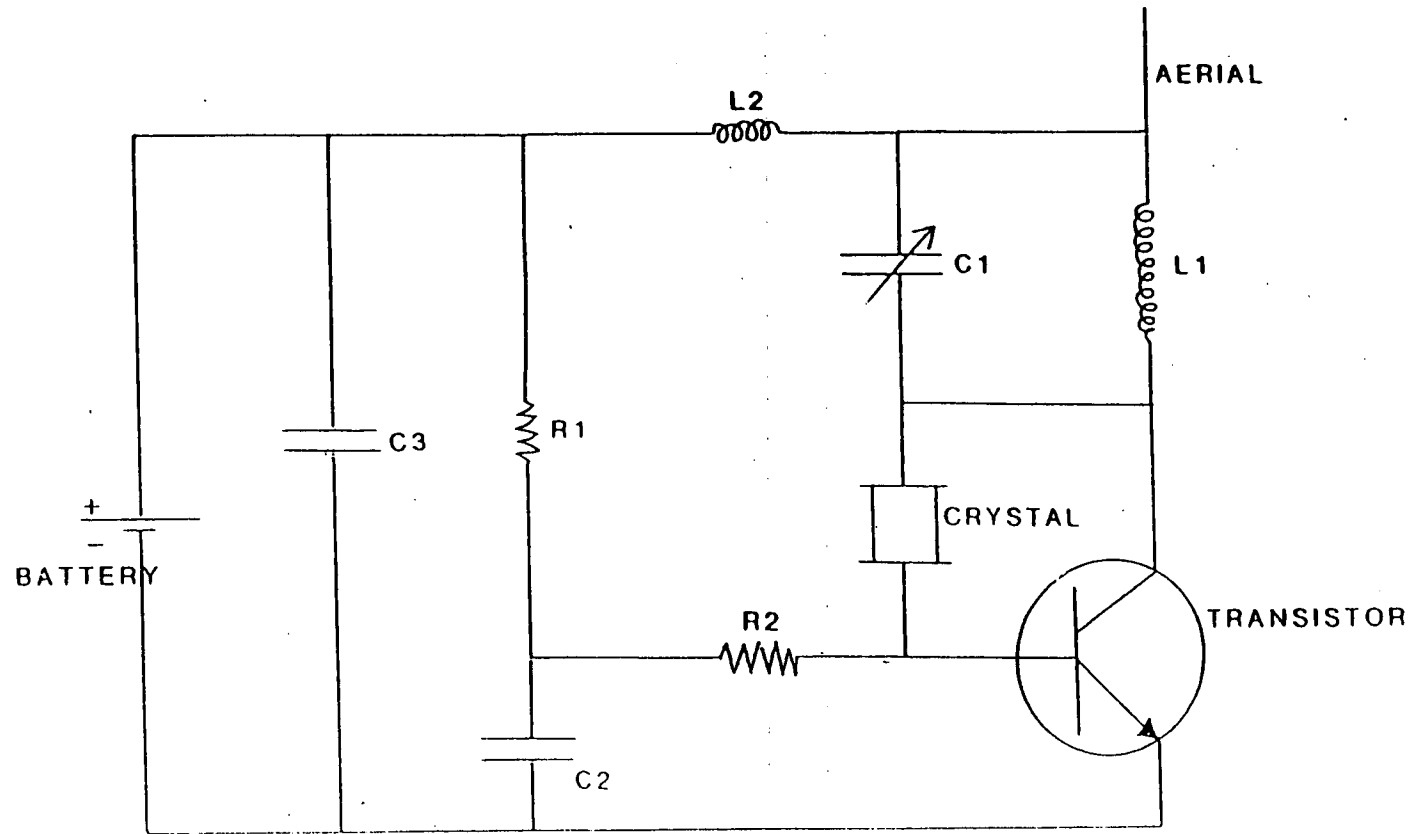


Table A1.1. Specification of components used in construction of Cochran transmitter.

COMPONENT	DESCRIPTION
C1	Trimmer (variable capacitor) 3.5-20 pF
C2	Capacitor (electrolytic) 4.7 μ F
C3	Capacitor 0.001 μ F
R1	Resistor 560 K
R2	Resistor 1.8 K
L1	Coil 17 turns 36SWG wire
L2	Coil 4 turns 36SWG wire
TRANSISTOR	Type 2N3904
BATTERY	Lithium Copper-Oxide 2.2v Type LC07
CRYSTAL	3rd Overtone Type HC-45
	Maximum resistance 35 ohms
	Maximum capacitance 2.4 pF
	Frequency 57.9-58.0 MHz

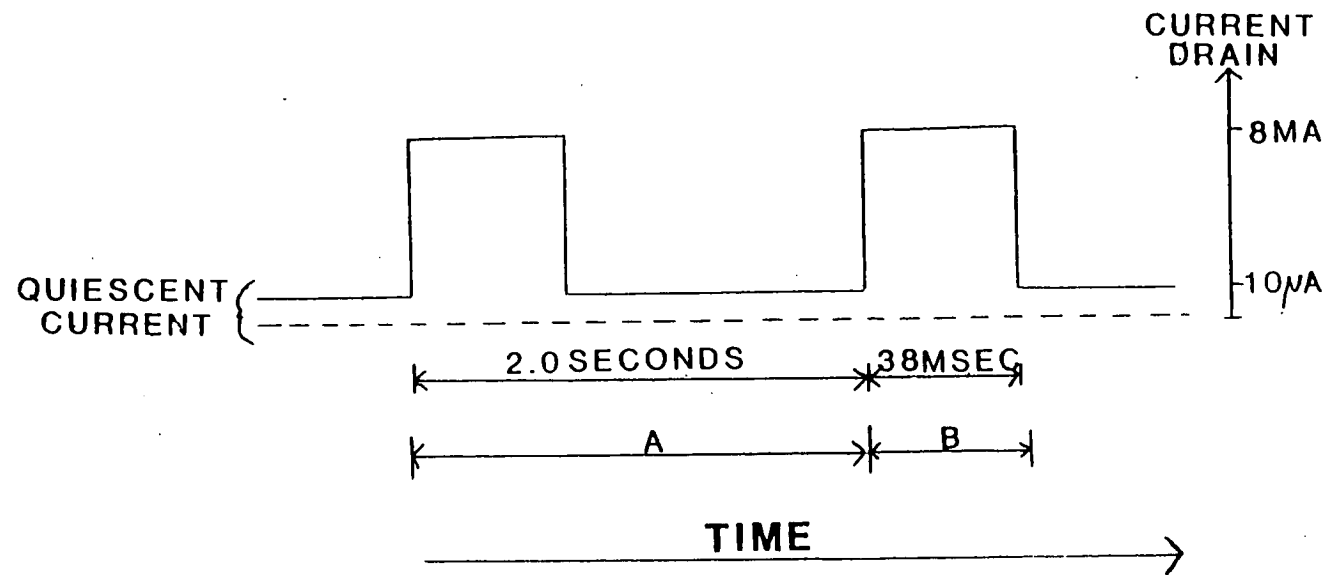
ALL COMPONENTS SUB-MINATURE

current through the transistor. The duration of the pulse is determined by the value of the resistor 'R2'. The pulse also travels through the coil 'L1', setting up a back electromotive force (EMF) as it does so, then charges the variable capacitor (trimmer) 'C1', thus building up a PD across C1. When the value of this PD exceeds that of the back EMF across L1, C1 will discharge back through L1 in the opposite direction, and so on for the duration of the pulse. The frequency of this current oscillation determines the frequency of the pulse transmitted through the aerial. L1 and C1 are collectively known as the oscillating circuit. To maintain accuracy, the current oscillation is entrained to the mechanical oscillation of the crystal. The nearer the frequency of current oscillation is to the frequency of mechanical oscillation of the crystal, then the more efficient the transmitter, therefore I used a trimmer at C1. By varying the value of C1 the frequency of current oscillation can be changed, so tuning the transmitter (see below). C3 is present to protect the battery from any back EMF and L2 is a choke coil to help match the impedance of the antenna to that of the air.

Together, C2 and R1 form the timing circuit. Increasing the value of R1 will slow the rate of charge of C2 and thus decrease pulse rate. I selected a value of R1 to give a pulse rate of about one every two seconds. The slower the pulse rate, the longer the life of the battery, but there is a trade off, since the chances of locating an animal which is moving quickly decrease with pulse rate.

Package life: the theoretical lifespan of the transmitter and battery pack is a function of battery capacity and average current drain. If these factors are known, then the life-expectancy of the radios can be estimated. I decided to use a lithium copper-oxide 2.2v cell (type LCO7, size 14mm x 12.5mm) which has a capacity of 1.4 ampere-hours (AH). The average current drain of a prototype device is shown in Fig. A1.2. This gives a theoretical expectancy of

Fig. A1.2. Representation of current drain. Quiescent (drainage) current can be ignored since it is so small. Average current drain $= 8/2 \cdot 38/100 = 0.152\text{mA}$. Battery life $= 1.4/0.152 \cdot 1000 = 9210.5\text{h}$, $= 384$ days. A = Interpulse Interval, B = Pulse Width (duration).



1.4 x 1000/0.152 hours, or 384 days.

Choice of frequency: Crystals are manufactured to specified frequencies, so it is important to know the desired operating frequency before ordering them. This was achieved by dividing the permitted frequency band for transmission (173.7–174MHz) into twelve to give the reception range for each of the 12 channels on the receiver (Table A1.2). Initially I had hoped to build 24 transmitters. It is desirable to operate with the largest possible separation between transmission frequencies, since devices are subject to frequency 'drift' in the field. Therefore I chose to operate with two devices per channel, with a separation of 12.5MHz (Table A1.2). The crystals I used were third overtone, which meant that I had to divide the desired operating frequencies by three in order to calculate the necessary crystal frequencies. It is also necessary to include a correction factor, the 'offset', into this calculation. The value of the offset can be measured by building a prototype transmitter with a crystal frequency of desired operating frequency/3, then determining the actual operating frequency. In my case the offset was -2.9MHz.

Coil construction: coils were made by wrapping the required number of turns of 36swg insulated wire around an empty inner tube of a 'Bic' biro. A weight was hung on both the free ends of the coil ('hackle pliers', used in tying fishing flies were found to be ideal for this purpose). The top of the coil was sealed with cyanoacrylate adhesive and left to dry for a few minutes. Finally the 'Bic' tubing was trimmed to the edges of the complete coil with a razor blade.

Antenna construction: The most suitable antenna for tracking is a whip aerial (Wilkinson & Bradbury 1985). Guitar strings were often used for this purpose, but they can become brittle and break. Like Green (1985), I used 45lb breaking-strain nylon coated, steel trace wire. Ideally the length of the antenna should be one quarter, one eighth or one sixteenth of the transmitted wave

Table A1.2. Calculation of required crystal frequencies from desired operating frequencies (see text for method).

	BAND WIDTH	CHANNEL	OPERATING FREQ.MHz	OPERATING FREQ./3	CRYSTAL FREQ.
1	173.700	A	173.706	57.9021	57.8992
	173.725	B	173.718	57.9062	57.9033
2	173.725	A	173.731	57.9101	57.9075
	173.750	B	173.743	57.9146	57.9117
3	173.750	A	173.756	57.9188	57.9159
	173.775	B	173.768	57.9229	57.9200
4	173.775	A	173.781	57.9271	57.9242
	173.800	B	173.793	57.9311	57.9284
5	173.800	A	173.806	57.9354	57.9325
	173.825	B	173.818	57.9396	57.9367
6	173.825	A	173.831	57.9438	57.9408
	173.850	B	173.843	57.9479	57.9459
7	173.850	A	173.856	57.9521	57.9492
	173.875	B	173.868	57.9563	57.9534
8	173.875	A	173.881	57.9604	57.9575
	173.900	B	173.893	57.9646	57.9617
9	173.900	A	173.906	57.9688	57.9659
	173.925	B	173.918	57.9729	57.9002
10	173.925	A	173.931	57.9771	57.9742
	173.950	B	173.943	57.9813	57.9784
11	173.950	A	173.956	57.9854	57.9825
	173.975	B	173.968	57.9896	57.9867
12	173.975	A	173.981	57.9938	57.9909
	174.000	B	173.993	57.9979	57.9950

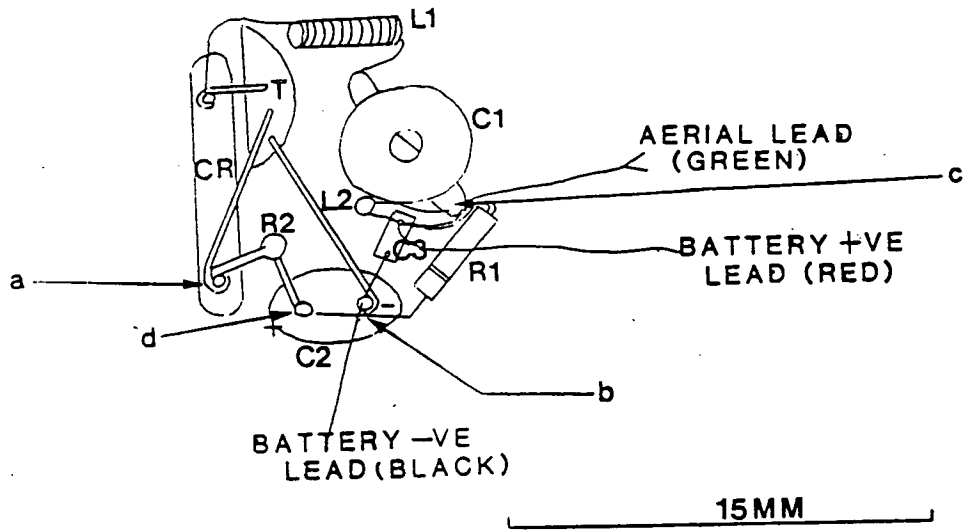
length (Amlaner 1980). Wavelength can be easily calculated by dividing the velocity of light by the operational frequency, in my case this was found to be about 1.73m. I used antennae one quarter of this length i.e. 43cm. About 2cm of the nylon insulation at the base of the antenna were removed and a small wire trimmed from a resistor lead was soldered to the steel using 10% orthophosphoric acid as flux. The trace wire was stiffened by consecutively shrinking a 40cm length of 1.6mm, a 25cm length of 2.4mm and a 15cm length of 3.2mm diameter heatshrink tubing around the nylon coating.

A1.3 Assembly of transmitters.

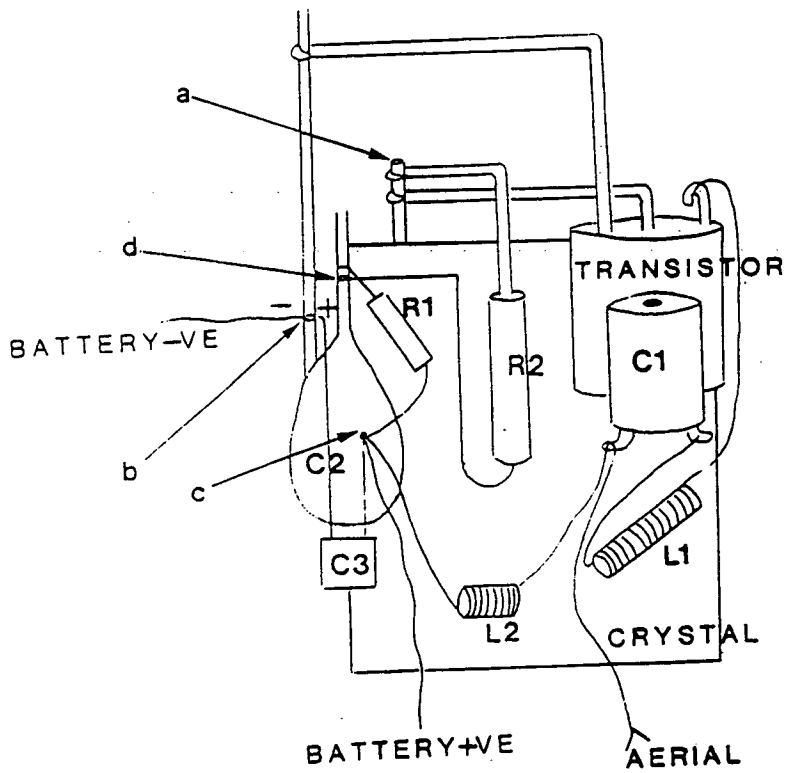
Prior to assembly all component leads were scraped clean of their oxide coating with the tips of sharp-nosed pliers. All leads and wires to be soldered were 'pre-tinned' by touching the tip of a pencil soldering iron to the lead/wire and the solder simultaneously and letting the molten solder run evenly over the lead. After each joint cooled it was inspected; if the joint was shiny and the meniscus concave, the joint was considered good. If the solder was tarnished, pitted or convex the joint was dismantled and remade. Before soldering all joints were made mechanically sound (self-supporting) by bending the component leads into the necessary shape. The build design is shown in Fig.A1.3. As is common in most commercially built transmitters, no circuit board was used; instead the device was constructed around the crystal casing. Firstly the mechanical joints between the transistor and the crystal leads were made, then those between R2 and the crystal. Joint 'A' could now be soldered. Mechanical joints were then created between R2 and C2, the transistor and C2, and C3 and C2 (care must be taken to ensure C2 is in the correct orientation). The battery negative lead was then placed in position and joint 'B' soldered. R1 was then placed in position and the battery positive lead and L2 were attached to C2 before soldering joints 'C' and 'D'. The trimmer, C1, was then soldered to the transistor, L2, L1 and the aerial lead. Finally L1 was soldered to the crystal.

Fig. A1.3. Build design of transmitter. C= capacitor, R= resistor, L= coil, CR = crystal. See Table A1.1 for component specification. Letters indicate joints referred to in text. See text for build order. Component separation exaggerated for clarity.

DORSAL VIEW



LATERAL VIEW



It is good practice to make all mechanical connections at any given joint before soldering; this helps prevent overheating through repeated application of the iron. The aerial lead was then soldered to the antenna. At this point the transmitter was tuned by temporarily connecting it up to a battery, then carefully adjusting the value of C1 using a specially designed 'trimming tool' until peak output was reached, as indicated by the needle deflection on the receiver, or the audio output.

A1.4 Potting and final assembly.

The assembled transmitter was cleaned by dipping it into a degreasing primer. I decided to pot transmitters in hard, transparent plastic specimen tubes (1.5cm deep x 1.3cm). An epoxy-resin potting mixture (Radio Spares part no. 555-077) was used, which when mixed with a catalyst (1:1 weight ratio) cures at room temperature in 24h. Each tube was half filled with the epoxy-catalyst mixture, then the transmitter and the antenna base were gently inserted into the tube, so that the potting compound was displaced up and around all the components. During this process the battery leads were held clear of the compound. This method alleviated problems with air bubbles in the compound. It was important to ensure that the base of the antenna was firmly potted; strain or breakage of the connection between antenna and aerial is a common cause of package failure (Wilkinson & Bradbury 1985).

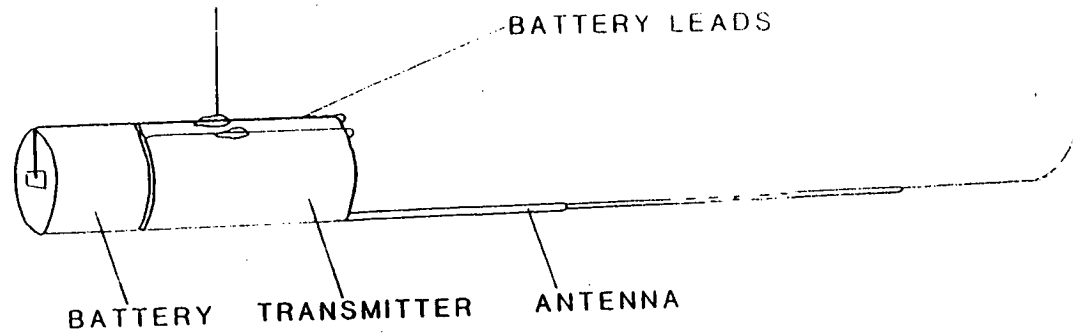
Once the potting compound had cured, insulated wires were soldered on to the battery terminal tags, and the battery was then glued on to the base of the potted transmitter (Fig. A1.4) using 'Araldite Rapid'. The positive and negative leads from the transmitter were then soldered to their counterparts from the battery. These connections were insulated with 1.6mm heatshrink tubing. Battery leads were glued to the dorsal surface of the package. The whole assembly was then sealed by painting it with a thin coating of silicon adhesive. Smears of this waterproof sealant were also painted around the

Fig. A1.4. Final assembly of transmitter package. A) fixing battery to transmitter, B) position of elastics.

HEATSHRINK INSULATION
OF CONNECTIONS

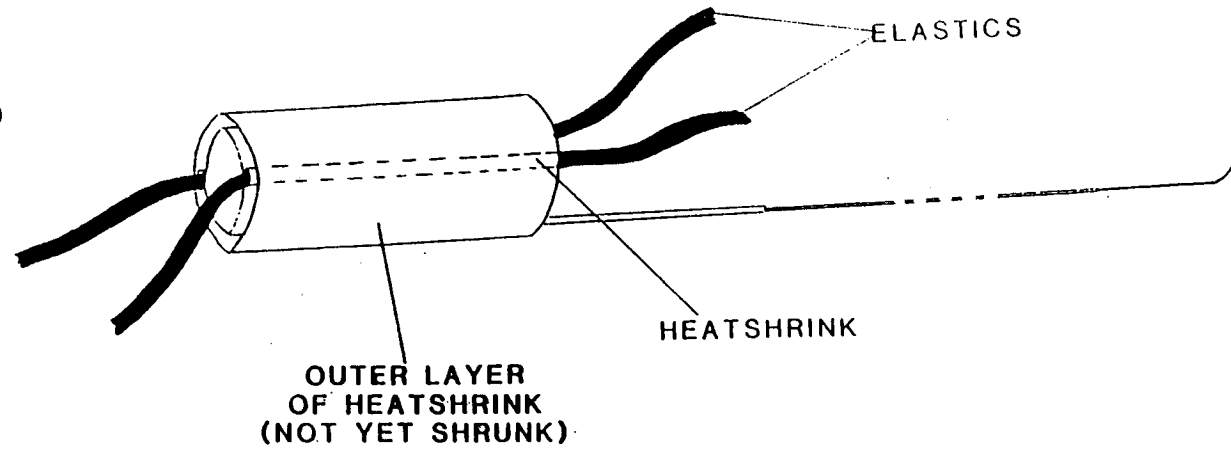
BATTERY LEADS

A)



30MM

B)

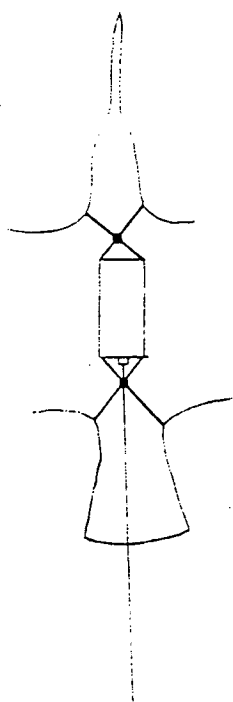


joints in the heatshrink sleeving around the antenna. Finally, two 1m lengths of six-cord flat 'knicker elastic' were cut, fitted with a 4cm length of 3.2mm heatshrink tubing at their mid-points and placed with their mid-points along the length of the assembly, one either side of the transmitter (Fig. A1.4). These were held in place by reducing a 4cm length of 16mm heatshrink tubing around the transmitter/battery assembly. The elastic strings on either side were joined in a reef knot immediately anterior and posterior to the package.

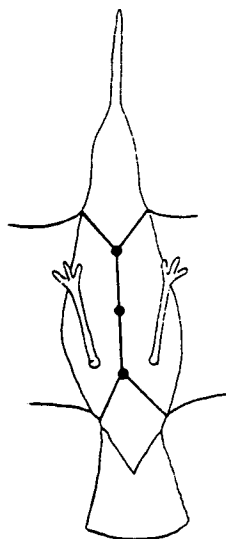
A1.5 Attachment of radios to birds.

There are three commonly used methods of attaching radio-transmitters to birds; backpacks, tail-mounts and leg-mounts (Kenward 1985), although breast-mounted packages powered by solar cells are becoming increasingly popular with researchers studying gamebirds. I rejected any thought of leg-mounts (often used on raptors) because of the problems associated with myopathy in curlew. Tail-mounts involve either sewing or glueing the package to the shaft of a tail feather. This would have caused problems with the positioning of the antenna, and obviously transmitters are dropped when the bird moults. Given that shock-moult is fairly common after attachment and that curlew were proving difficult to catch, I opted to use a back harness similar to that employed by Green (1985) on jackdaws, *Corvus monedula*. Prototype packages were attached to two birds and the final design to nine individuals. Attachment was the last operation before release of the bird. Two people were required to fix a transmitter in place; one held the bird in both hands, one either side of the wings, thumbs holding the package in place between the scapulas. The other took the two forward elastics one each side of the neck, and, applying slight downwards tension in order to draw the elastics into the base of the wings, fastened them in a double reef knot across the sternum (Fig. A1.5). The backward elastics were brought down behind the trailing edge of the wings and tied in a double reef knot between the legs. The

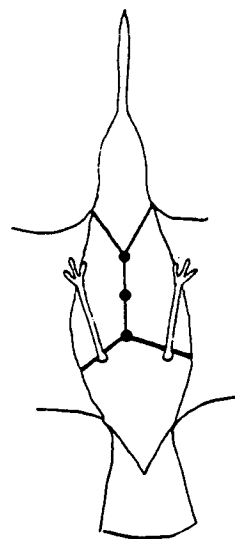
Fig. A1.5. Attachment of transmitter package to bird.



DORSAL VIEW



VENTRAL VIEW
METHOD 'A'



VENTRAL VIEW
METHOD 'B'

loose ends were brought through the legs and tied off to the loose ends of the forward elastics. On four birds the posterior elastics were taken in front of the legs before tying. The relative success of the two methods of attachment is discussed below. All loose ends were then trimmed and singed with a cigarette lighter to prevent fraying. It was important to apply the right amount of tension before tying any knots; if the package was too slack it could cause abrasion to the back and possibly interfere with flight whilst too much tension could cause severe restrictions on movement or feeding.

A1.6 Effect of radio-transmitters on birds.

Data collected in any study which involves placing a marking device on a free-ranging animal are only meaningful if the device is in no way detrimental to the individual marked. Cochran *et al* (1967) state: "It is axiomatic that attachment of a transmitter to a bird affects its behaviour.". If this is accepted as true (and in the absence of detailed behavioural data on colour-marked birds before and after attachment of radio-packs it is dangerous to dismiss the idea) then it is necessary to try and assess the degree to which packages affect their subjects. If there is an adverse effect upon survival or dispersal the technique is obviously unsuitable. If there is a short term reversible affect on other behaviours, this might be acceptable in the light of the data being collected. Several authors have already assessed the effect of radio-packages on avian subjects. Radio-transmitters did not impair the ability of red grouse, *Lagopus l. scotius*, to secure or hold a territory, but radio-marked birds were amongst the last to be flushed and slowest to accelerate although there was no evidence that this lead to increased mortality levels (Lance & Watson 1977). Boag (1972) discovered that captive red grouse marked with dummy radios showed lower levels of activity and lower food consumption among females than unmarked captive birds. These differences, however, were only apparent in the first week after attachment of the packs and no difference was observed in the pattern of

habitat use by marked and unmarked birds. Radio-transmitters appeared to cause atypical breeding behaviour (especially hampering courtship flight) in male woodcock, *Philohela minor*, (Ramakka 1972). Captive mallard, *Anas platyrhynchos*, and blue-winged teal, *Anas discors*, suffered feather wear and skin irritation after radio-attachment, but appeared to behave normally (Greenwood & Sargent 1973). Sargent *et al* (1973) did find that radio-marked teal *A. discors*, were more likely to be killed by mink, *Mustela vison*, than were unmarked birds. Johnson and Berner (1980) found no difference in the survival, dispersal or weight-gain of radio-tagged and untagged ring-necked pheasants, *Phasianus colchicus*, providing the birds were above a given weight.

It is thus impossible to make generalisations about the effect of radios on birds; this needs to be assessed for each species, with each transmitter design and each method of attachment. Two birds were fitted with prototype transmitters using the first method of attachment (elastics taken through the legs) during the 1985/6 season. On 18/9/86 a further nine birds had transmitters attached, although one was removed on the following morning as the bird was unable to fly and was suffering from myopathy (see chapter 1). This left six birds that carried radios attached by the first method and four attached by the second method (elastics taken in front of the legs) (section A1.5). Qualitative observations on all six birds with the first method of attachment suggested that these individuals appeared to be unaffected in the following behaviours: foraging, flying and preening although one individual appeared to have difficulty in adopting the normal roosting position, with the bill under the scapulars. The four birds with the elastics taken in front of the legs fared much worse; one was found dead two days after the catch (myopathy may have been causal here), one died approximately 10 days after the catch and another died 25 days after attachment. This last bird was found to have moderate to severe abrasion of the back, on both feather and skin as

reported for mallard (Greenwood & Sargent 1973). The fourth bird bearing a transmitter attached by the second method survived the winter and migrated, but appeared to be slow to flush (*cf* Lance & Watson 1977). The difference in mortality between the two methods of attachment (0% and 75% respectively) is significant ($\chi^2 = 6.492$, $p < 0.05$). I suspect that the mortality experienced using the second method of attachment may have been due to insufficient tension in the elastic, allowing the package to rub, causing irritation and hampering flight.

A1.7 Success of radio-packages.

Final transmitter packages met all the design specifications (Table A1.3). Package size was 3.8cm x 1.5cm, with a mass of 19.7g, well within the prescribed limit of 5% of body mass. Reception was adequate at ranges up to 4km. A prototype assembly kept transmitting for 13 months in the laboratory, but both prototypes placed on birds lasted for only 2 weeks in the field. I suspect that this was due to water entering the package by capillary action along the heatshrink sleeving of the antenna. I recovered one of the prototypes and there appeared to be some degree of corrosion within the encapsulation. Wanless *et al.* (1985) encountered a similar problem with packages for guillemots, *Uria aalge*. On the final assembly I took special care to waterproof these joints and did not encounter this problem again. Of the five successful radio-packs attached to birds on 18th September 1986, one stopped transmitting effectively after 47 days, two after 188 and 189 days respectively. The remaining two were still functioning when the birds migrated 223 and 231 days after attachment. Battery life in the field can be shorter than expected due to fluctuating temperatures (Macdonald & Amlaner 1980). Four out of the seven successful packages were known to have been shed by the birds between 9 and 12 months after attachment due to the rotting of the elastics.

SPECIFICATION OF RADIO TRANSMITTERS

PACKAGE SIZE: 3.8 X 1.5cm

PACKAGE WEIGHT: 19-20g

PACKAGE LIFE: 47- >231 days

PACKAGE RANGE: 5.6km

PACKAGE COST: approx. £12.50

ASSEMBLY TIME:

WIRING: 45mins

ASSEMBLY: 30mins

POTTING+CURING: 24H

Table A1.3. Specifications of completed transmitters.

APPENDIX 2.

AN INCIDENT OF TERRITORIALITY IN CURLEW FEEDING ON FIELDS.

A2.1. Introduction.

Territoriality, defined as priority of access to resources within a geographically defined area acquired by exclusion of conspecifics through social interaction (Kaufman 1983) is a behaviour pattern well documented in wintering curlew, *Numenius arquata*, feeding on the intertidal zone (Ens 1979, 1984, Phillips 1980, Townshend 1981a, Baber 1988). Cost/benefit approaches have often been adopted to explain this behaviour (Myers 1984, Townshend *et al* 1984). It seems likely that a major factor influencing territoriality in curlew is that birds feeding on the intertidal zone suffer from interference (an immediate and reversible drop in intake rate due to the presence of conspecifics, Goss-Custard 1980) as described by Zwarts (1979) and in chapter 4 of this thesis, rather than insurance against depletion of food stocks (Ens 1984).

Curlew also feed in field habitats during the winter (Elphick 1979, Townshend 1981b) where they form medium sized flocks, rather than feeding solitarily. In field-feeding flocks aggression is rare, normally being restricted to an occasional attempt at kleptoparasitism (pers.obs.). To my knowledge, territoriality in curlew has never before been documented on field habitats. Here I describe an incident of territorial behaviour on fields shown by one individual in abnormally severe conditions.

A2.2. Methods.

During a three year study of individual foraging specialisations of curlew at Scoughall, E.Loathian I made regular counts of birds feeding in fields, by driving a set route around the study site (chapter 3). One such census was made on 16/01/87 after a period of 6 days of deep snow cover. On this day there were sporadic snow showers and snow and ice were still preventing access by the birds to any field except a small corner of 'Knox Brook' (see Fig.

1.2). Here, a small triangular area, 16m x 20m, bordered on one side by deciduous woodland and on another by a small brook, was free of snow or ice cover (Fig. A2.1). In this region there were 11 curlew, 4 feeding under the trees, amongst fallen leaves, 6 trying to gain access to the snow-free patch but being prevented from so doing by the behaviour of the last bird. This individual was a male (based on my estimation of its bill length; see chapter 3) and exhibited all the behaviours associated with territoriality, including threat postures, hunched runs and/or short flights at intruders accompanied by the characteristic 'bubbling' call (Cramp & Simmons 1983). The boundaries of the territory were defined exactly by the edges of the snow cover and pursuit of intruders by the territorial bird never continued beyond this point.

I observed the behaviour of the birds between 11:20am and 12:26pm, when all were disturbed by a horseman. During this period I made 6 'focal animal' observations on the territory holder and one on each of the 6 intruders. These lasted between 1 and 6min and during each observation I counted the number of swallows made. Observations were conducted alternately to permit matched-pairs analysis. After the birds had been disturbed I took 30 measures of the ground penetrability within the territory and repeated these outside the territory. Penetrability was measured using the apparatus shown in Fig. A2.2. Basically this comprised a sharpened metal rod, 15cm in length by 0.6cm in diameter, attached to a wooden shaft 1.5m in length. A free-sliding grip was fitted over the shaft and attached to the spring of a spring balance. The top of the casing of the balance was secured to the shaft. Thus, by applying downward pressure to the grip, I could measure the pressure required to drive the tip (first 2cm), first half (first 8cm) and all of the rod into the substrate. Pressure was measured simply in pounds. Maximum pressure that could be recorded was 10 pounds; beyond this the ground was considered impenetrable.

A2.3. Results.

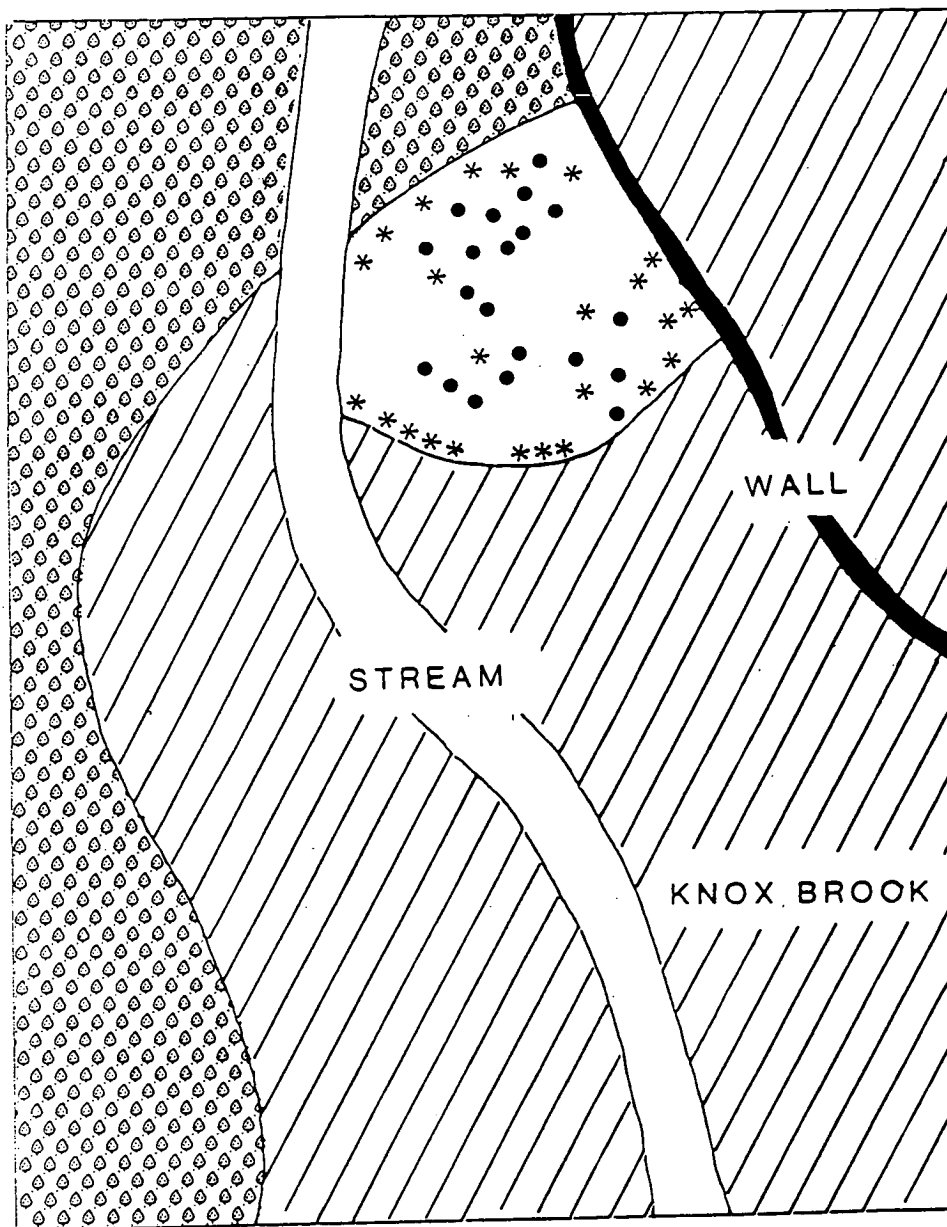
Fig. A2.1. Map of territory held by individual curlew on field.

Snow cover = 

Deciduous woodland = 

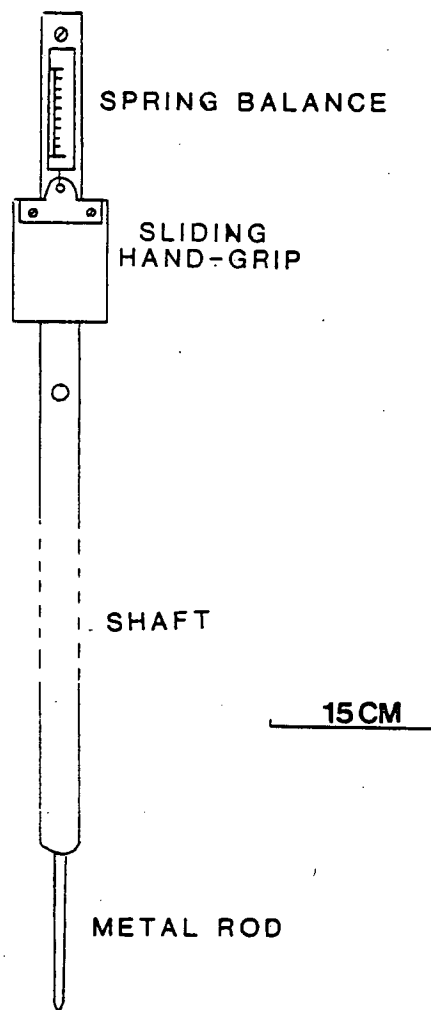
Sighting of territory holder feeding = ●

Supplant of intruder by territory holder = ✱



20M

Fig. A2.2. Apparatus used to measure substrate penetrability.



During the observation period I saw the territory holder drive out intruders on 24 occasions (0.36 supplants/min). Eight of these supplants were made against males, 3 against females and 13 against birds of undetermined sex. The six observations on the territorial bird totalled 13.1min during which time it swallowed 21 times, whilst only 2 swallows were seen during the six observations on intruders (9.7min). Both these were achieved from within the territory whilst the territory holder was itself feeding. The swallow rate of the territorial bird was in fact significantly higher than that of the intruders (Table A2.1, Wilcoxon matched-pairs signed ranks test, $T_s=0$, $N=6$, $p < 0.025$). The ground inside the territory was much softer than that outside (Table A2.2). It required significantly more pressure to insert the tip of the rod outside the territory than inside (Mann Whitney U-test, $W=608.5$, $p < 0.005$). At levels deeper than 2cm the ground outside the territory was mostly impenetrable. In fact the incidence of penetrability of both half and all the rod was higher inside the territory ($\chi^2 = 11.35$, $p < 0.001$, $\chi^2 = 8.23$, $p < 0.005$ respectively).

A2.4. Discussion.

My observations of this unusual behaviour pattern highlight the adaptive nature of territoriality. The territory holder spent much of its time in active defence, but nevertheless its swallow rate was consistently higher than that of intruders. Indeed, food availability outside the territory was effectively zero, since the ground was virtually impenetrable and the intruders only managed to capture prey at all within the territory whilst the territorial bird was itself feeding. Of course the swallow rate of the territorial bird would have increased had it not had to consistently defend the snow-free area. Since field-feeding curlew do not suffer from interference (chapter 4) it is likely that the major benefit gained by the territory holder was prevention of short-term depletion of prey in the snow-free area by conspecifics. This is in contrast to the situation on the intertidal zone where territories are probably defended to prevent

PAIRED OBSERVATIONS	
T ^y HOLDER	INTRUDER
1.794	0
5.037	0
0.578	0.375
0.791	0
0.705	0
1.361	0.508

Table A2.1. Results of matched-pairs observations of swallow rate (swallows/min) of territory holder and intruders.

TIP		HALF		ALL	
IN	OUT	IN	OUT	IN	OUT
6	9	9	*	*	*
9.5	*	*	*	*	*
6.5	10	9	*	*	*
9.5	10	*	*	*	*
8.5	10	10	*	*	*
8	9	10	*	*	*
4	10	7	*	8.5	*
8	*	10	*	*	*
5	*	9.5	*	9.5	*
9.5	8.5	*	*	*	*
8.5	6.5	*	*	*	*
9.5	9	*	*	*	*
5.5	*	9	*	9	*
5.5	5.5	9	9	*	*
9	8.5	*	9	*	*
7.5	9	*	*	*	*
8	9	9.5	*	*	*
4	9.5	8	*	10	*
5.5	7.5	7	9	8	*
3	9	5	*	*	*
2.5	10	5	*	8.5	*
8.5	9.5	10	*	*	*
6.5	*	8.5	*	*	*
8	9.5	10	*	*	*
6	*	7	*	7	*
8.5	*	9.5	*	9.5	*
9	*	10	*	10	*
9.5	*	10	*	*	*
7.5	9.5	9	*	*	*
9.5	8.5	10	*	*	*

Table A2.2. Pressure (in pounds) required to insert the tip, half and all the metal rod into the substrate inside and outside the territory. * indicates a pressure greater than 10lb required, therefore the ground was considered impenetrable.

interference (Ens 1984).

*"I'm closin' the book
On the pages and the text
And I don't really care
What happens next
I'm just going
I'm going
I'm gone"*

BOB DYLAN 1973.