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FACTORS INFLUENCING THE  
FORAGING AND ROOSTING BEHAVIOUR  
OF WINTERING BLACK-TAILED GODWITS  
(LIMOSA LIMOSA)

Brian A. Combes

Submitted in fulfilment of the Ph.D. thesis  
at the University of St. Andrews



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## ABSTRACT

This thesis examined the behaviour and ecology of a small population of black-tailed godwits wintering on the Eden Estuary, Scotland.

The godwits exhibited the typical behaviour of waders using an inter-tidal habitat during the non-breeding season. However, the godwits spent a surprisingly low proportion of the day feeding and formed a low-water roost. Energy intake during the day was not enough for overall requirements and much feeding must have been occurring at night. The frequency of the two foraging methods of the species was dependent on their relative energy intake rate.

Kleptoparasitism occurred between godwits. Although this behaviour was rare, the specialisation of the attacking bird was marked. A food-stealing attempt was targeted in such a way that the probability of a high energy item being taken was great.

The godwits were gregarious. Assessing the costs, of interference, and advantages, mainly to do with predators, to an individual of flocking, helped to explain the relative spacing behaviour of birds using the two feeding methods.

Godwits feeding in their preferred area were adversely influenced by the presence of roosting gulls and plovers. When these heterospecifics were present fewer godwits fed there and those that did foraged in deeper, less profitable, water. In the

presence of the roosting flock, the godwits reduced their vigilance rate. However, for most individuals this advantage was not great enough to allow them to maintain their feeding performance.

Juvenile godwits have much lower foraging rates than adults. An analysis of the components of foraging investigated the causes of the difference.

A detailed study of the low-water roost was made. Although there were microclimate and foraging benefits of being in the roost the overriding advantages were concerned with vigilance and predators.

CHAPTER 1  
INTRODUCTION

This study investigates the foraging and roosting behaviour of black-tailed godwits (Limosa limosa (L.)) wintering on the Eden Estuary, Fife, Scotland.

The details in this paragraph are taken from the review of the species in Cramp and Simmons (1983). The black-tailed godwit is a large wading bird (up to 240g), family Scolopacidae, with a long bill (up to 120mm) and long legs (up to 100mm). In common with many other sandpipers, the species exhibits sexual dimorphism with the female about 5% larger than the male. The bird breeds in damp open habitats in the north of the Palearctic. The nominate race, which summers in parts of western Europe, central Europe, and the U.S.S.R. east to the Yenisey, has a European population of about 100 000 pairs which winters mainly in west Africa north of the equator. The population of the Icelandic race (L.l.islandica), which breeds predominantly in Iceland, has increased markedly this century to about 20 000 pairs and winters in western Europe and around the Mediterranean. The Icelandic race has a bill on average 10% shorter than that of the nominate race, and has different

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summer plumage.

The status of the black-tailed godwit in the UK has changed over the last two hundred years. Formerly the species bred in England, principally in East Anglia and elsewhere north to Yorkshire, but by the middle of the nineteenth century it had become only a rare passage visitor (Cramp *et al.* 1983). Morley (1939) charts the improving fortunes of the black-tailed godwit in the first three decades of this century. Between 1900 and 1915 the species became more common both in the south of England and in Scotland. In the subsequent 20 years this increase continued in England, especially in the harbours and estuaries of Dorset and Hampshire, where records now occurred throughout the year and birds were beginning to winter in small numbers. It was during this period that black-tailed godwits were discovered wintering in large numbers in southern and central Ireland where previously they had been considered to be chiefly a passage migrant (Scroope 1940). Between World War II and about 1970, the wintering population in the U.K. and Eire increased further (Morley and Price 1956, Ruttledge 1966, Prater 1975), probably due to improved breeding success in Iceland caused by warmer springs (Prater 1975). From the mid 1960s there was a reverse in this climatic trend and in the early 1970s the winter population decreased in Britain. However, since then numbers have steadily recovered (Hutchinson 1986) and Ireland currently holds about 9 000 birds (Hutchinson 1979) and Britain roughly half that number (Prater 1981).

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The primary wintering areas of the species remain south and central Ireland and the south coast of England (Hutchinson 1986). The Shannon valley is the single most important site and has held flocks in excess of 1 000 birds for many years (for example Kennedy *et al.* 1954). At these favoured locations, there is a marked passage of godwits in April and between mid-August and mid-September (Hutchinson 1986). As well as becoming more common in winter, the black-tailed godwit resumed breeding in Britain in 1937 and has bred annually since 1952 (Cramp *et al.* 1983).

The national fortunes of the black-tailed godwit have been mirrored in Scotland. There were few records of the species in the country before 1900 (Baxter and Rintoul 1953), but, at the beginning of the century, there were observations at several coastal sites which continued in the east Fife area after 1915 (Morley 1939). Since 1930 there has been a steady increase in numbers in Scotland with the Lothians and Fife holding winter flocks and with regular breeding attempts occurring at a variety of sites (Thom 1986). The only regular site in Fife has been the Eden Estuary, which has a long-documented association with the black-tailed godwit. There are winter records of the bird on the Eden back to 1907 and wintering flocks have been present regularly from at least 1936 (Baxter and Rintoul 1953). The population on this estuary has built up from about 30 birds in the 1950s (Grierson 1962) to about 100 individuals in the late 1970s and early 1980s, although numbers may vary greatly from year to year (Dougall 1979, Smout 1986). This population, which is the most

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northerly wintering of the species (Cramp *et al.* 1983), is present from August to May, with a few birds present in the summer and a marked passage during April and again in September (Smout 1986).

Although we have this information on population fluctuation in Britain, there are few data concerning the behaviour and ecology of the black-tailed godwit. The species has been observed during the breeding season (for example Lind 1960), and a few studies have been made on birds wintering in Africa (Altenburg *et al.* 1985). However, little detail is known about the non-breeding habits in western Europe, although general observations in Britain have revealed that the species usually feeds in tight groups on fine mud in the inner stretches of estuaries (Goss-Custard 1970) and may take a large number of *Nereis* (Greenhalgh 1975).

The aim of this research was to describe the non-breeding behaviour and ecology of the black-tailed godwit and to look in detail at specific aspects of its foraging and roosting ethology during the winter. The characteristics of the study site and the methods commonly used throughout the study are outlined in Chapter 2.

The general behaviour of the black-tailed godwits is reported in Chapter 3. This section considers where the birds forage and how the numbers and time budget vary through the year. Subsequent chapters deal with aspects of the ethology of the godwits in winter.

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Chapter 4 investigates the general foraging behaviour of the birds in winter. The first section describes which areas within the preferred part of the estuary are used for foraging. There then follows a study of the energetics of foraging. The relative frequencies and energy intake of the two feeding techniques used by the species is looked at in relation to the tidal cycle. The results of the time budget analysis in Chapter 3 indicated that the black-tailed godwits on the Eden spend an unexpectedly large amount of the daytime roosting. An assessment was made as to whether energy requirements could be met during daylight hours with so little feeding.

Food stealing between black-tailed godwits is the subject of Chapter 5. Mathematical models are used to consider the nature of the behaviour and the degree of specialisation of the attacking bird. The energetic consequences of food stealing for both the attacker and its victim are also discussed.

Chapter 6 deals with the influence of conspecifics and other shorebirds on foraging performance. One section investigates flocking and spacing behaviour in relation to feeding and in terms of the benefits and costs to foraging and anti-predator efficiency. A large number of loafing gulls and plovers sometimes forms on the preferred feeding area of the godwits. In the second section, the influence of this heterospecific flock on the foraging behaviour and performance of the godwits is assessed.

## INTRODUCTION

A comparison between the foraging behaviour of juvenile and adult birds in early autumn is described in Chapter 7. Mathematical models are used to see which components of foraging are most important in determining the relatively poor performance of the juvenile birds.

The godwits formed low-water roosts on the Eden. Chapter 8 looks at the behaviour of birds at these gatherings in the light of contemporary ideas on the functions of communal roosting. There is a detailed report on the vigilance behaviour of sleeping birds.

Some concluding remarks are made in the final chapter.

CHAPTER 2  
STUDY SITE AND METHODS

2.1 STUDY SITE - THE EDEN ESTUARY

The Eden Estuary (56°degrees 22'N, 2°degrees 52'W; national grid reference NO475195) is centred 3km north-west of the town of St. Andrews, Fife, Scotland. Towards its west end the estuary passes through the village of Guardbridge and at the east flows into St. Andrews Bay (Fig.2.1). The estuarine system below Guardbridge is 5km long, mainly between 1 and 2km wide and consists of about 4.25km<sup>2</sup> of mud flats, which are divided by Martin's Point into Edenside Flat to the west and the larger expanse of Kincaid Flat to seaward (the areas are subsequently referred to as Edenside and Kincaid). These two areas differ substantially in aspects of their topography and, consequently, in their infaunas (Johnston *et al.* 1979). Edenside is the more muddy area and has relatively little vegetation, low salinity, and a long exposure time; it has relatively high concentrations of Macoma, Corophium volutator and Hydrobia ulvae. The eastern flats have large growths of Enteromorpha and abundant Cerastoderma edule and Arenicola marina.

## STUDY SITE AND METHODS

Nereis diversicolor is common in patches throughout the estuary.

Apart from a decline in wildfowl, which is probably related to the natural and extensive decrease in Zostera, the topography and ecosystem of the Eden have remained largely unchanged for at least 40 years (Johnson et al. 1979). This remarkable stability is linked to the lack of pollution; a paper mill at Guardbridge produces local effects, and R.A.F. Leuchars, which is adjacent to the estuary, creates a certain amount of noise, but these are likely to have had limited influence on the environment as a whole.

The Eden Estuary regularly supports nationally important numbers of grey plover (Pluvialis squatarola), bar-tailed godwit (Limosa lapponica) and redshank (Tringa totanus), and each winter holds between 8 000 and 15 000 waders (Moser 1983) which gives it one of the highest concentrations of shorebirds in Scotland (Bryant and McLusky 1976).

### 2.2 OBSERVATIONAL METHODS

This study was carried out mainly during the three winters 1984-5, 1985-6 and 1986-7.

Access was unrestricted along the south shore of the estuary, a hide (A) overlooked an area of saltmarsh used by shorebirds as a high-water roost (Fig.2.1). There was access to the north shore in the east and the west, with a hide (B) on a bank overlooking the Edenside Flats (Fig. 2.1).

## STUDY SITE AND METHODS

Preliminary studies confirmed the findings of Johnston *et al.* (1979), who suggested that black-tailed godwits used the high-tide roost on the southwest shore and usually fed west of Martin's Point. Subsequent observations were largely confined to the east of the estuary and were generally carried out from the hide on the north shore (referred to as the hide). The flats visible from this hide were defined as the study area. The other hide was only used to watch the high-water roost.

All observations were through a 60mm or 75mm telescope fixed to a tripod. A period of observations was referred to as a session. There was generally only one session per day.

Scan sampling (Altmann 1974) was used to investigate the overall behaviour of the birds under observation. The area was scanned from east to west, and the relevant details were recorded for each black-tailed godwit. Distance between birds was estimated in 'bird-lengths' - the horizontal distance between the breast and the tip of the tail in a normally standing bird, which is approximately 250mm (measured from stuffed specimens).

To study the details of behaviour, focal animal observation (Altmann 1974) was used. A bird was selected at random (random number tables were used to generate a number  $i$ ,  $i \leq$  the total number of birds, the  $i$ th bird in the scan was then used as the focal individual). If an interesting dichotomy, such as feeding alone and feeding in a group, was present, birds were alternately selected from the subsets. Once a bird was chosen it was watched

## STUDY SITE AND METHODS

for a fixed period timed by a digital audio timer; if an observation was interrupted during this time the data were ignored.

In the field, data were recorded on audio tape or paper and subsequently transferred to one of the St. Andrews University Digital VAX-11/780 computers. Statistical analysis was carried out using the SPSSX (SPSS Inc. 1986) and Minitab (Ryan *et al.* 1976) computer packages and followed Sokal and Rohlf (1981) and Siegel (1956). If necessary, data were transformed to meet the conditions of the statistical tests. Probabilities refer to two-tailed tests with significance taken at the conventional level of 5%. In some instances, the probabilities from independent tests of significance were combined using the procedures described by Sokal and Rohlf (1981: p779). Stepwise partial regression analysis was performed using the stepwise forward inclusion technique of SPSSX.

Further details of observational and statistical methods are given where appropriate in the text.

A few terms used throughout the study are described below.

Predicted high-tide (PHT) refers to the predicted time, and sometimes height, of the high-tide based on Admiralty Tide Tables. Day length is calculated as the time between sunset and sunrise, from the Astronomical Almanac at 56° latitude, plus an hour. This extra hour was added since, for a period before sunrise and after sunset, there is still much daylight; the figure is somewhat arbitrary, but gives a more sensible division between night and day. Diurnal refers to the time of daylight and not to a 24-hour

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period.

Parts of the study involved recording the length of various acts. Both short time intervals and the patterning of a behaviour were measured by making a continuous tone, on an audio tape that was running at a constant speed, during the period occupied by the apposite act. The duration of the tones could be measured by stopwatch at a later time.

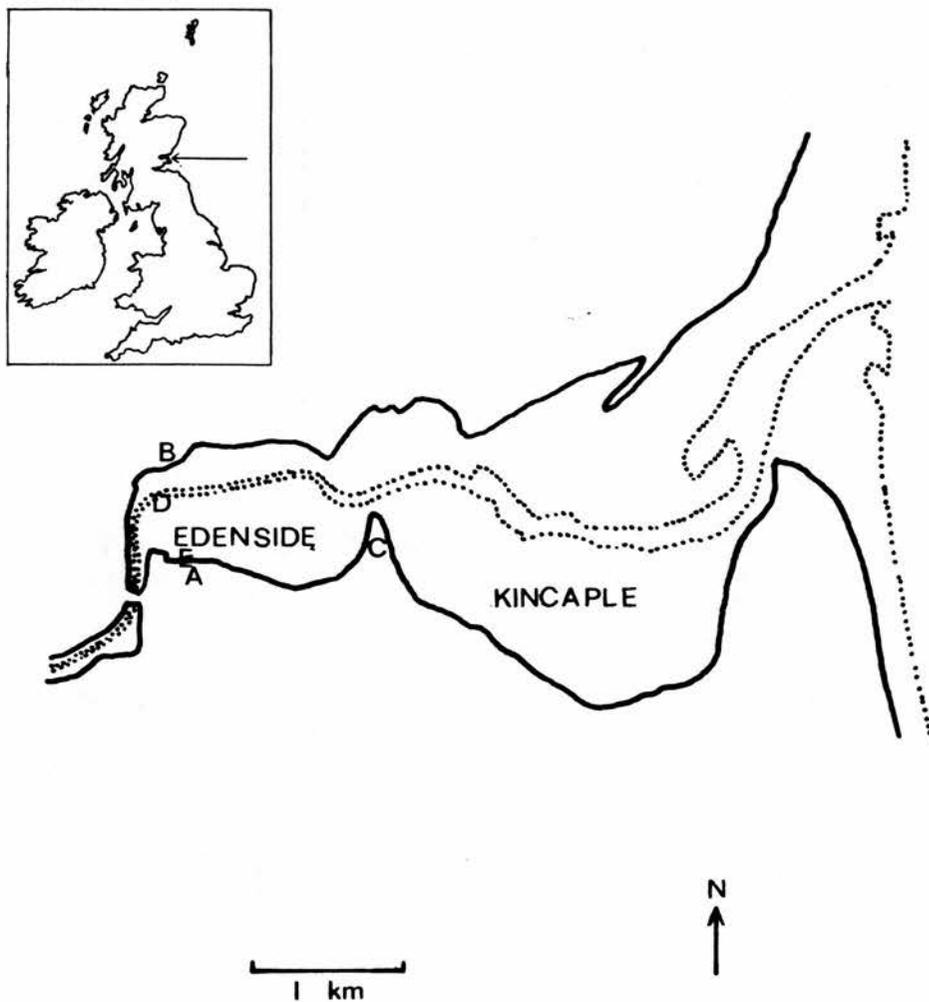
FIGURE 2.1

The Eden Estuary.

Inset indicates geographical position.

- A - hide on south shore
- B - hide on north shore
- C - Martin's Point
- D - position of low-water roost
- E - position of high-water roost

FIGURE 2.1



## CHAPTER 3

### GENERAL BEHAVIOUR

#### 3.1 INTRODUCTION

This chapter describes the general ethology and ecology of the black-tailed godwits on the Eden Estuary. There are two sections to the work: one looks at how numbers, habitat usage and diurnal time budget vary through the year, the other outlines the foraging and roosting behaviour. The chapter forms an introduction to the subsequent results, which deal in detail with winter behaviour.

#### 3.2 METHODS

##### 3.2.1 NUMBERS

At high-tide the black-tailed godwits stopped feeding and were present in one area. It is at this time that most wader counts are carried out, since during the rest of the tidal cycle birds are often dispersed throughout a habitat. However, counts at a high-water roost are likely to be inaccurate, due to the presence of other species and the high density of birds (Prater and Lloyd

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1987). These problems were encountered in this study and resulted in apparent black-tailed godwit numbers being lower at the roost that formed at high-tide on the saltmarsh at Guardbridge than just before or after it (Fig.3.1.). In addition, most behavioural observations were made from the north hide, from where it was not easy to see the saltings. For these reasons the high-tide was not an ideal time to assess total godwit numbers.

An experiment was carried out to see whether an accurate count could be made from the north hide. Counts made from the hide ('single' counts) were compared to counts made during a thorough search of the whole of Edenside Flats ('comprehensive' counts) (Fig.3.1). The comprehensive count remained fairly constant during the tidal cycle, and was therefore taken to be a good estimate of the number of godwits using the site. During low-tide and for most of the ebb and flow, the single count underestimated the number of birds. However, towards the end of the flood, the godwits usually formed a monospecific sub-roost or fed in a restricted area and were visible from the hide. Therefore, at this time, the size of the single count tended to coincide with that of the comprehensive count. Consequently, counts made at this time from the hide were used to monitor the number of black-tailed godwits using the estuary and were referred to as survey counts. Throughout the period November 1984 to May 1987 at least three survey counts were made each month.

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### 3.2.2 TIME BUDGET

To assess the mean amount of time the black-tailed godwits spent foraging requires an estimation of the proportion of birds foraging throughout the tidal period. This was carried out using scan samples taken at thirty minute intervals. The tide cycle was split into 12 sections, 1,2,...,12, where 1 covered the time between predicted high tide (PHT) and one hour after PHT, 2 the time between one hour after PHT and two hours after PHT, and so on. Section 12 was between 11 hours after PHT and the next PHT; due to the length of the tidal periods not being fixed, this last section had a correspondingly variable length, and for analyses its mean length of 1.41 hours was used.

For each month at least two scans were taken for every tidal section. The data recorded for a scan were the number of birds seen( $y$ ), and the number of these birds foraging( $x$ ). It was usually straightforward to decide whether a bird was foraging, since feeding birds generally had their bills either in the substrate or oriented towards it. However, between feeding bouts and between other activities, godwits sometimes walked short distances with their heads raised. Therefore, birds that were walking were watched until they started either feeding or another behaviour.

As described above, during most of the tidal cycle some of the godwits using the estuary were not visible from the hide. Observations on the birds away from the study area indicated that the proportion feeding was high and quite constant (0.9). This

## GENERAL BEHAVIOUR

allowed a correction factor to be used to estimate the percentage of the total population feeding for each scan ( $P_s$ ):

$$P_s = 100[v(z-y)+x]/z$$

$x$  = number of foraging birds visible from hide  
 $y$  = number of birds visible from hide  
 $z$  = total number of birds estimated from survey counts  
 $v$  = estimated proportion of birds not visible from hide that are feeding (0.9)

Scans were only used if at least 50% of the estimated maximum number of birds were directly represented in the sample. For each month, the mean percentage of the population foraging in each hourly section of the tidal cycle was calculated from the scan data:

$$P_i = \left( \sum_{x=1}^{x=n} P_s \right) / n$$

$P_i$  = estimated mean percentage of birds foraging during time interval  $i$   
 $P_s$  = estimated percentage of population foraging for a scan occurring in interval  $i$   
 $n$  = number of scans occurring in interval  $i$

The mean amount of time spent foraging during a tide cycle for

each month ( $P_m$ ) was then calculated:

$$P_m = \left( \sum_{x=1}^{x=12} P_i \right) / 12.41$$

Observations took place between August 1985 and July 1986.

### 3.2.3 Habitat Usage

The estuary was divided into 13 sections of unequal size, chosen mainly due to physical features which made delimitation of the sections easy in the field (Fig.3.2). At various tide heights it

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was noted which sections held or did not hold black-tailed godwits. To ensure a degree of independence, each survey was followed by at least three hours before the next. For every month a 'usage index' was calculated for each section as the percentage of occasions an area searched held one or more godwits. Observations took place between August 1985 and July 1986.

### 3.3 RESULTS

#### 3.3.1 NUMBERS

The variation in the mean monthly survey counts throughout the study is shown in Figure 3.3. The data were split into annual sections, with a year taken to finish at the end of May, by which time migrating birds had largely left the site. Each of the three years showed the same pattern: a few birds in summer, increasing numbers in autumn, but with no marked peak, a fairly stable winter population and a large passage in spring. This pattern can be considered in greater detail:

##### 1) Summer (June/July)

After the spring passage, a few birds (less than thirty) remained on the estuary. Characteristic of non-breeding waders remaining on the wintering grounds, these individuals did not develop summer plumage and were likely to have been young birds or adults in poor condition (Hale 1980).

##### 2) Autumn (August-October)

Numbers increased steadily in these three months as birds arrived from the breeding grounds; the initial build-up probably involved

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failed breeders, with large numbers of adults and juveniles causing a peak in October.

### 3) Winter (November-February)

The number of godwits remained quite level through this period, and stability over a period of days could be very high (Fig.3.4).

The winters 1984/5 and 1985/6 showed the same census pattern and also the same population level of about 110 birds. Maximum counts varied little between the months and the variation within the months was also small (coefficient of variation less than 7% in six of the eight months). Minimum counts varied more, with a marked trough in February which was related to climatic factors. Both these winters in Britain were severe and similar (Davidson and Clark 1985, Clark and Davidson 1986). In February 1985 there was very cold weather, including several days of extreme easterly winds combined with low temperatures. Again in the following February there were, towards the end of the month, strong winds as well as freezing conditions. These inclement periods coincided with the low counts.

The population level in the winter 1986/7 was lower than the preceding two years, with a mean monthly maximum of 80. With the exception of January, when there were very severe weather conditions, the pattern of numbers was similar to the other years, with little variation between months. In the inclement periods of 1985 and 1986, Scotland was less affected than England and intertidal areas generally remained unfrozen. However, during the cold spell in 1987, the Eden was frozen for several days, which

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resulted in the absence of godwits from the Estuary for at least four days (Fig.3.5). As soon as parts of Edenside became free of ice, birds returned. Over 30 birds were present within four days of the last of the sub-zero daytime temperatures, and by the end of the month the population was at the same level as before the cold weather.

### 4) Spring (March-May)

The counts in March were similar in pattern to those for the winter months; in March 1986 a relatively low minimum count was considered to be due to the continuation of the severe weather of the previous month.

In the three years April had the highest mean count, with all of the peaks occurring in the third week. By April the majority of birds had developed some summer plumage and many had completed their moult. The increased numbers during spring indicate that the estuary is used as a staging post by birds wintering further south, who were flying to the breeding grounds in Iceland. It is possible that, in the course of this passage, several hundred individuals pass through the estuary.

In 1985 there was a sharp decline in the population at the very end of April, with numbers fluctuating and staying around 50 for the duration of May (this is the general pattern of 1986, although there were fewer data for that year). In 1987 the decline in numbers was earlier and no more than ten individuals were seen in May, and none in full summer plumage. This relatively early migration coincided with very mild weather during April. Metcalfe

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(1984a) reported breeding waders leaving Scotland earlier than normal in response to warm conditions.

### 3.3.2 Time Budget

The black-tailed godwits on the Eden Estuary showed the activity pattern typical of waders feeding in the intertidal zone (see Puttick 1984 for a review). The vast majority of time was spent sleeping or foraging. At high tide, regardless of whether the substrate was totally covered or not, the birds roosted. Greatest feeding activity occurred during flooding and ebbing water, with a roost forming during low-tide.

The mean percentage of godwits foraging over the tidal cycle is shown for each month in Figure 3.6. There is a characteristic bimodal pattern, with the peaks in foraging activity occurring during the flood and, to a lesser extent, on the ebb. In spring, the ebb peak was more marked and more birds foraged around low-tide. Figure 3.6 also lists, for each month, the estimated mean percentage of the tide cycle a godwit spent foraging. Although there was little difference in the foraging intensity between the months, except in spring (March, April and May), foraging intensity was significantly influenced by the time of year, as well as by the state of the tide (two-way ANOVA: month  $F[9,677]=8.1$   $P<0.001$ ; tide  $F[11,677]=59.1$   $P<0.001$ ). However, foraging activity was not different between autumn and winter (ANOVA: season  $F[1,536]=3.2$  NS; tide  $F[9,536]=26.1$ ), but was greater in Spring than in the rest of the year (ANOVA: season

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$F[1,663]=45.6$   $P<0.001$ ; tide  $F[9,663]=21.3$   $P<0.001$ ). The interaction term in the last analysis was significant ( $F[9,663]=2.3$   $P<0.05$ ), which was due to the particularly large increase in foraging activity during low tide in the spring (see Fig.3.6).

An estimate of the mean number of diurnal hours spent feeding per day can be calculated for each month (Fig.3.7). This is carried out using the values for the mean percentage of the tide cycle spent foraging and the mean daylength. There is a trough in the value during the winter months (especially November, December and January). The number of hours is high in Autumn and especially great in Spring, with a peak in April.

### 3.3.3 Habitat Usage

Three of the thirteen sections that the Eden was divided into for monitoring habitat usage were never seen to hold black-tailed godwits (sections 3, 12 and 13 on Fig.3.2). One of these (3) was adjacent to the Paper Mill at Guardbridge and the mud there was polluted and often disturbed. The other two areas were part of Kincapple and formed the outer estuary, which was relatively sandy. The three other sections of Kincapple were used rarely and the species was largely restricted to Edenside.

The pattern of usage was fairly standard throughout the year and, for all months, the south-west quadrant of Edenside to the south of the river was the most regularly used section (Fig.3.8). For the three Flats (Guardbridge, Edenside and Kincapple) and for

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each season, calculations were made as to the number of occasions each Flat was used or not used by godwits. For each Flat the ratio of being used to not being used did not differ between autumn and winter, but in spring, compared to the rest of the year, there was significantly greater usage of Guardbridge ( $G[1]=15.7$   $P<0.001$ ), Edenside ( $Gadj[1]=4.1$   $P<0.05$ ) and Kincaple ( $G[1]=24.7$   $P<0.001$ ).

The usage data were concerned with the parts of the tide when mud was exposed. At high tide, the godwits invariably roosted on the saltings at Guardbridge, or on Edenside if this area was not entirely covered.

### 3.3.4 GENERAL BEHAVIOUR

#### Roosting Behaviour

The black-tailed godwits slept (see Amlaner and Ball 1983 for definition of avian sleep) at high-tide and to a lesser extent at low-tide. At both these times they gathered in a group.

Towards the end of the flood tide the godwits formed a sub-roost in a position close to the last area they had used for foraging. As the water flowed members of the flock periodically moved into more shallow water until most of the mud had been covered. At this stage, the godwits moved in groups or all together onto the adjoining saltmarsh often dispersing amongst other waders. When the high-tide left a boundary of mud or shallow water around the saltmarsh, the godwits often remained there in a

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discrete and monospecific group. This meant that during a neap tide the high-water roost could be some distance from the saltings.

The black-tailed godwit was one of the first species to start roosting during the flood-tide; after curlews and oystercatchers and before the smaller birds. This is the typical pattern for a multi-species roost (Hale 1980).

When the ebb uncovered the mud the smaller waders soon left the saltmarsh and started foraging. As the roost broke-up the black-tailed godwits often formed a sub-roost at the water's edge prior to feeding.

At low-tide a roost formed close to the water's edge on Edenside, opposite the paper mill. This flock tended to be linear and parallel to the tide-line, a similar pattern to the sub-roosts. Unlike its high-tide counterpart, this group did not tend to include all the godwits using the estuary, since there were usually some birds feeding at this time. As the tide flooded, this flock gradually began to break up as birds began to feed.

### Foraging Behaviour

Like roosting behaviour, foraging tends to be gregarious in the black-tailed godwit, although it is not uncommon for birds to feed alone.

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Under normal weather conditions, the species was only observed feeding on the estuary and rarely used the surrounding countryside (I Cumming, I Strachan pers. comm.). Fields adjoining the south side of the estuary were found to contain, usually at high-tide, ringed plovers, oystercatchers, curlews and redshanks, but never godwits. Within the estuary, foraging was restricted to the uncovered mudflats or water shallow enough to allow wading. However, in spring, birds sometimes foraged on the saltmarsh at high-tide and, during inclement weather, did very occasionally feed outside the estuary on the golf courses adjacent to the south side of Kincahle (I Cumming pers. comm.) and on fields around Guardbridge (D Bullock pers. comm.).

Black-tailed godwits can find food by tactile and visual means. The former involves moving the bill in the substrate until an item is encountered; in the latter sight is used to locate prey.

In waders, especially sandpipers, the visual cue is often not the animal itself, but an indication that it is below the surface at a specific point. The subsequent manipulation of such an item will be by touch and the forager will have used at least two senses in locating the invertebrate. Characteristically, a sandpiper foraging in this way walks while observing the substrate and occasionally pecking it lightly. These pecks are thought to be exploratory and may be followed by deeper probing to search for and handle prey.

## GENERAL BEHAVIOUR

Tactile foraging may be guided initially by visual cues to select an appropriate area; the bird then moves the bill continuously through the substrate, often while walking, until an item is found.

The method which tends to depend on a visual cue to find a particular item can be termed 'probing', and the technique where sight does not tend to be used to detect a specific prey can be termed 'stitching'. The godwits used both these methods.

Stitching was the more common feeding method and was especially prevalent during flood and ebb periods. Birds using this method often formed compact groups and generally fed along the tide-edge in shallow water.

Probing was relatively common during low-tide and was usually used on open mud. Birds feeding in this manner were frequently quite dispersed and sometimes solitary.

Periodic attempts were made through the winter months to collect pellets, regurgitated by black-tailed godwits while they roosted at high-tide. The area where the birds usually roosted was cleared of all pellets before the flock formed. The roost was then watched and, afterwards, any area which had been cleared and where only the godwits roosted, was searched. From eight successful occasions a total of 12 pellets was recovered: all contained both the jaws of Nereis and shell fragments from Macoma.

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During feeding there were occasional interactions between godwits, and, more rarely, encounters with heterospecifics. Other species regularly using the same part of the estuary were redshanks, curlews, dunlins, and oystercatchers and, during the autumn and winter, large numbers of roosting gulls, golden plovers and lapwings.

### 3.4 DISCUSSION

The Eden Estuary is used by wintering, passage and non-breeding summering Icelandic black-tailed godwits.

In winter the number of godwits was very stable, a feature of other wintering wader populations (for example Townshend 1981a), including those of marbled godwit (Kelly and Cogswell 1979, Gertensberg 1979). Some smaller shorebird species may be more vagile, including the sanderling (Myers 1984) and the knot, which can regularly move 30km during short periods and over 200km in a single winter (Pienkowski and Clark 1979). These two species are thought to be mobile due to the unpredictability of their food sources (Myers 1984, Pienkowski and Evans 1985). In this study, only in very adverse conditions did large numbers of godwits leave the estuary, and then only temporarily, suggesting that the movements were local. During one of these troughs in abundance, godwits were seen on the Tay at Kingoodie (N0335294) (J Steele pers. comm.), a site that has attracted the occasional party of black-tailed godwits, especially in Autumn, since at least 1937 (Baxter and Rintoul 1953). Another location where the godwits

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possibly visit is the Forth, which, like the Tay is a large open estuary more likely to be resistant to freezing than the Eden.

The peak spring passage counts were at least 50 percent greater than the winter population level and, due to turnover, which can be expected to be quite high at this time (Prater and Lloyd 1987), the total number of birds using the area may be considerable. The location of the Eden probably means that it will be the last feeding site for these godwits before they reach Iceland.

The autumn passage started in August and was less marked. Adults were the first to arrive, with the juveniles, which have probably not experienced an estuary before, arriving a month later.

Like the number of godwits using the estuary foraging activity also shows seasonal differences. In spring the proportion of the tidal cycle spent feeding is significantly greater than for the rest of the year. When daylength is taken into consideration, the number of diurnal hours spent foraging in spring is at least twice the figure for winter. Few shorebird studies have compared time budgets between seasons, although energy intake has been reported to increase during spring and also in autumn (Pienkowski *et al* 1984). The relatively high values at these times are related to moult, which can greatly increase metabolic demands (Kendeigh *et al* 1977), and preparation or recovery from migration. Unlike the birds in this study, many shorebirds increase the percentage of the tidal cycle spent foraging from autumn to winter; indeed, in

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winter, small species tend to feed whenever the substrate is available (Puttick 1984). In contrast, during the winter, black-tailed godwits spend, on average, about a third of the tidal cycle foraging; this compares with 50% for curlews and oystercatchers and 70% for bar-tailed godwits on the Wash (calculated from data in Goss-Custard *et al* 1977), and 60% for black-tailed godwits on the Ribble (calculated from data in Greenhalgh 1975).

Foraging activity also varies over the tidal cycle. The pattern is similar for all months, with the greatest feeding effort on the ebb and, especially, the flood. This is characteristic of other shorebirds (Puttick 1984), but the formation of a low-water roosting flock is not. There are reports of other waders roosting at this time (Townshend 1981a, Myers 1984), but these do not involve the majority of the population, gregariousness, nor the use of particular sites.

In spring, the godwits may be found in most areas of the estuary, while at other times the birds are largely restricted to Edenside. Like most of Edenside, the areas which tend to be used on Kincaple and Guardbridge share substrates that are glutinous mud (Johnson *et al* 1979); indeed, the fit between the two distributions is very close. This substrate is the characteristic habitat for black-tailed godwits in Britain (Cramp and Simmons 1983), and distinguishes the species from the bar-tailed godwit, which, although similar in morphology, tends to use sandy habitats (Cramp and Simmons 1983).

## GENERAL BEHAVIOUR

It might be thought that, because the Eden Estuary is the northern limit of its wintering range, the black-tailed godwits there would be under environmental stress. However, under normal winter weather conditions, this appears not to be the case. The species spends more time asleep during the tidal cycle than birds of comparable size in other studies, and has a stable winter population. Only during periods of extremely severe weather, which would have been encountered anywhere in Britain, did the population level fall and the birds exhibit behavioural signs of hardship.

This chapter has dealt with some general aspects of the behaviour of the black-tailed godwits on the Eden Estuary. Specifically, it has looked at how the population, habitat usage and time budget vary through the year, and has described general behaviour.

In the following chapters aspects of the foraging and roosting behaviour in winter will be outlined in greater detail.

FIGURE 3.1

Number of black-tailed godwits counted on the Eden Estuary (expressed as percentage of maximum count) through the tidal cycle. Data were collected for half a tidal cycle on two consecutive days in October 1985. Open circles are comprehensive counts taken from the north shore, closed circles are single counts taken from the north hide, and triangles are high-water roost counts taken from the south hide.

FIGURE 3.1

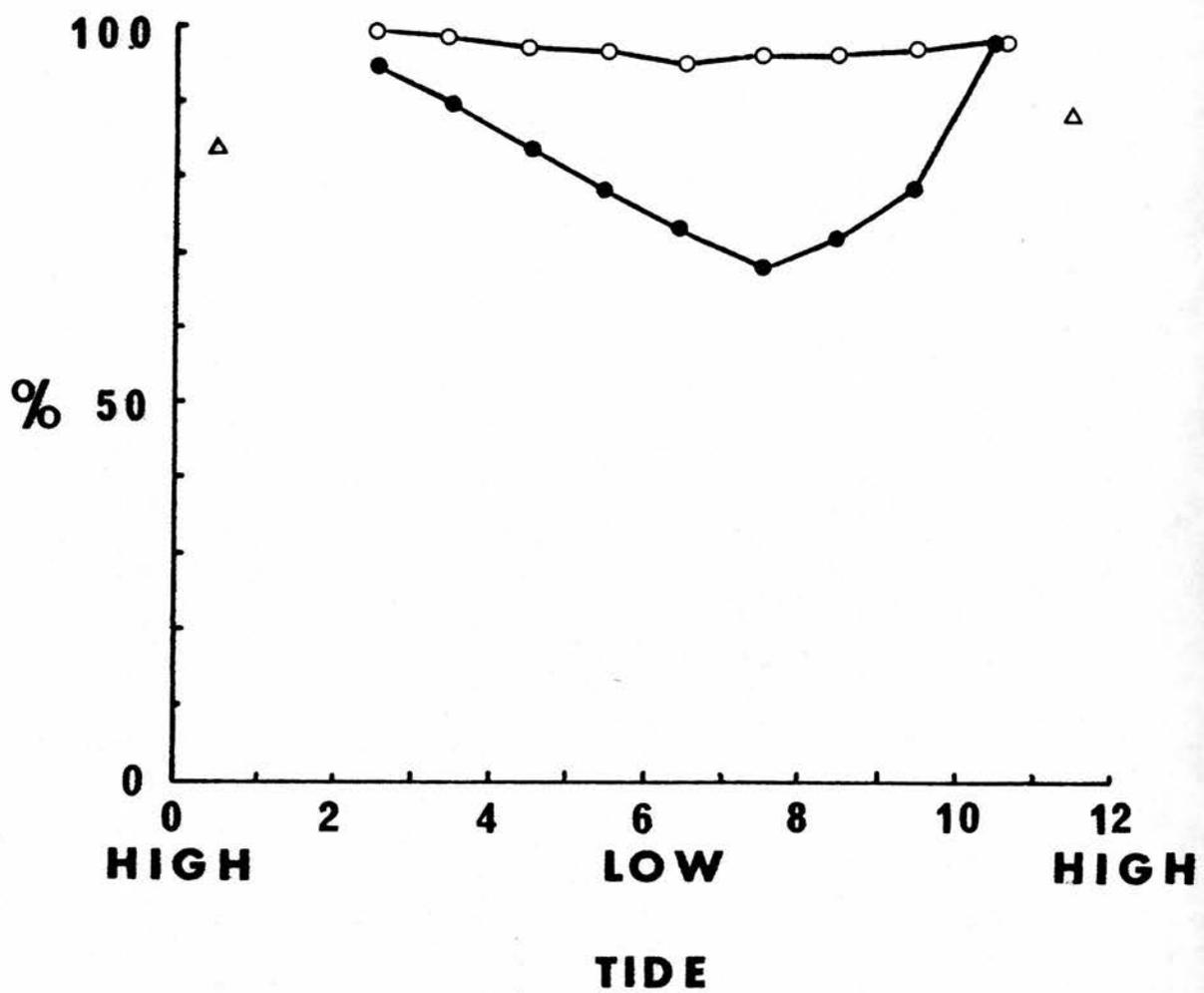


FIGURE 3.2

Division of the Eden Estuary into sections.

FIGURE 3.2

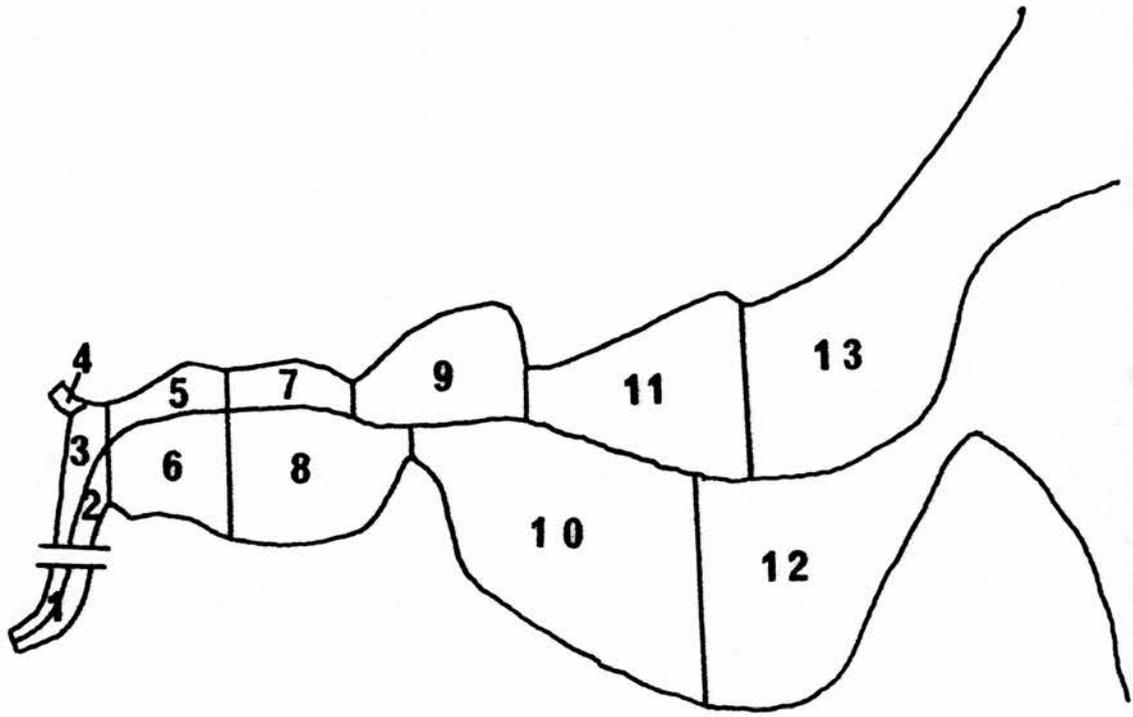


FIGURE 3.3

Variation through the year of the number (N) of black-tailed godwits using the Eden Estuary. The survey counts taken in each month were averaged. Bars indicate the range of the survey counts.

FIGURE 3.3

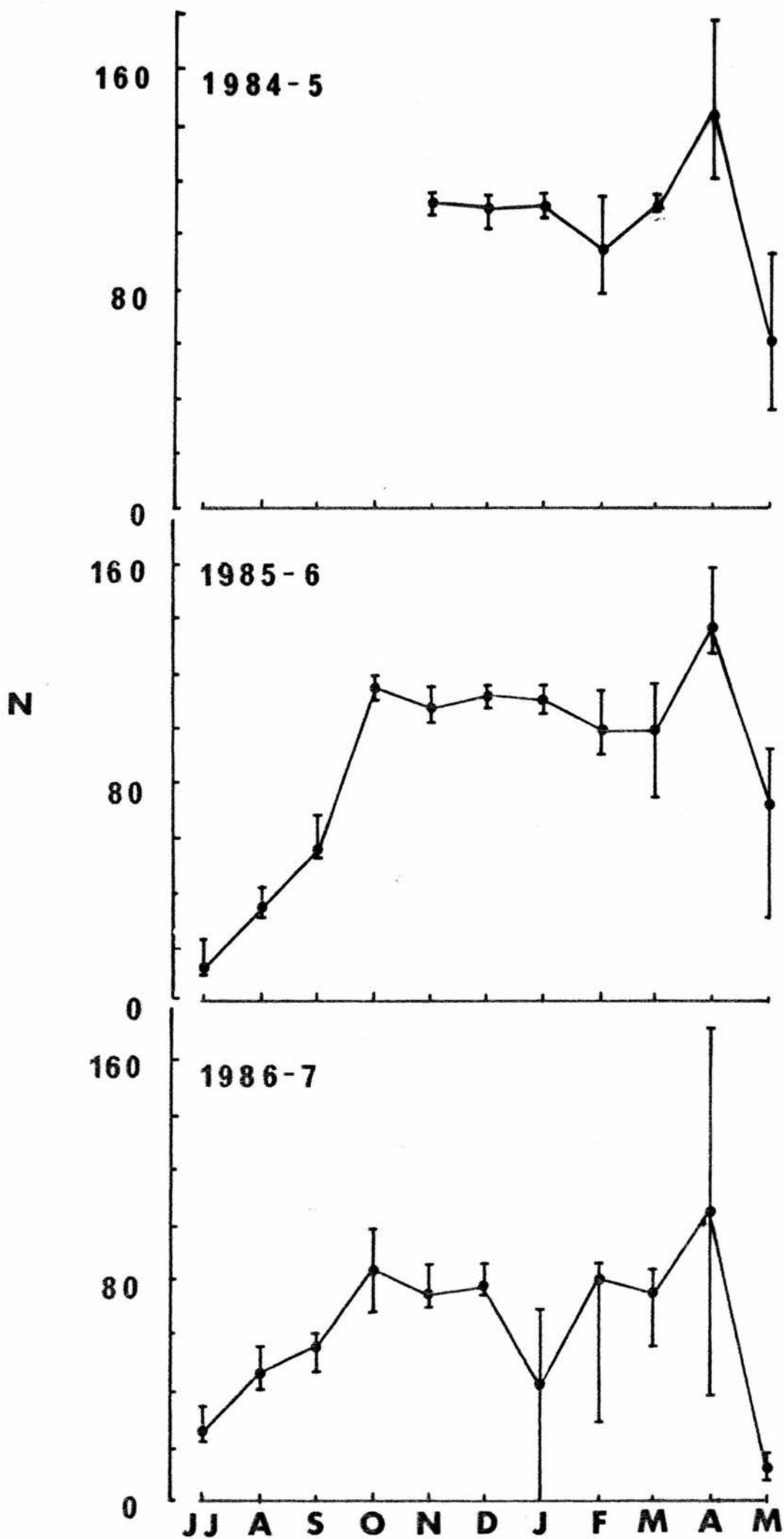
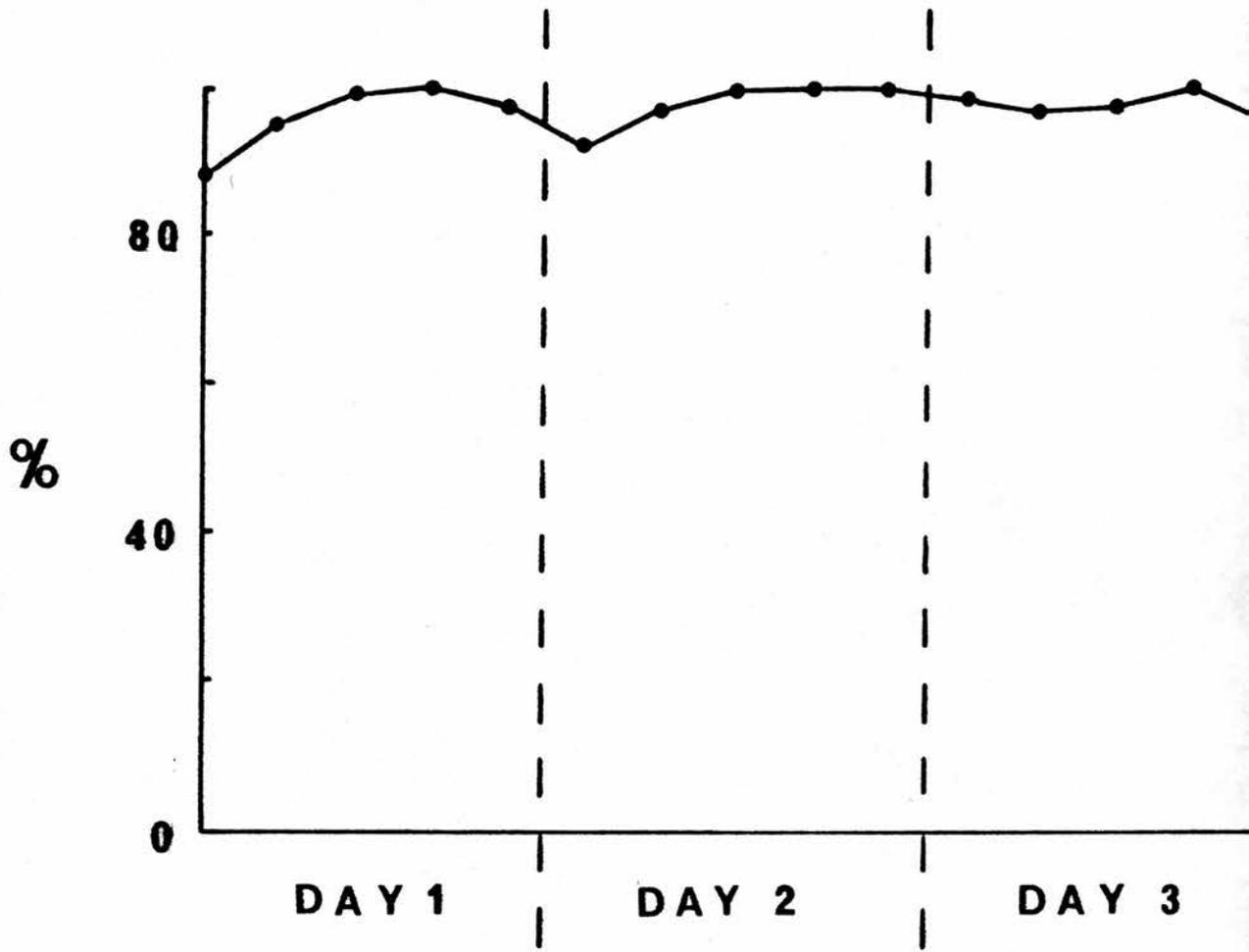


FIGURE 3.4

Stability in the size of comprehensive counts over a three day period during November 1985. The y-axis is the size of the comprehensive count as a percentage of the largest comprehensive count taken during the three day period. Each count was separated by at least one hour and was not made at high-tide. Data are plotted as a time series. Coefficient of variation = 3.5%

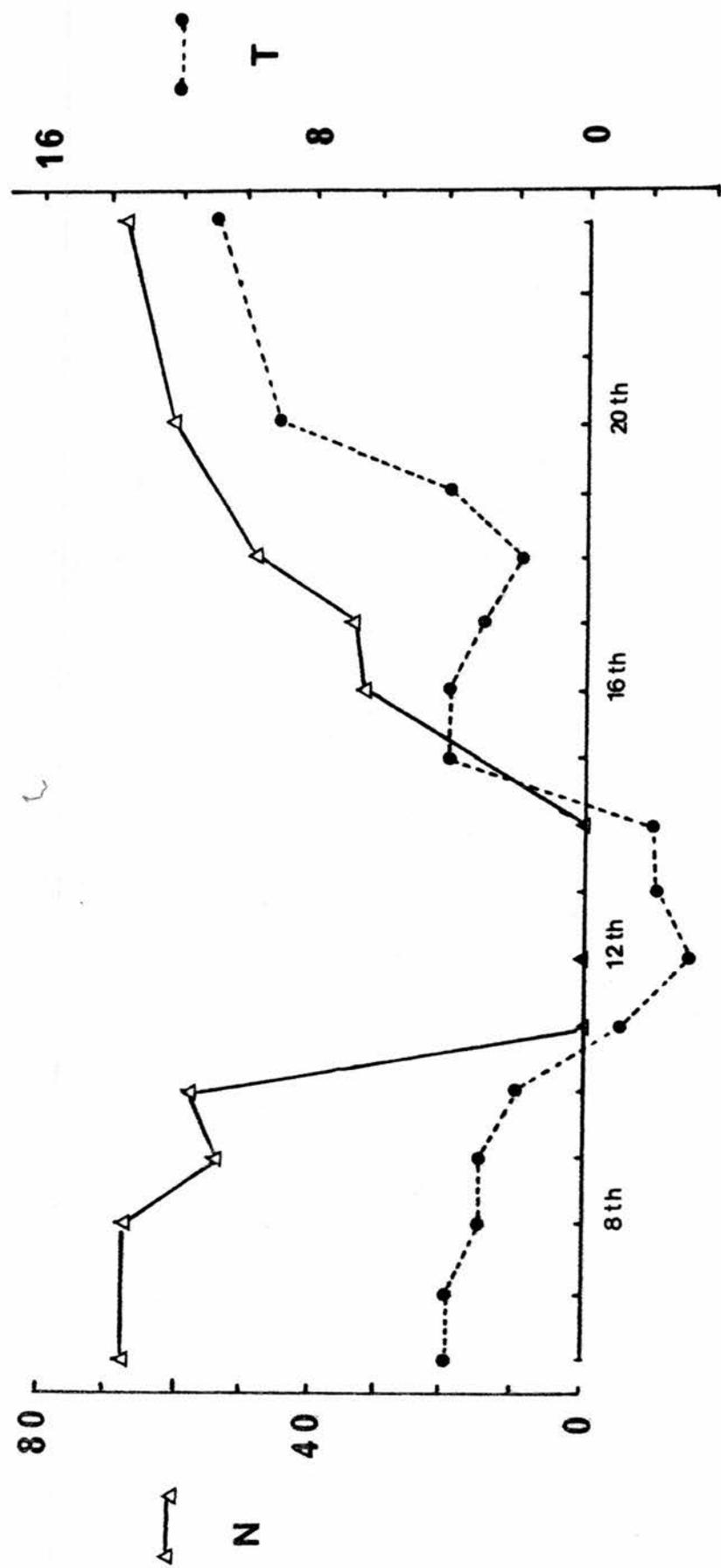
FIGURE 3.4



**FIGURE 3.5**

Counts (N) of black-tailed godwits and maximum daily temperature (T)(°C) in mid-January 1987. For the counts, a point represents the maximum number of birds seen on the day.

FIGURE 3.5

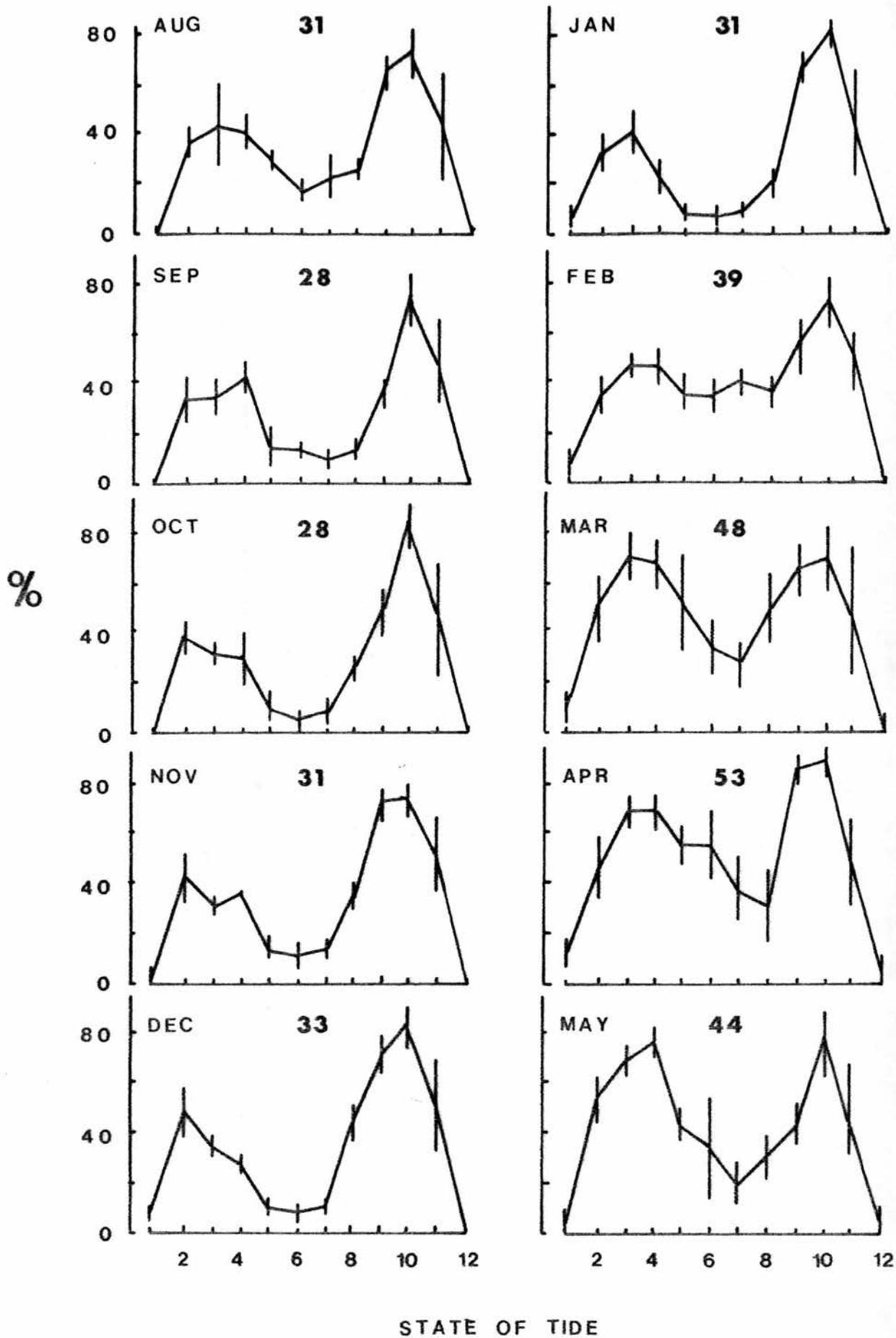


### FIGURE 3.6

Variation through the tidal cycle and through the year of the mean percentage of black-tailed godwits foraging. Bars represent SE of mean. Figure by the month label is the mean percentage of the tidal cycle that an average godwit spent foraging during that month.

Spring and neap tide observations were pooled. Although there was no marked difference in the behaviour of the birds between neap and spring tides care was taken not to bias the observations in a month towards a particular tide height.

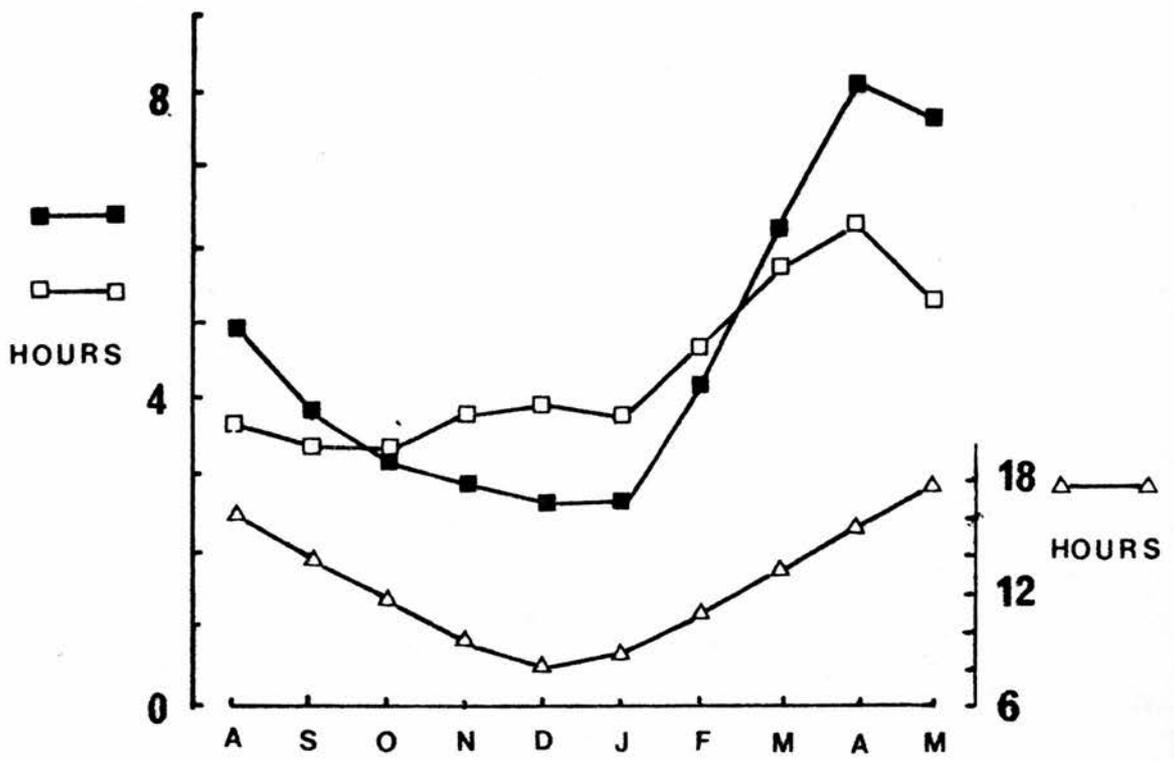
FIGURE 3.6



**FIGURE 3.7**

Variation through the year of the estimated number of hours a black-tailed godwit spent foraging. The open squares represent the number of hours spent foraging per tidal cycle, the closed squares represent the number of hours spent foraging per day, and the triangles represent the number of hours of light per day.

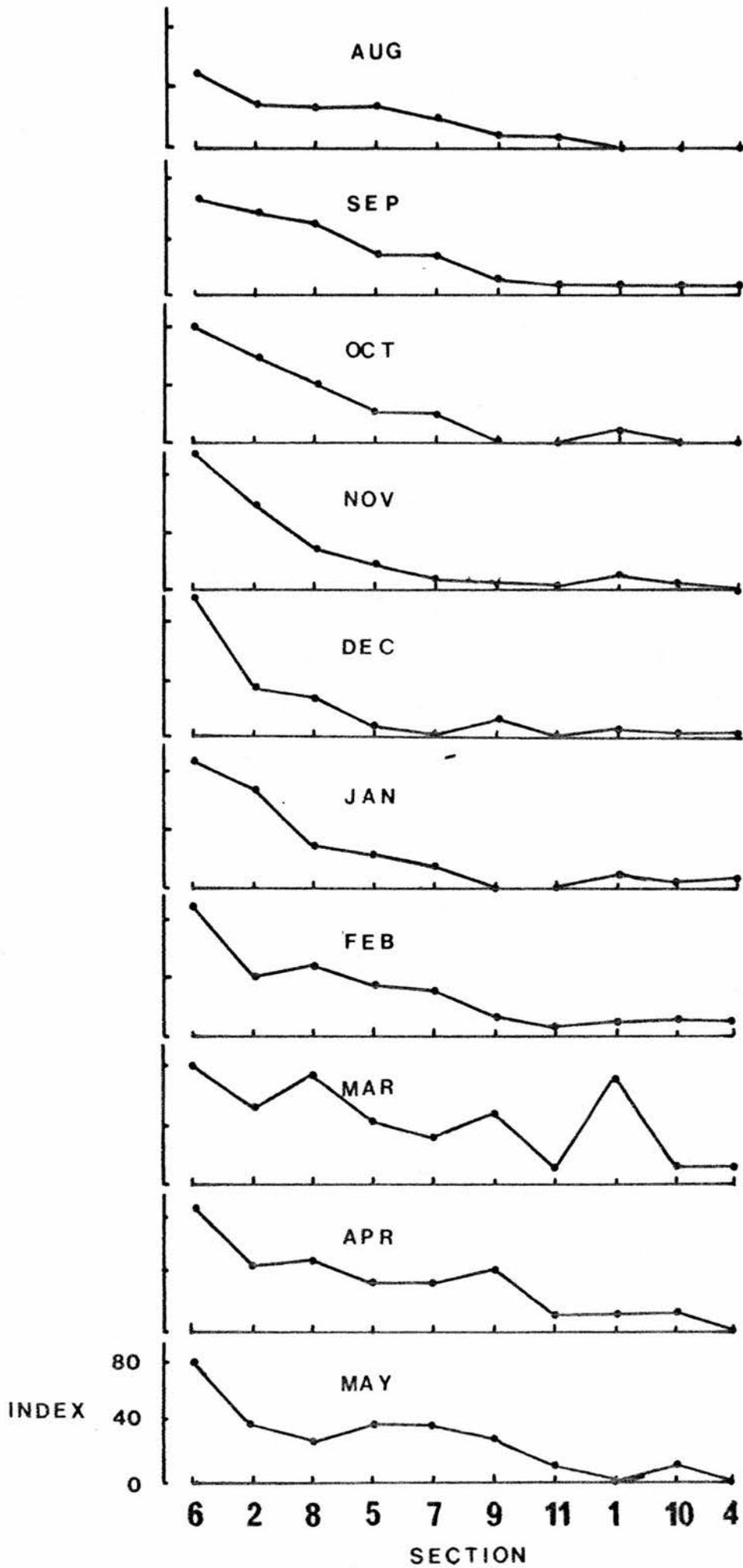
FIGURE 3.7



**FIGURE 3.8**

Variation through the year in the usage, by the black-tailed godwits, of the different sections of the estuary. The index is the number of times a section was surveyed and found to hold one or more black-tailed godwits, as a percentage of the total number of surveys of the section. Scale on the y-axis the same for each month.

FIGURE 3.8



CHAPTER 4  
WINTER FORAGING

4.1 INTRODUCTION

Two aspects of the winter ecology of the black-tailed godwits on the Eden are investigated in this chapter: the choice of foraging areas within the favoured part of the estuary, and the energy budget of the birds.

4.2 HABITAT USAGE

Black-tailed godwits using the Eden Estuary spend the majority of time on the Edenside Flats (see Chapter 3). This study looked at the way the birds used this preferred area; did they select certain parts of Edenside and, if so, was this linked to physical aspects of the habitat?

4.2.1 Methods

The use of Edenside by the black-tailed godwits was investigated by recording the positions of foraging birds at different times of the

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tidal cycle. During such a mapping, which was carried out from set points on the north side of the estuary, the approximate centre of each flock was marked on a map with reference to both landmarks and the tide-edge. In addition, for each flock a record was made as to whether the majority of the birds was within two metres of the water, in which case, the group was described as being at the tide-edge, and of group-size. Flock size was subsequently allocated to one of five categories:

- 1 <5% of total
- 2 5-<10% of total
- 3 10-<40% of total
- 4 40-<70% of total
- 5 70-<100% of total

Total refers to the estimated number of godwits using the estuary at that time (from survey counts; see Chapter 3).

Three maps were used, covering five tidal categories; one map represented the mud exposure of early-ebb (1-<3 hours after predicted high tide (PHT)) and late-flood (9-<11 hours after PHT), one map late-ebb (3-<5 hours after PHT) and early flood (7-<9 hours after PHT) and one map low-tide (5-<7 hours after PHT). High-tide was not considered as the birds roosted at this time. The actual amount of exposure at a specific time during the tide is dependent on the amplitude of the particular tidal oscillation. Therefore, mappings were not carried out at specific times of the tidal cycle, but when the state of exposure was close to that represented on the appropriate map. Discrepancies between the actual and mapped extent of the flats resulted in some inaccuracies in the plotting of the flocks. However, these errors were small and unimportant,

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since the analysis was based on relatively large areas (180m squares). For a specific tidal period, only one mapping was made for each tidal category. A total of 122 mappings was made, with at least 20 for each category of the tide.

The data were pooled for each tidal category in the following way. For all analyses, the maps were split into a standard grid of 180m squares and each flock was allocated to a square. For each square of a mapping, a record was made as to whether birds were present (positive record), and the number and size categories of flocks. In addition, three physical variables were calculated for each square of each of the three maps: the proportion of mudflats available, the length of the tide-edge, and (using the substrate maps of Jonnston et al 1979) the proportion of the available substrate that was 'glutinous heavy black mud' (black mud). For a particular map, a square was defined as 'active' and used for analyses if it contained some exposed mudflats or tide-edge (within 1m of mud), since foraging birds were confined to these areas. Within a tidal category, the data concerning the godwits were pooled for each active square: the usage index was calculated as the number of positive records divided by the number of mappings, and the flock size index as the sum of the flock size categories divided by the number of flocks. These two indices could then be correlated with the physical variables, to see if the presence or the flock size of birds in a square was related to the physical characteristics of that square.

## 4.2.2 Results And Discussion

Partial correlation was used to investigate the influence of the proportion of the square that was covered by mudflats, the amount of tide edge in the square, and the proportion of the flats which was black mud on the usage index of a square (Tab.4.1). For all tidal categories, the one significant partial correlation was with substrate type, the amount of black mud being closely related to the presence of black-tailed godwits.

Squares tended to have similar usage indices during early-ebb and late-flood (Pearson's  $r[17]=0.76$   $P<0.001$ ), and during late-ebb and early-flood, although this second relationship was not significant ( $r[24]=17$   $P=0.063$ ). The combined result was significant (test statistic[4]  $>19.3$   $P<0.001$ ). These results indicate that the black-tailed godwits use similar areas of Edenside when the tide is at a certain height, irrespective of whether the water is flooding or ebbing.

In four of the five tidal categories, the usage and flock size indices were significantly correlated (Tab.4.2), the exception being low tide, which may have been due to the smaller flocks which are present at this time (Tab.4.3). That is, an area which is used often by the godwits tends to be used by relatively large groups.

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For each tidal category, flock size categories were summed (total usage) for flocks feeding at the edge and for flocks away from the edge. Using the total area of open mud and edge (including water within 1m of the tide-edge where birds also fed) (Tab.4.4) the total usage of the two areas could be predicted, assuming there was no selection. A comparison of this predicted value with that observed clearly indicates that there is a huge preference for the edge area (Tab.4.5). In addition, the flocks on the open mud are significantly smaller than those present at the tide-edge (Tab.4.3).

Black-tailed godwits prefer certain sections of Edenside, with foraging birds using similar areas during the flood and ebb tide. Compared to other parts of the flats, the preferred areas are both used more often and tend to contain larger flocks. They are characterised by the presence of black mud. The godwits also showed a preference for the tide edge over the open mudflats.

### 4.3 ENERGY BUDGET

In Chapter 3 it was shown that during the winter the black-tailed godwits using the Eden Estuary foraged for less than a third of the tidal cycle. Figures 4.1 and 4.2 indicate the amount of time species of waders spent foraging in one study on the Ribble Estuary, England (data calculated from Greenhalgh 1975), and several studies on other inter-tidal flats (data calculated from Hopleston 1971, Smith 1975, Goss-Custard *et al* 1977, Puttick 1979, Townshend 1981a, Pienkowski 1982, Pienkowski *et al* 1984). There is

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an inverse relationship between the size of a wading bird and the proportion of the tidal cycle it devotes to foraging, but even the largest species are spending much more time feeding than the birds in this study. Indeed, other black-tailed godwits and the similarly sized bar-tailed godwits are feeding for at least 50% longer than the birds on the Eden.

This investigation was to assess whether the black-tailed godwits on the Eden Estuary can meet their energy requirements during the daylight hours with so little feeding.

### 4.3.1 Methods

To assess whether the black-tailed godwits are meeting their energy requirements requires an estimate of energy expenditure and a measurement of energy intake. These two aspects will be dealt with in turn.

#### Energy Expenditure

The basal metabolic rate (BMR) of an animal is its energy expenditure during rest under thermoneutral conditions (or at high relatively unstimulating ambient temperatures), and can be measured directly in the laboratory. In taxonomically related species this rate of energy utilisation is a function of body mass ( $M$ ) so, if the appropriate equation is available, an animal's BMR can be easily estimated. For non-passerine birds the relationship is given by Lasiewski and Dawson (1967):

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$$\log \text{BMR} = \log 78.3 + 0.723 \log M \quad \dots [1]$$

BMR in kcal per day    M in kg

The amount of energy expended by normally active animals (daily energy expenditure DEE) can be measured directly using doubly labelled water techniques. Within taxonomic groups, DEE is also dependent on body mass and two equations recently formulated for birds are given below (equation [2] from Walsberg 1983, equation [3] from Nagy 1987):

$$\ln \text{DEE} = \ln 12.84 + 0.610 \ln M \quad \dots [2]$$

$$\log \text{DEE} = 0.681 + 0.749 \log M \quad \dots [3]$$

DEE in kJ per day    M in g

Equation [3] is calculated entirely from free-living birds and is based mainly on measurements during the breeding season, due to the difficulty of recapturing individuals at other times. The relationship is therefore not particularly representative.

Energy expenditure is also dependent on the ambient temperature. Using the equations of Kendeigh *et al* (1977), the DEE can be estimated for a particular temperature:

$$\text{EM} = 1.46M^{0.626} \quad \text{at } 30^\circ\text{C}$$

$$\text{EM} = 4.24M^{0.532} \quad \text{at } 0^\circ\text{C}$$

EM in kcal per day    M in g

For non-passerines in the winter, where EM is the existence metabolism, which is the rate at which energy is expended by a caged bird maintained at constant mass when the bird is not reproducing, moulting, growing or showing migratory unrest. From

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EM(30°) and EM(0°) metabolism can be calculated for a bird at any temperature by manipulating the equation:

$$EM(t) = EM(0^\circ) - b t \quad \dots[4]$$

Where  $b$  is the temperature coefficient and  $t$  is the ambient temperature. DEE is then calculated as 107% of EM.

In general, the value for DEE in free-living birds is equivalent to between two and four times BMR (Pienkowski et al 1984).

### Energy Intake

To estimate diurnal energy intake requires the measurement of both the energy intake through the tidal cycle and the amount of daylight available. Observations were carried out between November 1985 and January 1986 and data were pooled over months and over spring and neap tides. To ensure the results were not influenced by adverse weather conditions or heterospecifics, data were not used if collected below an ambient temperature of 3.5°C, in strong wind and rain, or in the presence of roosting gulls and plovers (see Chapter 6). The two feeding methods probing and stitching, were dealt with separately; and therefore, information was required on the time budget and energy intake of the two techniques through the tidal cycle.

The tidal cycle was split into 12, sections 1,2,...,12 where 1 covered the time between high tide and one hour after high tide, 2 was the time between one hour after high tide and two hours after high tide and so on. Due to the variable length of the tidal

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period, section 12 was not of uniform length: for analyses its mean length of 1.41 hours was used.

During the scans used to estimate overall time budget (Chapter 3), the proportion of foraging birds which were probing (P) was also recorded. For each section of the tidal cycle, the mean percentage of the population foraging was found (as for Chapter 3) and, using P, the mean percentage of the population probing and stitching was calculated. Assuming an homogeneous population, the mean percentage of birds engaged in an activity during a section is equivalent to the mean percentage of that section a bird spends in the activity. In this way, the average number of minutes spent probing and stitching per bird in each section of the tidal cycle can be calculated.

Between the scan samples the energy intake of probing and stitching was measured. Two godwits for each of the foraging techniques were selected at random and watched for a set period recorded by an audio timer. On occasions, lack of foraging birds meant a reduction in the sample size. An attempt was made not to use the same bird more than once during an observation period. All probing godwits and those that were watched stitching during sections five, six and seven (when intake rate was lower) were recorded for three minutes, other stitching birds for two minutes. These periods were selected as they were the minimum length which ensured that, for most observations, the average feeding rate was reasonably stable (Fig.4.3).

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During probing, a large proportion of the prey taken could be identified as either Macoma balthica or Nereis diversicolor. A Macoma was held between the mandibles before swallowing and was clearly visible, with the larger items taking several seconds to handle and sometimes a few attempts to swallow.

The size of a Macoma was judged to be large, medium, small or 'probable'. The last category involved the bill being held open and rigid, but with the item too small to identify definitely. An experiment was carried out to calibrate these size categories to actual valve lengths. A large number of Macoma were collected from the edge of Kincapple and 14 selected which were stepped in valve length by 1mm from 5mm to 18mm. A life-size model was constructed of the silhouette of the head of a black-tailed godwit. The 'lower mandible' was pivoted so that the 'bill' could be opened and one of the selected bivalves, which were marked according to their size, was fixed by 'Blu-Tak' to the 'upper mandible' at a standard position. The bill was then closed. In this way, Macoma were presented by an assistant to the observer situated 100m away with a telescope. Each of the 18 bivalves plus an empty bill were presented for about two seconds on five occasions in a random order not known in advance to either assistant or observer. The observer noted the size category (none, probable, small, medium and large) that he considered each example belonged to. After the experiment these categories were shown to describe fairly discrete groupings of actual prey size (Fig.4.4). Although during observations godwits were observed at greater distances than the model, the

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magnification of the telescope in the experiment was restricted to 15x. In addition, with real birds the handling times were often longer than two seconds and varied depending on the size of Macoma being manipulated (see Chapter 5). Therefore the experiment was considered to have been a fair test and this allowed the size categories for Macoma assessed in focal observations to be expressed in terms of valve length: small >9-12mm, medium >12-15mm, large >15mm. Probables, up to 9mm long, were classed as unidentified prey items. Smith (1975), observing bar-tailed godwits, considered that bivalves could not definitely be recognised below about 10mm and Goss-Custard (1977a) suggested that those taken by redshank below 6mm were not visible in the field at all.

Nereis were briefly held across the bill and sometimes washed before being swallowed. Very few worms were larger than approximately half the bill length of the black-tailed godwits (up to about 50mm) and the smallest visible were considered to be about 20mm long. The size of large worms can be assessed by comparison with bill length (for example Goss-Custard 1977b); however this was difficult for smaller worms and for this reason it was not possible to to allocate worms to size categories.

Unidentified items were probably made up largely of Macoma up to 9mm in size and Nereis up to 20mm in length. On occasions when godwits were observed very close (<25m), as they probed in an area of low bivalve density, virtually all items were identifiable as Nereis.

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For each focal observation (N=598) of a probing bird the number of small, medium and large Macoma, Nereis, and unidentified items was recorded.

Energy content of Macoma is closely related to length (Prater 1972, Ingvarsson 1972, Greenhalgh 1975, Goss-Custard et al 1977, Hulscher 1982, Leopold et al 1985); this allows an average energy content per item to be allocated to the size categories: small 0.07kcal, medium 0.14kcal, large 0.24kcal. Likewise Nereis between 20-50mm long will have an average energy content of about 0.1kcal per item (Goss-Custard 1977b, Goss-Custard et al 1977, Smith 1975). Unidentified prey items include Macoma and Nereis both up to about 0.04kcal (calculations from above references), and possibly other species, although no evidence was found in pellets (see Chapter 3). An average figure of 0.02kcal was used for these items.

During stitching a smaller number of items could be identified, but those that were, were also Macoma or Nereis. The bivalves which were taken were virtually all small as categorised above (probables were treated as unidentified items). The Nereis eaten appeared similar in size to those taken during probing and the unidentified items were assumed to have the same energetic content for both foraging techniques. When birds were watched stitching from close to (<25m), many small (<20mm) Nereis were seen to be taken, and swallowing movements were only observed when the head was jerked up to bring the bill away from the substrate (see Chapter 3). It therefore appears that the apparent item intake

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rate was a good indicator of the actual number of items eaten and that many of the unidentified prey were small Nereis. It is possible that very small items were taken when the bill was still in contact with the water as reported for bar-tailed godwits with their beaks in mud (Smith 1975). Animals taken in this way might include Corophium and Hydrobia, although the close observations and the absence of these species in pellets, indicated that if they were taken it was only rarely. This scarcity, combined with their relatively low energy content per item of about 0.002kcal or less (Goss-Custard 1977, Hale 1980), makes them unimportant for the black-tailed godwits in this study.

For each focal observation of a stitching bird (N=541) the number of Macoma, Nereis and unidentified items was recorded. The energy content per item of these prey was taken to be 0.07kcal for Macoma, 0.10kcal for Nereis and 0.02kcal for unidentified prey.

For all observations a rate (items per min) was calculated for each category of prey taken. For each section of the tidal cycle these rates were averaged separately for probing and stitching birds, and the resulting means multiplied by the energy content of the apposite prey categories (kcal per item) to give the energy intake (kcal per min) for each foraging technique for each section. Combining this energy information with the time budget data gives, for each tidal section, the amount of energy intake for probing and stitching. Summation across the 12 sections and the two foraging techniques gives the total energy intake per tidal cycle. Finally allowing for the number of daylight hours will permit an estimate

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of the amount of energy eaten by a black-tailed godwit during diurnal foraging.

### 4.3.2 Results And Discussion

#### Energy Expenditure

Using a normal winter lean mass of 247.8g (Davidson 1981) in equation [1] gives a BMR for the black-tailed godwit of 28.6 kcal per day. Using the same mass the DEE estimated by equations [2] and [3] is equivalent to 3.1BMR and 2.5BMR respectively, and taking a mean ambient temperature of 6°C is 2.7BMR for equation [4].

#### Time Budget

The proportion of foraging birds that were stitching varied through the tidal cycle (Fig.4.5a). During the periods when most foraging occurred, the ebb and especially the flood, stitching was the favoured feeding method, while during low tide the vast majority of the foraging time was spent probing. This distribution of feeding techniques was closely related to the energy intake rate (kcal per min) of the two feeding methods (Fig.4.5b). The profitability of stitching fluctuated more than ten-fold between low tide and the peak of the flood tide. Probing was also more rewarding as the water rose but the increase was more modest. This results in stitching yielding a higher intake than probing in the hours around high tide and the reverse during low-water.

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### Energy Intake

It is important to consider that the values given below are estimations. The total energy intake for each feeding method over the tidal cycle is shown in Figure 4.5c. Probing contributes a fifth of the intake and over half of the total is obtained during the two hours of tidal sections nine and ten. The rate of item intake (items per min) of a bird was a good predictor of its energy intake (kcal per min); in regression analysis of all the data item intake explained 67.9% of the variance in energy intake.

The total intake per tidal cycle (12.41 hours) was estimated at 87.5kcal. The mean period of daylight for November, December and January was 8.67 hours (see Chapter 3) so the mean diurnal intake (MDI) during those months was:

$$\text{MDI} = \frac{87.5 \cdot 8.67}{12.41} = 61.1 \text{ kcal per day}$$

This is equivalent to 2.1BMR which compares with between 4.2-6.8BMR for other tidally feeding large sandpipers (Pienkowski *et al* 1984). Assuming 0.85 of energy taken is assimilated (Evans *et al* 1979), the total energy available to the black-tailed godwit is 52.0kcal per day which is equivalent to 1.8BMR. Thus the estimate for energy provision during the daylight period is markedly lower than the expected energy requirements over a complete day. On some days the interaction of tidal and diurnal periods will result in less time or less favourable parts of the tide being available, which will mean that the amount of energy intake during daylight will be even lower.

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The result is, of course, sensitive to the various parameters used, with the calorific content of prey particularly prone to error. However, the energy figures used were deliberately selected not to be conservative so that, if anything, the estimate for energy intake will be high. The energy content of identified Nereis was likely to be the least accurate due to the use of a single size category. However, if this energy figure for Nereis is increased by 50% from 0.10kcal per item to 0.15kcal per item the total energy available only increases by 17% to 2.1BMR.

It can be concluded that the black-tailed godwits as a whole do not appear to be fulfilling their energy demands purely by the foraging that occurs during daylight. If the requirements are as high as 4BMR then the birds may be receiving less than half the calories they need during the day. Therefore, it is expected that much nocturnal foraging is occurring.

Low MDIs have been reported in other shorebirds, especially plovers, which may obtain the majority of their energy at night (Dugan 1981, Pienkowski 1982, Pienkowski et al 1984). Nocturnal feeding has been recorded for many other estuarine waders, but is generally considered to occur only when requirements cannot be fulfilled during the day. This view has resulted from observations that night time foraging mainly occurs when conditions are adverse and is relatively inefficient. For example, Goss-Custard (1969) reported that redshank did not feed outside the day during the summer, but did so between November and December on dark nights and between October and March on bright ones. Lower feeding rates at

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night have been observed in oystercatchers by Hulscher (1982) and Goss-Custard and Durrell (1987c). However, some invertebrates, including species of Nereis (Dugan 1981), are more active at the surface of the substrate at night and are consequently potentially more available. Even so, smaller waders such as the plovers and dunlin (Pienkowski et al 1984) generally spend the majority of the available time during the day feeding (Figs.4.1 and 4.2), which is in contrast to the birds in this study which spend less than a third of the tidal cycle foraging. Other black-tailed godwits forage for more of the available time (Fig.4.1) and, on the Exe, often feed in fields during high-tide (Goss-Custard pers. comm.). This tends to suggest that nocturnal feeding is quite profitable for the black-tailed godwit on the Eden Estuary.

The RAF base at Leuchars which is adjacent to the north edge of the estuary ensures there is light cast on the mudflats at night, even when the sky is overcast. This illumination would allow the godwits to exploit the greater activity of Nereis and other invertebrates using visual cues by night. A few observations were carried out at night. On three occasions at low-tide no roost was present in the position where it would invariably have formed at this time in the tidal cycle during the day. In these three sessions and in three others during early flood a total of only 21 (0,0,3,3,5,10) godwits were located. All these birds were foraging; 18 stitching and 3 probing. It appears that the preferred feeding areas during the day were not the preferred areas at night. This is supported by the fact that sometimes at first

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light the study area was free from black-tailed godwits and, on these occasions, birds might arrive in large flocks from the east. In a study on grey plover Townshend et al (1984) found that the foraging areas used by an individual during the day were usually different from those used at night. It was suggested that the reason for this was that the relative profitability of areas was dependent on whether it was night or day.

TABLE 4.1

Partial correlations of the usage of a square by black-tailed godwits (usage index) and the amount of area in the square available to the godwits, the total length of the tide-edge in the square and the proportion of the available area in the square that is black mud. P is the significance of the partial correlation if the result is significant. The degrees of freedom for a tidal category is indicated in square brackets.

TABLE 4.1

	SIZE OF FLATS	AMOUNT OF TIDE-EDGE	AMOUNT OF BLACK-MUD
EARLY FLOOD [24]	-0.28	0.27	0.63 P<0.001
LATE FLOOD [15]	-0.37	0.00	0.86 P<0.001
EARLY EBB [17]	0.30	-0.45	0.71 P<0.001
LATE EBB [16]	-0.29	-0.21	0.24
LOW-TIDE [20]	-0.28	0.22	0.43 P<0.05

TABLE 4.2

Correlation between the flock index and usage index of a square at different times of the tide.  $r$  is the Spearman's coefficient of rank correlation and degrees of freedom are shown in the square brackets.

TABLE 4.2

	r	P
EARLY FLOOD	0.73 [12]	<0.005
LATE FLOOD	0.85 [6]	<0.01
EARLY EBB	0.71 [9]	<0.05
LATE EBB	0.57 [13]	<0.05
LOW-TIDE	0.27 [11]	NS

TABLE 4.3

Distribution of flock-size categories for black-tailed godwits using edge and open areas. G is the G-test statistic, degrees of freedom in brackets.

\* for low-tide, to generate enough data flock-size categories had to be allocated to one of two divisions: 1 and >1.

TABLE 4.3

		FLOCK-SIZE CATEGORY						
		1	2	>2	G	P		
EARLY FLOOD	EDGE	78	34	37	16.4 [2]	<0.001		
	OPEN	32	1	5				
LATE FLOOD	EDGE	28	38	61	14.4 [2]	<0.001		
	OPEN	13	2	5				
EARLY FLOOD	EDGE	47	26	18	2.9 [2]	NS		
	OPEN	19	4	6				
LATE EBB	EDGE	35	15	44	26.7 [2]	<0.001		
	OPEN	29	4	2				
LOW-TIDE*	EDGE	21	8		7.9 [1]	<0.001		
	OPEN	42	2					

TABLE 4.4

Areas ( $\text{km}^2$ ) of tide-edge and open mud at different times during the tidal cycle.

TABLE 4.4

	AREA OF TIDE-EDGE	AREA OF OPEN MUD
EARLY FLOOD / LATE EBB	0.012	0.64
LATE FLOOD / EARLY EBB	0.013	0.28
LOW-TIDE	0.013	1.03

TABLE 4.5

Observed (O) and expected (E) frequencies of black-tailed godwits using edge and open habitat; expected frequencies assume that there is no selection between the two areas. G is the G-test statistic. NA indicates that the G-test is not appropriate.

TABLE 4.5

		FREQUENCY				
		C	E	G	P	O/E
EARLY FLOOD	EDGE	257	5.82	1769	<0.001	44
	OPEN	49	300.18			
LATE FLOOD	EDGE	288	14.16	1590	<0.001	20
	OPEN	32	305.84			
EARLY EBB	EDGE	153	8.76	745	<0.001	18
	OPEN	45	189.23			
LATE EBB	EDGE	156	3.78	NA		41
	OPEN	43	195.22			
LOW TIDE	EDGE	38	1.06	NA		35
	OPEN	46	82.94			

FIGURE 4.1

Relationship between the number of hours spent foraging on inter-tidal flats during a tidal cycle by a wader and its wing length (mm). Wing length were taken as the mean of the limits given by Hayman et al (1986). Open circle black-tailed godwit on the Eden Estuary (this study), closed circles Ribble Estuary (Greenhalgh 1975):

- 1/ Dunlin
- 2/ Sanderling
- 3/ Turnstone
- 4/ Redshank
- 5/ Knot
- 6/ Bar-tailed godwit
- 7/ Black-tailed godwit
- 8/ Oystercatcher
- 9/ Curlew

The wing length explains 89.4% of the variance in the time spent foraging, and the relationship between the two variables is significant (from regression analysis:  $F[1,7]=68.3$   $P<0.001$ ) (excluding the result from this study).

FIGURE 4.1

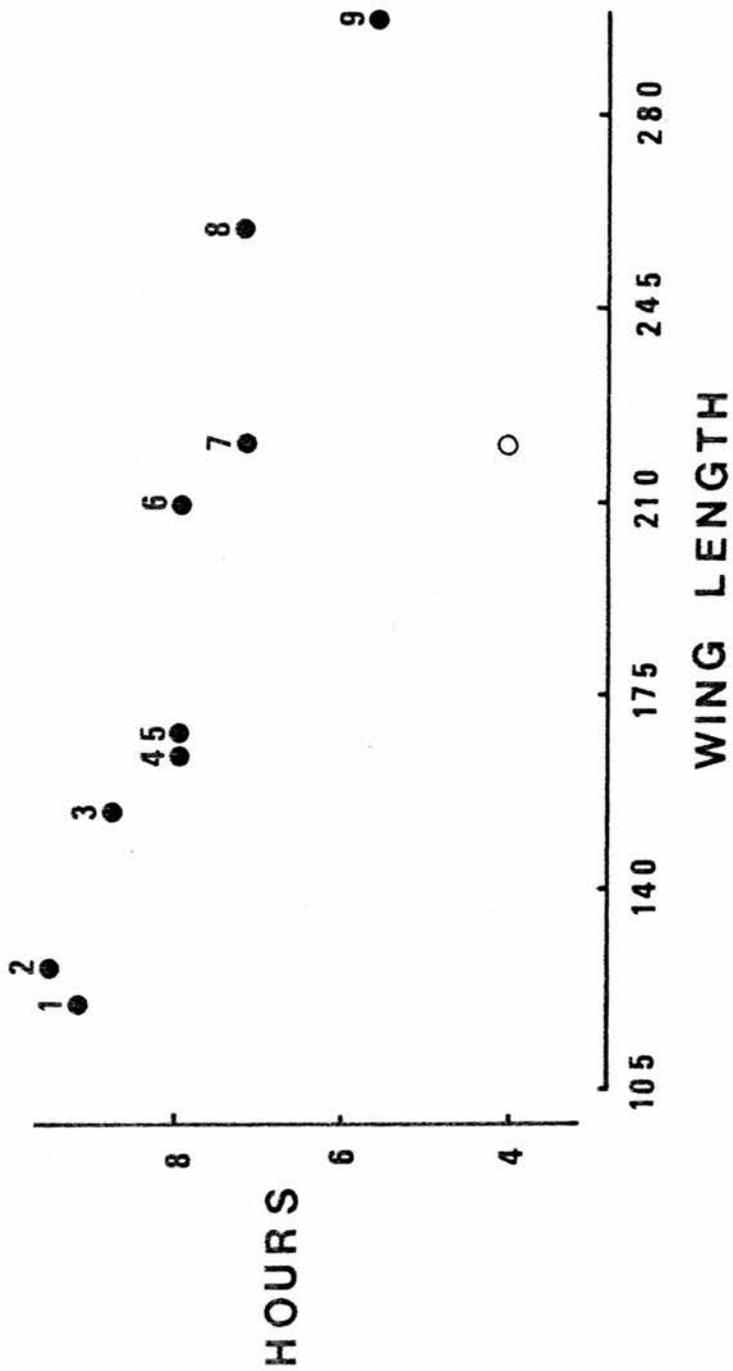


FIGURE 4.2

Relationship between the number of hours spent foraging on inter-tidal flats during a tidal cycle by a wader and its wing length (mm). Open circle black-tailed godwit on the Eden Estuary (this study), closed circles various estuaries:

- 1/ Ringed plover (Pienkowski et al 1984)
- 2/ Curlew-sandpiper (Puttick 1979)
- 3/ Grey plover (Pienkowski 1982)
- 4/ Grey plover (Townshend 1981a)
- 5/ Bar-tailed godwit (Goss-Custard et al 1977)
- 6/ Bar-tailed godwit (Smith 1975)
- 7/ Oystercatcher (Heppleston 1971)
- 8/ Oystercatcher (Goss-Custard et al 1977)
- 9/ Curlew (Goss-Custard et al 1977)

The wing length explains 37.2% of the variance in the time spent foraging, and the relationship between the two variables is significant (from regression analysis:  $F[1,7]=5.7$   $P<0.05$ ) (excluding the result from this study). Combining these data and those in Fig.4.1, the wing length explains 54.8% of the variance in the time spent foraging, and the relationship between the two variables is significant (from regression analysis:  $F[1,16]=21.6$   $P<0.001$ ).

FIGURE 4.2

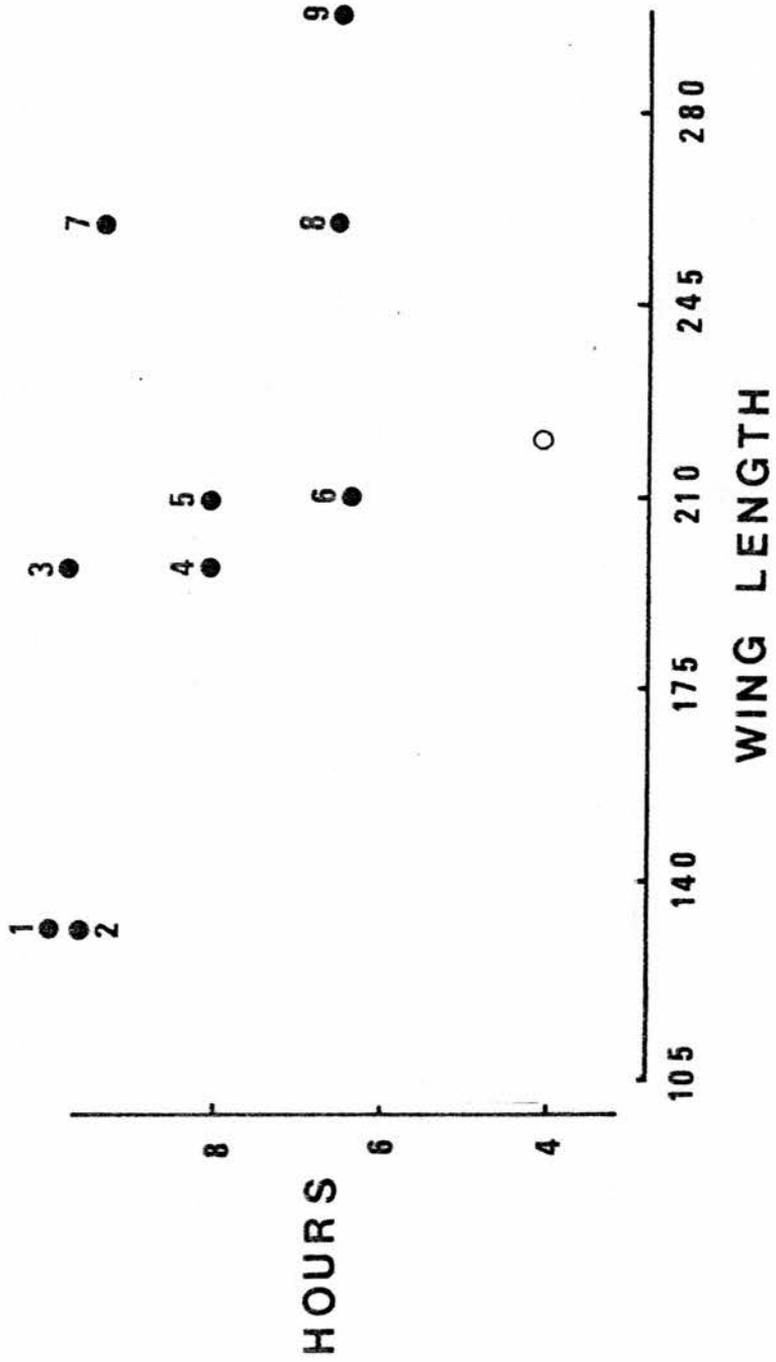


FIGURE 4.3

Change of mean feeding rate (items per minute), for a focal individual, with length of observation (time in seconds). Mean was recalculated every 10s. The figures represent two randomly selected data sets, one for probing (A) and one for stitching (B) (total sample = 20). The dashed lines represent the lengths of observation used in subsequent observations: 180s for all probing birds and stitching birds when intake rate was low, and 120s for other stitching birds.

FIGURE 4.3

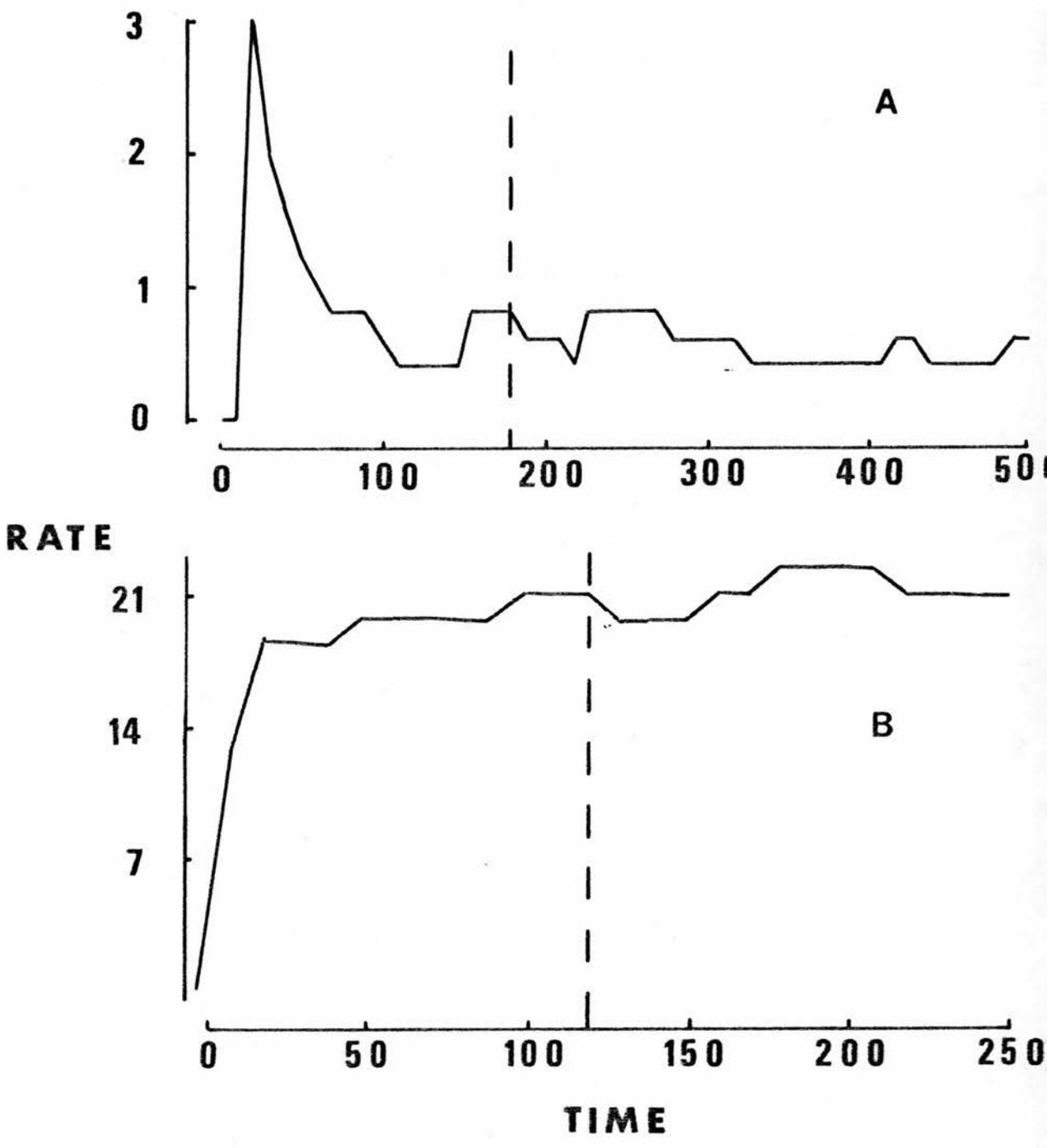


FIGURE 4.4

Experiment to relate estimates of Macoma size (estimate: L-large, M-medium, S-small, P-probable, N-none) to actual size (size: valve length in mm). The numbers on the graph are the number of presentations of a particular size which were allocated to the same category by the observer. The vertical dashed lines indicate the resulting calibration of estimates into actual sizes: s-small >9-12mm, m-medium >12-15mm and l-large >15mm.

FIGURE 4.4

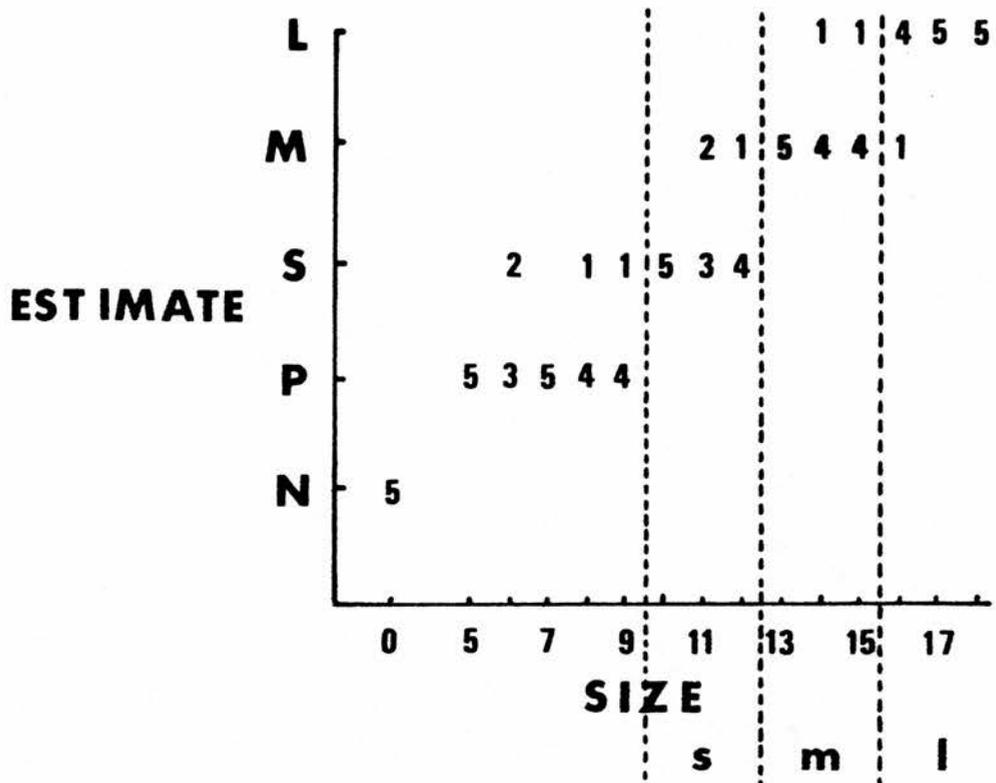


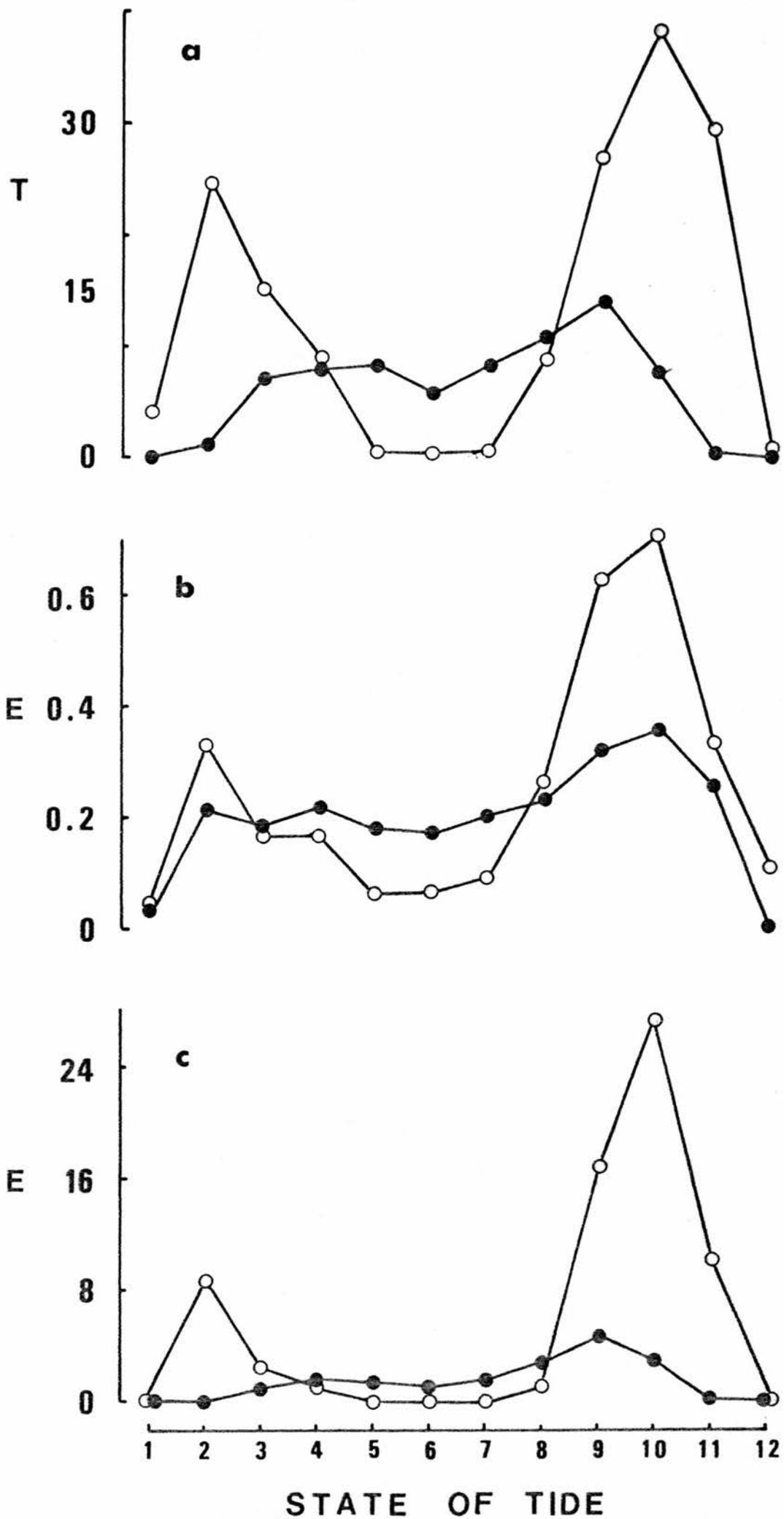
FIGURE 4.5

A/ Mean number of minutes (T) a black-tailed godwit spent probing (closed circles) and stitching (open circles) in each section of the tidal cycle (high-water during section 1 and 12, low-water during section 6 and 7). Mean total time spent probing per tidal cycle was 71.5 minutes and stitching 159.2 minutes.

B/ Mean feeding rate (E: kcal per minute) of a black-tailed godwit probing (closed circles) and stitching (open circles) in each section of the tidal cycle.

C/ Mean total energy intake (E: kcal) of a black-tailed godwit probing (closed circles) and stitching (open circles) in each section of the tidal cycle. Mean total energy intake per tidal cycle was, for probing, 17.5kcal and, for stitching, 70.0kcal.

FIGURE 4.5



CHAPTER 5  
KLEPTOPARASITISM

5.1 INTRODUCTION

Kleptoparasitism, which has been defined as the theft of already procured food from heterospecifics (Brockmann and Barnard 1979), is relatively common in birds (Brockmann and Barnard 1979) and particularly prevalent in Charadriiformes (Thompson 1986). The definition of this behaviour is somewhat loose. Stealing also occurs between conspecifics (for example Goss-Custard *et al* 1982) and it seems arbitrary to confine the term kleptoparasitism to encounters between species. In addition, the essence of kleptoparasitism is a direct encounter between two animals; however, procured food can be thought to include stored items that may be 'stolen' without an interaction with another individual. In an encounter, an attacker may gain an item that has not already been procured, but has been invested in and would otherwise have been taken by the individual being attacked. This is the case when the food is in the process of being procured when an attack occurs. We can therefore redefine kleptoparasitism or food-stealing as an encounter in which food procured or in the process of being

## KLEPTOPARASITISM

procured is ceded by one individual to another.

It is kleptoparasitism of food in the process of being procured that is the subject of this chapter. Black-tailed godwits using the probing method of foraging have characteristics which would be expected to lead to kleptoparasitism: they take large, high quality and visible prey, they forage in flocks (Brockmann and Barnard 1979) and they use an open habitat (Paulson 1985). In this species the kleptoparasitic act takes the form of an individual, which is in the process of procuring food by probing for it in the substrate, being displaced by a bird which takes over the feeding location. Birds which were kleptoparasitic were seen to feed normally during the remainder of the time and did not use this method as the sole provider of food. This is unlike some heterospecific kleptoparasites, which may gain all their food through theft and often have highly developed stealing techniques (Barnard and Thompson 1985). Other encounters not concerned directly with food also occurred between black-tailed godwits. It could be that the stealing behaviour is merely an epiphenomenon resulting from displacements that happen to result in the attacker obtaining food.

The main part of the chapter considers the nature and the degree of specialisation of the kleptoparasitic behaviour of black-tailed godwits; a secondary section describes the energetic consequences of food-stealing for both the perpetrators and those that are attacked.

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### 5.2 METHODS

#### 5.2.1 Observational Methods

Displacements and food-stealing occurred in groups of birds probing on open mud and were particularly prevalent when conditions were adverse. Observations were made throughout the study period, but mainly during February 1986 when it was particularly cold and these behaviours were common. During an observation session birds were selected at random and watched for five minutes (N=216). In addition 24 birds were each watched continuously for 20 minutes to assess behaviour over a longer period. Times were recorded by an audio timer and an attempt was made not to use the same bird more than once during a session. All the data were collected between 5 and 9 hours after the predicted time of the last-high tide, since probing was relatively common during this period (see Chapter 3).

#### 5.2.2 Description Of Displacements And Stealing

A godwit using the probing feeding method occasionally pecked the surface of the substrate as it walked with its head oriented downwards. Probes, often preceded by a peck at the substrate, were used to extract food items. A probe followed a standard sequence of events: the bird inserted its bill into the mud and, after a time, removed an item or gave up and moved to another site; the item was then either eaten, sometimes after being washed, or was discarded. The time between initial insertion of the bill and the item being brought to the surface, or the bird giving up, was

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defined as the probing time, and the period between the removal of the prey and the end of swallowing or discarding was referred to as the handling time. Manipulating time was taken as the sum of the probing time and the handling time. The food items taken during the observations were predominantly Macoma balthica, which could be allocated to the size categories small (0.07kcal per item), medium (0.14kcal per item) and large (0.24kcal per item), and also some smaller unidentified prey (0.02kcal per item) (see Chapter 4).

A displacement was where one bird ceded its position to another. The individual attempting the displacement was termed the attacker and the potential victim the target. The attacker walked, head up, often calling and with the back feathers raised, towards the target. This second bird usually moved away.

Kleptoparasitism was a consequence of the attacker displacing a bird which was in the process of probing. The target usually stopped probing and walked away, leaving the attacker free to continue the probe at the site. However, on a few occasions, the attacker was repulsed. If an item was removed before the attack was complete, the target moved off with the prey and the encounter finished. On no occasions was a target seen to start a probe after an attack had been initiated against it. A food-stealing attempt was defined as a displacement which was initiated during the period when the target was probing. The time between the attacker starting to walk towards the target and the onset of probing by the attacker after the displacement, or the end of the encounter if the attacker was repulsed, was defined as the attack time. An attack,

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also referred to as an assault, was the event covered by the attack time. The attack plus any resulting manipulation by the attacker comprised the stealing or kleptoparasitic act. In all cases attackers were seen to feed normally outside the stealing acts and spent the minority of their time engaged in kleptoparasitic behaviour.

In an attack against focal birds the time between the start of the probe and the interruption (target's probing time) was recorded if the attack was not repulsed. If an assault was repulsed the time between the target stopping and resuming probing (repulsion time) was noted. For an assault by focal birds the attack time, the outcome, and any resulting probing time, handling time and the nature of the prey item taken, were recorded. For all observations the number of non-kleptoparasitic displacements was also counted.

### 5.3 RESULTS AND DISCUSSION

#### 5.3.1 Frequency And Outcome Of Displacements

In the 1080 minutes covered by the five minute observations 635 displacements were observed and these could be broken down into those where the focal individual was the attacker and those where it was the target, and also into those that were kleptoparasitic in nature and those that were not (Tab.5.1). In all four categories of displacement the attacker was repulsed on about 10% of occasions.

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About 40% more displacements were non-kleptoparasitic than kleptoparasitic. If food-stealing was just a consequence of a displacement occurring by chance when a target was probing, the ratio of kleptoparasitic attacks to other displacements would be a reflection of the amount of time spent by the birds probing and not probing. The total number of probes in 1080 minutes was 1624 which is a mean rate of 1.50 probes per minute, and the mean probing time per probe was 4.85s (SE=0.05 N=2157). Therefore, the mean proportion of time spent probing was  $(1.5 \cdot 4.85)/60 = 0.12$  and, not probing, 0.88. Using these proportions we can calculate the expected number of the two types of displacement (Tab.5.2). The observed frequencies are very significantly different from those expected ( $G[1]=398$   $p < 0.001$ ). It can be concluded that it was particularly common for displacements to start while the target was probing.

Of 2157 probes only 139 (6.4%) were interrupted by a stealing attempt and, therefore, the behaviour appears to be quite uncommon. For this reason, kleptoparasitism may be relatively unimportant both for the attacker and the target, even during this period when the behaviour was at its most frequent. If this is the case, the expectation is that the skills involved in stealing will not be particularly well developed and that the energy consequences for attackers and targets will not be great.

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The next section examines whether or not stealing was highly developed and the energy consequences for attackers and targets are calculated in the final section.

### 5.3.2 The Art Of Stealing

The outcome of kleptoparasitic attacks is indicated in Table 5.3. About 10% of assaults are repulsed and a further 18% result in no item being gained by the attacker, due to the target making off with the prey or the attacker not locating any food. About 70% of attacks were rewarded by a medium or large Macoma. In the following section, we consider whether this performance was the result of random attacks or was due to targeting of assaults when they were likely to be successful. The following analyses consider stealing attacks which were not repulsed.

Although displacements preferentially occurred during the time that the target was probing, kleptoparasitic acts may occur randomly, that is, an attack may start randomly within a probing time. This might be expected, since foraging involves orientation of the head towards the substrate, which probably precludes observing other individuals. Indeed, surveillance peeks, whether for predators or conspecifics, appeared to occur only in the head-up position (see Chapter 6). It is a reasonable assumption that an attacker will have a random chance of breaking its own foraging bout to be vigilant and, therefore, will first observe, and perhaps attack, a bird that is a potential target at a random time into this second bird's probe. The performance of a randomly

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attacking kleptoparasite can be modelled and compared to the performance actually attained by the birds. To construct such a model requires a consideration of the process of probing.

### Description of Probing

As already seen, the great majority of probes (93.4%) were uninterrupted by food-stealing attempts. Table 5.4 shows the outcome of these probes. Three of the outcomes (unidentified items, discards, and give-ups) were relatively rare and were pooled into a single category (other:0) to simplify the subsequent analyses.

Figure 5.1 shows how probing and handling times vary between the different categories of outcome. The larger the item the greater the probing and handling time required. Profitability can be calculated as the estimated energy per item divided by the manipulating time (Fig.5.2), where manipulating time for a category was taken as the sum of the mean probing time and the mean handling time. Medium and large Macoma have similar profitabilities and small prey, due to their disproportionately short manipulating time, only about 15% less.

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### Predicting the Outcome of Stealing Attacks

A successful attack is one which culminates before the target has extracted the prey item. In other words, the assault must end as well as start during a single probing time of a target. There is an analogy between this situation and that involving a predator attacking a potential prey which is alternating between being vigilant and non-vigilant. The assault of the predator must start and end within a gap in vigilance (inter-peek interval) and the kleptoparasitic attack must start and end within a probing time. Models have been developed to predict the probability of success for a randomly attacking predator with a specific attack time using the frequency distribution of inter-vigilant periods (Hart and Lendrem 1984). In the case of stealing, the situation is more complicated since, if energy intake is to be assessed, the frequency distribution of probing times needs to be split into four according to the outcomes small, medium, large and other. However, the approach and apposite equations of Hart and Lendrem (1984) can be adapted to cater for this condition.

The frequency distribution of probing times for each category of outcome  $j=1,2,\dots,n$  ( $n=4$ ) is calculated for the time intervals  $i=1,2,\dots,c$  with the mid-point of the interval  $i = d_i$  (Fig.5.3). For example,  $j=1$  is the category for probings resulting in small Macoma being taken, and  $i=1$  is the time interval between 0 and 0.5s, therefore  $d_1=0.25$ . The  $x$ th interval has its upper limit equal to the attack time ( $T$ ) and  $f(d_i)_j$  is, for category  $j$ , the frequency of probing times in the interval with the mid-point  $d_i$ .

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The probability ( $P_{uj}$ ) that an attack was unsuccessful on a probe which will result in outcome  $j$  can be calculated:

$$P_{uj} = \sum_{i=1}^x g(di)j + \sum_{i=x+1}^c [T/di] g(di)j$$

where 
$$g(di)j = \frac{di f(di)j}{\sum_{j=1}^n \sum_{i=1}^c di f(di)j}$$

The probability that a probe will yield an outcome category  $j$  ( $P_{oj}$ ) is equal to  $\sum g(di)j$ . Therefore, the probability a random attack will be successful on category  $j$  is:

$$P_{sj} = P_{oj} - P_{uj}$$

and overall probability of success ( $P_s$ ) is:

$$P_s = \sum P_{sj}$$

We can also calculate success if the displacement was made, irrespective of whether the target was probing or not; in this case the overall probability of a random attack being successful ( $P_t$ ) is:

$$P_t = P_s \cdot P_p$$

Where  $P_p$  is the mean proportion of the time a foraging individual spent probing (0.12).

Figure 5.4 shows how the success of a bird attacking randomly varies with the attack time it uses. Since the proportion of time a foraging bird spends actually probing is small,  $P_s$  is much greater than  $P_t$ , which at best yields a success rate of 10%. On the other hand, an attack initiated at random while the target is

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probing will have a success rate of nearly 90% at an attack time of 0.5s. However, this performance deteriorates rapidly with increasing attack time.

Since the probability of a particular outcome at a given attack time is known (Fig.5.5), we can calculate the expected energy intake rate using the energy yield of the different outcomes,  $E_j$ , and the manipulating time for the items kleptoparasitised,  $T_{mj}$  (Tab.5.5 - there were no data for the category other so the value for non-kleptoparasitised records was used =2.92s). This assumes that the probability that an item is brought to the surface does not vary depending on whether one bird or two birds carry out the manipulation. For a given attack time, performance can be calculated:

$$R = \frac{\text{energy}}{\text{time}} = \frac{\sum P_{sj} E_j}{(1-P_s)T + \sum P_{sj} (M_{tj} + T)}$$

The term  $(1-P_s)T$  represents the contribution of time spent in unsuccessful attacks. Performance, like success, is greatest at shortest attack times (Fig.5.6).

### Expected and Observed Success and Performance

The actual attack times were not particularly short; less than 10% were shorter than 2s and the mean was 3.1s (SE=0.05 N=232). The attack time is constrained by the distance between the attacker and the target, which was quite large since the foraging groups were well dispersed.

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Taking the attack time as 3s, we can use Figure 5.5 to estimate the performance of a bird if it attacked randomly. The observed performance was much superior to that expected on the model (Tab.5.6): more attacks were successful, the estimated energy gained per act was greater and the estimated rate of energy gain was higher. It can be concluded that food-stealing was not occurring according to the random model.

The assumption of the model is that the attacker initiates an assault at random during a probe. Figure 5.7 plots the distribution of times at which the attack was initiated; if the process was random some form of negative exponential would have been expected, however, this is clearly not the case, as shown by the lack of short times. In addition, the distribution had little variance, with the majority of attacks starting between 2 and 4s into the probe. Consequently, the probing of the target was interrupted after several seconds in a fairly tight distribution with a mean of 5.9s (SE=0.10 N=151) and, on the large majority (>70%) of occasions, between 5 and 7s. That is, the attackers appear to be electing to attack at a specific time during the probe of the target.

Obviously the model of random attacks is not appropriate. However, since attacks are occurring at a fairly set time during the probe, a simple analysis using survivorship curves (Fig.5.8), constructed from the frequency distribution data, can be used to predict the outcome of attacks. This will indicate whether the birds were making selections beyond the decision as to when to

## KLEPTOPARASITISM

start their assault.

There are four outcomes for the unrepulsed attack: unsuccessful, other (k=1), small (k=2), medium (k=3) and large (k=4). If  $f(t)_k$  is the frequency of probes of outcome k that are longer than time t, then the probability of an assault of attack time T, initiated at time t seconds into the target's probe, being successful for a probing of outcome k is:

$$P_k = \frac{f(t+T)_k}{\sum_{k=1}^4 f(t)_k}$$

$$P_0 = 1 - \sum_{k=1}^4 P_k$$

Where  $P_0$  is the probability of an attack being unsuccessful due to a probe ending before an attacker reaches the target.

The observed performance was still much greater than expected (Tab.5.7); in particular, few attacks were unsuccessful. To achieve this the bird must be acting in such a way as to increase its chances of attacking during a long probe. This may be achieved if there is a heterogeneous population of potential targets and attacks are made on birds that tackle more large items or have longer probing times than average. There was no evidence for this and, since attackers did not appear to spend time in prolonged surveillance of their conspecifics, which would be required for such selectivity, the process is unlikely to be important. Alternatively, the kleptoparasites may be able to distinguish between probes which are going to be extended and those that are

## KLEPTOPARASITISM

not. If the latter explanation is correct a possible cue to the length of a probe may be the depth the bill is inserted into the substrate.

### Probe Depth

During probes of known outcome, estimates were made of the maximum depth the bill was inserted into the substrate. Categories of depth were 1/4 (0-1/4 of bill) 1/2 (1/4-1/2 of bill) 3/4 (1/2-3/4 of bill) 1 (3/4- whole of bill). The category of outcome is dependent on the maximum probe depth (Tab.5.8), with larger items being taken from greater depths. Interestingly, discarded items (2 medium and 4 large) were taken from relatively close to the surface. Diseased Macoma are found at lesser depths than healthy ones (Hulscher 1982), which may suggest that items may be discarded due to their being diseased. However, it appears that oystercatchers need to open Macoma before they can assess whether or not they are diseased with trematodes (Hulscher 1982). The godwits may be discarding items that they can detect, by touch, to be dead or to have damaged shells.

That larger items (those which tend to have longer probing times), have greater probe depths will only be of use to an attacking bird if the information is available in the first four seconds of a probe, since most attacks have been initiated by this time. Tab. 5.9 indicates that this is the case. Indeed, where the depth of probe was recorded at the start of an attack, in all cases depth was 3/4 of the bill or greater (N=20, expected

## KLEPTOPARASITISM

distribution for categories 1/4 and 1/2 was 10.0; for 3/4 and 1 was 10.0:  $G[1]=27.7$   $P<0.05$ ). An added advantage of selecting deep insertions is that for the same outcome category, their probing time is significantly greater than for shallower probes (Tab.5.10).

If the attacker randomly selected probes of depth category 3/4 or 1 between 2 and 4s into the probe, would the predicted feeding efficiency approach that observed? This was answered by constructing survivorship curves from the data on probing depths and using the same procedure as above.

The observed and predicted performances are relatively close (Tab.5.11). That the birds make fewer unsuccessful forays than expected may be due to the use of other visual cues not modelled here, and to the tendency of deeper probes to last longer.

It can be concluded that kleptoparasitic attempts were not an epiphenomenon and were also not occurring randomly. Attackers selected probes which were more likely to be longer and to provide higher quality items than average. This seemed to be achieved through the assessment of probe depth.

Interestingly, sometimes the depth of Macoma is inversely proportional to size (Hulscher 1982). Therefore, kleptoparasitic behaviour needs to be flexible, in order to deal with the particular conditions that are present.

### 5.3.3 Performance Of Attackers And Targets

## KLEPTOPARASITISM

In this section we consider the consequences of food-stealing for the attacker and the target. A focal bird which, in a particular observation period, was an attacker more often than a target, was defined as dominant; other birds were termed subordinate unless they were not involved in any stealing encounters, in which case they were called inactive. The percentage of focal individuals in the five minute observations which belonged to these categories was dominant-28%, subordinate-45% and inactive-27% (N=216). That there were over a third more subordinates than dominants suggests that the average kleptoparasitic bird undertook stealing attempts at a greater rate than an average target suffered them. The rate at which the behaviour occurred, and its estimated energetic consequences, can be looked at more closely by considering the 20 minute observations. In order to focus these longer observations on both birds which were attacking and those that suffered assaults, individuals were selected for observation on the basis of their behaviour in the previous five minutes. Half the birds chosen had initiated at least one kleptoparasitic act while suffering none in this period, and the other half had not made any assaults, but had been the target of at least one stealing act.

The data for each focal individual watched for 20 minutes were analysed to yield the following figures: an estimate of the energy gained through non-kleptoparasitic foraging; the number of times the bird was an attacker and a target; the total time spent in stealing acts and the estimate of the gross energy obtained; the total time lost as a target (target's probing time and repulsion

## KLEPTOPARASITISM

time) and the estimated gross energy forfeited. The amount of energy lost could not be estimated directly, since the outcome of the probes by the attacker was not observed. However, the mean energy that an attacker was estimated to gain per act (and therefore the mean loss to the target) can be calculated from the frequency distribution of the four outcomes (Small:11, medium:27, large:33, unsuccessful:16) and their estimated energy content (see above). This yields a mean figure of 0.14kcal per act.

Of the 24 birds watched, 14 were dominants and 10 subordinates (Fig.5.9). Although most dominants only attacked and most subordinates were only targets this was not always the case. Interestingly, dominants which made relatively few assaults were more likely to suffer attacks. However, the two groups were fairly discrete (Fig.5.9) and the population seemed to be split, at this time, into birds which were basically kleptoparasitic and those that were not.

The mean number of attacks made by dominant birds in twenty minutes was 6.9 (SE=0.76 N=14), which is a rate of 0.34 per minute, and the mean time spent in these attacks and subsequent manipulations was 74.2s (SE=8.93 N=14), which represents 6.2% of available time. The mean rate of energy intake from kleptoparasitism (total energy gained from acts divided by the total time engaged in them) was 0.80kcal per minute (SE=0.016 N=14), which is more than four times the overall intake rate; even assuming some cost of kleptoparasitism stealing was obviously very profitable. Indeed, the average contribution

## KLEPTOPARASITISM

stealing makes to the overall energy intake of a dominant bird was 24% (SE=8.7 N=14) and, for some individuals, was as high as a third.

The mean number of times a subordinate was a target in the 20 minute period was 2.5 (SE=0.40 N=10), which is a rate of 0.13 per minute, a figure significantly less than the number of attacks made by dominants ( $F[1,22]=20.3$   $P<0.001$ ). The mean time lost by subordinates to assaults was 15.1s (SE=2.32 N=10), which is 1.3% of the total time. The expected amount of energy obtained in the time period by a subordinate in the absence of being attacked (inactive state) can be calculated by summing energy actually obtained and the estimated energy lost to attacks. The mean proportion of energy lost to energy expected in an inactive state was 0.094 (SE=0.014 N=10) and, at highest, 0.15, that is, about 10% of the potential energy of a subordinate bird was being lost to kleptoparasitism. Therefore, it might be expected that dominants would have a greater overall energy intake but, although dominants are taking a quarter of their energy through displacements, their overall energy intake in 20 minutes (4.0kcal, SE=0.31 N=14) was not significantly greater than that for subordinates (3.2kcal, SE=0.46 N=10) ( $F[1,22]=2.4$  NS).

The expected energy intake rate in the absence of interactions can be calculated (sum of energy from uninterrupted probes and the estimated energy forfeited, divided by the sum of the time spent in uninterrupted foraging and the time lost to attacks). It might be predicted that this rate would be lower in dominants, since

## KLEPTOPARASITISM

vigilance for targets may reduce their own foraging efficiency, or if only individuals with low intake participate in kleptoparasitism. However, although the rate was higher for subordinates, 0.18kcal per min (SE=0.025 N=10) against 0.17kcal per min (SE=0.013 N=14), the difference was not significant ( $F[1,22]=0.16$  NS).

Therefore, although food-stealing was uncommon and the amount of time spent by attackers, and especially that lost by targets, was small, the energetic consequences may be important as dominants take a quarter of their energy from kleptoparasitic attacks and subordinates lose a tenth of their intake. The importance is heightened because the behaviour is at its most common during adverse weather when feeding conditions are poor.

TABLE 5.1

Frequency of intraspecific displacements in 1080 minutes. Rate is the number of events per minute. Attacks refer to displacements which were kleptoparasitic. Displaces refer to other displacements.

TABLE 5.1

	TOTAL (N)	RATE	FREQUENCY REPULSED(R)	R/N
FOCAL BIRD ATTACKS	155	0.14	17	0.11
FOCAL BIRD IS ATTACKED	139	0.13	11	0.08
FOCAL BIRD DISPLACES	191	0.18	21	0.11
FOCAL BIRD IS DISPLACED	215	0.20	16	0.07

TABLE 5.2

Frequency of kleptoparasitic displacements (attacks) and other displacements compared to the frequencies expected if displacements occurred randomly in time.

TABLE 5.2

	OBSERVED	EXPECTED
TOTAL NUMBER OF ATTACKS	294	84
TOTAL NUMBER OF OTHER DISPLACEMENTS	406	616
	700	700

TABLE 5.3

The outcome of kleptoparasitic acts.

The table indicates how many kleptoparasitic acts were repulsed and of those not repulsed how many lead to the attacker gaining no item, a small item, a medium item, or a large item.

TABLE 5.3

		FREQUENCY	PROPORTION OF TOTAL	PROPORTION OF THOSE NOT REPULSED
REPULSED		25	0.10	
NOT REPULSED	NO ITEM	46	0.18	0.19
	SMALL ITEM	16	0.06	0.07
	MEDIUM ITEM	66	0.25	0.28
	LARGE ITEM	108	0.41	0.46
		-----		
		261		

TABLE 5.4

The outcome of probes uninterrupted by displacements

TABLE 5.4

	FREQUENCY	PROPORTION
GIVE UP	88	0.041
ITEM DISCARDED	108	0.050
UNIDENTIFIED ITEM	211	0.098
SMALL ITEM	658	0.305
MEDIUM ITEM	565	0.262
LARGE ITEM	527	0.244
	-----	
	2157	

TABLE 5.5

Length of the probe after a successful attack. SE in brackets.

The table indicates the mean probing and mean handling time of an item gained through a successful attack. Manipulating time is the sum of the mean probing time and mean handling time.

Data are split according to the size class of the items.

TABLE 5.5

	MEAN PROBING TIME (s)	MEAN HANDLING TIME (s)	MANIPULATING TIME (s)
SMALL	2.1 (0.21)	2.1 (0.17)	4.2
MEDIUM	3.8 (0.10)	3.5 (0.07)	7.3
LARGE	6.3 (0.12)	6.8 (0.11)	13.2

TABLE 5.6

Performance of observed kleptoparasitic acts and performance predicted on the random model. For random attacks, attack time=3s; for observed attacks, mean attack time=3.1s.

The table indicates both the observed and expected frequencies of the various outcomes of attacks, and the length and energy consequences of attacks.

Small - small item gained

Medium - medium item gained

Large - large item gained

Unsuccessful - unsuccessful attack

Other - other outcome

TABLE 5.6

OUTCOME OF ATTACKS (PROPORTION OF TOTAL)		
	EXPECTED	OBSERVED
OTHER	0.00	0.04
SMALL	0.04	0.07
MEDIUM	0.13	0.29
LARGE	0.27	0.46
UNSUCCESSFUL	0.57	0.16
ENERGY PER ACT (kcal)	0.09	0.15
MEAN LENGTH OF ACT (s)	7.7	11.6
ENERGY RATE DURING ACT (kcal per s)	0.011	0.013

TABLE 5.7

Performance of observed kleptoparasitic acts and performance predicted if attacks started at random at 2 and 4s into the probe of the target. For random attacks, attack time=3s; for observed attacks, mean attack time=3.1s.

Table format as for Table 5.6.

TABLE 5.7

OUTCOME OF ATTACKS (PROPORTION OF TOTAL)			
	EXPECTED		OBSERVED
	ATTACK STARTED AT 2s	ATTACK STARTED AT 4s	
OTHER	0	0	0.04
SMALL	0.01	0	0.07
MEDIUM	0.17	0.01	0.29
LARGE	0.28	0.42	0.46
UNSUCCESSFUL	0.54	0.57	0.16
MEAN LENGTH OF ACT (s)	0.09	0.10	0.15
ENERGY PER ACT (kcal)	8.0	8.6	11.6
ENERGY RATE DURING ACT (kcal per s)	0.012	0.012	0.013

TABLE 5.8

Variation of outcome of probe with the maximum depth of probe.

Maximum depth expressed in terms of depth category.

Other does not include items that were discarded.

TABLE 5.8

-----					
FREQUENCY OF OUTCOME					
-----					
MAXIMUM PROBE DEPTH					
	1/4	1/2	3/4	1	TOTAL
-----					
OTHER	36	10	2	0	48
SMALL	17	16	5	0	38
MEDIUM	3	19	14	9	45
LARGE	0	4	16	21	41
DISCARDED	6	0	0	0	6
-----					

TABLE 5.9

The fraction of probes of maximum depth category  $3/4$  or  $1$ , that reach a depth category of at least  $3/4$  within  $2s$ ,  $3s$  and  $4s$  of the probe starting.

Data split according to the outcome of the probe.

TABLE 5.9

	FRACTION OF PROBES		
	2s	3s	4s
SMALL/OTHER	4/4		
MEDIUM	12/16	16/16	16/16
LARGE	4/15	8/15	14/15

TABLE 5.10

Probing times for medium and large items taken at different depths. Depths in terms of maximum depth category. In brackets sample size followed by SE.

Probing time significantly dependent on depth: for medium sized items  $F[3,41]=10.1$   $P<0.001$ ; for large sized items  $F[2,38]=15.0$   $P<0.001$ .

TABLE 5.10

MEAN PROBING TIME (s)				
	MAXIMUM DEPTH CATEGORY			
	1/4	1/2	3/4	1
MEDIUM	3.9 (3,0.17)	5.0 (19,0.20)	5.8 (14,0.20)	6.3 (9,0.24)
LARGE		6.6 (3,0.60)	8.2 (16,0.20)	8.7 (21,0.18)

TABLE 5.11

Performance of observed kleptoparasitic acts and performance predicted if attacks were random, but started between 2 and 4s into the probe of the target and were on probes of depth category 3/4 or 1.

Format of table as Table 5.6.

TABLE 5.11

OUTCOME OF ATTACKS (PROPORTION OF TOTAL)					
	EXPECTED			OBSERVED	
	ATTACK STARTED AT 2s	ATTACK STARTED AT 3s	ATTACK STARTED AT 4s	MEAN	
OTHER	0	0	0	0	0.04
SMALL	0.04	0	0	0.01	0.07
MEDIUM	0.46	0.21	0.05	0.24	0.29
LARGE	0.28	0.43	0.61	0.44	0.46
UNSUCCESSFUL	0.21	0.36	0.34	0.30	0.16
ENERGY PER ACT (kcal)				0.14	0.15
MEAN ACT LENGTH (s)				10.7	11.6
ENERGY RATE DURING ACT (kcal per s)				0.013	0.013

FIGURE 5.1

Probing (closed circles) and handling (open circles) times in seconds for different outcomes of probes. S-small item, M-medium item, L-large item, O-other outcome.

Sample sizes: S=657, M=566, L=526, O=408.

Bars represent SE.

FIGURE 5.1

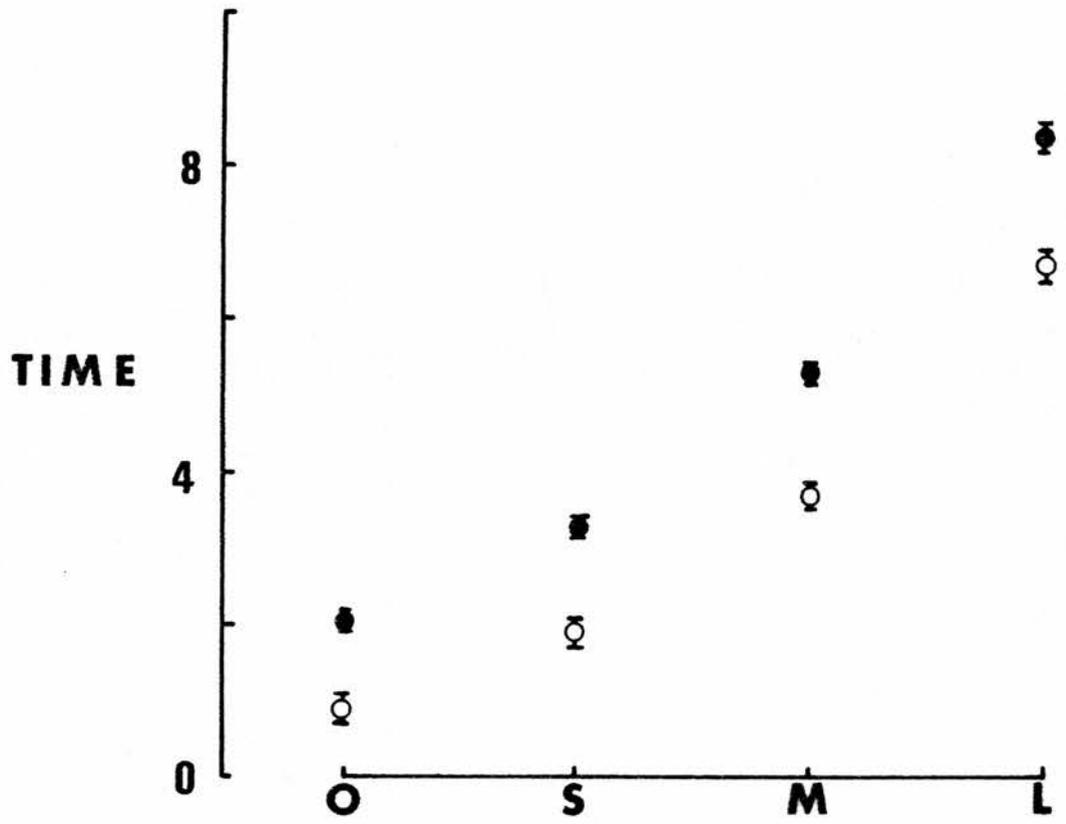


FIGURE 5.2

Estimated profitability of different outcomes of probes. Energy per probe ( $E$  in kcal), rate of energy intake ( $R$  in kcal per s). S-small item, M-medium item, L-large item, O-other outcome.

FIGURE 5.2

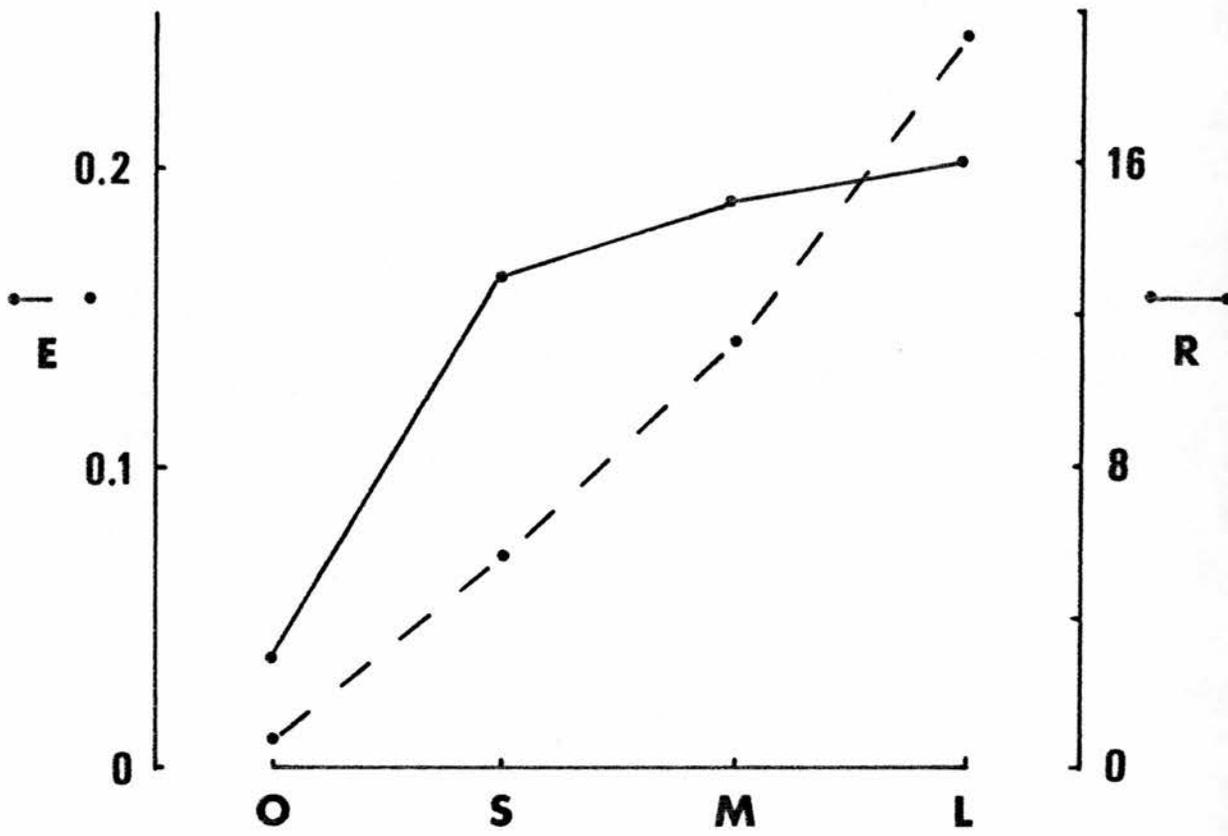


FIGURE 5.3

Frequency (F) distribution of probing times for different outcomes of probes. Time is split into half second categories. S-small item, M-medium item, L-large item, O-other outcome.

FIGURE 5.3

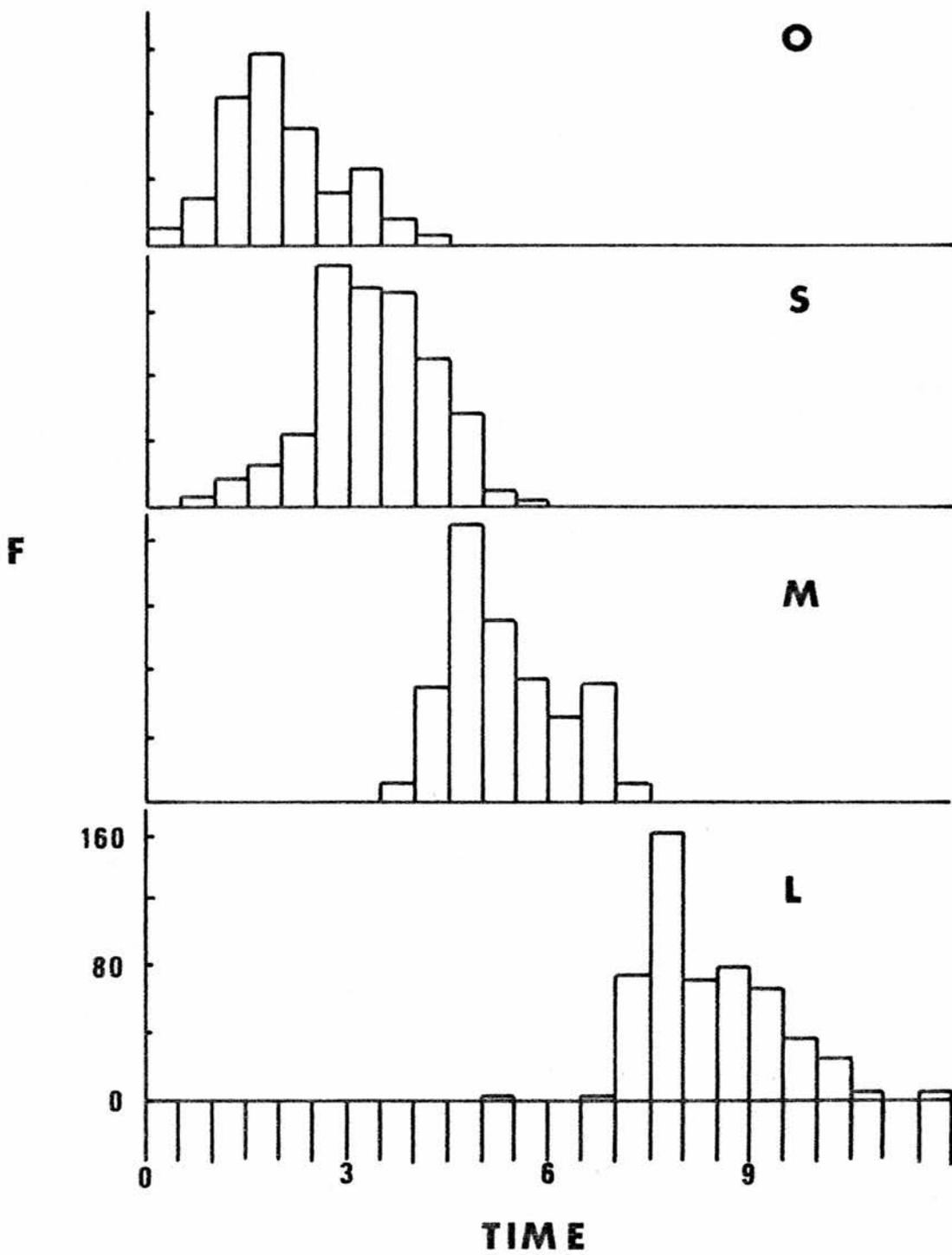


FIGURE 5.4

Influence of the length of the attack time (TIME in seconds) on the predicted probability (P) of an attack being successful.

Top line: success if attack is started at random while target was probing.

Bottom line: success if 'attack' is started at random irrespective of whether the target was probing or not.

FIGURE 5.4

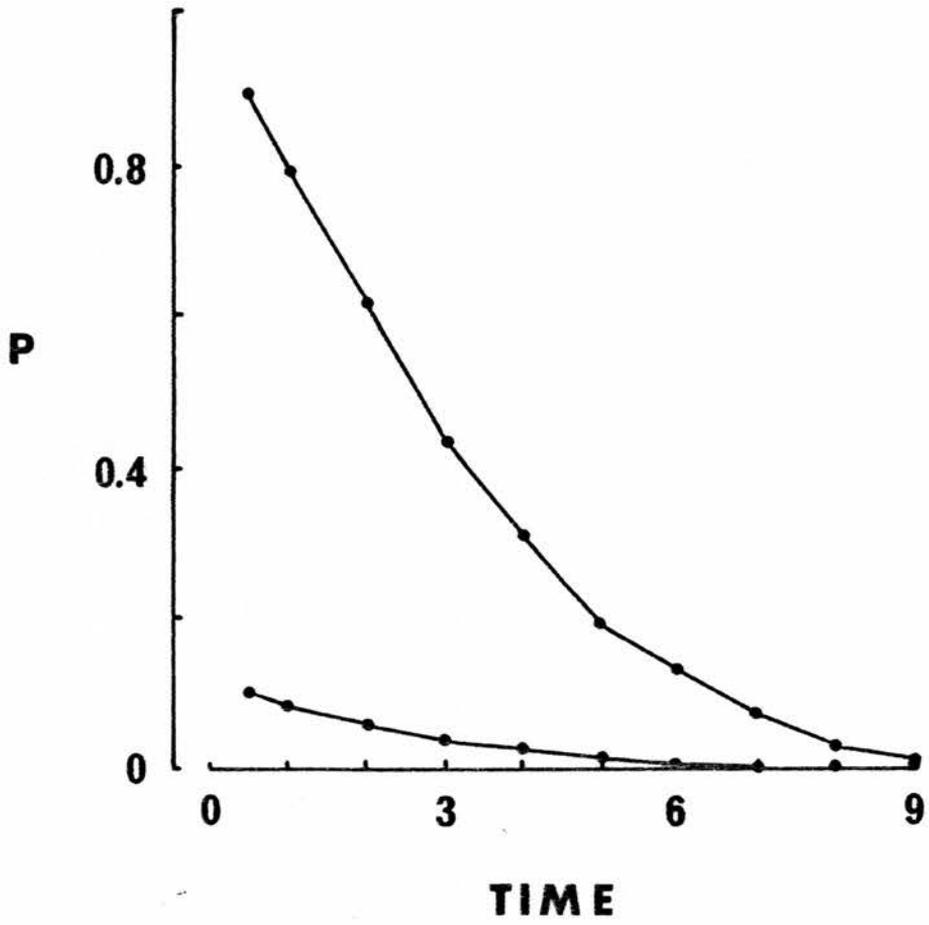


FIGURE 5.5

The influence of the length of the attack time (TIME in seconds) on the predicted outcome of an attack (probability, P, of a particular outcome).

b/ small item

c/ medium item

d/ large item

u/ unsuccessful outcome

a/ other outcome

FIGURE 5.5

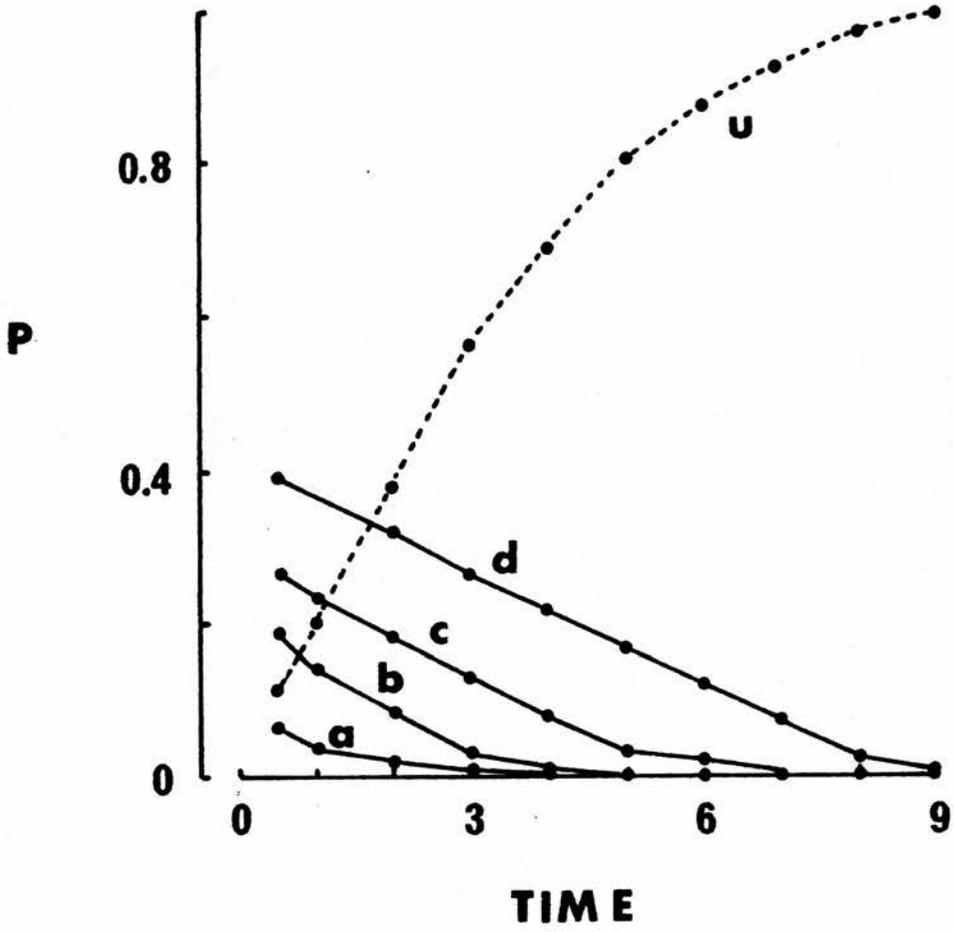


FIGURE 5.6

Influence of the length of the attack time ( $T$  in s) on the predicted mean rate of energy intake ( $E$  in [kcal per s] 1000).

FIGURE 5.6

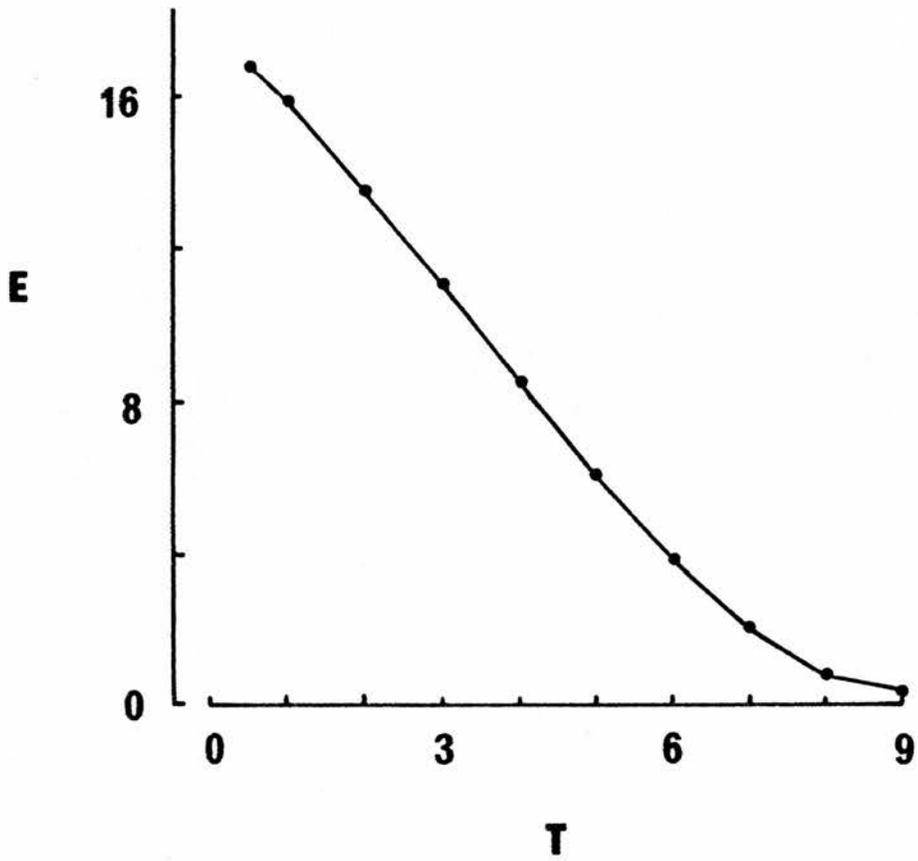


FIGURE 5.7

Frequency (F) distribution of when an attack was initiated in terms of how long the target had been involved in a probe. Time is divided into half second categories.

FIGURE 5.7

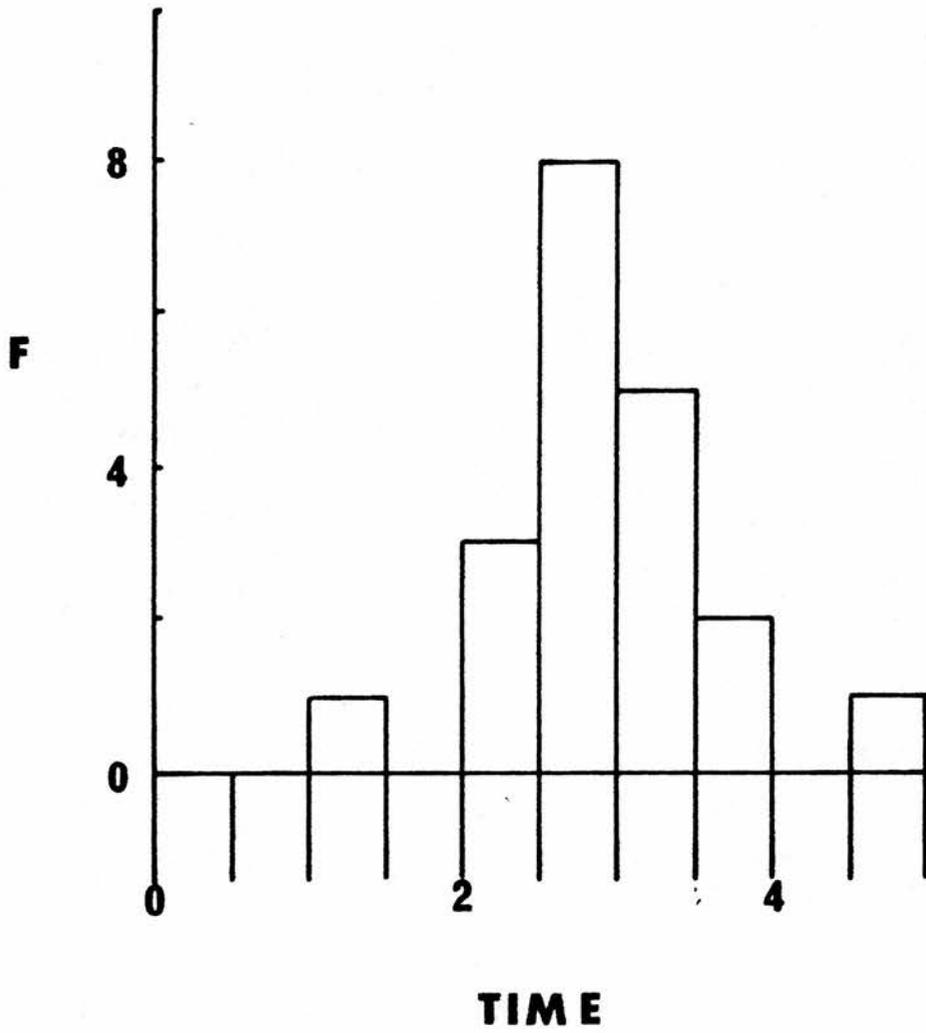


FIGURE 5.8

Survivorship plot of probing time (TIME in s) for probes uninterrupted by kleptoparasitic attacks. The solid line indicates how many probes (F) are longer than a specific length. The dotted lines divide the probes according to their outcome; for example, the probes represented between the top dotted line and the solid line are those that will yield a large item (l). Medium items are m, small items s and other outcome o.

FIGURE 5.8

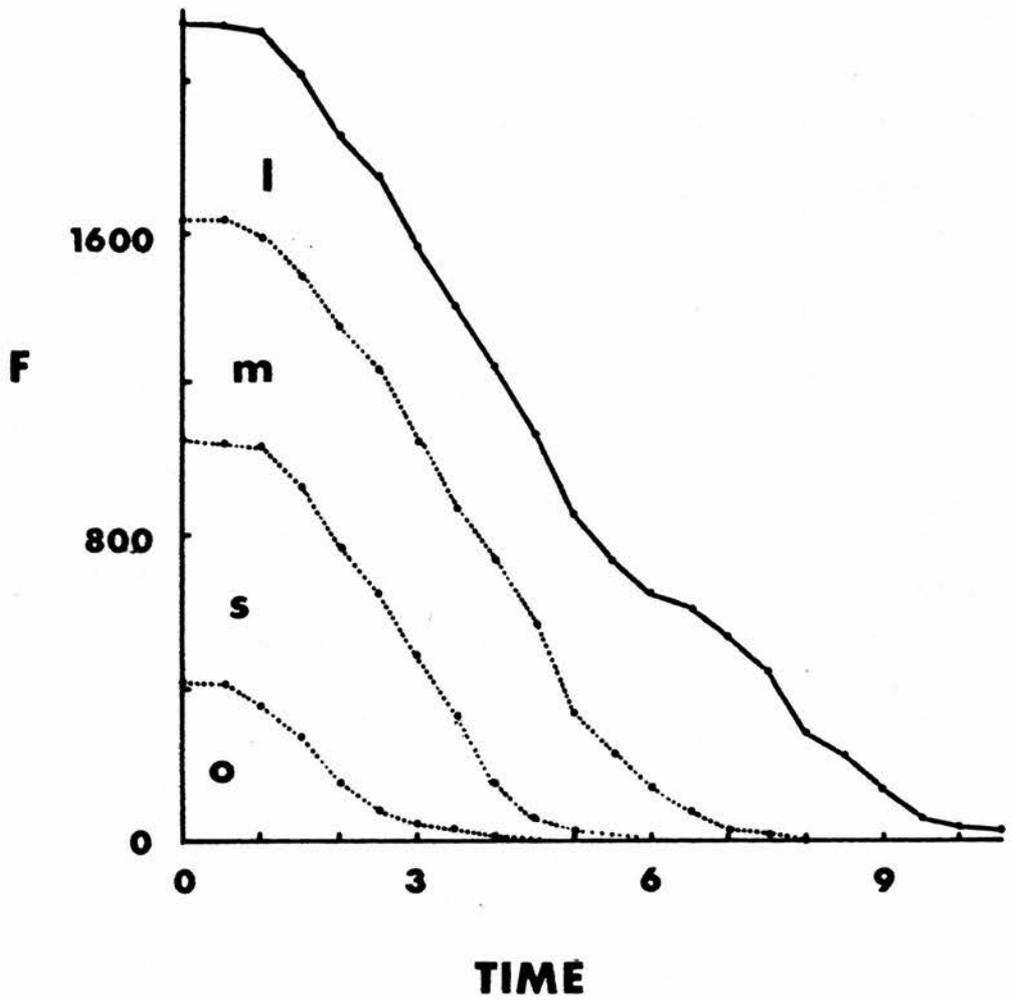
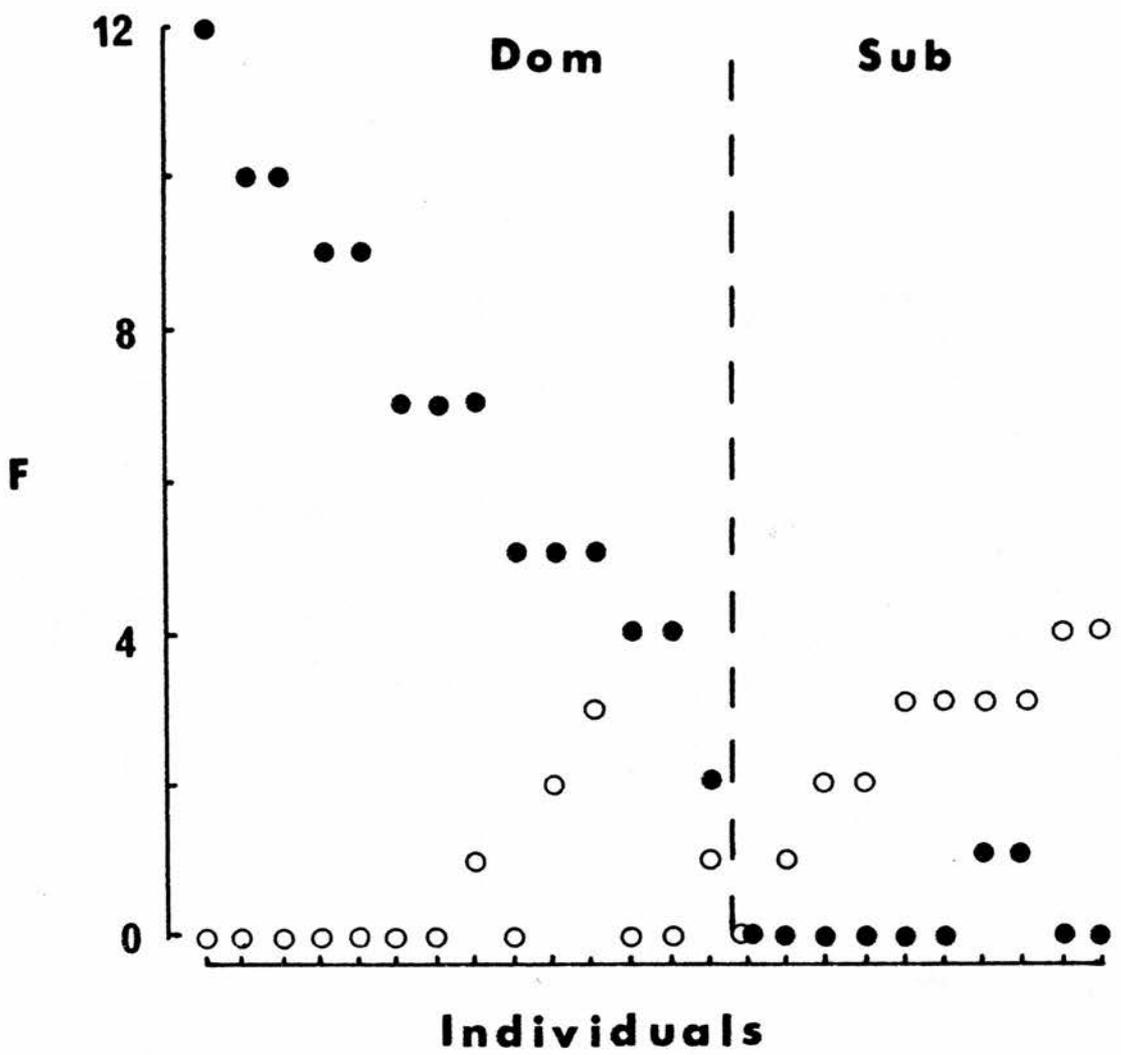


FIGURE 5.9

The frequency (F) of attacks undertaken (solid circles) and suffered (open circles) by 20 focal individuals each observed for 20 minutes. The birds have been divided into dominants (Dom) and subordinates (Sub).

FIGURE 5.9



## CHAPTER 6

### EFFECT OF CONSPECIFICS AND OTHER SHOREBIRDS ON FORAGING

#### 6.1 INTRODUCTION

An estuary usually attracts a large number of wintering shorebirds of various species. At such a site a foraging individual is therefore usually in the presence of both conspecifics and heterospecifics. The spatial relationships with these other birds may have a profound influence on the behaviour and the performance of a bird.

Within a species the spacing pattern may be random, clumped or overdispersed, persistent or ephemeral. Most non-breeding waders show great variability in their spacing, although flocking is the norm and the majority of a population rarely adopt a spaced-out formation (Myers 1984). Mixed species flocks are frequent at roosts, but form relatively uncommonly during foraging birds (Myers 1984). However, other shorebirds may have a large effect on behaviour by, for example, making an area unavailable through their physical presence.

## EFFECT OF CONSPECIFICS AND OTHER SHOREBIRDS ON FORAGING

There has been a considerable amount of interest in the reasons for birds adopting particular spacing patterns, and in the consequences of single and mixed species associations (general reviews: Bertram 1978, Pulliam and Caraco 1984, Barnard and Thompson 1985, reviews concerning shorebirds: Myers 1984, Goss-Custard 1980). This chapter describes two studies:

- 1) An investigation of flocking by stitching and probing black-tailed godwits in terms of the consequences for protection from predators and for foraging performance.
- 2) An investigation into the effect of loafing gulls and plovers on the behaviour of black-tailed godwits.

### 6.2 FLOCKING BEHAVIOUR

A bird presumably joins or remains part of a flock if it is advantageous to do so. There are two types of benefit from foraging in a flock: one concerns the efficiency of anti-predator behaviour, the other concerns the efficiency of foraging.

#### 6.2.1 DESCRIPTION OF FLOCKING

A quantitative study of the flocking and spacing of stitching and probing birds needs to be made before a consideration of the consequences of being a flock member can be assessed.

## EFFECT OF CONSPECIFICS AND OTHER SHOREBIRDS ON FORAGING

### Methods

Observations occurred between seven and nine hours after predicted high-tide. At this time a majority of the population was usually foraging and a large area of mud remained uncovered, meaning that available space was unlikely to be a controlling factor in determining flocking patterns. Once per session data were collected on all the flocks that were on the study area.

Probing birds usually formed discrete groups, with birds moving in the same general direction. For each probing flock, the number of birds was recorded and their spacing estimated by noting the nearest neighbour distance (NND) of each individual in bird-lengths.

Stitching birds usually gathered in a single line along the tide-edge and did not form discrete flocks which were easy to define. A record was made of the distances, in bird-lengths, in one direction, between the birds in such an array. A note was also made of the NND for each bird. The distribution of the size of gaps between the stitching birds (Fig.6.1) indicated that the birds were significantly under-dispersed, that is, the godwits were arranged in flocks. A log-survivor plot of the size of gaps allows an objective definition of a flock (Fig.6.2). Although there is no clean break in the plot, there is a flattening of the curve by the category of gap size nine or 10. Consequently, a flock was defined as birds not separated by more than 10 bird-lengths. Using this definition flock-sizes for stitching birds could be calculated.

## Results

Flock-size was twice as large for stitching birds as for probing birds (10.1 against 4.7).

Within flocks, the NND was shorter for stitching birds than for those that were probing (mean NND 2.7 against 4.4:  $G[9]=54.6$   $P<0.001$ ). If spacing within a flock was random, the distribution of NND would be expected to follow some sort of negative geometric. This is clearly not the case (Fig.6.3). There were a lot fewer short spaces between birds than would be expected, indicating that there was a tendency for a minimum distance to be maintained between individuals.

## 6.2.2 INFLUENCE OF PREDATORS ON FLOCKING

Raptors can inflict high rates of mortality on smaller waders (Page and Whitacre 1975, Whitfield 1985) and all shorebirds show alarm on the appearance of these predators. Compared to being solitary, a wader in a flock may benefit from enhanced predator detection, from reduced risk and disturbance if an attack occurs and from a lower commitment to vigilance, allowing more time to feed.

If predators are important in determining spacing behaviour, it would be expected that flocking tendency should change with predation risk.

## EFFECT OF CONSPECIFICS AND OTHER SHOREBIRDS ON FORAGING

### Influence of Raptors on Spacing

#### Methods

On nine occasions (five for stitching flocks and four for probing flocks), involving a total of 25 foraging groups, the NND for flock members was measured by chance before and within 15 minutes of alarm caused by a raptor and could be remeasured five to 10 minutes after the disturbance. The birds did not take off, but were alert after the disturbance and stopped feeding for a few minutes.

#### Results and Discussion

For both feeding methods, flock density was significantly greater after disturbance than before it (comparing the distribution of NND sizes in flocks before and after the event: stitching,  $G[3]=24.2$   $P<0.001$ ; probing,  $G[4]=19.1$   $P<0.001$ ). Of 13 birds that were solitary before the event nine joined a flock.

Thus predators have an effect on the spacing behaviour of black-tailed godwits. This phenomenon has been found in other studies; in the most extreme examples territorial buff breasted sandpipers (*Tryngites subruficollis*) (Myers 1984) and redshanks (Whitfield 1988) will group if a predator flies over. Myers (1984) concluded that predators may strongly influence not only spacing behaviour but also local movements of shorebirds. Similarly, Pulliam (1973) linked sociality with predator pressure and Caraco (1979) linked flock-size with frequency of encounters with predators.

## EFFECT OF CONSPECIFICS AND OTHER SHOREBIRDS ON FORAGING

### Reaction to Disturbance

It is important to detect a raptor before it attacks, since, if a wader is able to take off, the chances of being caught are low (Page and Whitacre 1975, Metcalfe 1984a), although shorebirds may sometimes be taken in the air (Blick 1980, pers. obs.). However, if a bird takes off when the danger is not great, foraging efficiency will be unnecessarily reduced. Therefore, the sooner a potential danger is detected the greater the time available for a correct decision to be made as to whether to fly or not. This section looks at this behaviour in the context of flock-size.

### Methods

The flats to the south of Guardbridge were used to conduct an experiment. Up to 15 godwits foraged at this site, usually on one particular area of the mud and mainly during late winter and early spring. A footpath along the bank of the estuary passed close to the favoured area and people and dogs using this track frequently caused disturbance amongst the birds. On 25 occasions spread between four months (February 1986, 1987 and 1988 and September 1987), a flock that was using the area and that had not been disturbed for at least 30 minutes was approached at a constant rate from along the footpath. When the first bird showed signs of an awareness of the observer by adopting an alert posture and an orientation towards him, and again when the flock took off, the observer marked his position and the position of the flock member closest to him on a map, with reference to landscape features. Subsequently, the map was used to estimate the distance between the

## EFFECT OF CONSPECIFICS AND OTHER SHOREBIRDS ON FORAGING

observer and the flock at the two moments of interest - the response distance and the flight distance. A note was also made of the size of the flock and whether the flock left the Guardbridge flats entirely after taking off. The data were not used if the reactions of other birds affected the response distance of the flock. Trials were separated by at least 60 minutes, with a maximum of three in any one session.

### Results and Discussion

The response distance was positively correlated with flock-size (Kendall's Tau [N=25]=0.46  $P<0.01$ ). However, the flight distance was negatively correlated with flock-size (KT [N=25]=-0.33  $P<0.05$ ). That is, there was an earlier response to the observer in a larger flock, but the flock was less likely to fly. Smaller flocks (<4 birds) were also significantly more likely to leave the area completely after taking off ( $G[1]=11.2$   $P<0.001$ ).

It can be concluded that larger flocks appear to detect potential predators sooner and are less likely to take off when disturbed. Therefore, an individual in a flock benefits from both reduced individual risk and reduced disturbance. Two reasons why a larger flock takes off later are: 1) that the earlier detection allows a less hasty response and 2) that individual risk is lower, meaning that, for a given situation, there is less need to fly. Similar results have been reported before (Lazarus 1979). However, in some studies larger flocks take off sooner (Murton 1971, Siegfried and Underhill 1975, Greig-Smith 1981). Some of this variation between the studies is probably due to the costs and

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benefits of early flight varying depending on the particular circumstances. For example, if the foraging cost of leaving an area is low, a large flock may be more likely to fly early.

Individuals in flocks are likely to gain other advantages concerning predation risk. Although lacking empirical evidence (Inman and Krebs 1987), models by Treisman (1975) have suggested that cryptic animals hunted from above would minimise predator encounter rate if they flocked. When an attack does occur, factors such as dilution (Hamilton 1971) and confusion (for example Milinski 1979) may confer benefits on a flock member.

### Budgeting for Stitching Birds

Since feeding in shorebirds involves orienting the head towards the mud, and is therefore mutually exclusive with scanning the environment, watching out for predators reduces foraging performance. By joining a flock an individual may be able to drop its vigilance rate while still benefiting from a high corporate vigilance (see Lendrem 1986). In this section the vigilance of solitary birds and flock members was compared. When a black-tailed godwit was stitching, the head was usually oriented towards the substrate and the eye was often closed thus preventing vigilance. However, when an item was swallowed the head was raised above the horizontal and the eye opened for a short period of time allowing vigilance to occur. In addition, the head was occasionally brought above the horizontal when food was not being swallowed, presumably for vigilance. In probing birds it was more difficult to discern

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when vigilance was shown. Therefore, only stitching birds are considered here.

### Methods

Since it was mutually exclusive with feeding, the variable of most interest was the vigilance not associated with swallowing food. Therefore, vigilance was defined as occurring when the bird was stationary with head held above the horizontal, and the bird was not handling or swallowing food. In addition 100 head-up times for swallowing birds were recorded for both solitary and flocking godwits.

### Results and Discussion

The mean amount of time spent vigilant by birds in a flock was very low (0.79s per min, SE=0.11 N=79) and not correlated with flock-size. Solitary birds spent four times as long as group members in vigilance (3.14s per min, SE=0.24 N=22), the difference was significant (Mann-Whitney U-test  $w=1981$   $P<0.001$ ). The swallowing head-up time was also significantly longer for solitary individuals (0.97s per event, SE=0.02 N=100, against 0.69s per event, SE=0.01 N=100:  $F[1,198]=137.6$   $P<0.001$ ).

Difference in vigilance rate related to flocking behaviour has been found in many birds (Abramson 1979, Barnard 1980, Bertram 1980, Jennings and Evans 1980, Barnard and Stephen 1983, Sullivan 1984, Lendrem 1984a, Metcalfe 1984b 1984c), and it appears that a general advantage of being in a flock is the lower commitment to vigilance.

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On average, a single bird spent 2.3 seconds per minute more in vigilance (extra vigilance) and 0.3 seconds per swallow more in head-up (extra head-up) than a member of a flock. Assuming feeding rate (outside extra vigilance and extra head-up) is the same for solitary birds and flock members, and vigilance behaviour is independent of foraging rate, how important is the difference in time budget?

let  $x$  = items taken per minute for a single bird

thus rate per second of foraging for single bird =  $X/60$

=> rate per second of foraging for flock member

$$= x / (60 - \text{extra vigilance} - \text{total extra head-up})$$

=> items taken per minute of foraging for a flock member

$$y = 60[x / (60 - 2.3 - (0.3x))]$$

Figure 6.4 plots the variation of  $y$  with  $x$ . The budget difference would mean that a solitary bird with a low intake rate of five items per minute would increase its performance by 7% on joining a flock. At a higher rate of 20 items per minute the advantage is much greater at 16%. The suggestion that the size of the budget advantage varies is interesting, since it means that the advantage of joining a group may be dependent on the foraging conditions.

6.2.3 INFLUENCES OF CONSPECIFICS ON FLOCKING

There may be consequences of flock feeding as well as the budget and disturbance benefits related to predators described above.

Foraging and Density

If there are direct feeding benefits from being in a group, a relationship between foraging performance and flock-size might be expected.

Methods

Observations took place between eight and nine hours after predicted high-tide, in order to control for tide height, which can have a large effect on foraging behaviour (see Chapter 4). A flock was selected at random from the study area. The size of the flock, the density of the flock (mean NND), temperature and wind speed were recorded. The foraging performance of the godwits within the flock was measured by focal bird observations for a total of six minutes per flock. Gross energy intake was calculated using the procedure described in Chapter 4. Data were collected for 47 stitching flocks and 45 probing flocks over 36 sessions. A given flock was only used once per session. Foraging performance was taken as the average energy intake per minute of feeding time, where feeding time was defined as observation time minus vigilance time and head-up time. This controlled for budget changes related to flock-size discussed above.

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### Results and Discussion

For stitching, both flock density and flock-size were positively related to foraging performance (Tab.6.1). Density and flock-size were correlated. For probing, density was positively related to foraging performance (Tab.6.2). These results are probably a reflection of flocks forming at good sites and flock density being greater in these areas. Food density was not measured in this study but other work has indicated that flock-size is largest where prey availability is highest (Barnard 1980, Curtis and Thompson 1985, Barnard and Thompson 1985).

If flocks form at good feeding sites, an individual can use a flock as an indication of a good position in which to forage. This being true, it might be expected that birds should move from one flock to another and solitary birds join flocks. Of 35 birds which were seen to leave flocks, all but three joined other foraging flocks. On three occasions, a solitary bird that flew off and joined a flock had been observed by chance prior to take off and was able to be recorded after becoming a flock member. For all three, the feeding method being used both outside and within the flock was stitching. Two of the three solitary birds that joined flocks had significantly greater foraging performance (data controlled for budget changes) in flocks than when they were alone ( $F[1,11]=18.4$   $P<0.05$ ;  $F[1,9]=9.3$   $P<0.05$ ;  $F[1,8]=0.96$  NS).

Godwits do actively join flocks, maybe because they indicate good feeding conditions. Once in a group, there are several possible direct consequences of being near conspecifics. Within a flock, area copying and opportunities for stealing food as observed in other species (Barnard and Sibly 1981, Feare 1984, Curtis and Thompson 1985) could occur. Kleptoparasitism was usually a rare event and under normal conditions will not make an important contribution to overall foraging performance, although when the weather is inclement it may be significant for probing birds (discussed in Chapter 5).

All the benefits mentioned in this and in the previous section will tend to decrease not only the risk of low feeding efficiency, but also the variance in performance which may also be important (Caraco 1981, Pulliam and Caraco 1984).

However, there are likely to be costs of being a group member, which may help to explain the variation of spacing in flocks and why some birds forage on their own. Basically there are two types of negative effect that other flock members can have on foraging performance - depletion and interference (Goss-Custard 1980). Depletion is the removal of food items. Interference is where intake rate is reversibly reduced by the presence of other birds. Interference may occur through prey being disturbed, thereby making them unavailable, or by reducing the searching or feeding efficiency. Depletion is a more long-term effect and it is interference that is of interest in this study.

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### Interference Within Flocks

Considering different flocks, it has been shown above that, when birds were closer together, foraging performance was higher. This was probably related to food availability. If interference was occurring within a specific flock, the foraging performance of an individual should be influenced by the closeness of its immediate neighbours.

#### Methods

Flocks were selected where there was a large variation of density with time. Within a flock, a bird was observed continuously for a minimum of 10 minutes. After each minute of the observation the NND was noted and also any large changes of NND throughout the period. Ten flocks of stitching birds and 10 flocks of probing birds were used; a flock was only used once per session. In order to record the spacing of the birds, observations occurred using low magnification which precluded detailed observations on food items; feeding performance was therefore recorded in terms of items. Compared to gross energy this is less accurate, but it has been shown that item intake is a good predictor of gross energy intake (see Chapter 4). For each minute of the observation, the number of items taken was calculated, as was the mean NND (mean of values at the beginning and the end of the minute plus any other noted changes). Although following individuals in this way is the only means to assess the influence of intraflock density on foraging performance, the data set for each observation is small and, combined with the influence of other factors, is prone to type II

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errors. To overcome this the combined significance of a series of observations was calculated (see Chapter 2).

### Results and Discussion

For each of the observations, the performance each minute was correlated (Kendall's Tau) with the NND. For eight of the 10 stitching birds, there was a trend for performance to be greater when NND was small. However, overall this result was not significant (for the eight birds: test statistic[16] =10.1 NS). For all 10 probing godwits, feeding rate was greater when NND was greater. This trend was significant for one of the birds and the combined result for the series was highly significant (test statistic[20] =45.2  $P < 0.005$ ).

Other shorebird studies have looked at interference. However, it is often difficult to interpret what the results indicate. For example, Pienkowski (1980) found that the energy intake rate of grey plovers declined with increasing flock-size. However, average intake of the flock was used, which is unfortunate, as the crucial variable is the intake rate of an individual as the size of the flock varies. Other workers report that feeding rate in terms of items is low in dense or large flocks; the phenomenon is taken to represent interference (Goss-Custard 1980). This conclusion assumes that item rate and energy rate are positively correlated. Although the relationship holds for this study, it may not always be the case, especially since dense or large groups may gather at good patches. At high prey density an individual should be more selective (for a review see Krebs and McCleery 1984), and therefore

energy rate may increase but item rate decrease.

#### Conspecific Interactions

One factor in interference may be the level of aggression within flocks.

#### Methods

Observations on interactions between flock-feeding black-tailed godwits took place during the collection of data on the influence of flock-size and density on foraging behaviour (see above). Each flock used in that investigation was observed for a further five minutes. During this period low magnification viewing was used so that all group members could be seen, allowing a record to be made of the total number of interactions. The mean number of interactions per bird per minute was calculated for each flock observed.

#### Results and Discussion

For flocks of stitching birds, one third of the variance in interaction rate was explained by flock-size and NND (Tab.6.3). Birds in larger groups and more dense groups have higher rates of aggression, flock-size being particularly important. There was also a trend for interactions to be more common when it was colder, but this was not significant.

Over a third of the variance in aggression levels of probing flock members was explained by, in order of importance, NND, temperature and group-size (Tab.6.4). In larger flocks, more dense

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flocks and when it was colder, the rate of interactions that a bird had with conspecifics was higher. In contrast to the situation for stitching flocks, density was a more important factor than group-size, and temperature had a significant effect.

Although the level of interactions is a function of flock parameters, it will not be an important factor in feeding interference, since, on average, encounters occur rarely and only last a matter of seconds.

### 6.2.4 GENERAL DISCUSSION

This investigation has shown that there are reasons related to both predator avoidance and foraging success as to why a black-tailed godwit would benefit from being in a group. These advantages are likely to be similar for both foraging methods. However, for probing birds, there is a cost of flock membership due to interference from other individuals.

Visual forms of feeding, such as probing, are expected to be prone to interference from close conspecifics (Goss-Custard 1980). Indeed, shorebirds that feed by touch do form the tightest flocks and species using both types of feeding method show the expected dichotomy in spacing behaviour (Goss-Custard 1970, Myers 1984).

### 6.3 INFLUENCE OF OTHER SHOREBIRDS ON FORAGING BEHAVIOUR

Other species of shorebird may not be of no significance to a foraging bird. Waders do form mixed-species flocks (for example

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Metcalfe 1984b) and, in terms of protection and information, an individual may gain similar advantages from a heterospecific as it does from a conspecific. Metcalfe (1984c) has shown that vigilance may be shared between species of shorebird foraging together and Thompson and Thompson (1985) have demonstrated that one species of wader may use another to indicate danger. There may also be costs of being in a mixed-species flock. Other species may steal food items (for example Barnard and Thompson 1985). An area can be rendered less available to a wader by the presence of another species. This can be a temporary condition, as, for example, sanderling being excluded from an area by gulls feeding on a wreck of sprats (Evans and Dugan 1984), or long-standing; for example, Pienkowski (1981) noted that grey plover exploited better feeding areas after bar-tailed godwits had vacated them in spring.

Black-tailed godwits foraging on the Eden Estuary rarely formed feeding associations with other foraging birds, and the only regular inter-species relationship was with loafing gulls and plovers.

### 6.3.1 DESCRIPTION OF THE INTERACTION WITH GULLS AND PLOVERS

During winter up to 2000 lapwings, 2000 golden plovers and 300 gulls used the Edenside area for roosting. The preferred site for this appeared to be the saltmarsh at Guardbridge, but the birds were often disturbed from here onto the mud around the saltings which is the favoured area for foraging black-tailed godwits. Although the flock was often large, it was not dense enough to

physically exclude feeding waders. The roosting flock was present here during the flood-tide on over a quarter of observations (19 from 67: 28%).

This study looks at how the presence of the gulls and plovers affected the foraging and vigilance behaviour of the godwits. The next section considers the effect of the roost on the number of godwits using their favoured area, and the following section considers the influence of the other species on the behaviour of the godwits.

#### Displacement of Godwits

##### Methods

One part of the study area that was easily delimited by topographical features was defined as the 'observed area'. The number of probing birds and stitching birds, as well as loafing gulls and plovers on this area, was counted during tidal section 10 (the period between nine and 10 hours after the predicted time of the last high-tide). Only one count was made during a session. A total of 31 counts was made over the winters 1985/86 and 1986/87.

##### Results

The presence of gulls and plovers had a significant effect on the number of godwits using the observed area. As the size of the loafing flock increased, the number of stitching and probing birds decreased and there were no probers present when there were more than 250 heterospecifics present (Fig.6.5).

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### Foraging Depth and Behaviour

This section looks at the relationship between the depth of water used by the godwits and their foraging performance and vigilance rate, and whether these were influenced by the loafing gulls and plovers.

#### Methods

Observation sessions occurred in the tidal sections nine and 10 (the time between eight and 10 hours after the predicted time of the last high-tide). A session generally lasted for the whole two hours. The two sections were divided into four half-hour periods. Twice in each period the depth of water each godwit was foraging in was recorded. The depth categories were (1) 0 to a quarter of the leg covered (2) a quarter to a half of the leg covered (3) half to three-quarters of the leg covered (4) three-quarters to the whole leg covered. To record the foraging performance and the time spent vigilant as defined above, a bird was selected randomly from flocks at least four times during a half-hour period, for one minute of focal individual observation. Due to the observational difficulties imposed by the loafing birds, foraging performance was recorded only as items taken. Ten observation sessions were carried out when there were no gulls and plovers present and 10 when at least 20 loafers were within 1m of the tide-edge. Solitary birds were rare, but 13 in the presence of the loafing flock were used for focal individual observation. There was not enough data to investigate the influence of the roosters on the foraging of these birds but their vigilance behaviour was compared to that of

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single birds observed in the absence of the loafers (see above).

In addition, a series of experiments was carried out to assess the effect of the loafing birds on the depth of water used by the stitching godwits. The gulls and plovers were relatively sensitive to disturbance. This wariness sometimes meant that an approaching observer caused the loafing flock to take off, but left the godwits to feed alone. On occasions all species of bird flew, but on three trials the roosters were selectively frightened away and left the area. On another occasion the loafers only flew and then returned after a few minutes. Three times the same stimulus was presented to foraging godwits when there was no roosting flock present. For these seven trials, a record was made of the feeding depth of all the godwits in the area 10 minutes before and 10 minutes after the experimental disturbance.

### Results and Discussion

#### Foraging Depth

Foraging depth was dependent on the state of the tide and on whether the loafing gulls and plovers were in the area (Tab.6.5). In the presence of the heterospecifics, the godwits used significantly deeper water and, as the tide flooded, the stitching birds also on average used slightly, but significantly, deeper water.

In the experiments, after the loafers were frightened away the stitching birds on average adopted shallower foraging positions ( $G[3]=75.3$   $P<0.001$ ;  $G[3]=23.5$   $P<0.001$ ;  $G[3]=9.3$   $P<0.05$ ). This result was not present in the controls ( $G[2]=0.5$  NS;  $G[2]=2.5$  NS;  $G[2]=4.7$  NS), nor in the trial where the gulls and plovers returned ( $G[3]=3.4$  NS).

#### Foraging and Vigilance Behaviour

The instantaneous foraging performance was affected both by the presence of the loafers and the foraging depth used by a godwit (Tab.6.6). Birds feeding in shallower water had a higher foraging performance, and, in addition, intake was improved in the absence of the gulls and plovers. Smith (1975) also showed that the performance of bar-tailed godwits feeding at the tide-edge was dependent on the water depth being used.

However, the amount of time spent in vigilance was lower for birds foraging in the presence of the heterospecific group (Tab.6.7). This budgeting advantage was limited, since godwits in flocks spend little time in this activity (see above) and the overall foraging performance was still lower for birds feeding in the presence of the loafing flock (Tab.6.8). There was a trend for birds in deeper water to spend less time in vigilance, but this was not significant. Solitary godwits in the presence of the heterospecific flock spent much less time in vigilance than single birds in the absence of the gulls (0.81s per min,  $SE=0.12$   $N=13$ , against 3.14s per min,  $SE=0.24$   $N=22$ : Mann-Whitney U-test,  $w=18.3$   $P<0.05$ ).

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The fact that the gulls and plovers were wary allowed the godwits to drop their vigilance rates. This phenomenon of a bird relying on another species to detect danger has been reported several times (Barnard and Stephen 1983, Burger 1984, Sullivan 1984, Thompson and Thompson 1985, Barnard and Thompson 1985). The reduced vigilance had relatively little consequence for flocking black-tailed godwits, but for solitary birds it probably means that they can at least maintain their foraging performance in the presence of the heterospecifics.

### 6.3.2 GENERAL DISCUSSION

The foraging performance of a black-tailed godwit at the water's edge during flood-tide was dependent on the depth of water it was in. The presence of gulls and plovers resting at the edge of the mudflats in the godwits' preferred feeding area has a large influence on the waders.

Although the roost was not dense enough to exclude other birds, the decrease in space probably caused three of the changes observed in the behaviour of the godwits: the number of the waders using the preferred area was lowered significantly, the godwits on average fed in deeper water where profitability was lower, and the mean feeding rates of the birds, controlling for the effect of water depth, was reduced significantly. In addition, in the presence of the loafing flock the mean time spent being vigilant was reduced significantly. The heterospecific group was very wary, which probably allowed the godwits to reduce the time they spent in

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predator surveillance.

This budget advantage to flocking godwits was not enough to compensate for the interference suffered. However, for solitary birds the drop in vigilance was more marked and should allow them to maintain their performance in the presence of the heterospecifics. Interactions between species of birds that are engaged in different activities may be more than a competition for space and may involve subtle changes in behaviour.

TABLE 6.1

Beta values from stepwise partial regression analysis of the relationship between foraging performance and flock and environmental variables, for stitching flocks. Adjusted  $R^2 = 0.51$ .

TABLE 6.1

	FLOCK DENSITY	FLOCK SIZE	TEMP.	WIND SPEED
BETA VALUE	-0.53	0.35	NS	NS
P	<0.001	<0.001		

TABLE 6.2

Beta values from stepwise partial regression analysis of the relationship between foraging performance and flock and environmental variables, for probing flocks. Adjusted  $R^2=0.10$

TABLE 6.2

	FLOCK DENSITY	FLOCK SIZE	TEMP.	WIND SPEED
BETA VALUE	-0.35	NS	NS	NS
P	<0.05			

TABLE 6.3

Beta values from stepwise partial regression analysis of the relationship between interaction rate and flock and environmental variables, for stitching birds. Adjusted  $R^2=0.32$ .

TABLE 6.3

	FLOCK SIZE	FLOCK DENSITY	TEMP.	WIND SPEED
BETA VALUE	0.43	-0.30	NS	NS
P	<0.01	<0.05		

TABLE 6.4

Beta values from stepwise partial regression analysis of the relationship between interaction rate and flock and environmental variables, for probing birds. Adjusted  $R^2=0.37$ .

TABLE 6.4

	FLOCK SIZE	FLOCK DENSITY	TEMP.	WIND SPEED
BETA VALUE	0.31	-0.43	-0.38	NS
P	<0.05	<0.01	<0.01	

TABLE 6.5

Effect of tide and the presence of the flock of loafing gulls and plovers on the foraging depth (mean depth) of the godwits. The higher the tide number the closer to high-tide. SE and sample size in brackets.

TABLE 6.5

FORAGING DEPTH				
TIDE	NO FLOCK		FLOCK	
1	1.2	(0.07 10)	2.1	(0.09 17)
2	1.2	(0.04 17)	2.3	(0.09 21)
3	1.4	(0.06 18)	2.4	(0.05 24)
4	1.7	(0.04 18)	2.8	(0.06 24)

TABLE 6.6

Effect of the presence of the flock of heterospecifics and foraging depth category on instantaneous feeding rate. SE and sample size in brackets.

MANOVA: presence/absence of flock,  $F[1,392]=6.6$   $P<0.05$ ; foraging depth,  $F[3,392]=156$   $P<0.001$ ; tidal category,  $F[3,392]=1.3$  NS. No interactions were significant.

TABLE 6.6

INSTANTANEOUS FEEDING RATE (items per min)				
DEPTH	NO FLOCK		FLOCK	
1	18.8	(0.51 77)	15.4	(0.60 43)
2	17.1	(0.82 47)	15.6	(0.36 98)
3	12.1	(0.70 33)	11.6	(0.43 78)
4	6.1	(1.00 23)	5.2	(0.97 25)

TABLE 6.7

Effect of the presence of the flock of heterospecifics and foraging depth category on vigilance rate. SE and sample size in brackets.

MANOVA: presence/absence of flock,  $F[1,392]=82.1$   $P<0.001$ ;

foraging depth,  $F[3,392]=1.0$  NS; tidal category,  $F[3,392]=2.0$  NS.

No interactions were significant.

TABLE 6.7

---

VICILANCE RATE  
(s per min)

---

DEPTH	NC FLOCK		FLOCK	
1	1.17	(0.21 77)	0.12	(0.12 43)
2	0.99	(0.24 47)	0.31	(0.14 98)
3	0.78	(0.23 33)	0.34	(0.15 78)
4	0.56	(0.13 23)	0.24	(0.17 25)

---

TABLE 6.8

Effect of the presence of the flock of heterospecifics and foraging depth category on overall foraging rate. SE and sample size in brackets.

MANOVA: presence/absence of flock,  $F[1,392]=16.9$   $P<0.001$ ;  
foraging depth,  $F[3,392]=195$   $P<0.001$ ; tidal category,  
 $F[3,392]=0.8$  NS. No interactions were significant.

TABLE 6.8

OVERALL FORAGING RATE (items per min)				
DEPTH	NO FLOCK		FLOCK	
1	18.5	(0.51 77)	15.4	(0.60 43)
2	16.8	(0.82 47)	15.5	(0.36 98)
3	11.9	(0.71 33)	11.6	(0.43 78)
4	6.0	(1.00 23)	5.2	(0.97 25)

FIGURE 6.1

Frequency (F) distribution of gap length categories (L) between stitching birds in a linear array. Expected distribution if birds were arranged randomly is represented by dashed lines. Comparing expected and observed,  $G[15]=240$   $P<0.001$

Category 1 contains gap lengths smaller than 1 bird-length, category 2 contains gap lengths between 1 and 2 bird-lengths, and so on.

FIGURE 6.1

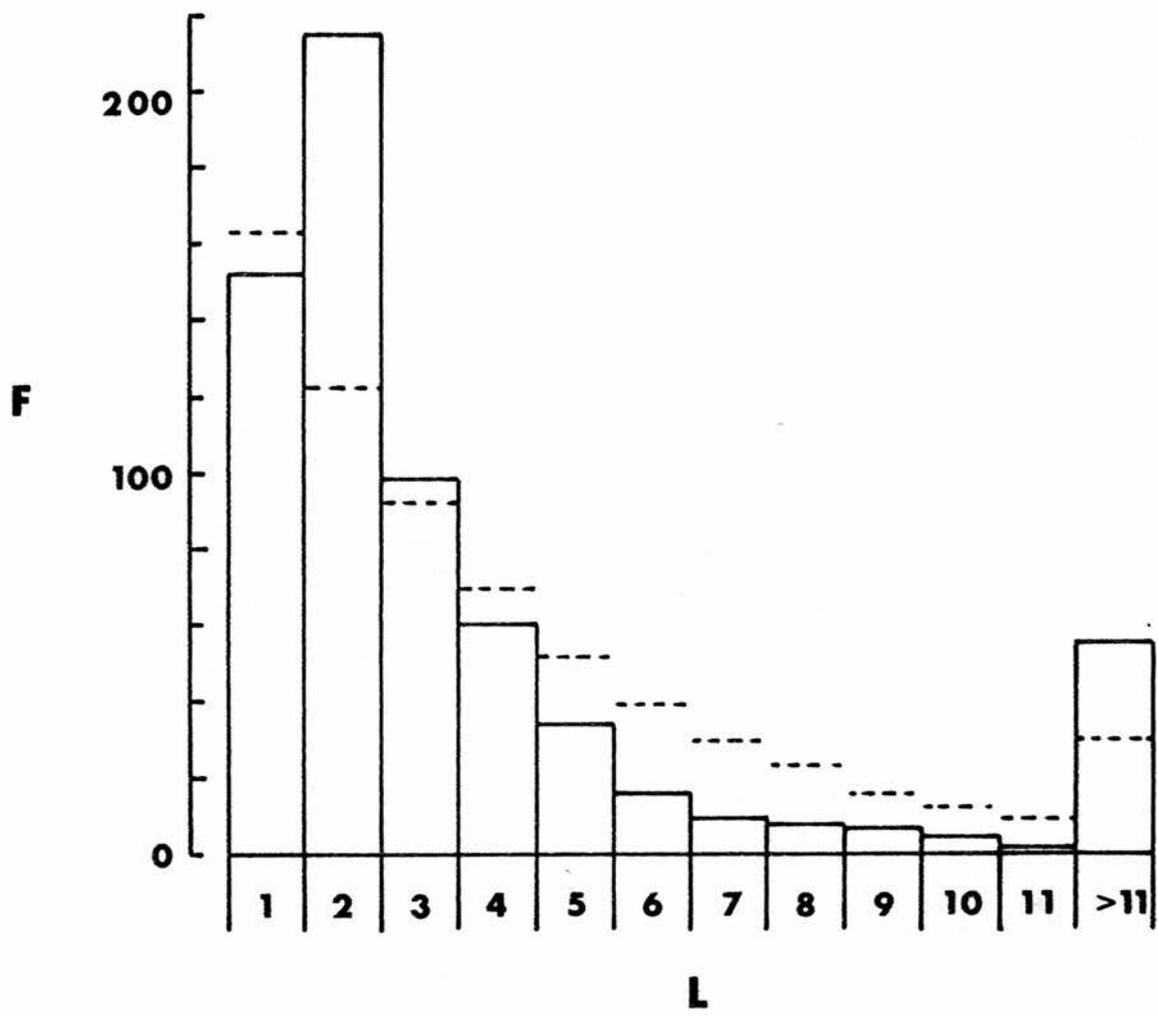


FIGURE 6.2

Log-survivor plot of gap lengths between stitching birds in a linear array.  $\log f$  is the log of the number of gaps longer than  $x$ .

FIGURE 6.2

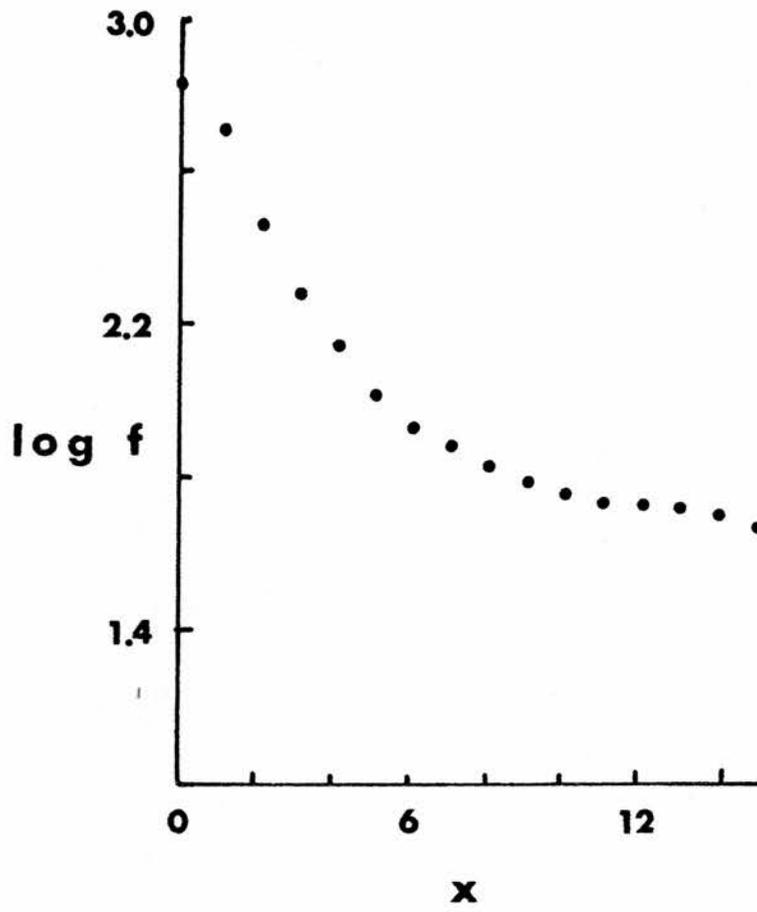


FIGURE 6.3

Frequency (F) distribution of NND categories (D) for stitching (s) and probing (p) birds.

Category 1 contains NND smaller than 1 bird-length, category 2 contains NND between 1 and 2 bird-lengths, and so on.

FIGURE 6.3

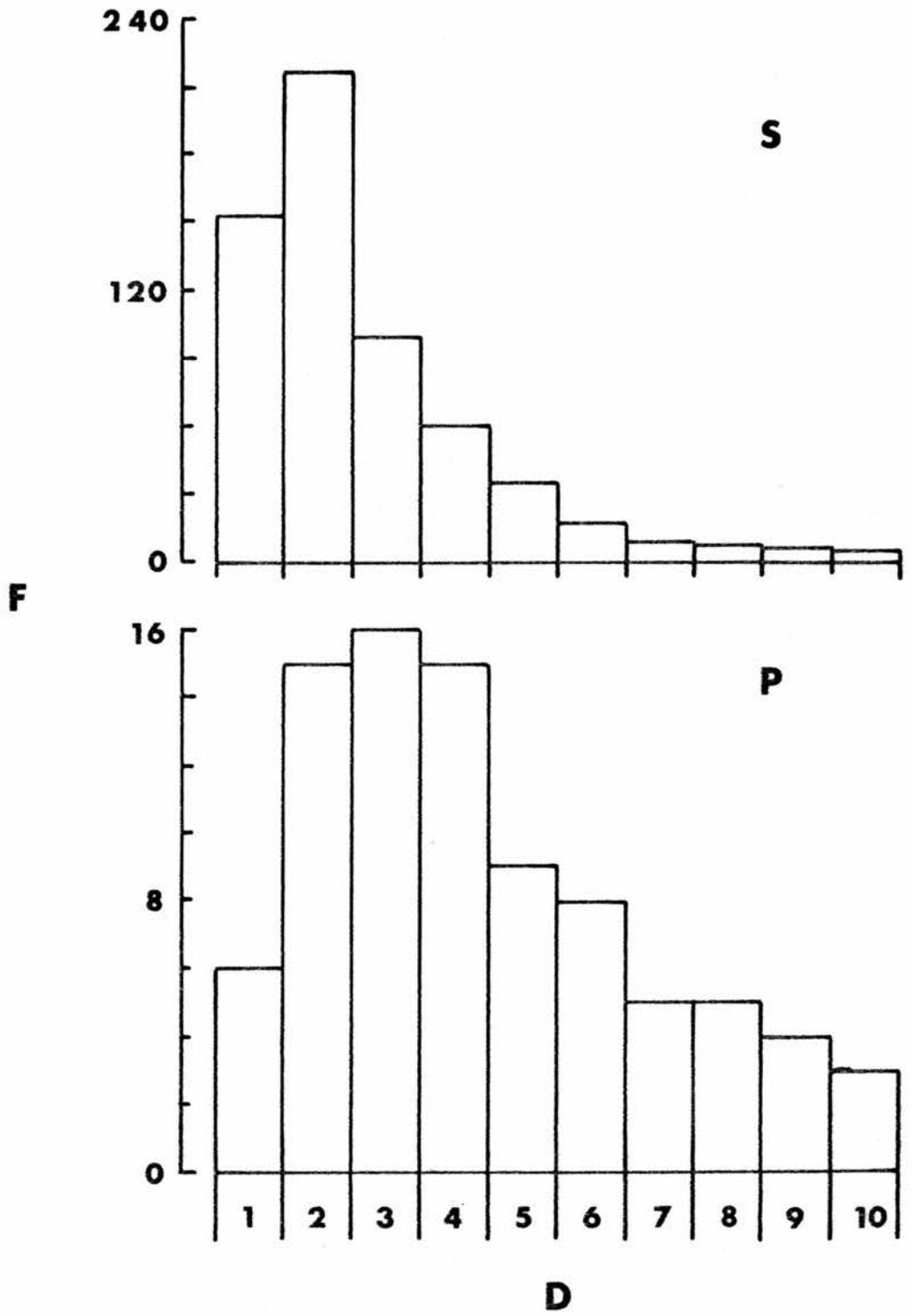


FIGURE 6.4

Expected foraging advantage of joining a flock, due to a lower commitment to vigilance.  $S$  is the performance (items per min) of a solitary bird,  $F$  is the performance (items per min) of a flock bird with the same instantaneous foraging rate. Dashed line represents  $F=S$ .

FIGURE 6.4

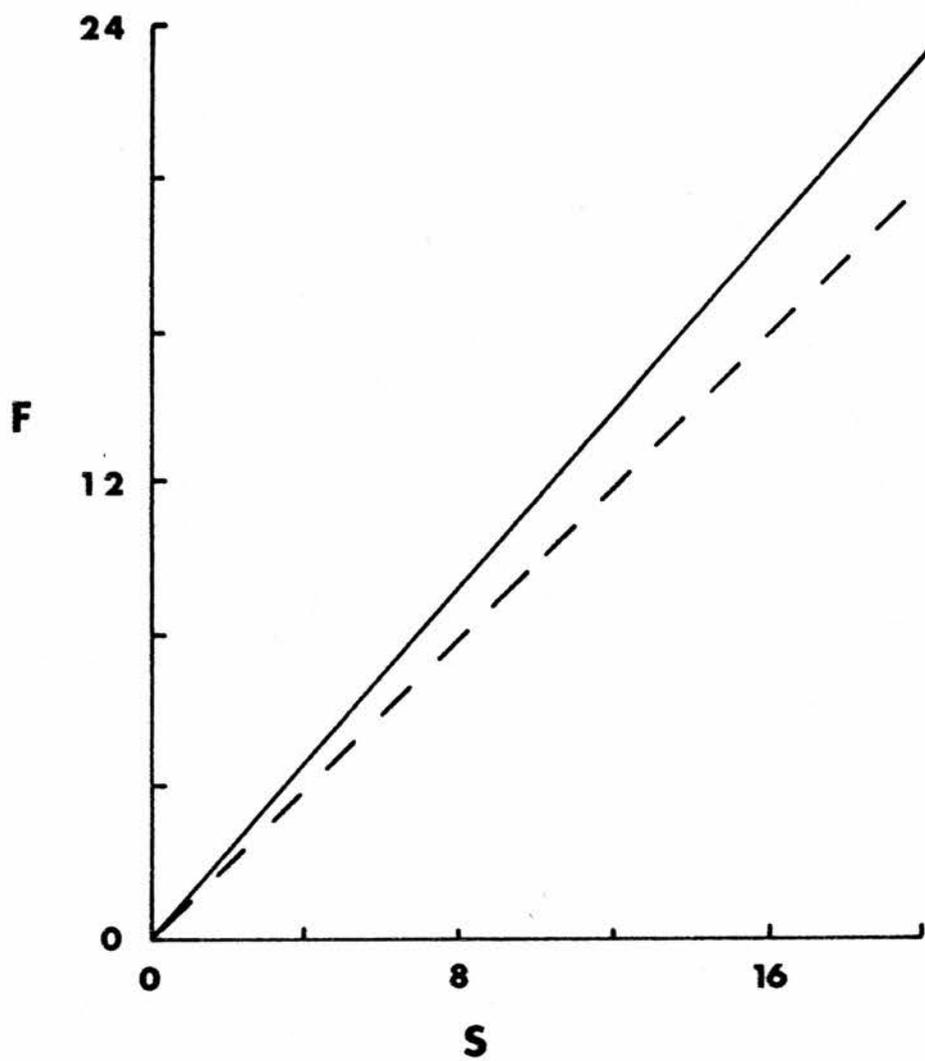
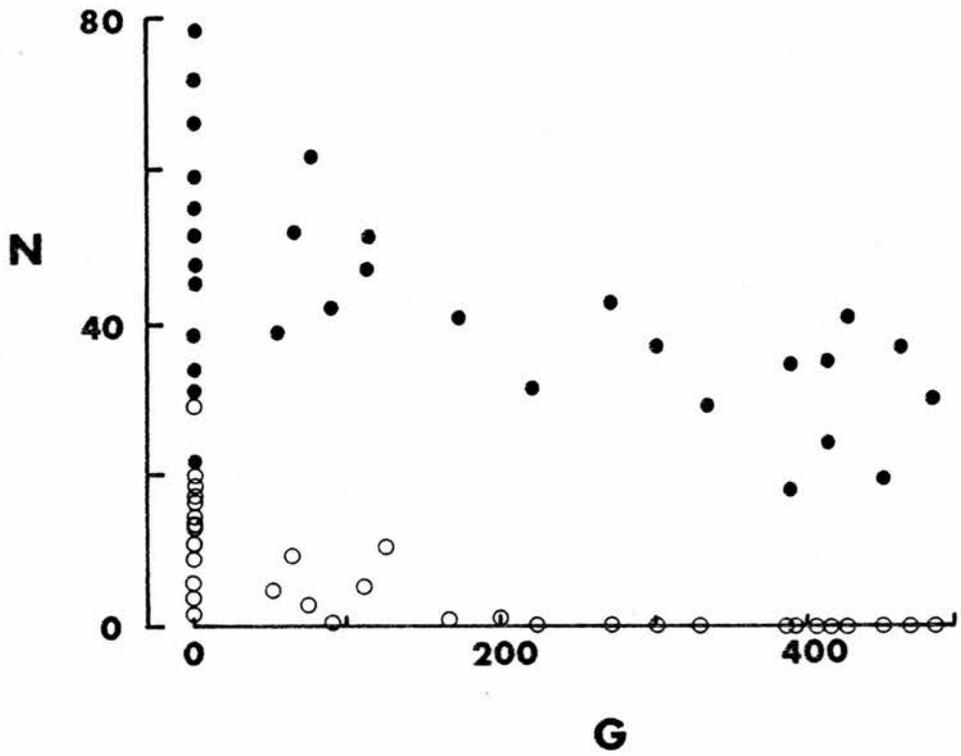


FIGURE 6.5

Influence of the number (G) of gulls and plovers on the number (N) of godwits using an area of mudflats. Closed circles stitching birds, open circles probing birds.

Kendall's Tau [N=31], for stitching birds,  $=-0.42$   $P<0.005$ ; for probing birds,  $=-0.69$   $P<0.001$ .

FIGURE 6.5



## CHAPTER 7

### AGE-RELATED DIFFERENCES IN FORAGING PERFORMANCE

#### 7.1 INTRODUCTION

This chapter examines the importance of various components of foraging in determining the relatively low intake rate of stitching and probing juvenile black-tailed godwits.

In many species of birds young individuals have lower feeding rates than adults (Davies and Green 1976, Groves 1978, Puttick 1979, Greig *et al* 1983, Gochfeld and Burger 1984, Higuchi 1986, Draulans 1987, Breitwish *et al* 1987). However, only a few studies (for example Espin *et al* 1983, Sutherland *et al* 1986) have investigated which aspects of feeding contribute to these differences in performance. The components considered in this study are the skills involved with finding and dealing with prey and the allocation of foraging time to actual feeding. There are additional factors that can effect the performance of young birds. For example, juvenile oystercatchers on the Exe Estuary are forced onto less favourable mussel beds (Goss-Custard and Durell 1984) and are also particularly susceptible to interference from conspecifics

## AGE-RELATED DIFFERENCES IN FORAGING PERFORMANCE

(Goss-Custard and Durell 1987a, 1987c). These two aspects were not relevant in this study since data were collected from juveniles and adults foraging in the same area and black-tailed godwits under the observed conditions were not prone to interference (see Chapter 6).

### 7.2 METHODS

#### 7.2.1 Observational Methods

Adult black-tailed godwits start to return to the Eden Estuary from the breeding grounds in July and the juveniles a month later (see Chapter 3). For the young birds it is possibly their first experience of an estuary. The study took place in August 1986 when there were between 20 and 70 birds present and juveniles and post-breeding adults could be distinguished relatively easily using plumage characteristics (Cramp and Simmons 1983).

Paired data were collected in order to control for environmental variables that have been shown to have a large effect on behaviour (see Chapters 3 and 4). An individual of each of the two age classes was selected at random and viewed for between two to five minutes of uninterrupted foraging, where foraging was defined as time not containing periods of resting, flying or preening. In all cases the two observations which made up a pair were not separated by more than two minutes and the same bird was not used twice during a session. Paired focal animal observations were made on both the following:

- 1) Birds from discrete flocks that contained both juveniles and

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adults using the same foraging technique.

2) Birds outside flocks using the same foraging technique.

Although this was the easiest time of the year at which to age the godwits it still proved to be difficult if the observing conditions were not ideal, and solitary birds were relatively rare. Consequently, there were few pairs of observations on single stitchers and, for most analyses, the single and flock data were combined. Data were collected for 14 pairs of probing birds and 16 pairs of stitching birds.

During the period of study probing birds were taking small and medium sized Macoma and stitching birds mainly unidentified small items (see Chapter 4). Foraging performance was defined as the number of items taken per minute of observation. Item intake rate has been shown to be a good predictor of energy intake rate (Chapter 4). Foraging performance, which is a measure of the overall or absolute feeding rate (as used by Lendrem 1984a), can be decomposed into constituent components.

### 7.2.2 Components Of Foraging

Within a foraging period activities occur which are not directly related to catching food. This allows the behaviour to be divided into feeding and non-feeding. Non-feeding includes surveillance, walking between bouts of feeding, and social interaction. Feeding itself is composed of searching for prey and capturing and eating prey. Therefore, foraging performance is dependent on the success in finding and dealing with prey and on the amount of time devoted

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to feeding within a period of foraging. The efficiency in searching for and handling prey determines the instantaneous feeding rate (as used by Lendrem 1984a), which is an indication of feeding skill.

A measure of how efficiently food is being found is the encounter rate (Holling 1959), which is the number of encounters per minute of search. Search time is the time spent feeding, minus the time between finding the prey item and starting to look for the next one (handling time). Often the number of attempts at taking prey is taken to be equivalent to the number of items encountered; this assumes that the animal tackles all the prey it detects. However, many species have been shown to be selective (see Stephens and Krebs 1987), including waders (for example Goss-Custard 1977b). Therefore, the term 'tackle rate' will be used instead of the traditional encounter rate. Tackle rate is defined as the number of items tackled per minute of search and therefore makes no assumptions about selectivity.

The values for the three foraging components (tackle rate, handling time and proportion of a foraging period spent feeding) in the adult can be compared to those in the juvenile. This will indicate which aspects of foraging are significantly different in the two age classes.

The relative importance of an age-related difference may then be gauged by estimating its impact on foraging performance. This assessment is carried out by constructing equations relating time

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devoted to feeding within a period of foraging, tackle rate, and handling time to the foraging performance. For each age-group, the mean values for these components of foraging are used in the equation to derive a figure for the average foraging performance. For the juvenile class, this foraging performance is then recalculated by changing the value of one of the components from the juvenile to the adult level. Hence, an estimate is made of the mean foraging performance the juveniles would have if, for example, they possessed the adults' mean tackle rate.

The form of the equation relating the components of foraging to the foraging performance is dependent on the feeding technique.

### Stitching

While feeding, a stitching bird was stationary or walked slowly. The bill was either oriented towards, or moved rapidly up and down in the substrate. An item was removed from the mud before being swallowed. Handling time was the time between an item being removed and the bill being replaced in the mud or reoriented towards the substrate. Therefore, the period when the prey was being manipulated below surface was included in the search time rather than in the handling time. The stitching bird sometimes held the bill away from the substrate, either while walking (non-feeding walking), or while standing stationary for more than a second (non-feeding looking). These two behaviours were the main activities within the foraging period that were not concerned directly with feeding. Table 7.1 lists the variables recorded or

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derived from a focal observation of a stitching bird.

Tackle rate is the number of items tackled per minute of search:

tackle = items tackled/search time  
rate

$$R = \frac{is}{f-is \cdot h}$$

Solving for foraging performance:-

$$is = \frac{R f}{1+R \cdot h} \quad \dots[1]$$

Equation [1] gives an expression for foraging performance in terms of the three foraging parameters: tackle rate, mean handling time, and proportion of time spent feeding.

### Probing

A probing bird walked, while holding its bill close to the substrate and occasionally pecking the mud lightly. These exploratory pecks were sometimes followed by a probe, where the bill was pushed to varying depths within the substrate. A successful probe removed an item, which was then swallowed. During a probe, the bird was locating the prey within the mud and handling the prey, before bringing it to the surface. The time from the start of the probe until the end of swallowing was termed 'manipulation' time. Therefore, the search time was the period when the bird was locating an appropriate site for a probe, and manipulation time was the period when an attempt was made to find an item within the mud and when the prey was handled both beneath

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and above the substrate. Probing birds also carried out non-feeding walking and looking as described above.

As with stitching, during probing there were periods of feeding, which were composed of search time and time spent dealing with prey, interspersed with non-feeding activities. However, in probing, unsuccessful manipulations of prey can be observed and this feature can be incorporated into the model. Table 7.1 lists the variables recorded and derived from a focal observation of a probing bird.

For probing, the tackle rate is taken to be the total number of items tackled per minute of search time.

$$R = \text{items tackled} / (\text{time feeding} - \text{total handling time})$$

$$R = \frac{i}{f - (1-p)i - m - p \cdot i \cdot \mu}$$

Solving for  $i$  :-

$$i = \frac{Rf}{1 + R(p \cdot \mu + (1-p)m)}$$

Now,  $i = i_u + i_s$  and  $p = i_u / (i_u + i_s)$

$$\Rightarrow \frac{i_s + p \cdot i_s}{1-p} = \frac{R \cdot f}{1 + R(p \cdot \mu + (1-p)m)}$$

Solving for feeding performance:-

$$i_s = \frac{R \cdot f(1-p)}{1 + R(p \cdot \mu + (1-p)m)} \quad \dots[2]$$

Equation [2] expresses feeding performance in terms of the five feeding parameters: tackle rate, proportion of time spent feeding, proportion of unsuccessful feeding attempts, mean manipulation time for successful probe, and mean manipulation time

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for unsuccessful probe.

### 7.3 RESULTS

#### 7.3.1 Foraging Performance

Table 7.2 shows the mean foraging performance (items eaten per minute of observation) of juveniles and adults for both foraging techniques. The juveniles were performing significantly less well than the adults, who, on average, were taking nearly twice as many items as the young birds.

#### 7.3.2 Foraging Components

##### Stitching

Table 7.3 lists the values of the components of stitching in juvenile and adult birds. Both tackle rate and the proportion of a foraging period actually spent feeding were significantly different for the two age classes. Using these means in equation [1] an estimate can be made of the mean foraging performance of the juveniles and of the adults. These derived values (Tab.7.4) for adult and juvenile feeding performance were within the 95% confidence limits of the mean of the observed values.

Both their lower tackle rate and the smaller proportion of time they actually spend feeding have a large influence on the relatively poor foraging performance of the young birds (Tab.7.4).

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The two main activities which made up non-feeding behaviour were looking and walking. On average, the juveniles spent significantly more time than adults in both of these behaviours (Tab.7.5a). Young birds were also more likely to have an interaction with a conspecific during their observation ( $G[1]=15.8$   $P<0.001$ ), although these were short-lived and rare. For all interactions involving both age-classes, the young bird was displaced by the adult.

### Probing

Table 7.6 lists the values of the components of probing in juveniles and adults. All the variables were significantly different for the two age-classes, except for the overall tackle rate. The tackle rate was higher for the adults, but was very variable. Using the means for the components of foraging in equation [2] an estimate can be made of the mean foraging performance of the juveniles and of the adults (Tab.7.7). These derived means are within the 95% confidence limits of the means of the observed values.

The two variables, which have the most single effect on the age-related differences in mean foraging performance, were the proportion of time actually spent feeding and the proportion of items tackled that were manipulated unsuccessfully (Tab.7.7).

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As in stitching, the juveniles spent significantly more time in both the main non-feeding activities occurring during foraging (Tab.7.5b).

### Sensitivity Analysis

The strength of the results concerning the relative importance of the different components in determining foraging performance is dependent on how accurately the parameters in the models have been estimated. There is no reason to suspect that there was undue error in the measurement of the behavioural variables, nor that the sample means were unrepresentative. This is confirmed by the fact that the derived values for overall foraging performance were close to the mean observed values. Sensitivity analysis indicated that, even if there was error in the estimation of the foraging components, the results were not sensitive to it. A model is generally considered sensitive to variation in a parameter if a percentage change in the parameter causes an equal or greater percentage change in the result (for example Krebs and Avery 1985). The analysis was carried out for both adult and juvenile data by altering each foraging component in turn by 20% (Tab.7.8). The models were sensitive only to the parameter of time actually spent feeding.

It can be concluded that the results of the component analysis are robust.

## 7.4 DISCUSSION

In this study, mathematical models have been used to investigate how important time-budget and feeding skills were in determining the relatively poor foraging performances of juvenile black-tailed godwits. The models were a simplification for they only consider the apparent behaviour of the birds. For example, in stitching it was impossible to measure the handling time before an item was brought to the surface. Therefore, the study was not a comprehensive investigation into foraging skills. However, the approach is useful as it helps us to understand the process of foraging and gives some indication of why juveniles are less efficient than adults.

Few previous studies have analysed age-related differences by looking closely at the components that contribute to foraging efficiency. Most workers express performance purely in terms of items taken per minute of observation (for example Groves 1978, Puttick 1979, Burger 1980). Even if the number of items taken provides a good measure of energy intake, a fact often not established by a researcher, this simplicity may obscure interesting processes and may even give the misleading impression that a difference in overall foraging rate invariably means that juveniles have relatively poor feeding skills. A difference in absolute rate may be due purely to different foraging budgets, to juveniles being forced into lower quality areas in the site (Have *et al* 1984, Draulans and Vessem 1985, Townshend 1985), or suffering high levels of interference (Goss-Custard and Durell 1987a, 1987c).

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Interference and age-related differences in feeding areas were not present in this study.

On average, the performance of juvenile black-tailed godwits in both stitching and probing was much poorer than that of adults. Part of this age-related difference was caused by young birds spending relatively little time actually feeding during foraging. The juveniles spent more time in non-feeding walking and looking. The non-feeding walking probably represented birds changing feeding areas or moving towards other birds. The non-feeding looking was distinct from rapid surveillance used by both adults and young (see Chapter 6), and involved a bird orientating towards a conspecific. It may be that young birds were gaining information on feeding techniques by observing other godwits, as reported for other bird species (Mason *et al.* 1984, Palameta and Lefebvre 1985). If this were the case, it might be expected that juveniles in flocks would carry out more looking than those that were single. This was so, but the trend was not significant, probably due to low sample size (proportion of time spent in this looking: means 0.062 and 0.046; Mann-Whitney U-test [N=11,5]  $z=-0.52$  NS).

As well as the budget differences, juveniles appeared less able to search for and deal with prey. In stitching, the juveniles' mean handling time was as good as the adults', but their tackle rate was lower. In comparison, in probing the young birds' ability to manipulate prey was relatively poor, although they did not tackle significantly fewer prey per minute of search time.

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Items taken during stitching were relatively small, and handling time was merely that needed for swallowing an item. It is therefore not surprising that there is little difference in the value of this variable between age classes. The searching in stitching is mainly tactile, with the bill being moved rapidly up and down in the substrate. It is likely that inexperience in this technique contributes to the young birds having a relatively low tackle rate. The rapid movement may be difficult in itself to perform and the process may actually involve manipulating prey below the surface, or interpreting tactile information, both of which would require some degree of learning. Alternatively, or in addition, the low tackle rate may be due to the juveniles feeding in poorer positions. That is, although each pair of observations was taken from the same flock, young birds may adopt poorer feeding stations within the group. If they do, this appears not to be due to social interference, as juveniles, apart from the rare agonistic interaction, moved freely within a flock and they were not systematically found in peripheral positions as in some shorebirds (Kus 1984, Whitfield 1985). The young may be having difficulty in finding the best locations and this could be a reason why they spent relatively more time non-feeding walking.

Interestingly, for juveniles and not adults, the proportion of time spent feeding by stitching birds was significantly correlated with tackle rate (Spearman's rho [n=16]; juvenile =0.53 p<0.05, adult =0.00 NS). This may suggest that juveniles with poor feeding ability are spending relatively more time in non-feeding

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activities involved with looking for better positions and gaining information from other birds.

Compared to those that were stitching, probing birds took large and deeply buried items. Consequently, the prey required relatively much more handling, especially below surface. Therefore, it was not surprising that the young were worse at manipulating such prey. Encountering prey is by visual means, and the tackle rates of the two age classes were not significantly different. This does not necessarily mean that the searching ability of the young bird approached that of the adult, since we have no information on prey selection. The adults could have been detecting prey at a higher rate, but have been much more selective. Such selectivity might explain why the adults had a greater chance of a probe being successful.

Therefore, the difference in the relative performance of the juvenile in searching for and handling prey between the two feeding methods, appears to be due to the specific learning problems which stitching and probing pose.

The relative importance of the different components in determining the juvenile's low feeding efficiency was assessed using models. An important cause in the poor performance of the young birds was the relatively large amount of time during foraging that was devoted to non-feeding behaviours. In stitching, of even more importance was the low tackle rate, and in probing it was the high proportion of items tackled unsuccessfully. Tackle rate in

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stitching, and items tackled unsuccessfully in probing, both reflect the ability of birds at encountering suitable prey. We can look at the feeding components (excludes the variable of how much foraging time was spent feeding) in more detail, by considering the results of the sensitivity analysis. In such an analysis, a component whose variation (error) has a large influence on the foraging rate, will be a component which, if improved by a godwit, will have a large effect on that individual's performance. For both age-classes and both foraging techniques, the feeding component that has greatest effect was tackle rate (Tab.7.8). Tackle rate, like encounter rate, will be dependent on food density. As long as prey are not super-abundant and handling/manipulating times are relatively short (usually the case for shorebirds taking infauna), the tackle rate will be the major determinant of the instantaneous feeding rate. Therefore, tackle rate will tend to be both the determinant of a successful bird within an age-class, and the most important aspect of foraging that a young bird needs to improve in order to emulate the intake of an older bird. An interesting facet of this is that, as food density becomes lower, that is, when conditions are hard, the tackle or encounter rate becomes increasingly important. This ties in with the study by Draulans (1987), in which the relatively poor performance of juveniles became less marked as food density increased, and disappeared when prey were common. Juveniles would therefore be at a particular disadvantage when prey availability was reduced by harsh weather, a time when they have been reported to do badly (for example Pienkowski 1984).

TABLE 7.1

Variables recorded or derived for each focal observation of a foraging black-tailed godwit.

TABLE 7.1

---

The foraging process in probing and stitching:

- o = length of observation (min)
- f = proportion of time feeding = total time feeding/o
- l = proportion of time in non-feeding walking  
= total time non-feeding walking/o
- w = proportion of time in non-feeding looking  
= total time non-feeding looking/o

The feeding process in stitching:

- n = number of items taken during o
- is = number of items per min of foraging  
= number of items per min of observation = n/o  
= foraging performance
- h = mean handling time (min per item)  
= total time handling/n

The feeding process in probing:

- n = no. of successful manipulations of prey during o
  - nu = no. of unsuccessful manipulations of prey during o
  - is = no. of items eaten per min of foraging = n/o
  - iu = no. of unsuccessful tackles per min of foraging = nu/o
  - i = no. of items tackled per min of foraging = is+iu
  - p = proportion of unsuccessful tackles = iu/(is+iu)
  - m = mean manipulation time for successful probes  
= total time in successful manipulations/n (min per item)
  - mu = mean manipulation time for unsuccessful probes  
= total time in unsuccessful manipulations/nu  
(min per item)
-

TABLE 7.2

Mean foraging performance (items taken per min foraging) of juvenile and adult black-tailed godwits. SE in brackets.

\*Wilcoxon matched pairs test: for stitching  $z[N=16] = -2.7$ ; for probing  $z[N=14] = -3.2$ .

TABLE 7.2

FORAGING PERFORMANCE			
	JUVENILE	ADULT	P*
STITCHING	6.9 (1.1)	12.0 (1.1)	<0.01
PROBING	1.9 (0.2)	3.6 (0.4)	<0.005

TABLE 7.3

Values of mean stitching components in juvenile and adult black-tailed godwits. SE in brackets.

\*Wilcoxon matched pairs test,  $z[N=16]$ : for R= -2.4; for f= -3.1;  
for h= -0.8.

TABLE 7.3

	JUVENILE	ADULT	P*
TACKLE RATE (R) (items per min)	12.6 (2.1)	18.6 (1.9)	<0.05
PROP TIME FEEDING (f)	0.68 (0.04)	0.82 (0.03)	<0.005
HANDLING TIME (h) (min)	0.013 (0.001)	0.013 (0.000)	NS

TABLE 7.4

Estimated effect on mean juvenile stitching performance of changing the values of juvenile foraging components to those of the adult. Figures in the brackets are the range generated from the 95% confidence limits of the adult parameter under consideration.

TABLE 7.4

	ESTIMATED FORAGING PERFORMANCE (items per min)	PERCENT IMPROVEMENT IN JUVENILE
ADULT	12.2	
JUVENILE	7.4	
JUV. WITH ADULT f	8.9 (8.3-9.5)	20.6 (12.5-28.7)
JUV. WITH ADULT R	10.2 (8.3-11.9)	38.7 (12.8-62.3)

TABLE 7.5

Mean proportion of time spent in non-feeding activities by juvenile and adult black-tailed godwits during: A/ stitching and B/ probing.

\*Wilcoxon matched pairs test:-

Stitching, z[N=16]: for walking = -3.3, for looking = -2.8.

Probing, z[N=14]: for walking = -2.7, for looking = -2.7.

TABLE 7.5

	JUVENILE	ADULT	P*
A/STITCHING			
PROPORTION OF TIME WALKING	0.19	0.10	<0.005
PROPORTION OF TIME LOOKING	0.06	0.01	<0.01
B/PROBING			
PROPORTION OF TIME WALKING	0.11	0.04	<0.01
PROPORTION OF TIME LOOKING	0.07	0.03	<0.01

TABLE 7.6

Mean values of the components of probing for juvenile and adult black-tailed godwits. SE in brackets.

\*Wilcoxon matched pairs test,  $z[N=14]$ : for R= -1.9, for f= -3.0, for p= -3.0, for m= -3.3, for mu= -2.5.

TABLE 7.6

	JUVENILE	ADULT	P*
TACKLE RATE (R) (items per min)	4.4 (0.8)	5.8 (0.7)	NS
PROPORTION OF TIME FEEDING (f)	0.73 (0.02)	0.85 (0.02)	<0.005
PROPORTION OF UNSUCCESSFUL PROBES (p)	0.19 (0.02)	0.07 (0.02)	<0.005
MANIPULATION TIME FOR SUCCESSFUL PROBES (m) (min per item)	0.071 (0.004)	0.041 (0.002)	<0.005
MANIPULATION TIME FOR UNSUCCESSFUL PROBES (mu) (min per item)	0.13 (0.01)	0.07 (0.01)	<0.05

TABLE 7.7

Estimated effect on mean juvenile probing performance of changing the values of juvenile foraging components to those of the adult. Figures in the brackets are the range generated from the 95% confidence limits of the adult parameter under consideration.  $\mu$ =mean time for unsuccessful probes,  $m$ =mean time for successful probes,  $f$ =proportion of time spent feeding,  $p$ =proportion of probes that were unsuccessful.

TABLE 7.7

	ESTIMATED FORAGING PERFORMANCE (items per min)	PERCENT IMPROVEMENT IN JUVENILE
ADULT	3.7	
JUVENILE	1.9	
JUV WITH ADULT mu	2.0 (1.9-2.0)	4.2 (4.2-4.2)
JUV WITH ADULT m	2.1 (2.0-2.1)	8.9 (7.3-10.0)
JUV WITH ADULT f	2.2 (2.1-2.4)	16.8 (11.0-23.0)
JUV WITH ADULT p	2.3 (2.2-2.4)	18.9 (12.6-25.1)
JUV WITH ADULT mu, m, AND p	2.5 (2.4-2.7)	33.0 (24.1-41.8)

**TABLE 7.8**

**Sensitivity analysis. The effect on foraging performance (percentage change) of altering a foraging component by 20%.**

TABLE 7.8

	JUVENILE	ADULT
STITCHING:		
TACKLE RATE	16.7	15.5
TIME SPENT FEEDING	20.0	20.0
HANDLING TIME	2.7	3.7
PROBING:		
TACKLE RATE	13.9	15.4
TIME SPENT FEEDING	20.0	20.0
PROPORTION OF PROBES UNSUCCESSFUL	5.5	1.9
MANIPULATION TIME FOR UNSUCCESSFUL PROBES	1.6	0.4
MANIPULATION TIME FOR SUCCESSFUL PROBES	3.5	3.4

CHAPTER 8  
THE LOW-WATER ROOST

8.1 INTRODUCTION

During the period around low-tide, the black-tailed godwits on the Eden Estuary generally formed a communal roost. This behaviour is not characteristic of many populations of wintering shorebirds (see Chapter 3) and has consequently received little attention. However, the low-water roost is interesting for, unlike its high-tide counterpart, it is a single species aggregation and it has a large choice of sites available for its positioning. Therefore, the social implications of communal roosting can be investigated without the complications of other species and habitat limitation. It has been found (Chapter 4) that, around low-water, the time when communal roosting occurs, the foraging performance is poor. This study investigates how being in a flock affects the energy conservation and anti-predator performance of roosting birds during this period when feeding appears unprofitable.

## THE LOW-WATER ROOST

The two main contributions to shorebird mortality during the wintering period are climate (Clark 1982, Davidson and Clark 1982, 1983) and predation (Page and Whitacre 1975, Whitfield 1985). Therefore, a sleeping wader should be maximising energy conservation while minimising the risk of predation. Figure 8.1 indicates some of the energy and predation considerations of a sleeping bird; all may be affected by roosting communally.

Predator and energy considerations occur simultaneously. An individual will have a conflict of interest between staying vigilant to reduce the chances of predation and sleeping to minimise energy expenditure (for example Ball *et al* 1984). Flocking may ameliorate this trade-off, by improving the anti-predator and energy conservation efficiencies of an individual.

Investigation of flock dynamics and of thermoregulatory behaviour was used to assess the energetic impact on an individual of joining a roost. Investigation of vigilance behaviour and of reaction to disturbance helped to examine the impact on anti-predator performance.

### 8.2 GENERAL METHODS

The low-water roost was watched from the hide on the north side of the estuary. The west end of Edenside Flats could be seen from this site and was defined as the study area. Observations were made at other positions along the north side of the estuary when a

## THE LOW-WATER ROOST

different viewing angle was required. The roost was generally situated on the study area at a distance from the hide of between 100 and 200m.

The density of the roost was usually greatest around its centre; towards the outside, the birds could be quite scattered. These peripheral individuals were considered as belonging to the flock if they were not separated from it by more than 10 bird-lengths.

During an observation period, flock-size, air temperature and wind speed were recorded at least every 30 minutes.

### 8.3 DYNAMICS

There is an energy cost of joining the roost, which is composed of the travel expenditure between the feeding site and the roost and vice versa. To minimise energy expenditure between feeding and roosting, a bird would roost where it completed foraging and, since all birds do not usually feed at a single site at this time (see Chapter 3), more than one roost would generally form. Minimising energy expenditure between roosting and feeding would lead to birds feeding close to the roost after departure. To minimise overall travel costs, an individual would either roost near the last feeding site or the next feeding site; for the latter to occur, a bird needs to know, prior to roosting, where it is going to feed on leaving the roost.

## THE LOW-WATER ROOST

An individual can increase energy intake after roosting communally through enhanced feeding efficiency. This can occur by gaining feeding information (information-centre hypothesis: Ward and Zahavi 1973), or through an increased chance of social feeding (for example O'Malley and Evans 1982), if this is desirable. Information transfer can only occur if there is asymmetry in the flock members' knowledge of food resources. Such a situation allows a bird to gain information on feeding sites by following other individuals from the roost. If this information transfer does occur, birds will leave the roost in groups; within these groups individuals that leave first will lead to unpredictable food sites, and the behaviour should be most common during times of hardship (heightened resource unpredictability). To investigate the possibility that information transfer was occurring, the break-up of the low-water roost was studied in particular detail.

### 8.3.1 Methods

The formation stage of the roost was taken to be the period when roost size was increasing.

A godwit arrived at the roost by flying, either from outside the study area (long flight) or from within it (short flight), or by walking from an adjacent feeding area. A flying bird was defined as joining the roost on alighting within the flock's boundary, although it may have washed and preened before actually roosting. Walking individuals were defined as joining the roost when they stopped feeding and took up a position in the flock.

## THE LOW-WATER ROOST

Birds flying to the roost always did so in discrete groups, whereas those walking to it did not. During the formation of the roost, it was unusual for birds to leave the flock, so a change in roost size was taken as representing the arrival of new birds.

On 11 occasions the size of a forming roost was recorded every two minutes and, during six of these observations, the arrivals were categorised as flying or walking. Between the roost counts on the other five occasions, and during an additional 10 formations, the whole study area was watched, in order to record the size of arriving airborne flocks and whether they had made short or long flights. These counts were usually made while the birds were in flight, but were otherwise possible on the ground, due to the flocks remaining spatially or behaviourally discrete.

The break-up stage of the roost was defined as the period when roost size was decreasing. A godwit was defined as leaving the roost when it either moved outside it or started to feed. A bird departed by flying, to outside the study area (long flight) or to inside it (short flight), or by walking to an adjacent feeding area. Birds flying away always did so in discrete groups; those that walked did not. When the roost was breaking up it was rare for birds to join the flock; therefore, a difference in two counts was taken to represent the number of birds that had left the roost.

On 14 occasions the reduction in roost size was recorded every two minutes. On eight of these times the roost was watched continuously and a record made of how many birds departed in each

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two minute period by flying or walking. Between the counts on the other six occasions, and during an additional nine roost break-ups, the size of departing flocks of flying birds and whether they made long or short flights was recorded.

On 10 days when the temperature was  $>2^{\circ}\text{C}$ , and on six days when  $<2^{\circ}\text{C}$ , flocks making long flights were watched from a position which gave a view of both the low-water roost and of feeding sites outside the study area. For each of these flocks it was noted whether: the first bird to leave the roost remained the leader of the flock and landed first, the flock landed together (within 20 bird-lengths), the flock (or the largest resulting flock) landed where other godwits were already present (within 20 bird-lengths), and the flock (or largest resulting flock) landed at a 'predictable' feeding site. A predictable feeding site was defined as one which had held godwits on at least three of the last four previous visits to the estuary at a comparable tide-height.

Sometimes, disturbance caused the whole roost or a major part of it to make a long flight. Such events were not present in the departure data analysed here.

The frequency pattern of the number of arrivals or departures in two minute periods will be described by a Poisson distribution if events occur at random and the underlying rate is both low and uniform. Considering departures, the underlying rate was uniform between 20-80% of the maximum count (Fig.8.2) and the two minute time period used ensured that the rate was low (for formation

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mean=2.6 birds per time interval; for break-down mean=2.3 birds per interval). Therefore, data between these limits can be tested for randomness by comparison with a Poisson distribution. The underlying rate of arrivals, even between 20-80% of the maximum count, was often not uniform due to large flights of birds joining the roost. Figure 8.3 shows the size distribution of all airborne flocks arriving during the 15 observations and indicates the large size of some of these groups. Such large arrival flocks may be due to disturbance, since, during the break-up of roosts, there were no departure groups larger than 15 individuals unless something had alarmed the birds. Therefore, for comparison with the random model, data were used between 20-80% of the maximum count and, in addition, large groups (>15) and arrivals after large groups were not considered. The arrival of the large flocks does not affect the overall peak size of the roost. In fact, the mean maximum count was higher for occasions when there were no very large arrival groups (>40) (92.0 [SE=5.1 N=9] against 84.7 [SE=5.8 N=6]), although the difference was not significant ( $F[1,33]=0.9$  NS).

Birds arriving and departing from the roost around its peak size (stable condition) were also investigated. A stable roosting flock was retrospectively defined as containing >90% of the peak count. The number of birds joining and leaving stable flocks in a total of 46 thirty-minute periods was recorded.

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The data used for all analyses were examined within the bounds described above unless specifically stated.

### 8.3.2 Results

#### Formation

The majority of birds flew to the roost (76%) and, of these, most had made long flights (82%).

The temporal pattern of all arrivals, flying arrivals and walking arrivals differ significantly from random (Fig.8.4). All three distributions show the same deviation from expected - a lower number of time periods with few arrivals and a greater frequency of periods with either many birds or no birds joining. That is, birds which join the roost either in flight or by walking are clumped in time. The mean flock-size of birds making long flights was 4.4 (SE=0.6 N=39) and short flights 2.0 (SE=0.2 N=19); this difference was significant ( $F[1,56]=13.7$   $P<0.001$ ).

#### Break-Up

As with the formation of the roost, the pattern of departure from the roost was significantly clumped for all birds, flying birds, and walking birds (Fig.8.5). Of those flying, most undertook long flights (86%). However, the majority of birds leaving the flock walked away (72%).

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The mean flock-size of birds making long flights was 4.6 (SE=0.5 N=41) and short flights 2.0 (SE=0.3 N=15), and the difference was significant ( $F[1,54]=15.8$   $P<0.001$ ).

There was no significant difference between the size of flocks arriving and departing by long flights ( $F[1,78]=0.2$  NS), nor those arriving and departing by short flights ( $F[1,32]=0.03$  NS).

Table 8.1 summarises the behaviour of the departing flocks making long flights which were watched until they landed. The bird which left the flock first remained leader and landed first on less than half of the occasions. More than a quarter of the flocks split up before alighting and about half of them landed in the presence of other godwits. There was little effect of low temperature on the observed behaviour, although during cold conditions there was a significant decrease in the proportion of flocks landing at predictable feeding sites. That birds landed at less predictable sites during inclement weather was probably a reflection of food itself being less predictable at these times.

### Stability

Figure 8.6 shows the temporal pattern of birds joining and leaving the roost while it is stable: both distributions are significantly clumped.

#### 8.4 THERMOREGULATORY BEHAVIOUR AT THE ROOST

An individual that joins a communal roost may gain the advantage of reduced energy expenditure over the roosting period. During sleep

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it is reasonable to expect heat conservation to be an important consideration.

A bird can reduce heat loss by minimising its surface area not covered by feathers, reducing wind resistance and occupying a favourable microclimate (for reviews see Calder and King 1974 and Kendeigh et al 1977). This is carried out by placing the bill in the back feathers and standing on one leg, facing into the wind, and by seeking shelter. In general, wind may be the major problem (Walsberg 1986); it will increase heat loss and has the indirect affect on roosting birds of decreasing stability, which may require that the bird stands on both legs. A flock will provide shelter from the wind; the relative quality of the shelter will depend upon the geometry of the group. Therefore, if it is important to the flock members that a communal roost provides a favourable microhabitat in terms of energy, the shape, orientation and density of the flock should be expected to change with climatic conditions, and an individual's thermoregulatory behaviour may be expected to be dependent on its position inside or outside the flock.

### 8.4.1 Methods

The behaviour of the low-water roosting flock was observed on 40 occasions. In analyses, to ensure independence, for each variable no more than one data point per observation session was used.

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The roosting flock was generally elliptical, with its major axis diameter(A) several times longer than the minor axis diameter(B). The orientation of the long axis of the flock, relative to the wind and the tide-edge at the time of formation, was recorded.

The lengths A and B were measured (in bird-lengths, then corrected to metres; see Chapter 2) for flocks which had not shown indication of disturbance for at least an hour. The proportion A/B was used as a simple index of the linearity of the flock, the larger the number, the greater the relative narrowness of the ellipse. The values of A and B were also used to estimate the area the flock covered and hence its mean density:

$$\begin{aligned}\text{mean density} &= \text{number/area} \\ &= N/(\pi AB/4)\end{aligned}$$

Using a roosting flock which, for the previous thirty minutes had not been disturbed or joined, a count was made of the proportion of birds on one leg and the proportion of birds facing directly into the wind. All birds in the flock were recorded. For each valid data point, at least five such counts were made over a period of at least thirty minutes. Directly after a count was made the wind speed and air temperature were recorded and, for each observation, the mean was taken for each set of values.

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Additional measurements were also collected for peripheral and central birds, and for solitary birds. A roosting bird was defined as peripheral if no other bird was sheltering it from the wind, and central if it was not peripheral; a solitary bird was one which was outside the roosting flock. At least five peripherals and five centrals were required for a valid observation. Solitary birds were recorded opportunistically.

### 8.4.2 Results

On 18 of 18 occasions when disturbance was not apparent, the low-water roost formed in the same position and was on the mud beside and parallel to the tide-edge, irrespective of wind-direction.

The mean value of the index of flock linearity (A/B) was 11.0 (SE=1.6 N=34) and the mean overall density was 5.7 birds per m<sup>2</sup> (SE=0.2 N=34). Table 8.2 shows the partial correlations of these two variables with temperature(K), wind speed(W) and flock-size(N). Linearity of the flock decreased significantly with lowering temperature and increasing wind speed. Flock density increased significantly with wind speed.

The mean value of the proportion of a flock standing on one leg was 0.78 (SE=0.05 N=34). Table 8.3 shows the partial correlations of this variable with temperature(K), wind speed(W) and flock-size(N). As the wind became stronger, significantly more birds stood on two legs.

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When there was little wind, the vast majority of individuals were on one leg and, at the highest winds, virtually all godwits were on two legs. Therefore, considering all wind speeds, there was no significant difference between central and peripheral birds. However, at intermediate wind speeds, central birds stand significantly more on one leg than do peripheral individuals (Wilcoxon:  $z[N=10]=-2.5$   $P<0.05$ ). Individuals roosting outside the flock were more likely to be standing on two legs than birds in the group. This was most marked in strong winds when the difference was also significant comparing solitary birds with those on the periphery of the flock (Tab.8.4). In the strongest of winds no birds were observed roosting alone.

The mean for the proportion of a flock facing into the wind was 0.85 (SE=0.04 N=30). Table 8.3 shows the partial correlations with temperature(K), wind speed(W) and flock-size(N). The proportion of birds facing into the wind increases with temperature and wind speed. There was no significant difference between central and peripheral birds ( $F[1,44]=0.1$  NS) or between solitary and group individuals, except at low wind speed (Tab.8.5).

### 8.5 ANTI-PREDATOR BEHAVIOUR

Anti-predator behaviour for a roosting individual can be split into three categories: vigilance as it relates to the probability of predator attack and detection, reaction to a potential predator, and behaviour during predator attack. For all categories flocking communally may be advantageous to the individual. In a flock, a

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bird may receive an increased corporate predator detection probability while reducing its vigilance rate. The behaviour of a flock after predator detection and during attack may reduce the chance of mortality and disturbance for each individual. Therefore, a roosting bird may, by joining a flock, increase its amount of sleep and decrease the likelihood of disturbance and mortality.

### 8.5.1 Methods

The birds on the low-water roost, when not preening or reacting to disturbance, spent the majority of time resting with the eyes closed and body stationary (except for any buffeting by the wind). However, each bird frequently took short peeks and occasionally twisted the body horizontally by 5-15°. The former activity is a standard component of the behaviour of sleeping birds and is taken to be surveillance for predators (for example Lendrem 1984b). The latter behaviour has not received attention, although it is present in other wading birds (oystercatcher, curlew and bar-tailed godwit: pers. obs.); it can be postulated to be a response to wind or part of the anti-predator system.

Vigilance can be considered in two ways; rate, which is the number of peeks per time period (for example Elgar and Catterall 1981), and pattern, which concerns the length and distribution of these peeks (for example Poysa 1987).

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Due to the contrasting colour of the white eyelid and dark eye in the black-tailed godwit, peeks can be observed easily if the bird is at close range and in the appropriate orientation. However, if the watching conditions were not good (not a rare event), the activity could not be seen adequately. For this reason observations could not occur to a planned schedule and were therefore made opportunistically. Data were collected at different flock-sizes, although, due to the nature of the low-water roost, there were no records for flocks below 15 individuals. Observations of rates involved recording the number of events in a one or two minute time period. Pattern data were recorded for between one and five minutes. An observation of the patterning of vigilance recorded how long the eye was open and closed. A period with the eye open is called a peek, with the eye shut an inter-peek gap.

The position in the flock of the focal bird was recorded. A peripheral bird was defined as one which, in plan, had a horizontal, continuous angle of at least  $135^{\circ}$  free of any part of another flock member (Fig.8.7). A central bird was one which was not peripheral. In practice, peripherals often had an unobscured angle of  $180^{\circ}$  or greater and centrals, a maximum unobscured angle of less than  $90^{\circ}$ . Therefore, only in rare instances did the flock need to be represented on paper for a judgement to be made. In addition, the elevated position of the hide made the judgements easier.

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Unless stated, data were collected from birds which had not been disturbed for at least thirty minutes. A bird was selected at random and only used once in an observation period. If possible, peripheral and central birds were watched alternately. During each observation period flock-size, wind speed and temperature were recorded every 30 minutes.

In addition to the vigilance data, behavioural records were collected on the responses of the roosting flock to disturbance. Disturbance was defined as an event which caused at least one godwit to show the minimum sign of wariness: sudden removal of the bill from the back-feathers and erection of the neck. This posture and the speed at which it was adopted was distinct from the waking which preceded either normal departure from the roost or preening. The response of one individual usually led to the alertness of the majority of the flock, and immediately, or after a short time the group would take off and perform complex aerial manoeuvres. After a few minutes, the flock would return again and gradually settle down after a period of washing and preening. Sometimes the birds would watch the source of disturbance and then settle down without taking off, but perhaps changing position.

In each case of disturbance, it was noted whether other species reacted, whether the godwits returned to the same area, and whether, after disturbance, the birds were closer to the tide-edge and more compact. The response of individuals roosting outside the flock to disturbance was also recorded if observed.

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Minor disturbances were probably under-recorded, especially those that elicited only a short-lived response and aroused only a few flock members.

The effect of disturbance on flocks leaving the roost was also investigated: the size of groups making long flights from the flock was recorded when there had or had not been disturbance in the previous 60 minutes.

### 8.5.2 Results

#### Rate

The observed peek rates of peripheral and central birds were allocated to broad categories of flock-size (Fig.8.8a). The peek rate of central individuals was significantly lower than that for peripherals (two-way ANOVA, see below for the result for flock-size categories,  $F[1,232]=110$   $P<0.001$ ). That is, birds at the edge of the flock made more glances than birds in the centre. Although there was a trend for peek rate to reduce with flock-size this was not significant (two-way ANOVA,  $F[3,232]=0.33$  NS).

Peripheral(p) and central(c) data were each pooled across flock-size and then compared to the peek rate for solitary(s) birds. The mean for solitary birds is significantly higher than for centrals ( $F[2,255]=123$   $P<0.001$ ; p and c, s and c sig. different at 5% level).

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To look more closely at the effect of flock-size and other factors on the peek rate, for both central and peripheral birds, data were averaged for each of 17 observation periods when at least five peripheral and five central birds were observed. Table 8.6 shows the partial correlations of peek rate for both peripheral and central godwits with flock-size, wind speed and temperature. The vigilance rate of central birds significantly decreases with increasing flock-size and decreasing temperature.

The observed rates of twisting for peripheral and central birds were allocated to the same broad categories of flock-size (Fig.8.8b). Central birds twisted significantly less often than peripheral birds, but there was no significant affect of flock-size (two-way ANOVA: central/peripheral,  $F[1,115]=14.9$   $P<0.001$ ; fock-size,  $F[3,115]=0.25$  NS). Peripheral and central data were each pooled across flock-size and then compared to the higher twisting rate of solitary birds. All three means were significantly different from each other ( $F[2,126]=23.1$   $P<0.001$ ).

The twisting data for both central and peripheral birds were averaged for each of 17 observation periods when at least three peripheral and three central birds were recorded. For both twisting rates, there were no significant partial correlations with flock-size, wind speed or temperature.

Some paired data were collected: an individual had its peek rate and twist rate measured in adjacent one minute periods. Other paired data involved taking readings close in time ( $<2$  minutes)

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from both a central and a peripheral bird. This method of collection allowed correlations to be made between various variables (Tab.8.7). Vigilance rate and twisting rate were strongly correlated in central birds; the trend was not significant for peripheral birds although it was for all birds.

### Pattern

Data were collected for 45 central, 32 peripheral and 10 disturbed birds (those that had shown alarm responses within the previous two minutes). Mean peek length was similar in the three groups: 0.27s (SE=0.01 N=548) for central birds, and 0.25s (SE=0.01 N=496; SE=0.01 N=205) for peripheral birds and disturbed birds. However, inter-peek gap length was markedly different for the three groups: mean gap length was 3.7s (SE=0.1 N=556) for central birds, 2.5s (SE=0.1 N=504) for peripheral birds, and 2.1s (SE=0.1 N=210) for disturbed birds ( $F[2,1267]=82.9$   $P<0.001$ , all three means different from each other at 5% level).

Using the mean peek length and the mean vigilance rates, the average proportion of time spent pecking ( $P_p$ ) can be calculated for each group (the vigilance rate for disturbed birds was 29.3 peeks per minute SE=1.4 N=10). For central birds  $P_p=0.07$ , for peripheral birds  $P_p=0.09$  and for disturbed birds  $P_p=0.12$ .

The distribution of inter-peek gaps (Fig.8.9) and the proportion of time spent pecking can be used to estimate the probability of a bird (or group of birds) detecting a randomly attacking predator (Hart and Lendrem 1984, Lendrem 1986).

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It is assumed that a bird which is pecking will detect a predator making an uncovered attack. If the proportion of time a bird spends pecking is  $P_p$ , then this proportion of attacks will be initiated during a peek and therefore detected. On the remaining occasions an attack will start during an inter-peek gap. For a solitary bird, the probability ( $P_a$ ) of detecting an attack of length  $T$  started at random within an inter-peek gap is:

$$P_a = \sum_{i=1}^x g(d_i) + \sum_{i=x+1}^c [T/d_i]g(d_i)$$

where 
$$g(d_i) = \frac{d_i f(d_i)}{\sum_{i=1}^c d_i f(d_i)}$$

$f(d_i)$  is the frequency distribution of the inter-peek gaps with classes  $i=1,2,\dots,c$ . The  $x$ th class has an upper limit equal to  $T$ .

Therefore, the overall probability ( $P_d$ ) of an individual detecting a randomly attacking predator is:

$$P_d = P_s + (1-P_s)P_a$$

This can be extended to groups of birds scanning independently; the probability ( $P_f$ ) of a flock of  $N$  birds detecting a randomly attacking predator is:

$$P_f = 1 - (1-P_d)^N \quad \dots[1]$$

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Equation 1 can be used to assess how predator detection performance varies with the number of birds in the group. Individual vigilance parameters have not been shown to be strongly correlated with flock-size in this study, so, within each subset (peripheral, central, and disturbed), the same data were used for all group sizes. The uncovered attack time was varied from 1-10s.

Figure 8.10 shows the predator detection probabilities for flocks of peripheral birds, central birds, and disturbed birds. For all three states of bird, predator detection asymptotes at unity at low flock-size.

Peripheral birds, as described, will tend to predominate in small groups. However, a flock may not be homogeneous and may contain central as well as peripheral individuals. Although small groups were rare and no systematic data were obtained on their composition, the abundance of peripheral and central birds can be estimated by simulating flocks. By specifying two values, bird density and group linearity, the spatial relations in a flock can be modelled. The parameters selected were a density(D) of 6 birds per m (approximate mean density of the roost) and a flock shape where the index of linearity (major axis diameter(A) divided by minor axis diameter(B)) was 5. The linearity was selected to be less than the observed average, in order to give a conservative estimate of the proportion of peripheral birds. For each flock-size(N), an ellipse was generated using the flock-size, density and linearity to find the major and minor diameters (A and B):

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$$D = N/\text{area}$$

$$D = N/(\pi AB/4) \quad \text{and} \quad B = 5A$$

solving for A

$$A = \sqrt{[4N/(5\pi D)]}$$

and  $B = 5A$

Once the flock ellipse was defined, the required number of birds was randomly positioned within it and the number of peripheral and central individuals recorded. This procedure was repeated five times for each flock-size. Figure 8.11 shows how the numbers of peripheral and central birds increase with increasing group complement. Even with this conservative estimate for peripherals, for flocks of up to six individuals all birds were peripheral, and, for a group size of ten, on average only two were central.

From this we can see that central individuals would be too rare to influence the predator detection probability before it reaches unity. Therefore, the best estimate of predator detection probability of flocks up to the size of ten birds is shown by Figure 8.10b.

It can be seen from Figure 8.10b that the advantage, as regards predator protection, of not being solitary is great. The analysis assumes that solitary birds have the same pattern and peek behaviour as peripheral birds (they have the same vigilance rates). This is reasonable as the nature of patterning is much the same in central, peripheral, and disturbed birds and birds at greater

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predation risk do not have longer peeks (peripheral and disturbed not significantly different: see above).

### Disturbance

There were 61 recorded disturbances during 136 hours of observation, an average of one every 134 minutes. The rate was independent of the month ( $G[3]=1.5$  NS). In 45 of these events the specific cause of the disturbance was ascertained (Fig.8.12). Two-thirds of these were accounted for by aerial predators, the peregrine being the most common species (at least three individuals were observed in the winter 1985-86).

The data were split into aerial disturbances (birds of prey and planes, which elicited similar responses, but not helicopters, which caused great distress) and ground disturbances (dogs and humans). The birds reacted differently to these two categories. Ground disturbance was more likely to cause the birds at the roost to take off (Tab.8.8) and move position (Tab.8.8), whereas aerial disturbance was more likely to cause the roost to move into deeper water or closer to it (Tab.8.8). A general consequence of disturbance was the roost adopting a more compact formation (Tab.8.8).

On seven occasions flock length(A) and width(B) had been measured prior to disturbance and could be remeasured after it. This allowed a quantitative description of the change in flock compactness. Mean density was 5.5 birds per  $m^2$  before disturbance and 13.5 birds per  $m^2$  afterwards. This difference was significant

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(Wilcoxon:  $z[N=7]=-2.4$   $P<0.05$ ).

The size of flocks leaving the roost and making long flights was dependent on whether there had been disturbance at the roost: mean flock-size for undisturbed roosts was 3.8 birds and for disturbed roosts 7.5 birds ( $F[1,18]=32.0$   $P<0.001$ ).

Birds defined as being outside the flock sometimes acted independently. Eight times when the main roost flock took to the wing, the behaviour of those birds outside the roost was observed. On five of these occasions the outsiders remained on the mud.

### 8.6 DISCUSSION

#### 8.6.1 Factors Influencing Roosting Birds

Around low-tide, roosting black-tailed godwits tend to form a single flock. What consequences does this have for an individual bird? Figure 8.1 lists some energy and predator considerations of a roosting bird. The data collected can be used to assess the influence of communal roosting on each of these considerations, and hence give an indication of why a roosting flock forms.

#### Energy considerations before a roost forms

A communal roost may just be a consequence of social foraging if a bird: minimises its travel costs between feeding and roosting, feeds gregariously before roosting, and synchronises its behaviour with the rest of its flock. However, the black-tailed godwit roost was formed by the arrival of groups of birds from different feeding

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areas and at different times.

Over three-quarters of birds arriving at the roost had flown and over half had flown from outside the study area. Therefore, most birds are not minimising energy expenditure between feeding and sleeping and consequently, there is an energetic cost of joining the roost. However, the distances covered are relatively minor compared to those of some species of wader joining high-water roosts (Myers 1984), or of passerines joining overnight roosts (for example Yom-Tov *et al* 1977, Morrison and Caccamise 1985).

### Energy considerations during roost

It is reasonable to expect that, in winter, a prime reason for roosting communally may be heat conservation. Unless the roost is in an undesirable microhabitat, and there was no evidence for this, a bird joining the flock will not incur any energetic cost during the period of roosting.

The geometry of the roost varies with climatic conditions. The flock becomes more compact with increasing wind speed and decreasing temperature, and the density of birds increases with increasing wind speed. In addition, birds outside flocks, especially in strong winds, stand more on two legs than individuals within the roost. Clearly the roost provides energetic advantages for a sleeping bird, especially during harsh conditions. It is during periods of strong winds and with low temperatures that shorebirds are most stressed (Dugan *et al* 1981). At these times, feeding may be inefficient (for example Davidson 1981), or even

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impossible (Townshend 1985), so energy conservation at the roost may be very important.

If the only, or main, reason for joining the roost was to reduce energy expenditure during the time of sleep, it would be expected that the geometry and orientation of the flock would reflect this. One prediction would be that flock shape should be elliptical, with the major axis parallel to the direction of the wind (thus minimising the number of birds which were not sheltered). The shape of the flock was invariably an ellipse, but the orientation, regardless of wind direction, was always parallel to the shore. Another expectation would be that the communal roost would only be present regularly through the inclement months. Instead, the roost was found throughout the year. The relative size of the roost did fall in the spring, but this was due to the increase in the time spent feeding during this season (see Chapter 3).

### Energy considerations after the roost

If a bird does not feed in the immediate vicinity after finishing roosting there is an energetic cost on leaving the roost. Over 70% of birds departing from the roost start feeding close by and less than a quarter of individuals make long departure flights. Therefore, many birds are minimising energy expenditure between sleeping and feeding. However, the estuary is small and travel costs will always be relatively small.

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The quality of feeding after roosting may be affected by joining a flock. However, there is little support for any information transfer between flock members. This is a common observation (Morrison and Caccamise 1985, O'Malley and Evans 1982), although the hypothesis has been supported at breeding colonies (Waltz 1987) and roosts (Rabenold 1987). However, it could be that information is transferred but only rarely, presumably during times of stress. Although uncommon, it could be crucial to an individual gaining access to an unknown feeding site at a time of food shortage.

The roost may enhance the chance of social feeding after roosting. This will be advantageous if flock foraging is favoured, and such a benefit has been postulated to be a function of colonial breeding (O'Malley and Evans 1982). However, the feeding areas of black-tailed godwits on the Eden are predictable and an individual will have little difficulty in finding feeding conspecifics, although the roost may allow synchronisation of this behaviour.

### Vigilance Considerations

There is a trade-off between sleeping and surveillance for predators (for example Lendrem 1983). As in many species (for example Metcalfe 1984b, Knight and Knight 1986, Beveridge and Deag 1987), being part of a flock allows a black-tailed godwit to reduce its vigilance rate.

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As well as a reduction in the need for anti-predator behaviour, the flock member also benefits from a higher corporate predator detection probability. At a predator approach time of two seconds (estimated to be the minimum for the roosting flock in its characteristic position), the detection rate (probability of attacker being detected) of a solitary godwit would be 0.7, of two birds, 0.9, and, of four birds, tending to 1.0. The advantage of not being solitary, in terms of predator detection, is great, although it asymptotes at a very low flock-size (<10 birds).

Predators may also be less likely to encounter birds if they are flocked. Although modelling (Treisman 1975) has suggested that cryptic animals hunted from above would minimise the chances of a predator encountering them if they flocked, this has not been found in practice (Inman and Krebs 1987).

### Considerations after predator detection and during predator attack

In the air, a bird is safe from potential ground predators and often safe from aerial predators (Metcalf 1984c). Therefore, flying at the first sign of danger confers most safety, although it results in the greatest amount of disruption to the individual's roosting behaviour. Since many disturbances may actually pose little threat, much unnecessary perturbation may occur. In a roost, security in numbers may mean that flight only occurs where there is maximum danger. In addition, the higher probability of detection in a flock means that a disturbance will tend to be

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observed sooner, which may allow more time to assess the nature of the disturbance. However, the response of the flock to over three-quarters of disturbances was to take off and there was no apparent influence of flock-size on the degree of response.

During an attack, there may be added advantages of being in a flock (for example Page and Whitacre 1975, Morgan and Godin 1985, Landeau and Terborgh 1986).

### Synthesis

That the black-tailed godwit low-water roost is communal is not an epiphenomenon. It is not merely a consequence of gregarious feeding prior to its formation, nor is it caused by habitat limitation. Birds actively join the roost and appear to obtain both energetic and anti-predator benefits from membership. There are general advantages during roosting of decreased vigilance, increased corporate alertness, and shelter from the environment. A communal roost may promote advantageous social feeding after sleeping and, although not a common feature, may allow information transfer. These advantages must outweigh any travel cost incurred from joining the communal roost.

Anti-predator advantages will be ever-present, while microclimate benefits will not be important in warmer months. In addition, the orientation of the flock suggests that anti-predator considerations are overriding. Prior to disturbance, the roost is linear and parallel to the tide-edge, irrespective of climatic conditions. When birds land again at the roost after being

## THE LOW-WATER ROOST

disturbed, they land in or closer to water and, even if the disturbance is not great enough to cause flight, the birds often move towards or into the tide-edge. Proximity to water appears to represent safety, especially from potential aerial predators, and it appears that it is important for an individual to remain close to it. It may be that raptors are less likely to make an attack on birds standing in water. In an observation on the high-water roost a redshank which was being pursued by a merlin landed in a water filled creek. The merlin broke off the attack and perched on the edge of the channel from where it watched the wader from a distance of a few metres. During the next few minutes the redshank, on three occasions, took off, but returned to the creek moments <sup>later</sup> with the merlin in pursuit. The raptor was driven off by mobbing crows before the encounter was resolved.

If the sheltering function of the communal roost was paramount, it would be expected that the space between birds would be minimal. However the density, except during adverse conditions, was not great. Highest densities of birds were found after disturbance. At other times it could be that high concentration of individuals may interfere with vigilance, as has been reported by Siegfried and Underhill (1975) for doves at high feeding densities, or hinder rapid flight. Peripheral members of the flock tend to be more dispersed (after taking edge-effect into account); this group is assumed to be at higher risk (reflected in their higher vigilance rate), and the fact of having more space around them may enhance vigilance and taking-off ability.

Hence, from the above arguments it is reasonable to postulate that, whatever the reasons for joining a flock, the main advantages for an individual at a roost are concerned with predators.

#### 8.6.2 Roost Size And Siting

The low-water roosting flock of the black-tailed godwit on the Eden often contains all the birds that are sleeping in the study area and may sometimes contain the entire population of the estuary (see Chapter 3). Usually many flocks are formed during feeding (see Chapter 6) and birds are well spread out. Patchy food and disadvantages of gregarious feeding are usually put forward as reasons for dispersed foraging amongst birds (Goss-Custard 1980). There are no analogous disadvantages to roosting communally, so larger and denser roosting flocks may be expected. However, there may be a disadvantage in large groups of obscured vigilance and, in addition, anti-predator advantages seem to asymptote at relatively small flock-sizes. Even if there are net drawbacks for individuals in large flocks, since the groups joining the roost are relatively small, flock-size would be expected to be greater than that which is optimal for the individual for reasons discussed by Sibly (1983).

If there is no major disadvantage of group membership, why are some birds outside the flock? The definition of a flock member used here was arbitrary, and individuals outside the flock may be better described as peripheral. Indeed, most birds described as solitary were within sight of the main roost. However, at least

## THE LOW-WATER ROOST

some of these birds were distinct behaviourally from the individuals in the flock. When the flock flew due to aerial disturbance, these solitary birds did not always follow. Eshel (1978) speculated that, in complicated aerial displays, individuals were trying to out-manceuvre slower birds in order to detach them from the flock, thus making them more vulnerable to the predator. It might be advantageous for such a slow individual not to be part of a display. However, by remaining within sight of the group, the individual may make use of the flock's high detection capability. If this were the case, the same individuals might be expected to be solitary. Indeed other studies have shown that social structure exists in roosts (Pienkowski and Dick 1976, Furness and Galbraith 1980, Noske 1985, Still et al 1987, Summers et al 1987).

Although there was no habitat limitation, the position of the roost was fixed on the same piece of mud and adjacent to the tide-edge throughout the study. Similarly Myers (1984) reported that sanderlings roosting on an apparently homogeneous beach continually selected the same site. It may be that choice is dependent upon very small microclimatic differences.

The siting near the water's edge may be partly a consequence of washing and preening prior to roosting. This position appears to have anti-predator advantages, but also allows an individual to track the state of the tide, which may be relevant to feeding after roosting (see Chapter 3).

TABLE 8.1

Effect of temperature on behaviour of flocks making long flights from the roost. Flocks were watched under warm conditions on 10 occasions and under cold conditions on six occasions. Comparing warm with cold conditions: leader lands first,  $G[1]=0.7$  NS; flock lands together,  $G[1]=2.4$  NS; main flock joins other godwits,  $G[1]=2.6$  NS; main flock lands at predictable site,  $G[1]=16.5$   $P<0.001$ .

TABLE 8.1

FREQUENCIES						
	TOTAL	LEADER LANDS FIRST	FLOCK LANDS TOGETHER	FLOCK JOINS GODWITS	FLOCK LANDS AT PREDICT- ABLE SITE	
WARM CONDITIONS:						
FLOCK SIZE	2	9	5	8	4	7
	3	8	3	4	4	6
	4	4	1	3	3	4
	5	4	1	2	3	3
	>5	6	1	3	3	5
	31	11	20	17	25	
		35%	65%	55%	81%	
COLD CONDITIONS:						
FLOCK SIZE	2	7	4	6	1	2
	3	4	2	4	1	1
	4	3	1	3	2	0
	5	2	1	1	1	1
	>5	3	1	2	1	1
	19	9	16	6	5	
		47%	89%	32%	26%	

TABLE 8.2

Partial correlations of linearity of roost and density of roost with flock-size, wind speed and temperature. For all cases DF=30.

TABLE 8.2

PARTIAL CORRELATIONS						
	FLOCK-SIZE		WIND SPEED		TEMPERATURE	
LINEARITY	0.06	NS	-0.42	P<0.05	0.38	P<0.05
DENSITY	0.04	NS	0.56	P<0.001	-0.29	NS

TABLE 8.3

Partial correlations of proportion of birds on one leg and proportion of birds facing into the wind with flock-size, wind speed and temperature. For proportion on one leg DF=30, for proportion facing into wind DF=26.

TABLE 8.3

PARTIAL CORRELATIONS						
	FLOCK-SIZE		WIND SPEED		TEMPERATURE	
PROPORTION ON ONE LEG	0.13	NS	-0.67	P<0.001	0.04	NS
PROPORTION FACING INTO WIND	0.17	NS	-0.51	P<0.001	0.38	P<0.05

TABLE 8.4

Influence of wind speed and position of roosting bird on the frequency of birds standing on one and two legs. Low wind speed = wind speed 1, moderate wind speed = wind speeds 2 and 3, high wind speed = wind speed 4 and 5.

TABLE 8.4

	FREQUENCY			COMPARISON BETWEEN:	
	FLOCK (F)	PERIPH- ERAL(P)	SOLI- TARY(S)	F AND S	P AND S
LOW WIND SPEED:					
1 LEG	553	95	24	G[1]=4.7 P<0.05	FISHER NS
2 LEG	32	11	5		
MODERATE WIND SPEED:					
1 LEG	558	120	14	FISHER P<0.01	FISHER NS
2 LEG	60	20	7		
HIGH WIND SPEED:					
1 LEG	560	91	3	G[1]=28.5 P<0.001	G[1]=17.1 P<0.001
2 LEG	229	59	18		

TABLE 8.5

Influence of wind speed and position of roosting bird on the frequency of birds facing wind and not facing wind. Low wind speed = wind speed 1, moderate wind speed = wind speeds 2 and 3, high wind speed = wind speed 4 and 5.

TABLE 8.5

		FREQUENCY		COMPARISON BETWEEN:
		FLOCK(F)	SOLITARY(S)	F AND S
LOW WIND SPEED:				
FACING	358	12		G[1] = 8.1
NOT FACING	104	12		P<0.01
MODERATE WIND SPEED:				
FACING	456	16		FISHER
NOT FACING	62	0		NS
HIGH WIND SPEED:				
FACING	641	19		FISHER
NOT FACING	51	0		NS

TABLE 8.6

Partial correlations of vigilance rate of central and peripheral birds with flock-size, temperature and wind speed. For all cases DF=13.

TABLE 8.6

	PARTIAL CORRELATIONS					
	FLOCK-SIZE		TEMPERATURE		WIND SPEED	
CENTRAL VIGILANCE RATE	-0.71	P<0.01	0.69	P<0.01	0.18	NS
PERIPHERAL VIGILANCE RATE	-0.40	NS	0.37	NS	-0.22	NS

TABLE 8.7

Correlation coefficients between paired vigilance and twist data.

TABLE 8.7

	CORRELATION COEFFICIENT		P
CENTRAL VIGILANCE RATE AND TWIST RATE	r[31]	0.55	<0.01
PERIPHERAL VIGILANCE RATE AND TWIST RATE	r[33]	0.19	NS
ALL VIGILANCE RATES AND TWIST RATES	r[66]	0.51	<0.01
PERIPHERAL TWIST RATE AND CENTRAL TWIST RATE	r[56]	0.25	NS
PERIPHERAL VIGILANCE RATE AND CENTRAL VIGILANCE RATE	r[37]	0.09	NS

TABLE 8.8

Comparison between the responses of the roosting flock to aerial disturbances and ground disturbances.

TABLE 8.8

	FREQUENCY		
	AERIAL DISTURBANCE	GROUND DISTURBANCE	
TAKES OFF	21	11	FISHER P<0.05
DOES NOT TAKE OFF	11	0	
AFTER DISTURBANCE FLOCK IN SAME PLACE	32	4	FISHER P<0.05
AFTER DISTURBANCE FLOCK MOVES TO NEW AREA	0	7	
FLOCK CLOSER TO WATER AFTER DISTURBANCE	27	1	FISHER P<0.05
FLOCK NOT CLOSER TO WATER AFTER DISTURBANCE	5	4	
FLOCK MORE COMPACT AFTER DISTURBANCE	23	4	FISHER NS
FLOCK NOT MORE COMPACT AFTER DISTURBANCE	9	4	

FIGURE 8.1

Some aspects of roosting which may be effected by roosting  
communally.

FIGURE 8.1

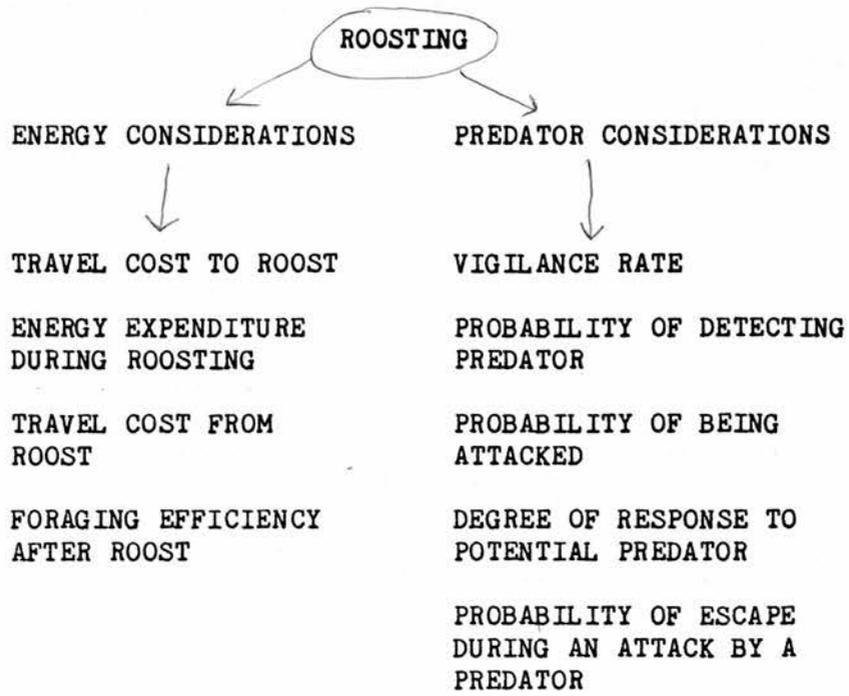


FIGURE 8.2

An example of the variation in the number (N) of black-tailed godwits on the low-water roost, with time, in minutes, as a roost breaks up. Dashed lines indicate 20% and 80% of the maximum roost size.

FIGURE 8.2

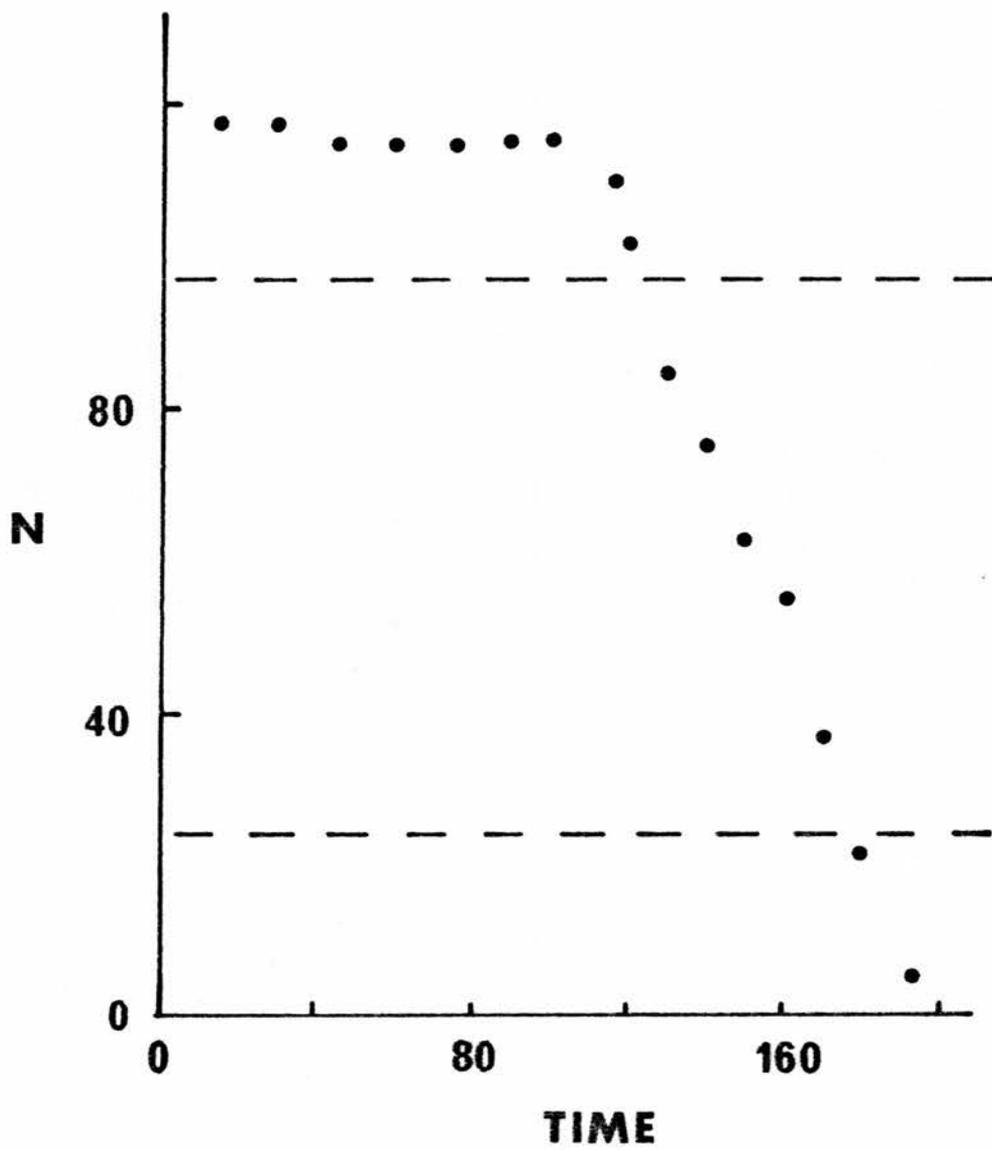


FIGURE 8.3

Frequency (F) distribution of flock-size (N) for all arriving flights at the low-water roost.

FIGURE 8.3

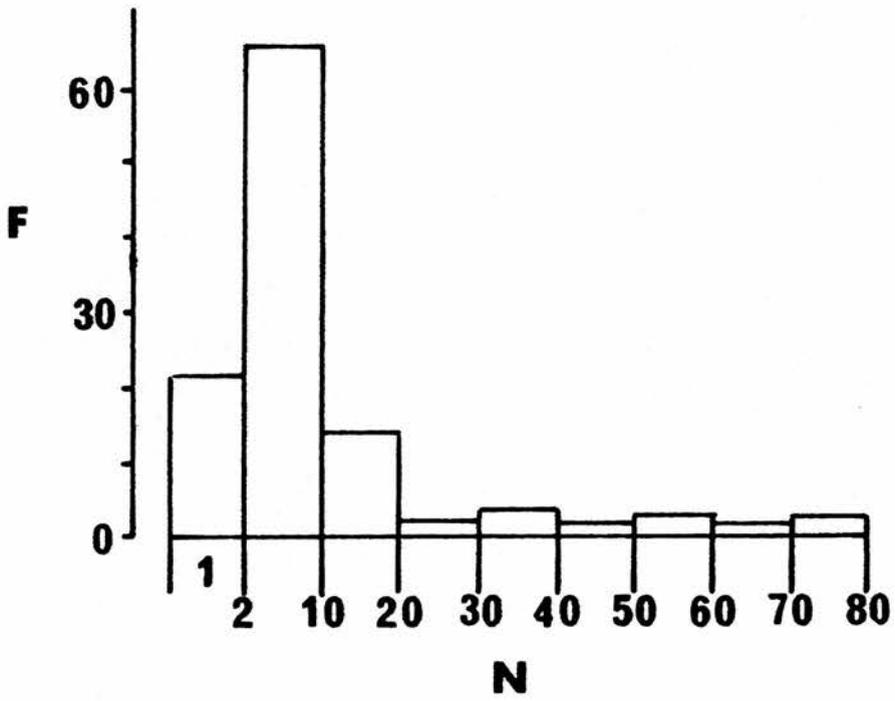


FIGURE 8.4

Frequency (F) distribution of the number (N) of black-tailed godwits arriving at the roost in two-minute periods; data collected between 20 and 80% of maximum roost count. Dashed lines indicate the expected distribution if the birds were arriving randomly in time.

a/ All arrivals; 11 observations and a total of 467 birds, observed different from expected:  $G[5]=214$   $P<0.001$ .

b/ Arrivals by flight; 6 observations and a total of 206 birds, observed different from expected:  $G[4]=91.2$   $P<0.001$ .

c/ Arrivals by walking; 6 observations and a total of 65 birds, observed different from expected:  $G[2]=24.3$   $P<0.001$ .

FIGURE 8.4

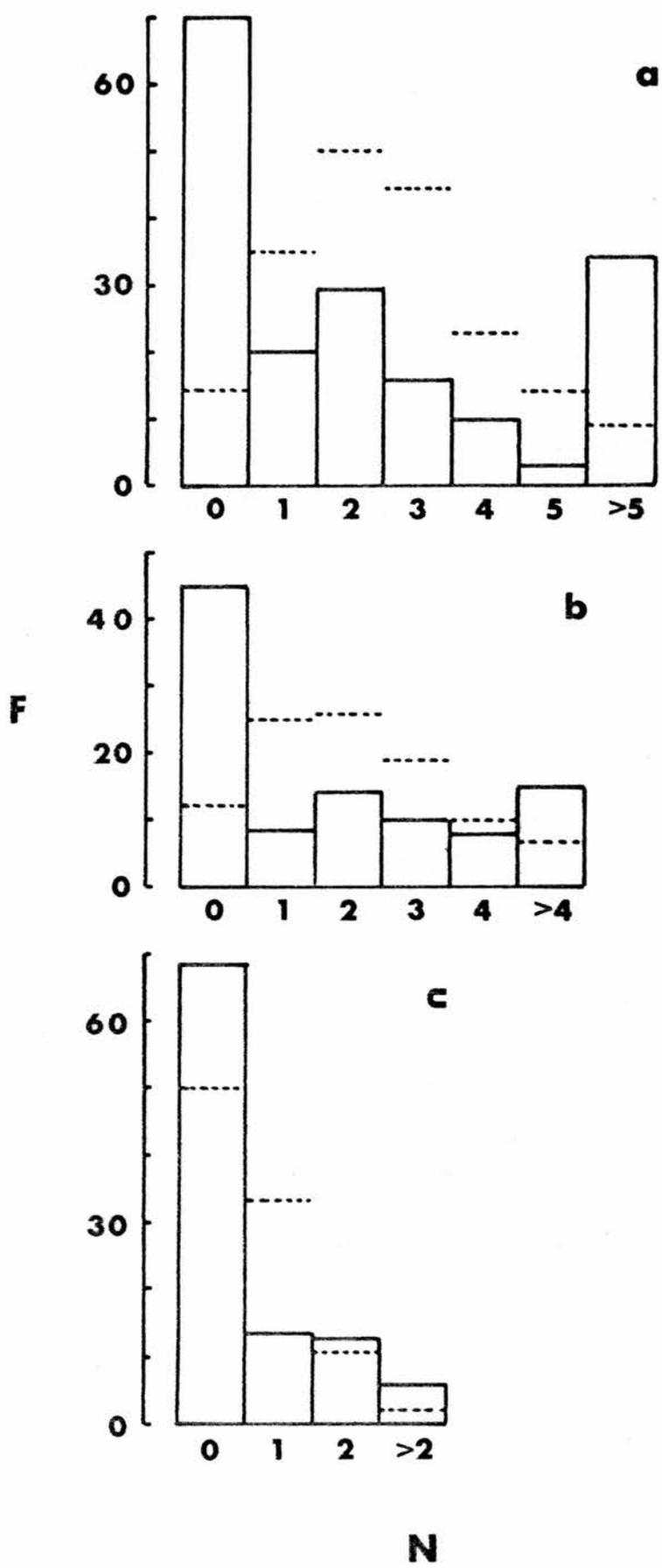


FIGURE 8.5

Frequency (F) distribution of the number (N) of black-tailed godwits departing from the roost in two-minute periods; data collected between 20 and 80% of maximum count. Dashed lines indicate the expected distribution if the birds were departing randomly in time.

a/ All departures; 14 observations and a total of 648 birds, observed different from expected:  $G[5]=294$   $P<0.001$ .

b/ Departures by flight; 8 observations and a total of 97 birds, observed different from expected:  $G[1]=81.2$   $P<0.001$ .

c/ Departures by walking; 8 observations and a total of 251 birds, observed different from expected:  $G[4]=65.9$   $P<0.001$ .

FIGURE 8.5

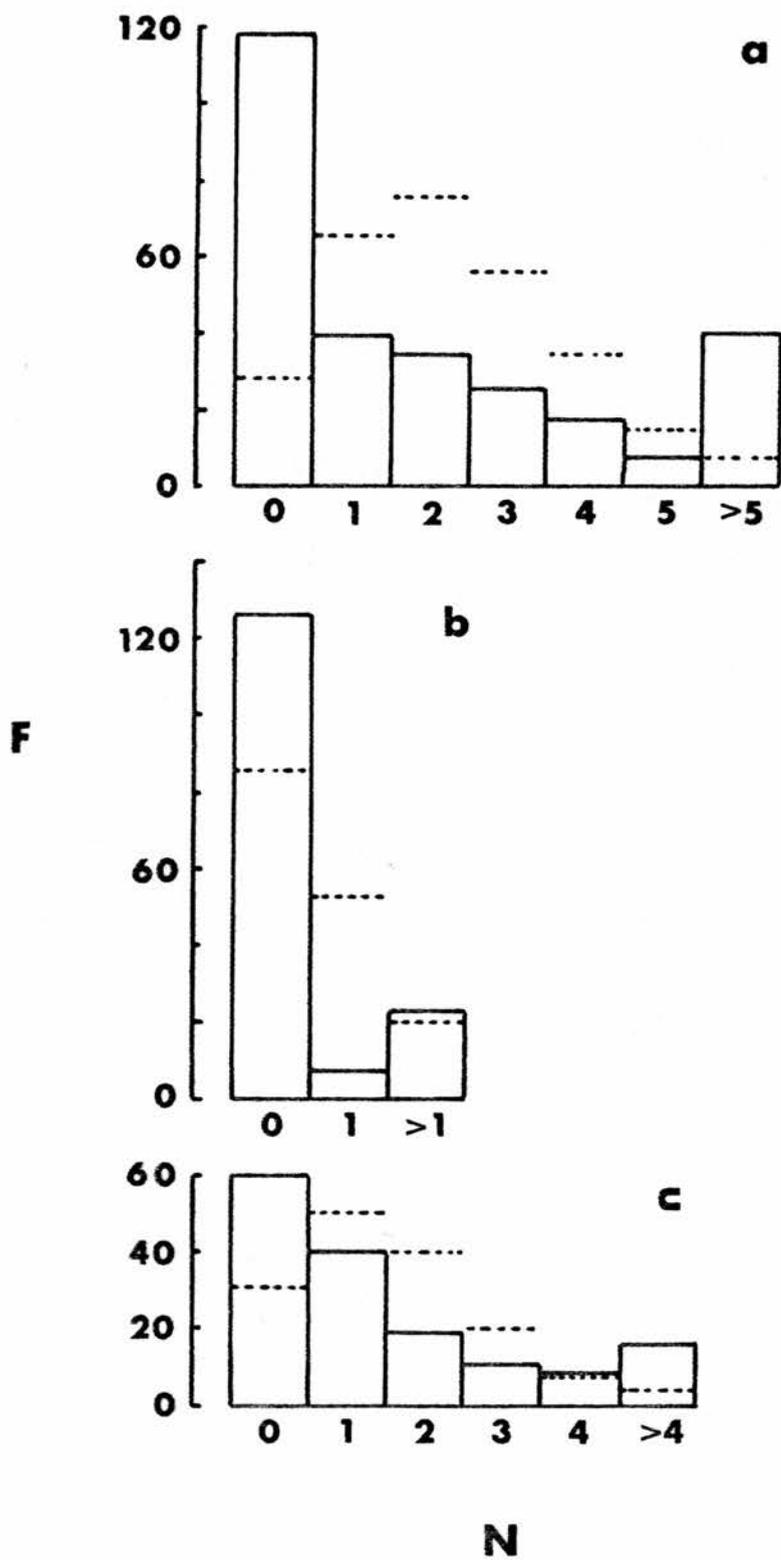
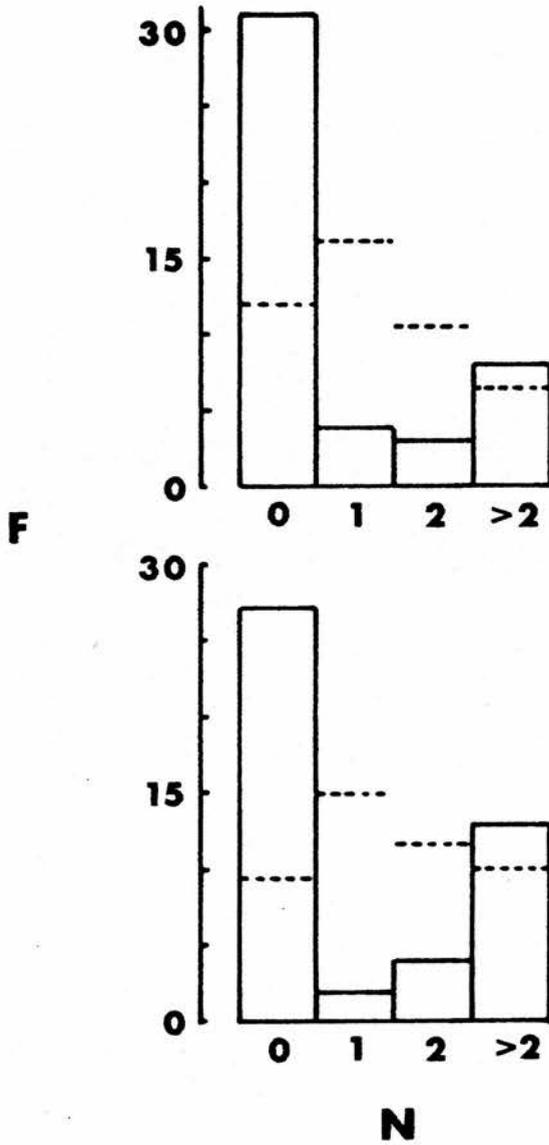


FIGURE 8.6

Frequency (F) distribution of the number (N) of black-tailed godwits joining (top section) and leaving (bottom section) a stable roost in 30-minute periods. Dashed lines indicate the expected distribution if the birds were joining and departing randomly in time. Comparison between observed and expected: for joining,  $G[2]=39.8$   $P<0.001$ ; for departing,  $G[2]=56.1$   $P<0.001$ .

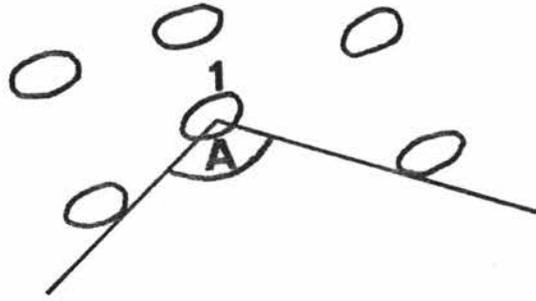
FIGURE 8.6



**FIGURE 8.7**

Definition of peripheral and central birds. Plan view of flock, oblongs represent birds. The largest continuous horizontal angle which contains no flock members is measured. For bird 1 this angle is  $A$ , which is  $<135^\circ$ ; therefore, bird 1 is defined as central. All other birds in this example are peripheral.

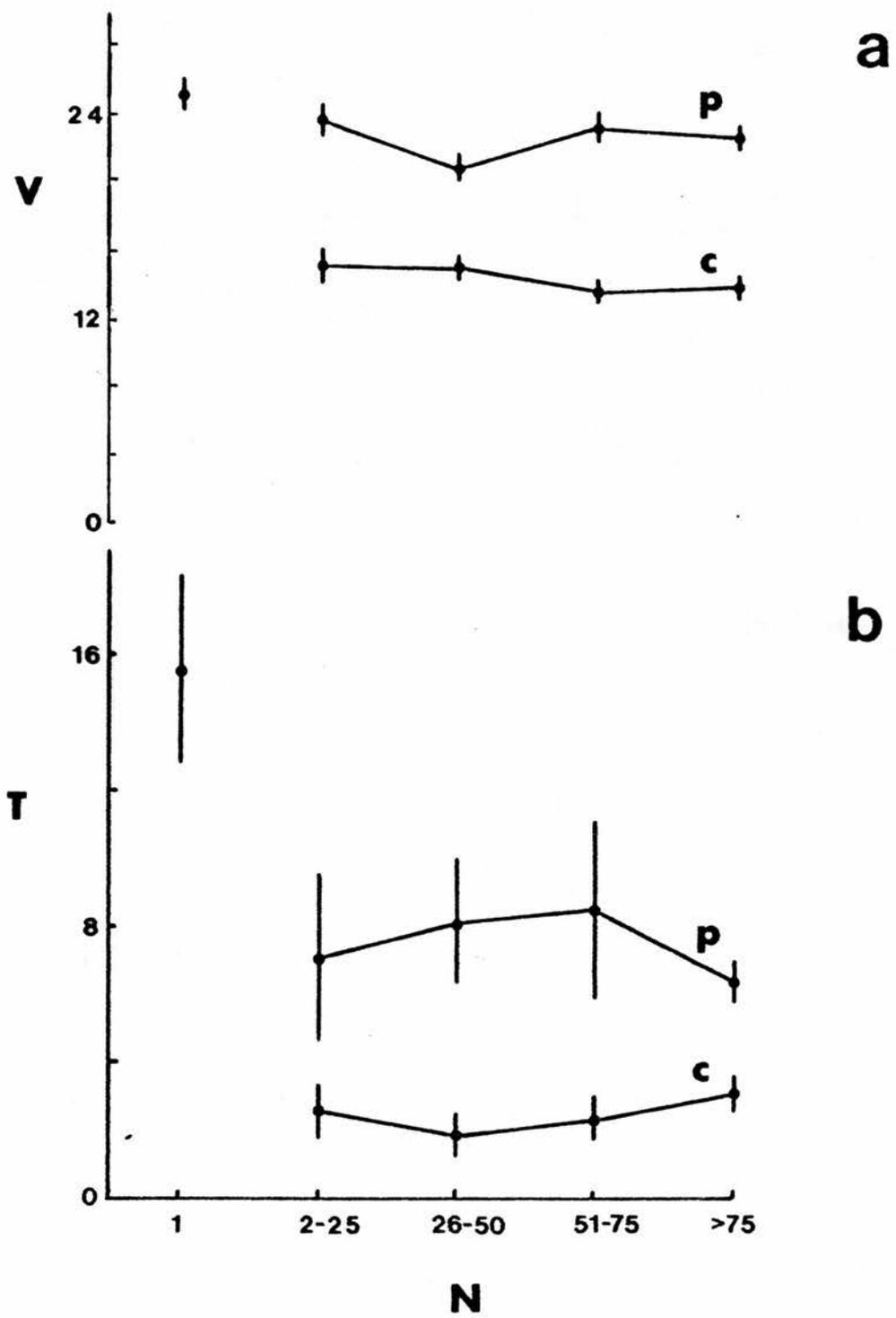
FIGURE 8.7



**FIGURE 8.8**

Mean vigilance rate (V in peeks per min) and mean twist rate (T in twists per min) of peripheral (p) and central (c) birds in different sized flocks. Bars indicate SE.

FIGURE 8.8



**FIGURE 8.9**

Frequency (F) distribution of inter-peek gap lengths (L) for central (C) peripheral (P) and disturbed (D) birds. Gap lengths have been allocated to 1s categories.

FIGURE 8.9

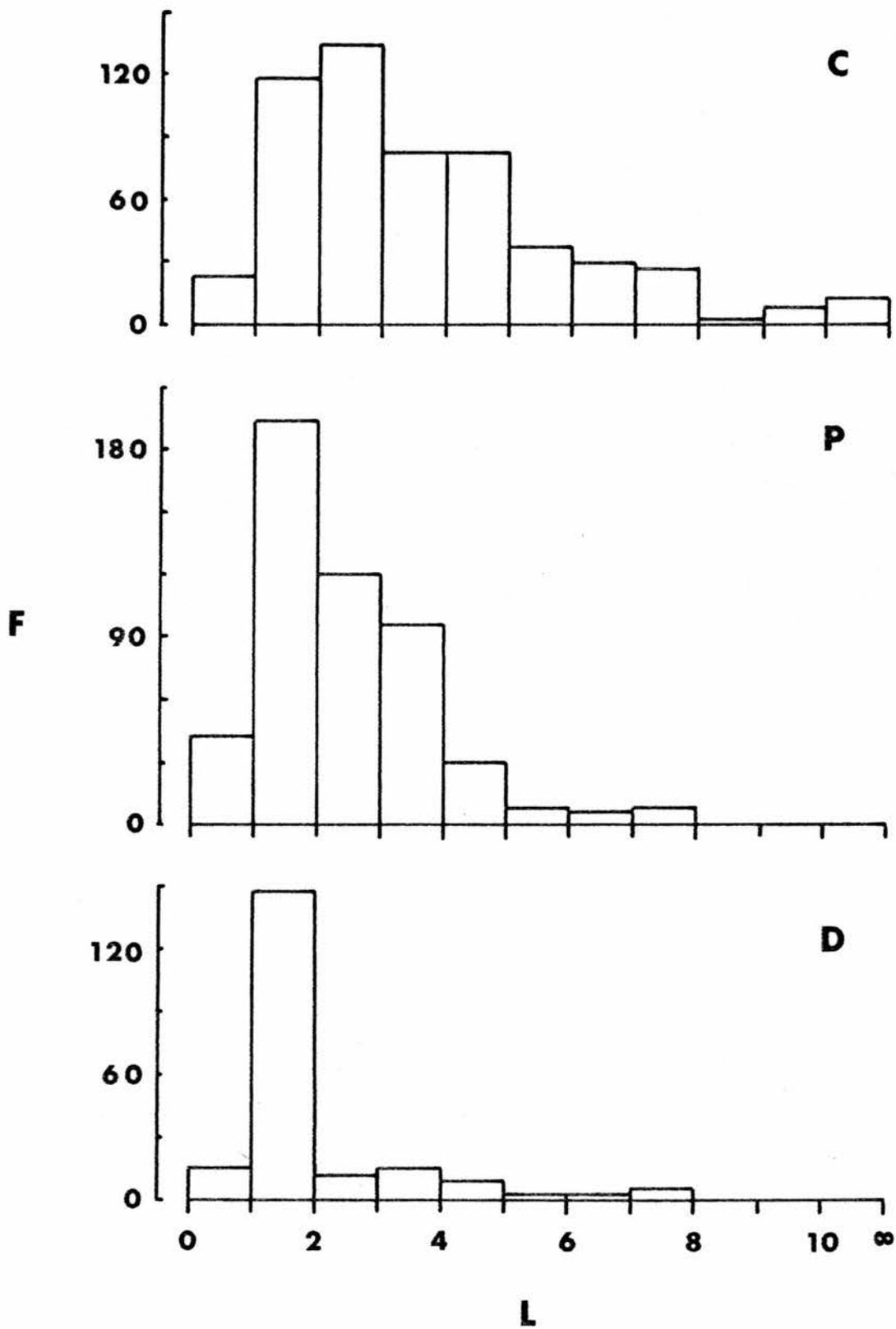


FIGURE 8.10a

Estimated corporate probability of detecting a predator against uncovered attack time ( $T$  in s) using vigilance parameters for central birds. a/ For 10 birds in roost, b/ for 5 birds in roost, c/ for 3 birds in roost, d/ for 2 birds in roost, e/ for a single roosting bird.

FIGURE 8.10a

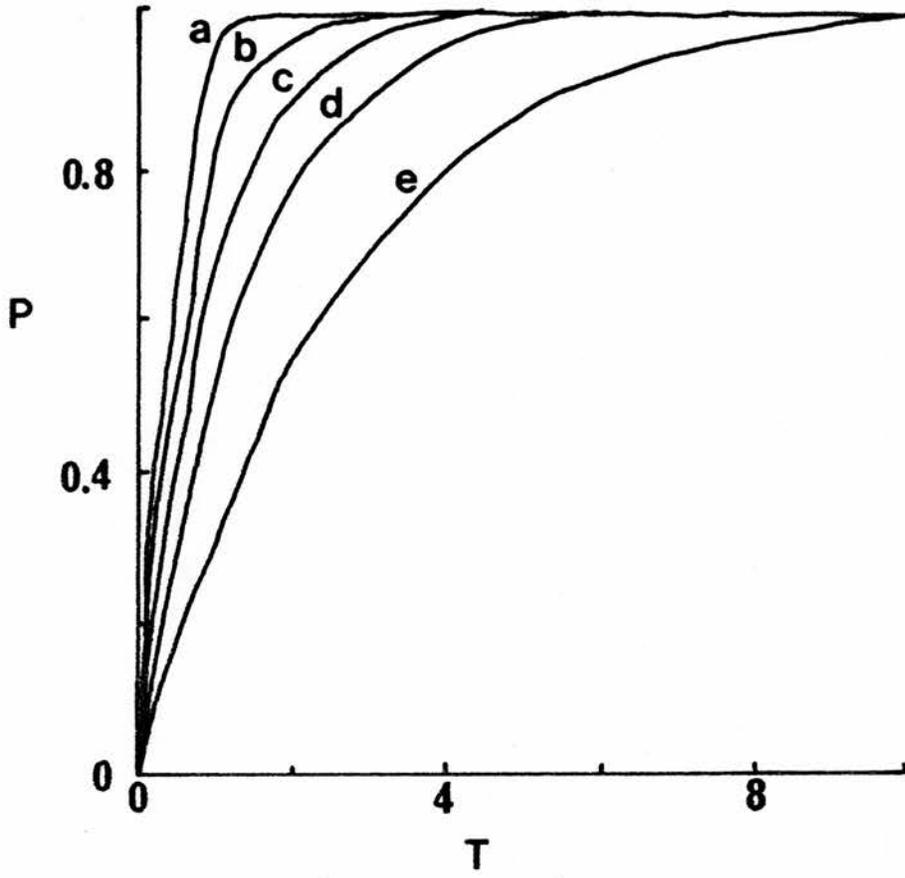


FIGURE 8.10b

Estimated corporate probability of detecting a predator against uncovered attack time (T in s) using vigilance parameters for peripheral birds. a/ For 10 birds in roost, b/ for 5 birds in roost, c/ for 3 birds in roost, d/ for 2 birds in roost, e/ for a single roosting bird.

FIGURE 8.10b

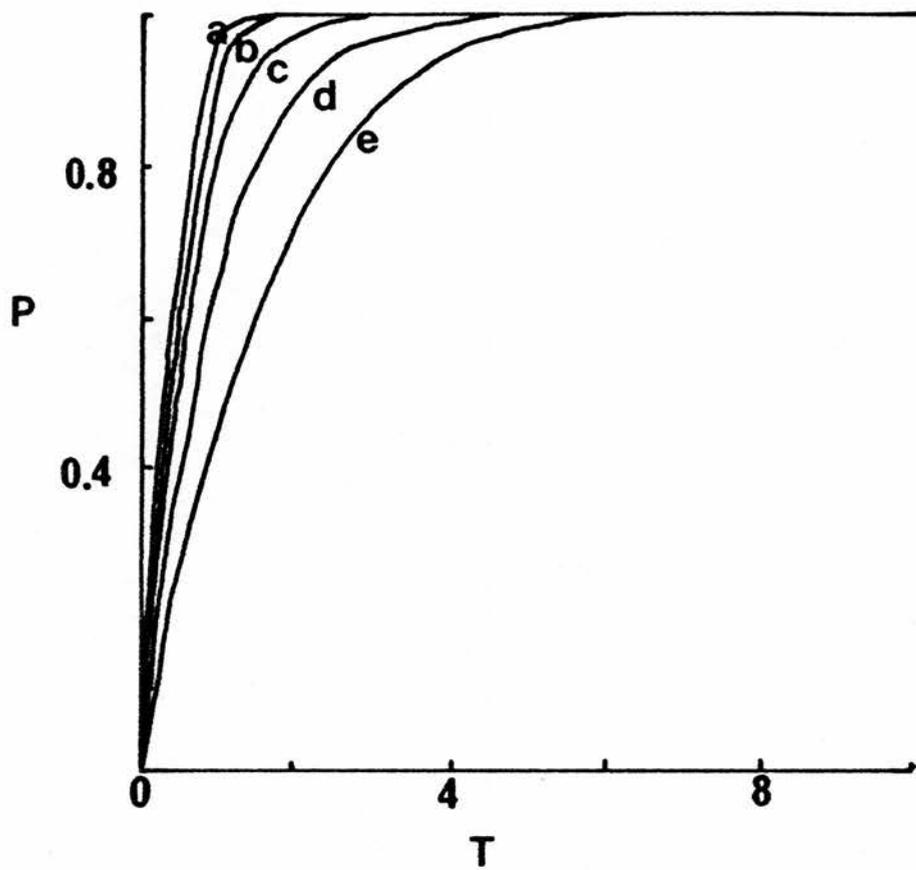


FIGURE 8.10c

Estimated corporate probability of detecting a predator against uncovered attack time ( $T$  in s) using vigilance paramaters for disturbed birds. a/ For 10 birds in roost, b/ for 5 birds in roost, c/ for 3 birds in roost, d/ for 2 birds in roost, e/ for a single roosting bird.

FIGURE 8.10c

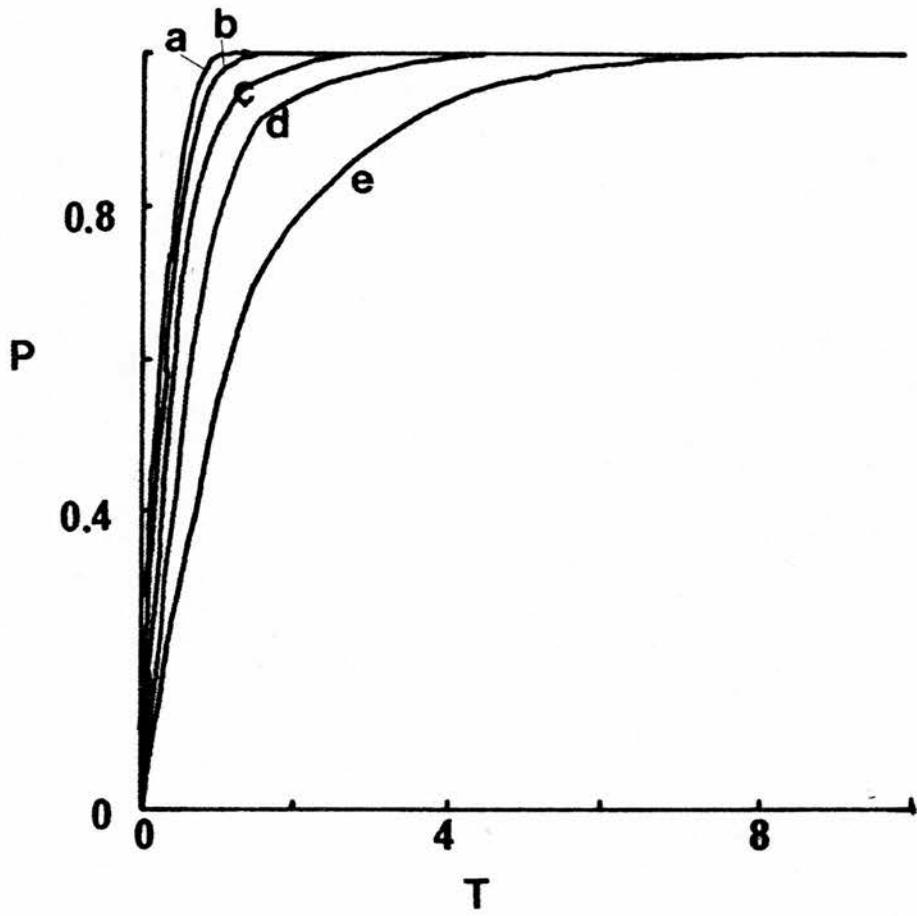
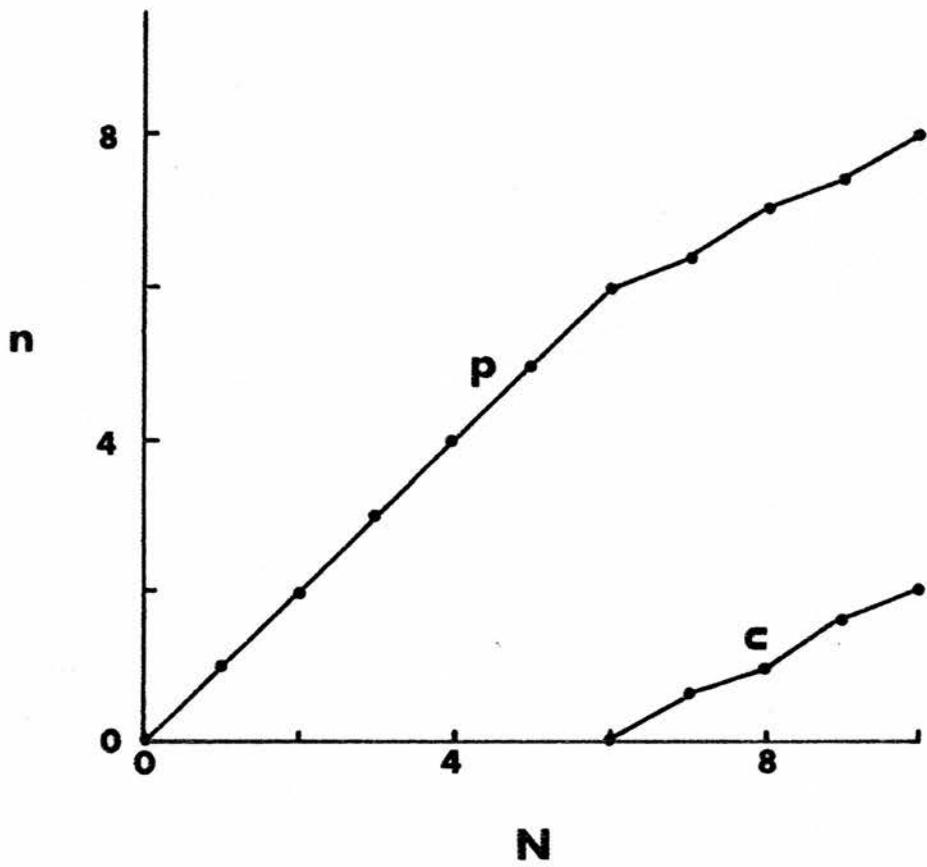


FIGURE 8.11

Mean number ( $n$ ) of peripheral( $p$ ) and central( $c$ ) birds in flock of different size ( $N$ ). Data from simulation of flocks.

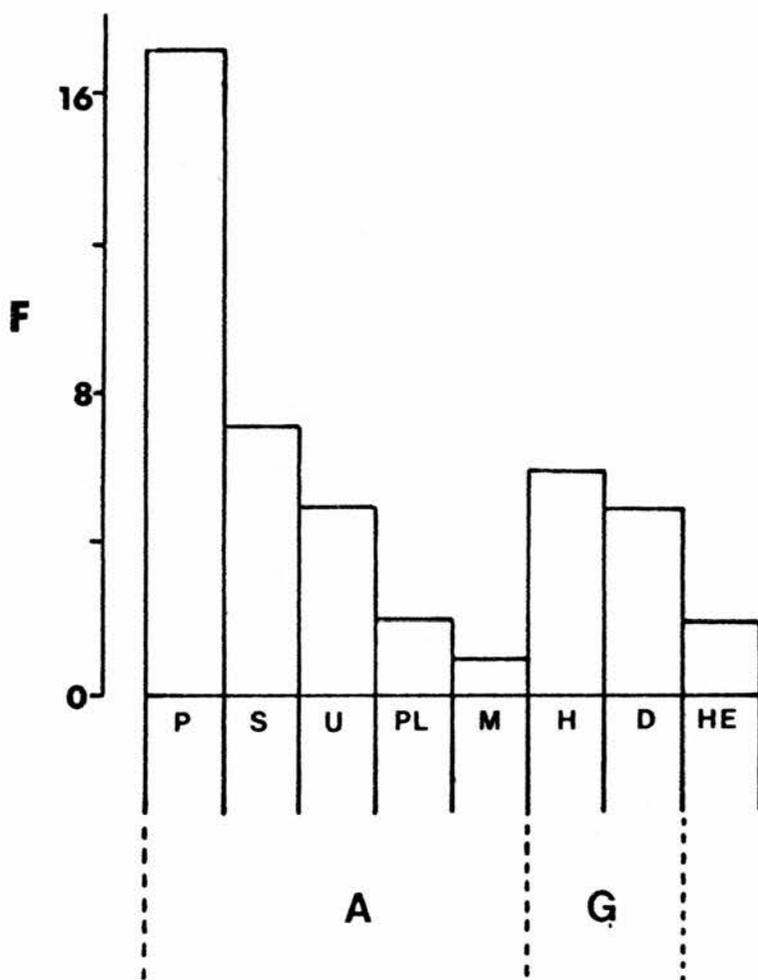
FIGURE 8.11



**FIGURE 8.12**

Frequency (F) of different causes of disturbance of the low-water roost. P for peregrine, S for sparrowhawk, U for unidentified raptor, PL for plane, M for merlin, H for human, D for dog, HE for helicopter. A indicates those disturbances which were defined as aerial and G those which were defined as ground.

FIGURE 8.12



CHAPTER 9  
DISCUSSION

This study attempted to do two things: to describe the general behavioural ecology of the black-tailed godwits wintering on the Eden Estuary, and to look at specific aspects of the ethology of these waders.

General Ecology

The godwits fed on fine mud in the inner part of the estuary, and ate mainly Macoma and Nereis; this confirms previous observations made on the species in Britain (Goss-Custard 1970, Greenhalgh 1975, and see species review in Cramp and Simmons 1983). Most aspects of the general behaviour of the birds were typical of waders wintering on an inter-tidal habitat (for a review see Puttick 1984). However, a noticeable exception to this was the formation of a low-water roost and the consequently small amount of time devoted to foraging during daylight. This time budget is an indication that the birds on the estuary are not very stressed under normal weather conditions. This observation is interesting

## DISCUSSION

as the black-tailed godwits on the Eden Estuary are at the northern limit of their non-breeding range.

There has been recent controversy as to which factors are important in determining the winter range of shorebirds. Trade-off models (for example Greenberg 1980) suggest that there is a trade-off between migrating to southern latitudes, where winter survival is expected to be high due to the mild conditions, and migrating to more northern latitudes where migration costs are lower. Competition models (for example Pienkowski and Evans 1985) suggest that a bird should attempt to winter as close to the breeding area as practicable; birds less able to compete move to more southerly sites. If the trade-off mechanism is of paramount importance, it would be expected that birds wintering further south should have lower winter mortality than members of the same species in the north. However, there is little evidence for this, and Pienkowski and Evans (1985) suggest that the opposite may in fact be true, although their data compare mortality across species, and do not take account of body size which may be an important factor.

There is intraspecific competition in various wader species on estuaries in northern Europe. Within an area, the density of a species has been positively related to the density of its main prey (Goss-Custard *et al.* 1977, Bryant 1979), and, within an estuary, best sites are filled first (Meire and Kuyken 1984, Goss-Custard 1977c). Juveniles may be excluded from the best sites in the autumn (Have *et al.* 1984) and throughout their first winter (Goss-Custard and Durell 1984), and it has been shown that young

## DISCUSSION

grey plover on the Tees have been forced to move further south to winter as a result of competition with adults (Townshend 1985). In addition, areas at the southern edge of at least some species' ranges only appear to be used when populations are particularly high (Pienkowski and Evans 1985). Competition is evidently an important aspect of the distribution of waders. There is also a great deal of evidence of populations of waders wintering in relatively close proximity to their breeding grounds (see species reviews in Cramp and Simmons 1983). Birds breeding in temperate latitudes may winter locally, as is the case with oystercatchers in Britain.

However, the northern limit of a non-breeding distribution is probably related to weather. For example, although curlews are found throughout Britain during the winter, their density in southeast Scotland is a tenth of that in southeast England at the same invertebrate density (Evans and Dugan 1984 using data from Bryant 1979). In addition, other species or populations of waders have more southerly distributions than would be expected from the competition model. For example, turnstones from Scandinavia pass through Britain to winter in Africa (Summers 1986) even though non-breeding conditions for the species are good in this country (Metcalfe 1984a). It is possible that there is competition with birds from Canada and Greenland.

## DISCUSSION

In the Icelandic black-tailed godwit, birds have only wintered in Britain since the breeding population has increased (see Chapter 1). Before this time, the wintering population was entirely more southerly. This pattern is the reverse of what would be expected from the competition model.

Obviously the situation is complicated. It is probable that the trade-off model has at least some relevance in determining the broad range of a wintering shorebird. However, within this range, especially where there is little variation in winter mortality over a wide band of latitude, competition will play a major role in the distribution of birds.

### Behaviour

The relatively short period of time spent foraging during the day by a black-tailed godwit on the Eden Estuary was not sufficient to provide it with enough energy for a 24-hour period. It appears that the birds are gaining a considerable proportion of their intake at night. Other wader species using the estuary were not seen to form a low-water roost in the study area, although it is possible that they did so elsewhere on the estuary. This suggests that the godwits find nocturnal feeding particularly rewarding; if this is the case, the reasons are obscure. The whole area of night-time foraging by shorebirds on the Eden is worthy of investigation. It could be that, during the study, the relative conditions for nocturnal feeding were particularly good for the species. In previous winters godwits have apparently made regular

## DISCUSSION

use of fields for feeding in during high-water (R W Byrne pers. comm.); this behaviour also occurs on the Exe (J D Goss-Custard pers. comm.). However, in the three years of research, godwits were only observed feeding outside the mudflats during cold and windy weather, and even then rarely.

During harsh conditions, the behaviour of the black-tailed godwits changes in several ways; for example, kleptoparasitism becomes more common (Chapter 5). Although overall food stealing was an uncommon event, the specialisation of the behaviour of the attacker was marked. An assault was targeted in such a way that the chance both of success and of a high energy item being taken was great. Therefore, the possibility of suffering a kleptoparasitic act was a disadvantage of being in a flock. However, this cost was confined largely to times when there was inclement weather, and, in general, foraging in a flock was advantageous.

Other costs and benefits of flocking were considered in Chapter 6. Flocks of black-tailed godwits appear to form at good feeding sites and, consequently, birds may use groups to indicate profitable areas. Once in a flock, a bird gains anti-predator benefits which are usually considered an important reason for joining a group (Goss-Custard 1985). On the cost side, those godwits that are probing suffer interference (in the sense of Goss-Custard 1980) from other members of the flock. It is likely that it is this cost which leads to groups of probing birds being more dispersed than those of stitching individuals. A

## DISCUSSION

consideration of the costs and benefits to an individual of flocking can explain the spacing characteristics of stitching and probing birds, and, likewise, a consideration of the energetic intake of the two techniques can explain their relative frequencies (Chapter 4).

Godwits feeding by either method were adversely influenced by the presence, on their preferred foraging area, of roosting gulls and plovers (Chapter 6). The waders responded by moving into deeper water where profitability was lower. However, a few godwits which were solitary probably maintained their feeding rates through a marked reduction in the amount of time they spent vigilant. The overall effect of the heterospecifics on the average daily intake of the godwits was not very great. However, if gulls commonly roost on mudflats, their impact on feeding waders could be considerable. As discussed above, young birds may be at a disadvantage in a competitive situation and it could be that they are suffering the worst consequences of the presence of other species.

On arrival at the estuary after migrating from their natal area, the foraging performance of juveniles was much poorer than that of the adults (Chapter 7). A breakdown of the components of foraging indicated that probing and stitching presented different learning problems to the young birds. The analysis also pinpointed the low rate at which suitable prey were encountered, as the major determinant of the young birds' poor feeding skills. It is not known how long it takes the juveniles to improve their performance.

## DISCUSSION

In oystercatchers it may take three years (Norton-Griffith 1967), but this species uses particularly specialised feeding techniques. In most other waders the situation is not clear. Some other birds learn quickly, such as juvenile moorhens which only need a few months to improve their performance (Sutherland *et al* 1986). Juveniles can compensate for their inefficiency, at least in part, by foraging for longer than adults (for example Burger 1980). However, as discussed above, juveniles may be disadvantaged in other ways. The fate of the young birds is important since, even if they suffer a small density-dependent mortality, this may have important consequences for the size of the whole population (Goss-Custard 1980, Goss-Custard and Durell 1984).

The fact that black-tailed godwits form a low-water roost on the Eden Estuary provided an excellent opportunity to investigate roosting behaviour (Chapter 8). Usually waders only roost regularly at high-tide, when they form mixed-species flocks on saltmarshes (Hale 1980). At high-water, the choice of a suitable roosting area may be extremely limited and it is possible that the behaviour is communal purely because of this. In contrast, a godwit at low-tide has a large expanse of mudflats over which it could choose to sleep. A communal roost under these conditions is definitely a functional phenomenon. Ydenberg and Prins (1984) reported that, for several groups of birds, there is a correlation between communal roosting and feeding parameters. There may be foraging advantages for a godwit in joining a roost, but these were not thought to be large. Once in a roost, a bird gained

## DISCUSSION

microclimate benefits and, above all, benefits concerning anti-predator behaviour. Myers (1984) was surprised at the large size of roosts since most benefits appeared to asymptote at low flock-size, as they did in this study. However, for reasons independently formulated by Sibly (1983) and Pulliam and Caraco (1984), such large aggregations are to be expected under these conditions.

There are still many aspects of the wintering behaviour of black-tailed godwits that are worth investigating. A comparative study at a site in southern England would be fascinating. This study has deliberately paid little attention to individual and sex differences in behaviour and ecology. An investigation of these would be particularly interesting, especially one which followed the fortunes of juvenile birds through their first winter.

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