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ASPECTS OF THE SUMMER FEEDING ECOLOGY OF A COASTAL POPULATION OF CURLEW (NUMENIUS ARQUATA)

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CHAPTER 1

INTRODUCTION

The curlew (Numenius arquata), is the largest member of the family Charadriidae, commonly termed waders. Curlew have a widespread distribution, breeding south of the arctic circle throughout much of northern Europe. Most continental birds migrate west to southwest before each winter. In Great Britain some birds are present all year round. Its breeding haunts are mainly open moorland, particularly in northern regions, although other areas of damp, open country are also used. In winter, curlew occur in greatest numbers on estuaries, rocky shores and coastal meadows. They generally arrive at the coasts between June and October, and depart in March and April (Bainbridge and Minton 1978). Most adult curlew undergo their annual complete moult between June and October (Bainbridge and Minton 1978), soon after they arrive at the coasts. In the summer, most curlew move to the breeding grounds, although some, mainly second year birds and some adults which do not try to breed (Boere 1976), remain on the coast.

The aim of my study was to look at the summer feeding ecology of a coastal population of curlew, with particular reference to the effects of moulting on the daily food intake.

The energy demand of moulting is an area of research in which relatively little has been published. Most of the early work (published before 1960) was concerned with measuring the basal metabolic rates (BMR) of moulting and non-moulting birds. This work has shown that, in moulting birds, BMR increases by up to 25% in *Fringilla coelebs coelebs* (Koch and Debont 1944); 45% in the domestic fowl (Perek and Sulman 1945); 14% in *Emberiza citrinella* and 26% in adult *Emberiza hortulana* (Wallgren 1954).

It seems likely that the increase in BMR in moulting birds, is due to a combination of three factors:

Firstly, an increase in heat production to cover additional heat losses from the skin, resulting from the lower insulation provided by the reduced plumage (Sturkie 1954).

Secondly, an increase in heat production related to an increase in blood flow to growing feather papillae (Wallgren 1954).

Thirdly, the increase in protein synthesis required for the formation of new feather material. Maqsood (1952), however, points out that moult is often associated with an increase in thyroid activity, and suggests that moult and increased BMR are not necessarily cause and effect, but have a common basis in increased thyroid activity. Whatever the reasons, an increase in BMR during moult does occur.

When considering the energy demands of moult, the energy content of the raw materials needed for building new feathers must also be considered. Davies (1955) calculated that, during the postnuptial moult of the house sparrow (*Passer domesticus*), an average bird must produce about 1·7 grams of keratin. In energy terms, this represents about 9·4 k cals of new feathers. Taking into account the costs of converting raw materials into feathers (assumed by Davies to be a process with 10% efficiency), but not the costs of increased heat loss due to the lack of insulation etc., Davies estimated that an extra 94 k cals were needed by moulting birds. Blackmore (1969) measured the metabolised energy intake of Passer domesticus under three different temperature conditions, and found an increase of 165 k cals per bird, during moult, in birds kept under constant ($20^{o}C$) temperature conditions. Similar results were fould by Dolnik and Gavrilov (1979), namely, that a minimum of 140 k cals were needed by Fringilla coelebs to produce 1·4 grams of new feathers, while being kept under thermoneutral ($26^{o}C$) conditions. Dolnik and Gavrilov concluded that, during the first part of moult, increased food consumption at this temperature was brought about, primarily, by the need to obtain specific sulphur--containing amino-acids for feather synthesis, and that the food required to meet these needs contained more energy than was needed by the birds for thermoregulation and other metabolic processes. From these data, one might expect the food intake during moult to vary according to the amino-acid content of the food, and the quantity of feathers being grown at each stage of the moult. While this may be true of captive birds kept under thermoneutral conditions, under more natural conditions there are several reasons to suppose that the amino-acid content of the food will have little or no effect on the daily food intake. These are:-

1) Captive birds, unlike wild birds, are provided with food, they do not have to search for it. As searching for food is an energy demanding process, non captive birds will have greater food requirements than captive birds. For example, Smith (1975) found that free living bar tailed

godwits (*Limosa lapponica*) consumed approximately 68 k cals per day (2 x BMR) more than captive birds kept under the same environmental conditions. The greater rate of food intake of free-living birds, related to energetic needs, may thus create a surplus, or at least reduce the extra amounts of particular amino-acids needed for keratin synthesis.

2) The energy costs of moving from roosts to the feeding grounds may be increased further, in free-living birds, by the effects of moulting on the efficiency of flying. For example, Sach (1968), found that, during primary moult, curlew had to increase their wingstroke frequency from 240 to 280 strokes per minute, in case of head wind or calm, in order to attain the same speed as non- moulting curlew.

3) Other energy demanding activities carried out exclusively by free-living birds, for example territorial defence, will also increase the food intake of such birds.

4) Air temperatures in the wild are usually below a bird's thermoneutral zone. Experiments by Blackmore (1969) and Dolnik and Gavrilov (1979) have shown that, at some temperatures below the range of thermoneutrality, the food intake of the species studied increased, during moult, to levels beyond those required to provide sufficient sulphur containing amino-acids, Although this may not happen in the wild if the food eaten contains fewer essential amino-acids than the food provided for captive birds, the increased food intake needed to balance the increased heat loss due to lower temperatures may help to reduce the amino-acid deficit.

5) Air movements, such as those caused by flying and by

winds, increase the rate of heat loss from the body. This effect will be particularly important to moulting birds with reduced insulation provided by deficient plumage. Although these factors are likely to influence the food intake of free-living birds, their influence will be minimal in the captive situation.

It is clear from this discussion, that the energy expended during the "normal" activities of free-living moulting birds, is likely to be much higher than the energy expended by captive birds kept at thermoneutral temperatures. Judging from the effects of one of the above "energy demands", the effects of low temperatures, on the food intake of captive moulting birds, it is thought that the combined effects of all of the above mentioned "energy demands", would necessitate a food intake which would provide a more than adequate supply of essential amino-acids. Another point revealed by this discussion is that, as well as having greater overall energy demands, free-living birds will also experience a greater change in total energy demands when they start moulting, than would captive birds.

Although the laboratory experiments on the food intake of moulting birds have been useful in determining particular relationships, for example between temperature and the energy demands of moult itself, they are unlikely to give a true indication of the energy demands of moult in free-living birds, or of the ways in which these demands are met. Captive birds were given a plentiful supply of food; in the free-living situation, however, food will not be so easily obtained, and a bird's fat reserves may need to be utilised. Dolnik and Gavrilov point out that fat reserves cannot be used to synthesize new feathers since they contain no amino-acids. In the free living situation, sufficient raw materials for feather synthesis may be provided in the normal "non-moulting" diet of birds. In this situation it may be possible for fat reserves to compensate for the increased energy demands of moult. In free-living yellow wagtails (*Motacilla flava*), (Ward 1964) and several other passerine species (the white crowned sparrow (*Zonotrichia leucophrys*), (King et al 1965), the bullfinch (*Pyrrhula pyrrhula*), (Newton 1968), and the redpoll, (*Acanthis flammea*), (Evans 1966)), the start of the moult is associated with a lowering of the body fat levels. As far as I know, however, there have been no published studies comparing the daily food intake of moulting and non-moulting birds in the wild. It is not known, therefore, to what extent birds in the wild rely on their fat reserves, and to what extent they increase their daily food intake during the moulting period, if indeed they need to, since they might become less active then, for example fly less.

Very few estimates of the daily food intake of carnivorous birds exist, apart from those held in captivity. Most of the reliable "field" estimates have been made on shorebirds (Goss-Custard, 1969 on redshank (*Tringa totanus*), Heppleston, 1971 on oystercatchers (*Haematopus ostralegus*), Prater, 1972 on knot (*Calidris canutus*), and Smith, 1975 on bar tailed godwits (*Limosa lapponica*)), and were carried out between autumn and spring, when large populations of shorebirds are found on the coasts. Very little work, apart from that of Hulscher (1976) on captive oystercatchers, appears to have been carried out during the summer months.

Most field estimates of the daily food intake of shorebirds, have been made by calculating the average time spent feeding by an "average" bird, and multiplying this by an estimate of the average ingestion rate. In order to obtain accurate estimates of the daily food intake, using this method, a number of temporal, environmental and other variables need to be considered, especially if the data on the time spent feeding, and the data on ingestion rates are collected on different days. These variables include:

1) The area in which feeding is observed. Ingestion rates may vary between feeding areas (since the density of food may vary), as may the time spent feeding on each area by an "average" bird. Ideally, then, this should be taken into account when calculating the average ingestion rate.

2) State of the tide. Ingestion rates may differ, on the same feeding area, at different times during the tidal cycle, since prey availability may vary.

3) The sex of the bird observed. In birds with a marked sexual dimorphism, such as curlew and bar tailed godwits, ingestion rates may differ between the sexes.

4) The time of high water. Each daytime high tide occurs approximately one hour later than the corresponding high tide of the previous day. The amount of potential feeding time during daylight hours may thus vary from day to day, according to the time of high water in relation to dawn and dusk.

5) Height of tide. This may affect the total time available for feeding and/or the size of the areas on which feeding

can take place.

6) Inland feeding and night feeding. An "average" shorebird may not obtain sufficient food to meet its daily requirements from the intertidal feeding areas during daylight. Feeding may also occur at night, and/or on inland feeding areas.

7) The weather. Particular weather conditions may affect the feeding behaviour of shorebirds, either by influencing a bird's capacity to hunt effectively, or by affecting the availability of prey, or by influencing the energy requirements of a bird. Fuller details of the ways in which this may occur are given by Evans (1976).

8) Population size. Changes in the total numbers of birds using the feeding areas may also affect each bird's feeding behaviour, through interference leading to a depression of prey capture rate.

It is possible that, at one extreme, on the days that ingestion rates are measured, birds are feeding for a very short time but with high ingestion rates, while, at the other extreme, on the days that feeding times are measured, birds are feeding for a long time but with low ingestion rates. Estimates of the total daily food intake, based on these extremes of data, would thus be excessively high. Similarly, if most feeding rate data were to be collected from the most successful sex of bird, feeding on the most favourable areas, during the most favourable times of the tidal cycle, then the "average" intake rate would, again, be overestimated. While these extremes are unlikely to be encountered in practice, there could be considerable errors in the estimates, if the above points are not considered.

One way of reducing the variability in the error of estimates of the daily food intake, would be to use feeding time and ingestion rate data, collected only under similar tidal and weather conditions, and during times of more or less costant population size. An alternative method of reducing the variability in the error of estimates of the daily food intake of shorebirds, would be to look at the feeding behaviour of shorebirds over a range of environmental conditions, and to quantify, and make allowances for, the effects of particular variables. Such an investigation, however, requires considerable time and effort. Most workers have therefore limited their studies to the detailed analysis of only a few of the many possible factors which may influence shorebird feeding behaviour. For example, Goss-Custard (1969) looked in detail at the effects of daylength and temperature, on the feeding behaviour of redshank. His estimates of the daily food intake of redshank also took into account the following:

1) Differences in the ingestion rate between areas.
2) The effects of temperature and state of tide on the time spent feeding, on each area, by an "average" bird.
3) The effects of temperature on the ingestion rate.
4) The seasonal variations in the size of prey taken.
5) The seasonal variations in the use of inland feeding areas.
6) Seasonal variations in the use of coastal feeding areas at night.

Some of the variables that Goss-Custard did not consider were included in the study carried out by Smith (1975) on bar tailed godwits. In addition to other variables, Smith looked at the effects of the state of tide on ingestion rates; differences in the use of spring and neap tides; differences in ingestion rates of male and female godwits; and some of the effects of wind on the behaviour of the main prey species Arenicola marina, and its possible effects on the feeding behaviour of godwits. Sex differences and the effects of the weather have been studied in more detail by Townshend (1980), looking at curlew during the autumn, winter and spring. Much of this work involved observations on individually recognisable (marked) birds, and revealed, amongst other things, that individual curlew follow different patterns in their use of fields and mudflats. Details of this and other work will be discussed in later chapters.

Although none of the studies, mentioned here, have been definitive with respect to shorebird feeding ecology, they have, along with other studies, helped to piece together a more complete picture of the ways in which shorebirds react to changes in their environment. One of the areas in which available information is still inadequate, however, is the effect of different tidal conditions on shorebird feeding behaviour. Heppleston (1971), looking at oystercatchers, and Prater (1972) looking at knot, found that there was no significant difference between the time spent feeding on neap and spring tides. Smith (1975), however, found that, during the autumn and winter, bar tailed godwits fed for a shorter time, and had higher ingestion rates on spring tides than on neap tides. In the spring, however, godwits fed for a longer time on spring tides, but still attained a higher intake rate than during neap tides. In his study, however, spring tides were associated with a reduction in the amount of potential daylight feeding time, so the seperate effects of height of tide, and the time of high tide were obscured.

Another topic on which more work is needed, is the effect of increased densities of birds on their feeding behaviour. This is particularly relevant when considering the effects of reclamation. Knights (1974,1975) studied the effects of reclamation on a number of species of shorebird overwintering on the Tees Estuary. On the Tees, recent reclamation had resulted mainly in the loss of upper shore feeding areas. This caused a reduction in the available feeding time, but, during Knights' study, had relatively little effect on the densities of birds using the remaining areas, as the number of birds using the Tees Estuary were, in most species, lower than in pre--reclamation years. Goss-Custard (1977) suggests ways in which shorebirds might respond to higher densities of birds, but these remarks were based on observations of the sequence of occupation of feeding areas, rather than on daily observations at different population sizes. As far as I know, there have been no detailed quantitative studies on the effects of population size on shorebird feeding behaviour.

Observations during the summer months provided an ideal opportunity for me to look at the effects of tidal conditions and population size on the feeding behaviour of curlew. During the summer, the long daylengths allow the effects of height of tide and time of high tide to be quantified sep~~e~~arately. The large influx of curlew during late summer also allowed the quantitative analysis of the effects of increases in population size.

This study attempts to quantify the effects of these variables on the feeding behaviour of curlew. The effects of moult on curlew feeding behaviour and daily food intake were also studied.

CHAPTER 2

THE STUDY AREA

The study was carried out between May and August 1980. The main study area was "Seal Sands" on the Tees Estuary (approximately 54° 34'N, 1° 12'W). Fields and other areas nearby were also used by curlew.

2.1. Seal Sands.

This is a large area of mudflats situated on the north side of the Tees Estuary (see Fig. 1.). The mudflats are bordered on their southern side by a reclamation wall running east-west, and on their eastern side by a sandy peninsula, and on their western edge by another reclamation wall which separates them from Greenabella Marsh, an area of rough pasture and brackish pools. Along the northern edge, the mudflats are bordered by a low rocky wall, which is covered at about mid-tide. The mudflats themselves contain a number of mudbanks and drainage channels. It was thus possible to distinguish a number of discrete areas (see Fig. 2.). These are:

1) Mid Tide Wall Bank. This is a small bank of mud, firm in the centre but soft at the edges. It is situated just north of the western tip of the low rocky wall (Mid Tide Wall). On spring tides it is just exposed 3¾ hours after high water; however on very low neap tides, it is not exposed until about 4½ hours after high water.

2) Mid Tide Wall Channel. This area includes the channel separating the Mid Tide Wall from the Mid Tide Wall Bank, and the channel separating the Mid Tide Wall from the "Central Bank". The southern channel is deepest at its

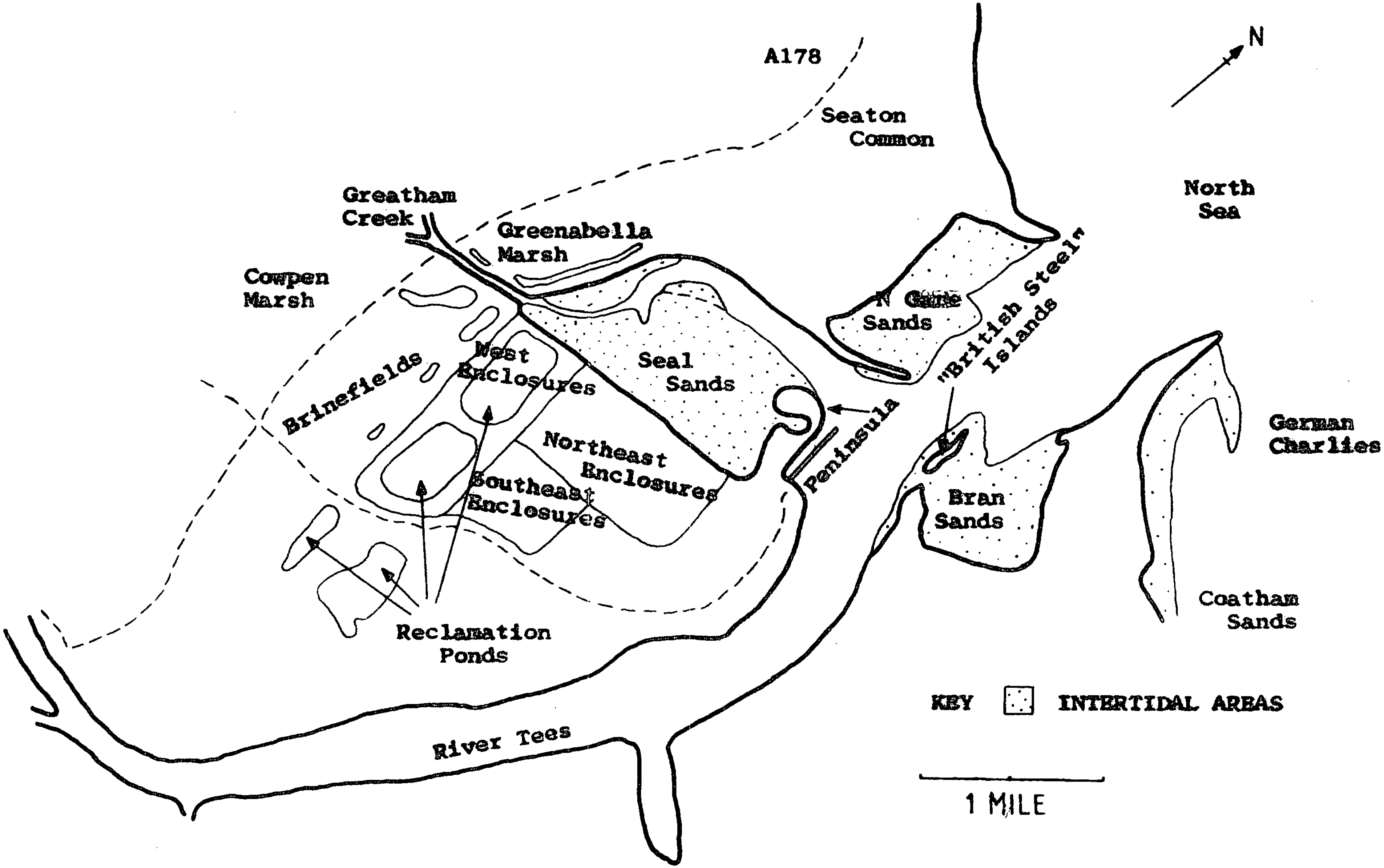


FIGURE 1 The Position Of Seal Sands On The Tees Estuary

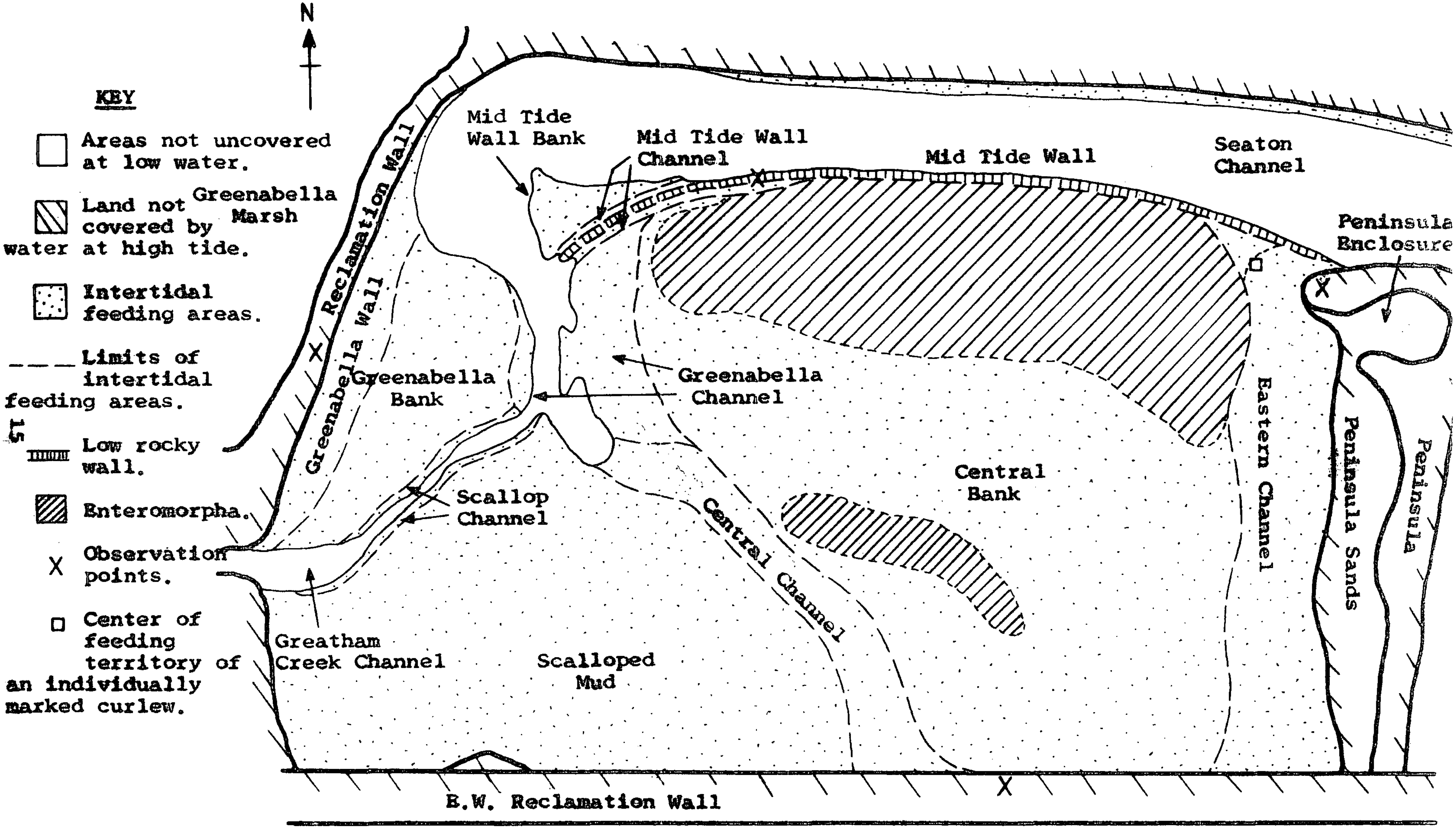


FIGURE 2. Diagram of Seal Sands Showing The Positions Of Different Feeding Areas.

western end; the eastern end merges with "Central Bank" about 75 metres along its length. The channels are about 6 - 10 metres wide, and made up the smallest of the eleven areas I distinguished.

3) Mid Tide Wall. This is the low lying rocky wall bordering the northern edge of Seal Sands. The wall is about 15 metres wide and rises about 1·5 metres above the low tide water levels. The surface of the wall is comprised of loose and embedded rocks, much of which is covered with fucoid seaweeds and Enteromorpha.

4) Greenabella Wall. This area comprises the loose rocks at the base of the Greenabella reclamation wall, and the soft mud immediately to the east of it. At its northern end, this area extends eastward to Seaton Channel. At the southern end, "Greenabella Bank" marks its eastern limit.

5)Greenabella Bank. This is an area of firm mud between Greatham Creek Channel, Seaton Channel, and the Greenabella Wall. This mudbank is exposed slightly before the Mid Tide Wall Bank, but later than either "Scalloped Mud" or the "Central Bank".

6) Greenabella Channel. This area comprises the soft mud on the eastern edge of Greenabella Bank and the soft mud on the western edge of "Central Bank". Between these areas there is also a small "island" of mud where the convergence of Greatham Creek Channel and the Central Channel is incomplete. At low tide this "island" of mud is linked to the western edge of Central Bank by soft mud.

7) Scallop Channel. This area includes the narrow strips of soft mud on the northwestern edges of "Scalloped Mud" and the south eastern edges of Greenabella Bank. Like

Greenabella Channel, the extent of mud exposed at low tide depends upon the height of the tide.

8) Scalloped Mud. So named because of the scalloped appearance of its surface. This is the second largest mud bank on Seal Sands, and the first to be exposed on the ebbing tide. On neap tides, a small portion of scalloped mud may be left exposed at high tide.

9) Central Channel. This is a broad channel separating scalloped mud from the "Central Bank". This is the drainage channel from the former northeast enclosure of the now reclaimed south area. This area is empty of water on all low tides.

10) Central Bank. This is an extensive area of slightly raised flats shelving from south to east, the higher areas being formed of sandy material. About one quarter of the surface is covered in summer by two patches of Enteromorpha, a large patch at its northern end, and a smaller patch in the south western corner. The Central Bank is the largest mud bank on Seal Sands.

11) Eastern Channel. This is a broad shallow channel which, at low water, is exposed as far as the Mid Tide Wall on all tides. It is bordered on the west by the Central Bank, and on the east by the peninsula, where the substrate is more sandy.

2.2. Other areas used by curlew.

The main roosting sites for curlew were on the sand between the Eastern Channel and the peninsula, in the peninsula enclosure, and on the north east and west enclosures. The northeast and west enclosures are large areas of wasteland lying just to the south of Seal Sands. These areas were reclaimed between 1973 and 1974 and, like the peninsula, are unsuitable for curlew feeding.

The Brinefields is a site known to be favoured by curlew for field-feeding in previous years (Knights 1974, 1975, Townshend 1980). This site, lying just to the south west of Seal Sands was also used by curlew during this study. Immediately to the northwest and west of Seal Sands lie extensive areas of rough pasture, which may also have been used by field-feeding curlew.

CHAPTER 3

METHODS

The following aspects of curlew feeding ecology were quantified:

1) The proportion of each "12½ hour" tidal cycle spent feeding, on each area of Seal Sands.

2) The number of paces and the number of "probes" observed per unit of feeding time.

3) The number, type and size of prey items eaten per unit of feeding time.

4) The biomass (dry weight) and calorific content of prey items of different sizes.

The food intakes of individual birds were also measured, as were the uses of areas other than Seal Sands. Observations were carried out using a telescope (x15 - x60) and binoculars (10x50), and were recorded either directly, in a note book, or by spoken commentary on a cassette tape. Tapes were transcribed the following day.

3.1. Monitoring the number of curlew feeding on Seal Sands.

Preliminary observations had shown that the greatest change, during a single tidal cycle, in the proportion of curlew feeding (as opposed to present but not feeding) on Seal Sands, occurred between two and four hours after high water (HW+2-HW+4) and between eight and ten hours after high water (HW+8-HW+10). During these times, counts of the number of curlew feeding and not feeding were made at approximately fifteen-minute intervals. At other times (HW+4-HW+8), counts were made at thirty-minute intervals. As well as recording the total number of birds visible and the proportion feeding, the numbers of birds feeding on each area of Seal Sands were also noted. These observations were made on 20 days throughout the study, under different tidal conditions, and with different total population sizes.

From each set of data, the proportion of a "12½ hour" tidal cycle, used for feeding by an "average" curlew (the percentage of feeding time), was calculated. It was assumed that the average proportion of the tidal cycle used for feeding by all curlew observed, was equal to proportion of that tidal cycle that an "average" individual used for feeding (Goss-Custard, 1969; Heppleston, 1971; Smith, 1975). This assumption, however, is valid only if feeding and non-feeding birds are equally visible.

The best estimates of total population size were obtained at about HW+3 and HW+9, when most curlew were concentrated into a relatively small area. At other times, a varying proportion of the population were not visible. Preliminary observations had shown that curlew fed on the southern and eastern parts of Seal Sands during the early and later stages

of the tidal cycle, but fed mainly on the northern and northeastern areas during the middle stages. In order to minimise the number of curlew that disappeared from view, observations were made from the E.W. reclamation wall between HW+2-HW+4 and HW+9-HW+11, and from the Greenabella reclamation wall between HW+4-HW+9 (see Fig. 2). It is thought that any curlew that disappeared from view were birds using the eastern side of Seal Sands, or the numerous small drainage channels on Central Bank.
Difficulties in observing these birds were brought about by heat haze, strong winds, the considerable distance of their feeding areas from the observation point, and the obstruction caused by the sides of the drainage channels. Observations from other positions, however, provided no evidence to suggest that either the small drainage channels, or the eastern side of Seal Sands, were used for feeding or resting to a greater extent than the other areas of Seal Sands.
The assumption that feeding birds and non-feeding birds were equally visible, was, therefore, thought to be valid.

Most observations were carried out on tidal cycles that were completed within the long hours of daylight of midsummer. Each day, however, there is a second tidal cycle, part of which overlaps with the hours of darkness. Attempts to count the number of birds arriving to feed just after dusk on the ebbing tide, and attempts to follow the activity of a single bird throughout the hours of darkness were unsuccessful. The total amount of feeding carried out at night was estimated from the number of birds observed feeding at dawn and dusk, and from what was known about daytime changes in the proportion of birds feeding in relation to the state of the tide. By adding this to the total amount of feeding carried out during the day (the amount of feeding carried out on the daytime tidal cycle plus the amount of feeding carried out during the daylight portion of the previous or following tidal cycle) it was then possible to estimate the proportion of two consecutive tidal cycles (25 hours) spent feeding on each area, by an "average" curlew.

3.2. Measurements of food intake rates.

The collection of these data involved observations on feeding curlew; the sampling and measurement of invertebrates on Seal Sands; and the laboratory determination of biomass (dry weight) and calorific content of prey items.

3.2.1. Observations.

During observations of feeding curlew, the number of paces, the number of "probes", and the number, type and size of food items taken, in measured time intervals, were recorded on cassette tape. Probes are defined as movements, during which the curlew inserts its bill, partially or fully into the mud. The most numerous food items taken by curlew were the polychaetes *Nereis diversicolor* . When taken, these worms were often seen hanging from the tip of the curlew's bill, immediately after being pulled from the mud. The size of worms taken were estimated in relation to the size of the bill. The following size classes were distinguished; less than ¼ the length of the bill (¼); between ¼ and ½ the length of the bill (½); between ½ and ¾ bill length (¾); and greater than ¾ bill length (1). Curlew are sexually dimorphic, the males being smaller and having shorter bills than the females. Townshend (1980), using data from dissected birds and from measurements of captured curlew, found that most males had bills less than 122mm long, and that most females had bills greater than 129mm long. During this study four size classes of curlew were distinguished, and labelled; small male; large male; small female; and large female. Using Townshend's data the mean bill length, for each of the four size classes of curlew, were estimated (see appendix 1). Details of the conversion of estimated relative worm size, into estimates of absolute worm size, are given in section 3.2.2.

The other major prey species taken was the shore crab Carcinus maenus. The sizes of crabs taken were estimated in relation to bill width when they were clearly observed. Section 3.2.3. deals with the sizes of crabs and other food items not clearly observed.

Observations on the feeding behaviour of curlew were carried out on each area of Seal Sands used for feeding by curlew. Many observations were made inbetween counts of the numbers of curlew feeding, but observations were also made on other days. On several occasions it was necessary to erect a canvas hide on the Mid Tide Wall, in order to get close enough to observe the feeding behaviour of birds in particular areas. As well as recording information on the feeding behaviour of each bird observed, the following were also recorded: the area on which feeding was taking place, the date, the state of tide (in terms of the number of hours after high water), the size class of the bird, and the duration of the observation period. Pace rates, probe rates and prey capture rates were calculated by dividing the number of each activity observed, by the duration of the observation period. In most cases, the duration of the observation period was five minutes. In some cases, however, disturbances or observational difficulties rendered the duration of the observation period less than five minutes. Heppleston (1977) points out that this method of estimating prey capture rates may be subject to error, as the observation period may begin just after, or just before a bird has eaten a food item. If the observation period begins just before a food item is eaten, the estimate of prey capture rate may be excessively high; the reverse would occur if the observation period begins just after a food item is eaten. This error is negligible , however, if a long enough observation period is used. In order to determine the minimum length of observation period required to obtain consistent results, a number of long observations (at least 10 minutes duration) were made, and records kept of the number of food items eaten each minute. Prey capture rates were then calculated using 1 minute of data, 2 minutes of data, 3 minutes of data, and so on, until all the data for that observation was used. The prey capture rates were then plotted against the duration of the observation, in order to find the minimum duration of observation, above which estimates of food intake rates varied only within narrow limits. (see appendix 1.). This was found to be four minutes in most cases. Therefore, only observations of four or more minutes duration, were used in the calculation of average prey capture, biomass intake or calorific intake rates.

3.2.2. The conversion of estimated worm sizes into absolute worm sizes.

Before determining the biomass and calorific content of different sizes of worms, worm sizes were measured after they had been killed with 70% alcohol. This method of killing resulted in contraction of muscles in the body wall of Nereis, and so caused a shortening of the body. When live worms are pulled from the mud and held in a curlew's bill, the worm's body muscles are likely to be in a more relaxed state than those of worms killed in alcohol. Estimates of "live size", based on the length of the curlew's bill, and the relative sizes of the worms, are therefore likely to be greater than the "dead sizes" of the same worms.

In order to convert estimates of the relative "live size" of worms into estimates of "dead size", it was necessary to measure the "dead sizes" of different "live size" categories of worms. This was carried out, firstly by collecting a large number of fresh, live *Nereis diversicolor* of different sizes, and placing them in a large enamel tray. Each worm was then, in turn, picked up with forceps by an assistant and held against the tip of the bill of a stuffed curlew. (The worms were held near the head, so that most of the body hung vertically from the forceps). I watched these actions through a telescope, and estimated the size of each worm in relation to the length of the curlew's bill. The results of each estimation were signalled to the assistant holding the worms, so that worms of differnt relative size classes could be placed in different containers. These worms were later killed with 70% alcohol and measured, and the median "dead size" of each size class calculated. This procedure was carried out twice. On the first occasion, a stuffed curlew, whose bill was equal in length to the mean size of a "large female's" bill (15·2cm) was used. On the second occasion, the bill was marked with white sticky tape, so that the length of the bill, from the tape to the tip, was equivalent to the mean size of a "large male's" bill (11·5cm). Only this section of the bill was then used for estimating the relative sizes of worms.

Methods, similar to those just described were also used to calibrate the estimates of relative crab size.

3.2.3. Estimation of the sizes of food items not clearly observed.

On a number of occasions, curlew were observed to make swallowing movements, immediately after probing, but it was not possible to see clearly the size of worms eaten. On these occasions, the size of worms eaten was assumed to be equal to the mean size of worms, taken by that size class of curlew on that area on other occasions. At other times, curlew were observed to take food items, mainly Nereis, from the surface of the mud or from the surface of the Enteromorpha on Central Bank. Most of these items, instead of being picked up and held clear of the surface before being eaten (in the way that most of the worms were held after probing), were eaten immediately, with the bird still leaning over the food item. The mean size of "surface items" was determined after collecting all the surface invertebrates, of a size likely to be taken by curlew, within fifteen 10 m^2 areas. This was carried out on Central Bank and on the Eastern Channel, the two areas where surface items were taken.

There were also difficulties in determing the size of crabs taken on the Mid Tide Wall. The sizes of crabs were estimated easily if the curlew picked up and swallowed the crab whole. However, on a number of occasions a curlew could be seen making pecking and swallowing movements, but sight of the crab being eaten was obscured by rocks. On these occasions, the size of crab eaten was taken to be equal to the "mean" size of crab present on the Mid Tide Wall. (Crabs larger than 4·0 cm had very hard carapaces, strong claws, and many other hard parts on their body, and it was thought that they were unlikely to be taken by curlew. These crabs were therefore ignored when calculating the "mean" size of crab present on the Mid Tide Wall). The "mean" size of crab present on the Mid Tide Wall was determined after collecting all the crabs present in a 1 m^2 area, at five points along the length of the wall.

3.2.4. Determination of the biomass and calorific content of food items.

Invertebrates were collected for measuring on two dates, one at the end of June, the other at the beginning of August. "Buried" worms and "Surface" worms, of different sizes were collected from the Mid Tide Wall Channel, the Central Bank, and Eastern Channel at the end of June. Due to the large quantity of material to be processed in June, crabs were not collected until the beginning of August. After killing the worms with 70% alcohol, each set of worms were measured and sorted into length classes of 1 cm intervals. For each length class, the length, dry weight and calorific content of an average worm was determined. The worms were dried in a vacuum oven at 60°c. Calorific contents were determined with a Gallenkamp ballistic bomb calorimeter. Before each set of determinations, a calibration curve was obtained by combustion of six "pellets" of four different weights of dried A.R. benzoic acid.

Crabs were measured across the width of the carapace. It was known, from observations of curlew feeding on crabs, that small soft bodied crabs were eaten whole. Larger crabs (larger than 2cm), however, have hard carapaces and other hard parts, which may not be eaten by curlew, or if eaten, are unlikely to be assimilated. For this reason, the carapace, the tips of the legs and the ends of the claws, were removed from crabs larger than 2cm, before they were weighed and bombed. Apart from this, the crabs were treated in the same manner as the worms.

3.3. Observations on individual birds.

On 3 days, attempts were made to follow the activity of a single bird throughout the tidal cycle. On the morning of the 25th May and on the evening of the 27th May, attempts were made to follow the activity of a single bird feeding on and near the small patch of Entermorpha on Central Bank (see Fig. 2.). These birds were not individually recognisable, so it was not possible to follow their activity after they flew away from this area after 4 hours.

The other bird observed was a uniquely marked bird with a feeding territory on the north western edge of the Eastern Channel. This bird was observed throughout most of the tidal cycle, and a minute by minute account was kept of its feeding activities, and of its use of different areas of its territory. These observations were made in order to compare the activity and food intake of an individual curlew, with the activity and food intake estimated for an "average" curlew.

3.4. Monitoring the use of areas other than Seal Sands.

As the flood tide covers Seal Sands, curlew are forced off this area. On all occasions that this was observed, the areas to which curlew flew on leaving Seal Sands were noted. Curlew were also observed leaving Seal Sands in the evening. Again their flight directions were noted whenever possible.

On two occasions, visits were made in late evening to the Brinefields, in order to determine whether curlew were feeding on this area.

3.5 Estimation of the numbers of curlew moulting.

The number of curlew moulting, and the stage of moult attained, were estimated from photographs of the birds, taken as they flew over the E.W. reclamation wall from Seal Sands. The photographs were taken at mid morning on the 22nd August, when it was thought that most, if not all curlew flew to the N.E. and W. enclosures to roost over the high water period. Photographs were taken with a Praktika camera, using a 135 mm lens and Ilford HP4 (ASA 125) film. The photographs were examined by eye and under a binocular microscope, and the proportion of birds that had reached different stages of primary moult were noted. The stage of moult was determined by noting the last primary feather to have dropped (see photographs on pgs. 104 and 105). Using data from Sach (1968), and assuming similar rates of moult in Germany and England, the time taken to reach each stage of moult was estimated. These estimates were then used to determine the approximate date at which each bird (photographed) had started to moult. Using these data, and data collected during this study on changes in curlew population size, the proportion of birds in moult at different dates during the study, were estimated.

CHAPTER 4

RESULTS AND DISCUSSION

4.1. Seasonal changes in the number of curlew using Seal Sands.

By the middle of May, when this study began, most adult breeding curlew had left Teesmouth, and only a small population of non-breeding birds remained. The size of this population was estimated to be about 90 birds. Counts of the number of curlew using Seal Sands decreased at the end of May to 73 birds, increased at the beginning of June to 143 birds, and increased again during the first two weeks of July to 450 birds (see Fig.3). The birds which left at the end of May may have been from the Scandinavian population, which starts breeding later than the British birds. The increase in June probably comprised curlew returning to the estuary having failed in their attempt to breed. The increase in July was much larger and spanned a longer time period, and probably consisted of successful breeders and perhaps some juveniles arriving at their overwintering feeding grounds. These seasonal changes are similar to those reported by Boere (1976) in the Netherlands, and Bainbridge and Minton (1978) in Britain.

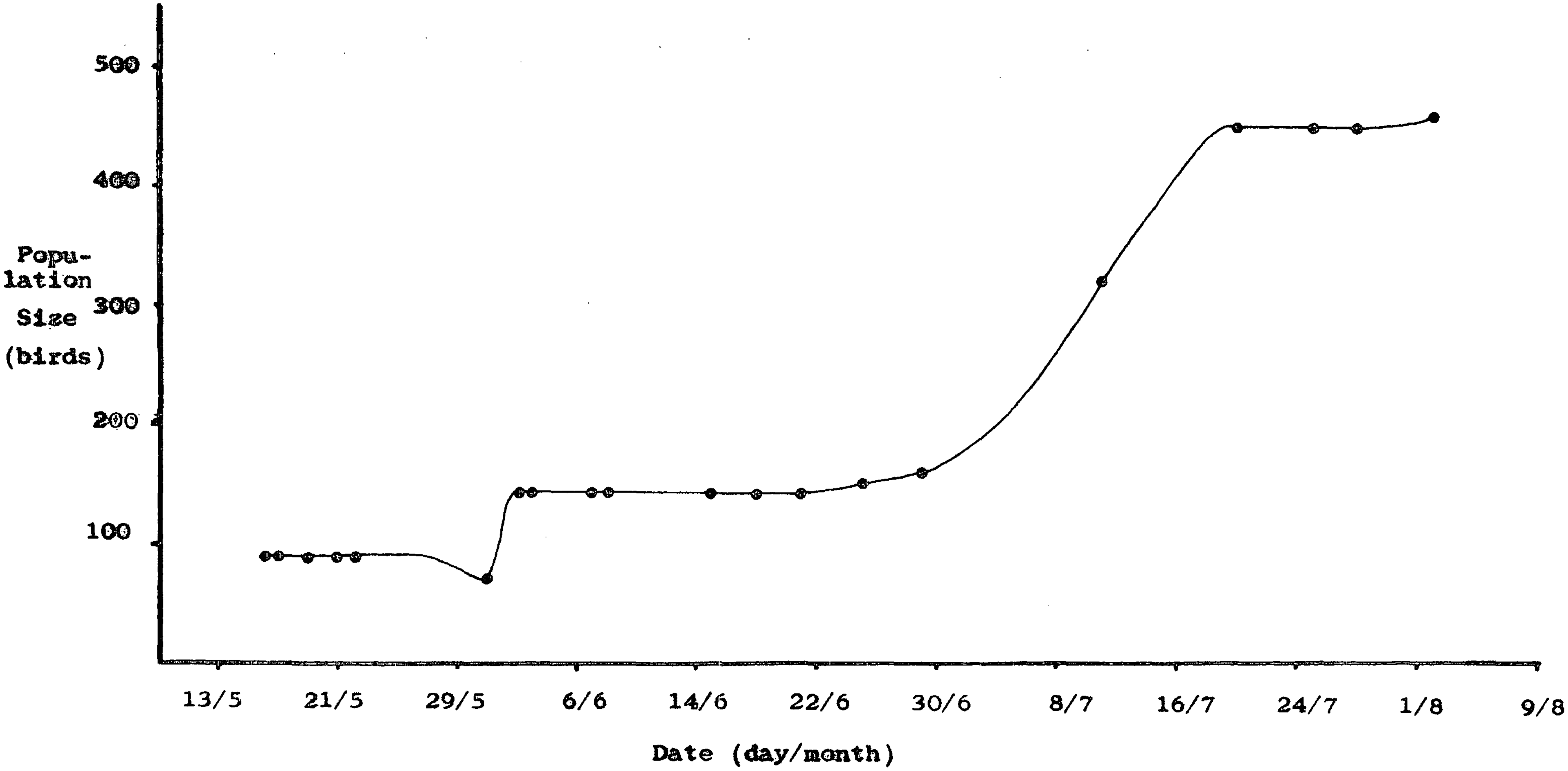


FIGURE 3. Seasonal Changes In The Number Of Curlew Using Seal Sands.

4.2. Variation in the use of different areas of Seal Sands.

In this section I will limit myself mainly to the quantification and description of the changes in the use of different feeding areas. These results will be discussed in relation to the profitability (the net energy gain per unit of feeding time) of the different areas in later sections.

The total use (for feeding) of a particular area during one tidal cycle, was measured using a quantity called Gross feeding time (GFT), which was calculated using equation (1).

(1) $GFT = \Sigma ni.ti$

ni= the number of curlew observed feeding on a particular area, at stage i of the tidal cycle.

ti= the time interval between counts made at stages i and $i+1$ of the tidal cycle.

As well as being a measure of the total use (the number of "bird hours" spent feeding) of a particular area, this quantity could also give a measure (assuming a constant food intake rate) of the total impact of curlew on their food resour~~s~~ces in that area.

Although GFT is a useful quantity for comparing the total use of different areas, it does not show how or when changes in the use of particular areas occur. By plotting the number of birds feeding against the state of the tide, for each feeding area, it is possible to look at these aspects of the changes in the use of different areas, and to look at them in relation to the use of the different possible feeding areas.

As population size increases, it is useful to know to what extent, if any, different areas accommodate a greater number of feeding birds. If the proportion of the population feeding on the most profitable areas decreases as population size increases, then (assuming a constant time spent feeding on these areas by each bird using them) the overall time needed by the whole population to obtain their daily intake of food, may increase. A measure of the proportionate use of each area, taking into account both the proportion of the population feeding on a particular area, and the time spent feeding, is therefore useful. This measure, called the relative feeding index (RFI), was calculated using equation (2).

$$(2)\ \mathrm{RFI} = \sum \frac{pi.ti}{12.5}$$

pi= the percentage of the population observed feeding on a particular area, at stage i of the tidal cycle.

ti= the time interval between counts made at stages i and i+1 of the tidal cycle.

This quantity represents the proportion of the box shown in Fig. 4, taken up by the shaded area, and equals

$$\frac{\mathrm{GFT}}{12.5} \times \text{population size.}$$

Estimates of GFT and RFI, for each feeding area, and for each daytime tidal cycle observed, are listed in Tables 1 and 2, together with information on the height of each tide, the date of each observation, and the population size on each day of observation. A detailed consideration of these results is presented in appendix 2. The main points are summarised below. These are:

1) Maximum use of the upper shore feeding areas, such as the Central Bank, Eastern Channel and Scalloped Mud, occurred just after these areas were exposed (before the middle and lower shore areas were exposed) and, to a lesser extent, just

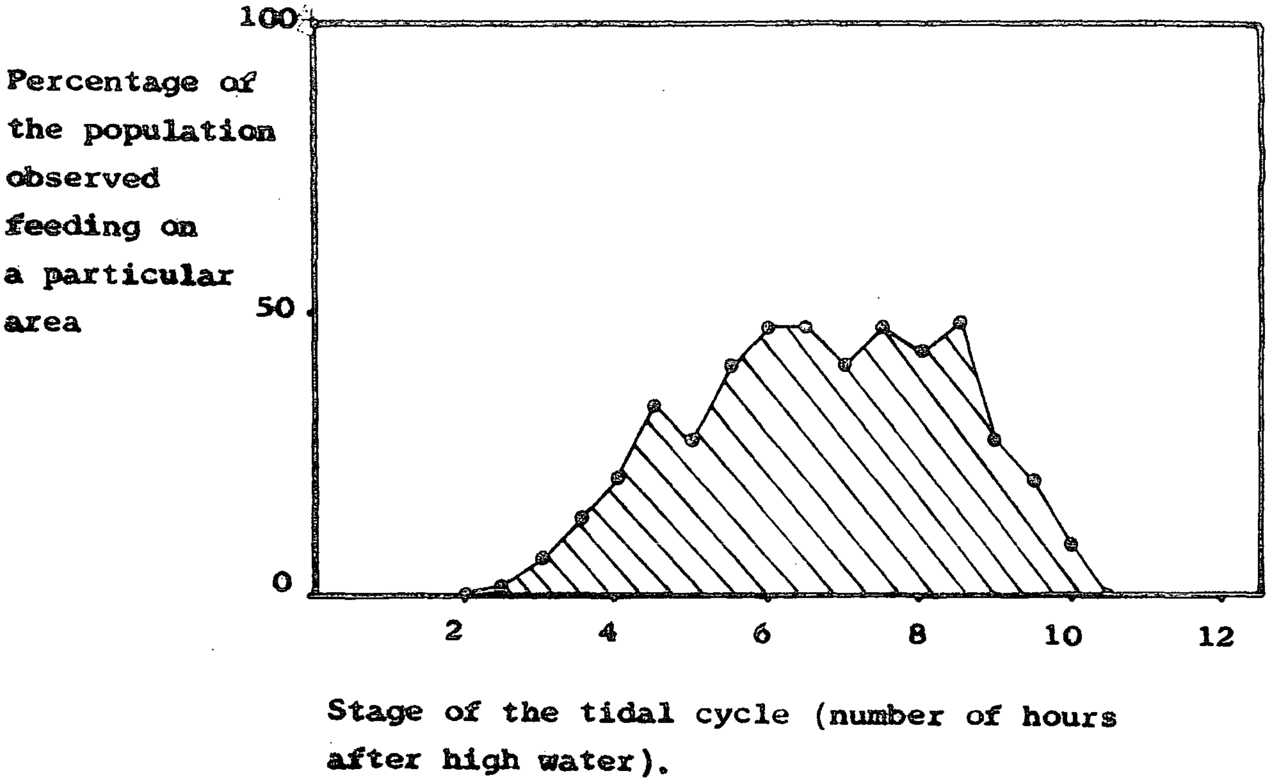


Figure 4 Box graph showing the proportion of the population feeding on a hypothetical feeding area at different stages during the tidal cycle.

TABLE 1. ESTIMATES OF GFT FOR EACH FEEDING AREA OF SEAL SANDS.

ATE	HEIGHT OF HIGH TIDE (m)	POPULATION SIZE (birds)	GROSS FEEDING TIME (GFT) IN BIRD HOURS										
			MWB	MWC	MW	GW	GB	GC	SM	SC	CB	EC	NO
6/5	5.1	91	36.00	17.50	N/N	N/N	17.50	14.00	13.50	12.50	56.75	8.50	129.70
7/5	5.0	91	45.00	11.00	N/N	N/N	20.75	8.00	28.00	16.00	103.75	7.50	128.30
9/5	4.6	91	40.50	40.50	33.25	N/N	10.00	17.50	8.25	11.50	176.00	48.25	64.27
1/5	4.2	91	27.00	15.50	29.00	2.50	8.50	0.50	16.00	9.50	89.25	34.00	114.66
2/5	4.1	91	32.50	20.00	31.00	6.00	8.50	0.50	10.50	2.50	163.50	6.50	96.80
1/5	4.8	73	24.00	15.50	44.75	0.50	7.00	2.00	3.25	5.50	135.00	56.00	22.00
/6	4.8	143	50.50	16.00	95.00	2.00	4.00	2.00	0.25	4.00	245.25	25.75	81.33
/6	4.7	143	44.00	20.25	58.00	3.50	14.50	5.50	14.50	5.00	242.50	28.50	84.91
8/6	4.6	143	7.00	8.00	37.00	0.00	0.00	0.50	10.50	0.50	305.75	1.00	48.62
1/6	4.1	143	10.50	0.00	45.00	6.50	7.00	2.00	11.00	0.00	264.00	9.00	311.07
5/6	4.3	150	12.90	0.00	19.50	1.50	3.50	9.00	11.00	0.00	359.00	13.50	146.62
9/6	4.9	160	24.75	10.50	26.25	2.50	11.50	36.50	12.50	2.50	301.50	1.50	150.60
1/7	4.8	320	23.50	10.00	18.75	6.00	29.50	244.00	30.75	18.50	484.50	229.00	148.00
0/7	4.2	450	21.75	0.00	23.00	14.50	140.00	247.25	72.00	5.00	849.75	26.75	262.70
5/7	4.4	450	19.00	5.50	12.00	21.00	66.75	367.25	51.75	5.00	640.25	56.00	101.25
/8	4.9	460	19.50	16.25	21.50	21.50	64.75	307.75	44.50	24.00	829.25	66.75	330.62

.B. The figures shown are for daylight tidal cycles only.
bbreviations used:
WB - Mid Tide Wall Bank, MWC - Mid Tide Wall Channel, MW - Mid Tide Wall, GW - Greenabella Wall, GB - Greenabella ank, GC - Greenabella Channel, SM - Scalloped Mud, SC - Scallop Channel, CB - Central Bank, EC - Eastern Channel, /N - Feeding was not noticed on these areas on these dates, NO - Estimated amount of feeding carried out on areas of Seal Sands which were difficult to observe from the main observation points, due to the distance involved or bad viewing conditions. (See Page 21).

TABLE 2. ESTIMATES OF RFI FOR EACH FEEDING AREA OF SEAL SANDS.

DATE	HEIGHT OF HIGH TIDE (m)	POPULATION SIZE (birds)	RELATIVE FEEDING INDEX (RFI)										
			MWB	MWC	MW	GW	GB	GC	SM	SC	CB	EC	NO
16/5	5.1	91	3.17	1.54	N/N	N/N	1.54	1.23	1.19	1.10	4.99	0.75	10.23
17/5	5.0	91	3.96	0.97	N/N	N/N	1.83	0.70	2.46	1.41	9.13	0.66	11.28
19/5	4.6	91	3.56	3.56	N/N	N/N	0.88	1.54	0.73	1.01	15.48	4.25	5.65
21/5	4.2	91	2.38	1.36	2.55	0.22	0.75	0.04	1.41	0.84	7.85	2.99	10.08
22/5	4.1	91	2.86	1.76	2.73	0.53	0.75	0.04	0.92	0.22	14.38	0.57	8.51
31/5	4.8	73	2.63	1.70	4.90	0.60	0.77	0.22	0.36	0.60	14.79	6.13	2.41
2/6	4.8	143	2.80	0.90	5.32	0.11	0.22	0.11	0.01	0.22	13.72	1.44	4.55
3/6	4.7	143	2.46	1.12	3.25	0.20	0.81	0.31	0.81	0.28	13.58	1.59	4.75
18/6	4.6	143	0.39	0.45	2.07	0.00	0.00	0.03	0.59	0.03	17.11	0.05	2.72
21/6	4.1	143	0.59	0.00	2.52	0.36	0.39	0.11	0.62	0.00	14.77	0.50	17.40
25/6	4.3	150	0.69	0.00	1.04	0.08	0.19	0.48	0.59	0.00	19.15	0.72	7.82
29/6	4.9	160	1.24	0.53	1.31	0.12	0.58	1.83	0.62	0.12	15.07	0.08	7.53
11/7	4.8	320	0.61	0.25	0.47	0.15	0.74	6.10	0.77	0.46	12.11	5.72	3.70
20/7	4.2	450	0.39	0.00	0.41	0.26	2.49	4.40	1.28	0.09	15.11	0.48	4.67
25/7	4.4	450	0.34	0.10	0.21	0.38	1.19	6.53	0.92	0.09	11.38	1.00	1.80
2/8	4.9	460	0.34	0.28	0.37	0.38	1.13	5.35	0.78	0.42	14.42	1.16	5.75

N.B. The figures shown are for daylight tidal cycles only.

For details of abbreviations used see Table 1.

before these areas were covered (after the middle and lower shore areas were covered). Similar patterns of use also occurred on the middle shore areas such as the Greenabella Bank and the Mid Tide Wall. Maximum use of lower shore areas occurred at low water (see Figs. 5 and 6).

2) The Central Bank was the largest feeding area, and supported the greatest amount of feeding throughout the study.

3) The second major feeding areas (after the Central Bank) were the Mid Tide Wall (MW), the Mid Tide Wall Bank (MWB) and the Mid Tide Wall Channel (MWC), during May and the early part of June, and the Greenabella Channel in July. In late June there was no second major feeding area. GFTs on Central Bank were proportionately greater (RFIs were greater) during late June, than at any other time (see Fig. 8).

Although the second major feeding areas did not accomodate as much feeding as the Central Bank, they were much smaller areas, were not exposed for as long, and so, often supported greater densities of feeding birds than the Central Bank. (On the Greenabella Channel this only occurred in July).

4) On several areas (MWB, MWC and Scallop Channel) a reduction in GFT occurred in June. All of these areas are bordered (partly) by the tide edge at low water. The reduction in GFT appeared to be associated with a reduction in the use of middle shore feeding areas (see appendix 2).

5) On all the areas bordered (partly) by the tide edge at low water (all areas containing lower shore feeding grounds), GFTs were higher during spring tides than during neap tides, presumably because the lower shore areas were exposed at a greater rate, and to a greater extent on spring tides (see Figs. 6 and 7, and Table 1). On neap tides, GFTs were

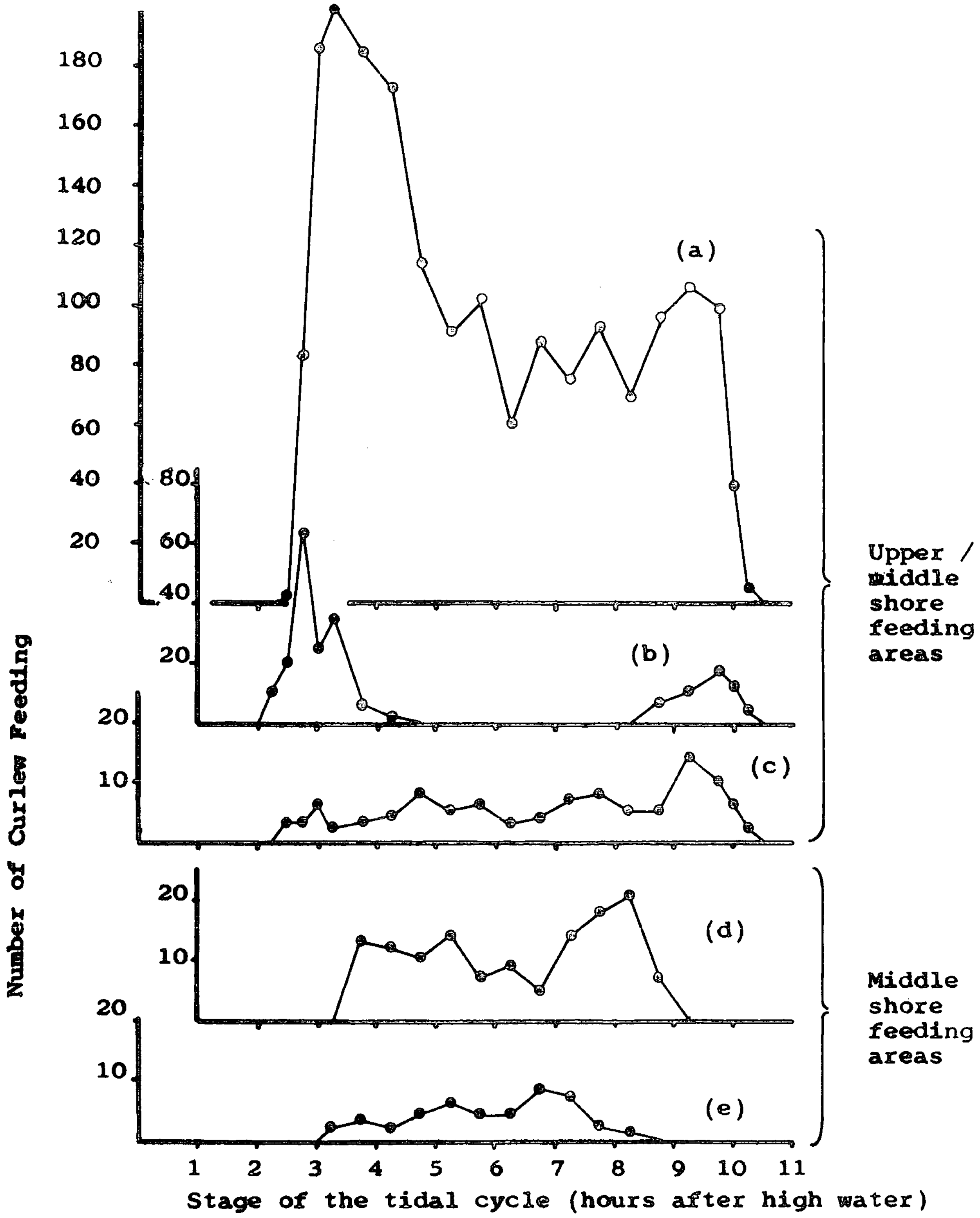


FIGURE 5. Variation in the number of curlew feeding in relation to the state of the tide on 2nd August (tide ht. 4.9m)

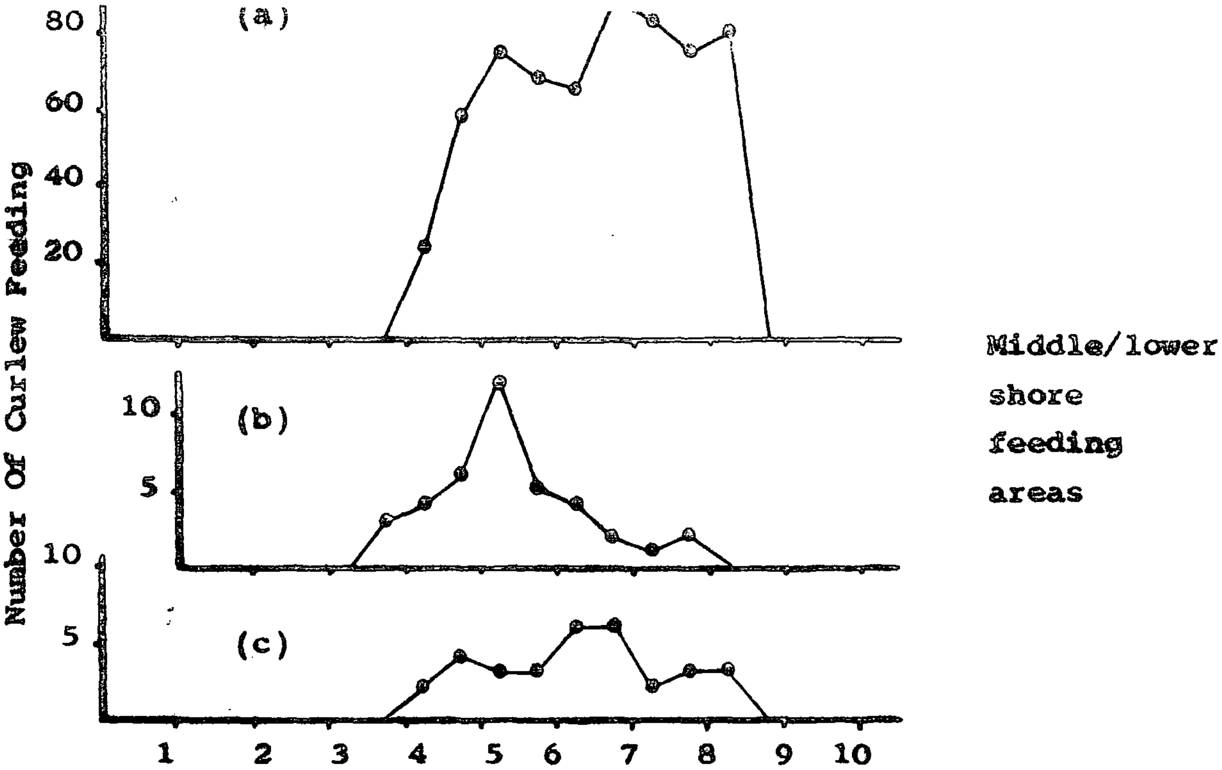
(a) on Central Bank

(b) on Eastern Channel

(c) on Scalloped Mud

(d) Greenabella Bank

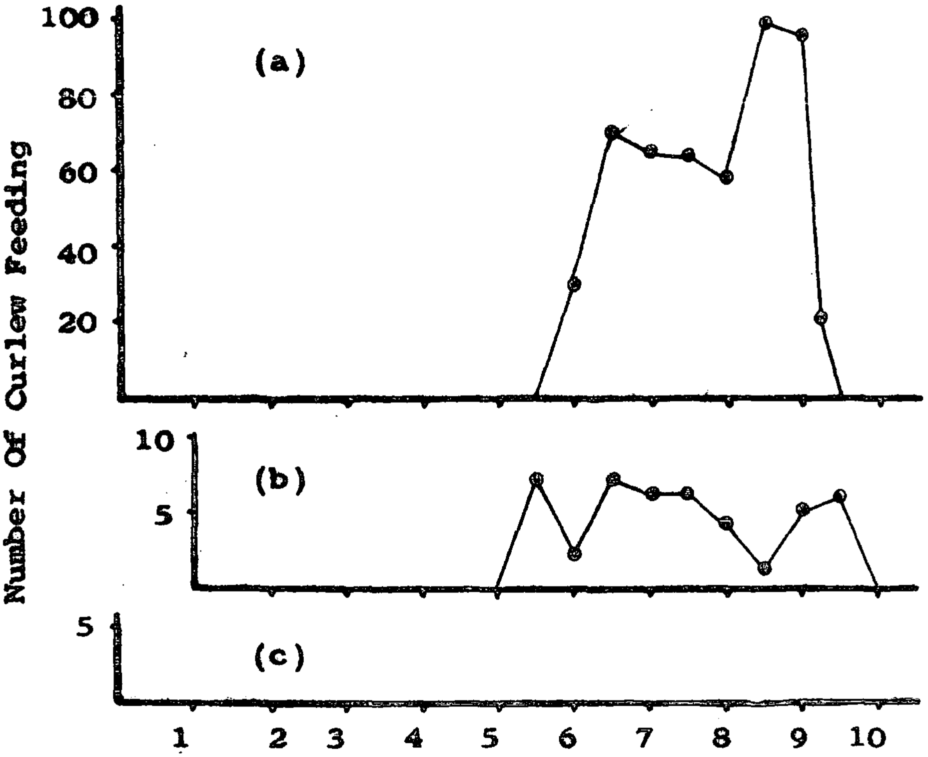
(e) on Mid Tide Wall



Stage Of The Tidal Cycle (hours after high water)

FIGURE 6. Variation in the number of curlew feeding in relation to the state of the tide on 2nd August. (tide height 4.9m)

(a) on Greenabella Channel
(b) on Mid Tide Wall Bank
(c) on Mid Tide Wall Channel



Stage Of The Tidal Cycle (hours after high water)

FIGURE 7. Variation in the number of curlew feeding in relation to the state of the tide on the 20th July (tide height 4.2m)

(a) on Greenabella Channel
(b) on Mid Tide Wall Bank
(c) on Mid Tide Wall Channel

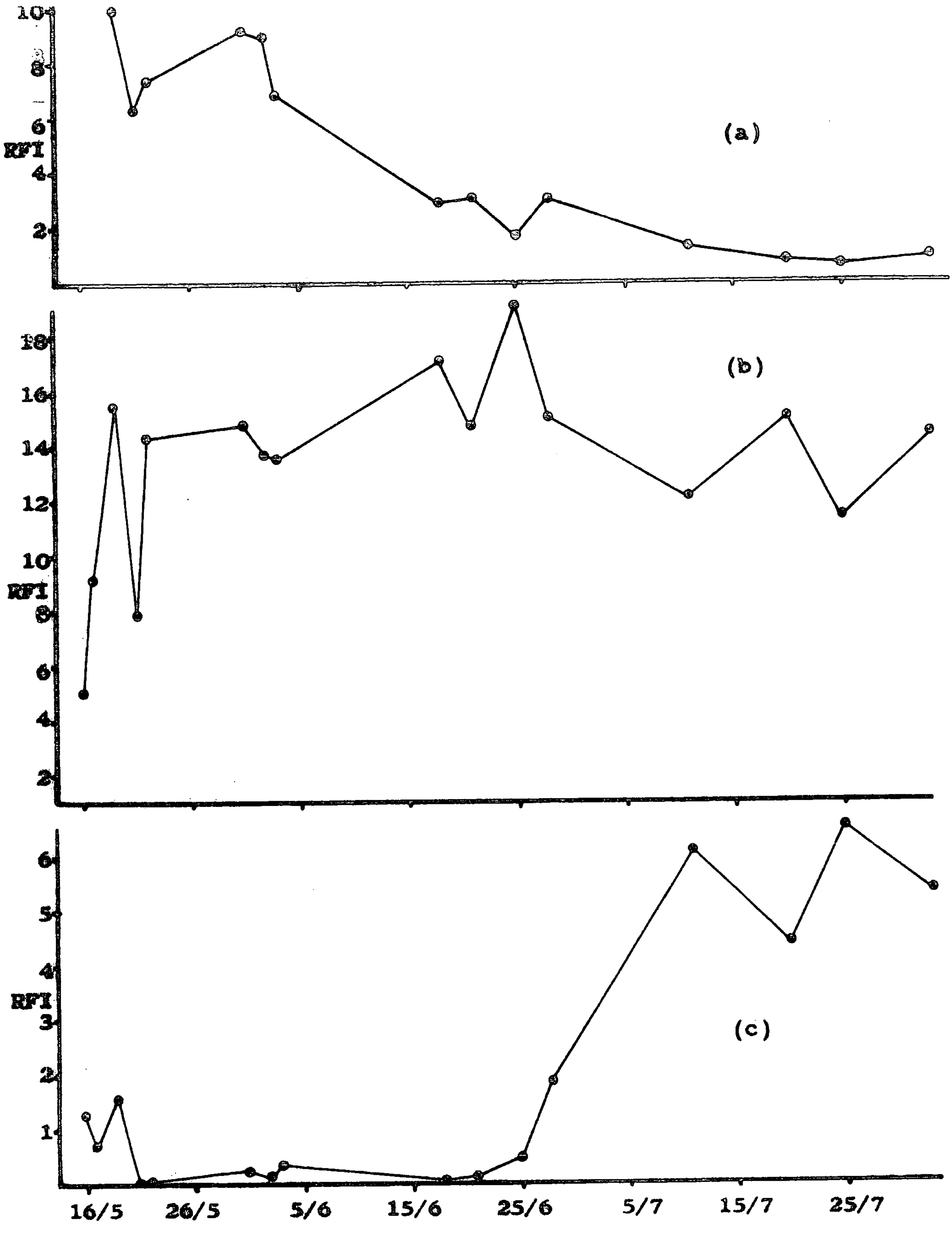


FIGURE 8 Variation in RFI on 3 areas during the study period.

(a) The combined RFIs for the 3 Mid Tide Wall areas

(b) Central Bank

(c) Greenabella Channel

higher on the upper and middle shore feeding areas such as the Central Bank and, in July the Greenabella Bank and the upper parts of the MWB. At intermediate tide heights, the Greenabella Channel supported a greater amount of feeding than on spring tides. It is likely that the other lower shore feeding areas were preferred to the Greenabella Channel, but could not support as much feeding during the intermediate tides.

6) On the middle and lower shore areas the duration of feeding did not appear to vary between spring and neap tides. This, however, may have been due to innaccurate timing, as these results were based on half-hourly observations. On the upper shore areas, namely the Central Bank, the Eastern Channel and Scalloped Mud, the duration of feeding was longer on neap tides than on spring tides.

4.3. Observations on the use of areas other than Seal Sands.

Conclusions on the use of areas other than Seal Sands were based on the following observations.

1) On all observation days when high tide occurred in the morning or early afternoon, curlew were observed flying to their main roosting sites as the flood tide forced them off Seal Sands. No curlew were observed flying to other areas at these times. On five occasions curlew were observed to remain on their roosting areas throughout the high water period. A similar activity was assumed for other occasions. The main roosting sites were the northeast and west enclosures, although the peninsula enclosure and the sand between Eastern Channel and the peninsula were also used (see Figs. 1 and 2). On one occasion (18th June) many curlew were observed flying to Seal Sands (as the tide ebbed) from the east. These birds arrived later than expected, and may have been roosting on the British steel islands (bulldozers were operating on the /u.c. peninsula during the high water period, and may have disturbed curlew during this period). All the roosting areas mentioned are unsuitable for curlew to feed.

2) On the 22nd May and 21st June, when high tide occurred late in the evening (11·15 pm and 11·30 pm), curlew were again observed flying to the northeast and west enclosures (between 8·30 pm and 9·30 pm) as the flood tide forced them off Seal Sands.

3) On the morning of the 18th June, observations began at dawn. Shortly after dawn, curlew were observed walking on to Seal Sands from the peninsula. Many "newly arrived" curlew were also seen walking from the southern part of Scalloped Mud (the area of Seal Sands closest to the northeast and west enclosures) to other areas of Seal Sands at this time.

4) On the 25th June a group of 3 curlew were observed leaving Seal Sands at 7·30 pm, just before low water (HW+5). Between 7·30 pm and 10·00 pm, single and groups of between 2 and 6 curlew were seen and/or heard leaving Seal Sands on about 10 occasions. These birds were flying in a westward direction above Greatham Creek. On 4 occasions curlew were observed landing on or near the Brinefields.
5) On other evenings (29th June, 11th, 20th, 25th and 28th July) curlew were again observed flying towards the Brinefields. On most of these occasions it was difficult to estimate the number of birds flying towards the Brinefields as I was making observations on Seal Sands at these times.
6) On the 20th July (high tide 11·30 pm), late evening observations took relatively little time, as the flood tide concentrated curlew into a relatively small area. More detailed observations on the movements of curlew were therefore possible. On the 20th July curlew were first observed flying towards the Brinefields at 4·30 pm (HW+6·75). The rate of movement towards the Brinefields appeared to increase from this time, as the evening progressed. Between 8·00 pm and 9·30 pm, the flood tide forced all the curlew remaining on Seal Sands to leave. During this period a flock of between 140 and 160 curlew flew to the northeast and west enclosures. All other curlew observed leaving Seal Sands flew westward towards the Brinefields.
7) On two occasions (20th July and 3rd August) visits were made to the Brinefields in the evening. On both these occasions no curlew were observed.

These observations suggest that, during the daytime, all curlew flew to roosting areas and did not feed over the high water period. Prior to the 25th June a similar activity occurred during the high water periods that occurred in the evening, and, for many curlew, the low water periods that were covered by darkness as well. On and after the 25th June, some curlew flew towards field areas in the evening. This activity occurred regardless of tidal conditions. Although field feeding was not observed directly, the areas to which curlew flew were known to have been used by curlew for feeding in past winters (Knights, 1974, 1975; Townshend, 1980). On the 20th July it was estimated that 150 curlew (33% of the population) did not use the field areas. The start of the use of field areas was not related to an increase in population size, although it is possible that an increase in the use of field areas may have occurred (curlew were observed flying towards the fields earlier in July) when the population size increased in July. The start of the use of field areas occurred just after the decrease in the use of the MWB, MWC and MW feeding areas. It is also possible that the very wet weather in mid and late June, may have influenced the timing of the start of the use of field areas, by raising the water table and forcing earth worms nearer to the surface, so that they become available to curlew.

4.4. Variations in the time spent feeding on Seal Sands, throughout the study period.

The proportion of a 12½ hour tidal cycle used for feeding on Seal Sands, by an "average" curlew (the percentage feeding time), was calculated using equation (3).

$$(3)\ \mathrm{PFT} = \frac{\Sigma pi.ti}{12\cdot 5}$$

pi= the percentage of the population observed feeding on Seal Sands, at stage i of the tidal cycle.

ti= the time interval between counts made at stages i and i+1 of the tidal cycle.

Estimates of percentage feeding time (PFT) varied considerably from one tidal cycle to another (see Table 3), depending on the height of the tide, the time of high water and the season.

4.4.1. Non-seasonal variation in PFT between tidal cycles completed within the hours of daylight.

In this section I shall show that the percentage of each tidal cycle in which curlew fed was greater on extreme neap and on spring tides, than on intermediate tides, in all months for which I have observations. Possible causes of variation in PFT will also be examined.

Figs. 9-11 show the effects of the height of the tide on PFT for tidal cycles completed within the hours of daylight (daylight tidal cycles). Estimates of PFT made in different months (May, June and July) are plotted separately. Before discussing these results, however, the "reliability" of some of these estimates need to be considered. These are:
1) In Fig. 9, estimates of PFT made on the 16th, 17th, and 19th May (open circles) are included. These estimates were calculated from data collected on the first three days of observations. At this time my ability to recognise and determine the activities of curlew, observed from long distances, was poor (for example on the first two days I failed to notice

TABLE 3. ESTIMATES OF PFT FOR ALL TIDAL CYCLES OBSERVED.

DATE	PERCENTAGE FEEDING TIME (PFT)	TIDE HEIGHT (metres) HIGH WATER	TIDE HEIGHT (metres) LOW WATER	HRS OF DARKNESS DURING LOW-WATER PERIOD	TIME OF HIGH TIDE (BST)	POPULATION SIZE	MISC. IMFORMATION
16/5	25.1	5.1	0.5	0.00	0530	91	(5.5)
17/5	32.4	5.0	0.6	0.00	0610	91	(6.0)
19/5	38.8	4.6	1.2	0.00	0740	91	(5.75)
21/5	30.4	4.2	1.8	0.00	0930	91	(3.8)
22/5	33.1	4.1	2.0	0.00	1030	91	(2.75)
31/5	34.6	4.8	1.0	0.00	0510	73	(5.5)
2/6	29.4	4.8	0.9	0.00	0630	143	(6.0)
3/6	29.1	4.7	1.1	0.00	0705	143	(6.0)
8/6	8.7	4.2	1.2	2.00	0002	143	
15/6	22.9	5.0	0.7	0.00	0550	143-	helicopters disturbed feeding for 3hr
18/6	6.9	4.5	0.9	6.00	1950	143	
18/6	23.4	4.6	1.4	0.00	0800	143-	bulldozer disturbance
21/6	14.1	4.0	1.5	3.50	2220	143	
21/6	37.0	4.1	2.0	0.00	1040	143	
25/6	30.8	4.3	1.6	0.00	0211	150	
25/6	17.0	4.3	1.4	2.50	1430	150-	curlew 1st observed to fly towards fields
29/6	29.0	4.9	0.9	0.00	0445	160	
29/6	10.4	4.8	0.9	5.25	1715	160	
11/7	31.1	4.8	0.9	0.00	0330	320	
11/7	17.0	4.8	1.0	3.80	1550	320	
20/7	15.0	4.1	1.5	4.50	2130	450	
20/7	29.6	4.2	1.8	0.00	0945	450	
25/7	23.9	4.4	1.5	0.00	0220	450	
25/7	12.6	4.4	1.4	2.75	1445	450	
28/7	23.6	5.0	0.7	0.00	0430	450-	large flock of gulls present
28/7	11.8	5.0	0.8	5.00	1700	450	
2/8	30.4	4.9	1.0	0.00	0815	460	(6.0)

Brackets indicate the number of hours of darkness during the low-water period of the following (not observed) tidal cycle.

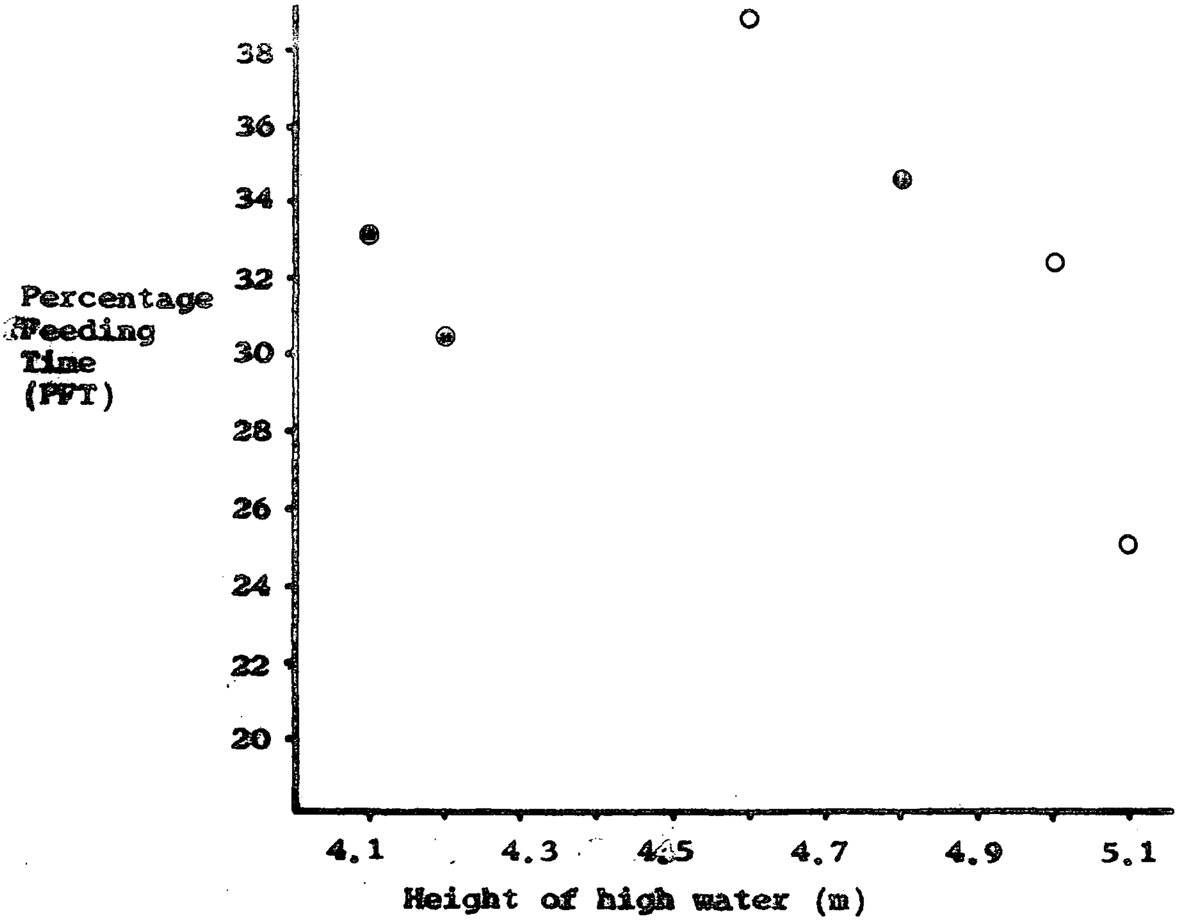


FIGURE 9 Variation in PFT with tide height in May (population size 73-91 birds). See text for explanation of symbols

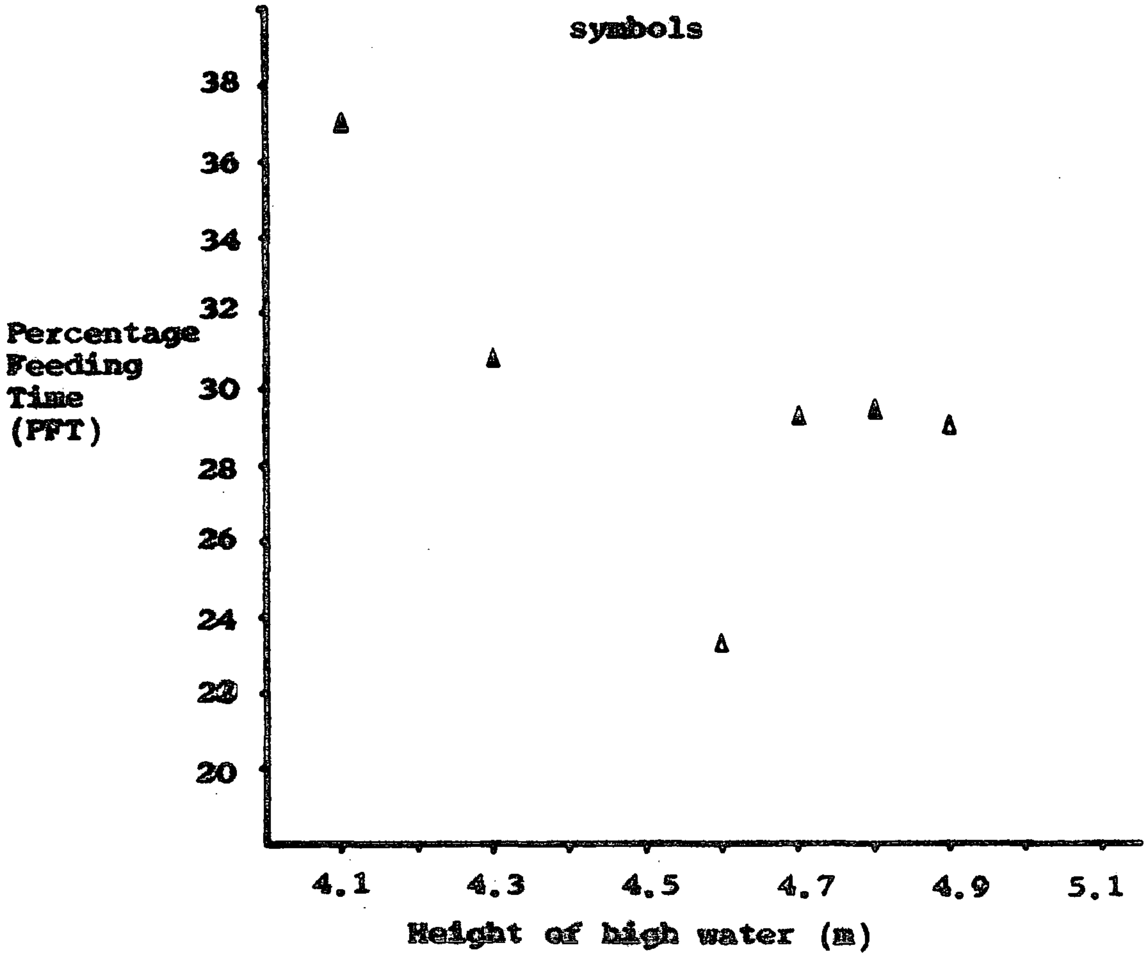


FIGURE 10 Variation in PFT with tide height in June (population size 143-160 birds). See text for explanation of symbols.

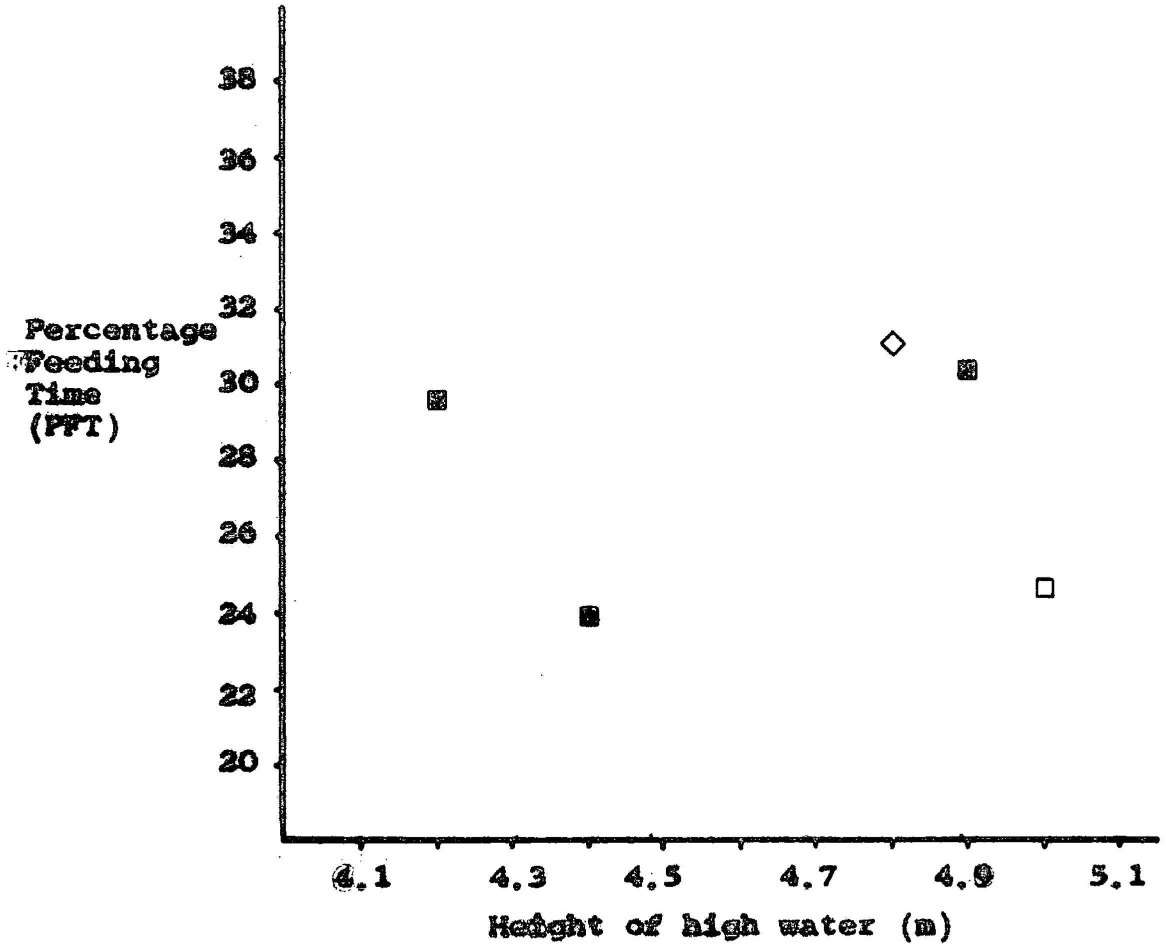


FIGURE 11 Variation in PFT with tide height in July (population size 450-460 birds (squares), or 320 birds (diamond)).

curlew amongst the rocks on the Mid Tide Wall). The accuracy of these estimates is therefore in doubt.

2) Towards the end of June, curlew were known to use the pastures adjacent to Seal Sands, probably for feeding (see section 4.3.). On these days (29th June (open triangle at tide height 4·9m, in Fig 10) and possibly 25th June), estimates of PFT on Seal Sands are likely to be less than would have been expected had the pastures not been used. During July, it was assumed that there was no day-to-day variation in the use of field areas.

3) On the 18th June (open triangle at tide height 4·6m, in Fig. 10), some curlew arrived at Seal Sands an hour later than "usual", presumably because they were disturbed by bulldozers working on the peninsula. While it is possible that these curlew may have compensated for this "loss" of feeding time by feeding to a greater extent during the rest of the tidal cycle, it is also possible that they did not, and that PFT was lower than would be expected for undisturbed tidal cycles of the same height.

4) The estimate of PFT made on the 11th July (open diamond in Fig. 11) may also be "unreliable" when considering the effects of height of tide on PFT in July, as population size was considerably less than on other July observation days.

5) The estimate of PFT made on the 28th July (open square in Fig. 11) is also thought to be unreliable in determining the effects of height of tide on PFT. On the 28th July a large flock of several thousand gulls were present on Seal Sands over the daytime low water period. Prior to this occasion, large flocks of gulls were seen on Seal Sands only at night. The interference caused by the gulls was thought to have been the reason why approximately 60 curlew formed a

"non-feeding" flock on the south-western corner of Central Bank. This flock was present throughout the low tide period. The presence of gulls may also have influenced the feeding behaviour of other curlew.

As mentioned earlier, Figs. 9-11 show the effects of tide height on PFT for each month that curlew were observed. Unfortunately there are not enough "reliable" points on the individual monthly plots for precise relationships to be determined for each month. By combining the data for all months, a general picture of the effects of tide height on PFT is obtained (see Fig. 12). Although this treatment of the data results in the confusion of possible seasonal and non-seasonal variation, a number of general trends can be seen, for example, in all months there is a similar decrease in PFT (with increase in tide height) within the tide height range 4·1 - 4·4m. The results for June and July also suggest that PFTs for tides in the tide height range 4·7 - 5·0m are greater than PFTs for tides in the height range 4·4 - 4·6m. With the data presented so far, it is difficult to determine the relationship between PFT and tide height within the upper range of tide height (4·7 - 5·0m), as there are fewer "reliable" estimates of PFT in this range.

The height of the tide affects several aspects of the exposure of intertidal feeding areas, including the extent of exposure, the rate of exposure, the rate at which feeding areas are covered, and the timing of the beginning and end of the exposure period (in relation to the time of high water). The results shown in section 4.2 indicate that the extent of exposure of lower shore areas at low water, is likely to have been a major factor influencing the choice of feeding areas. These results, however do not show whether the extent of

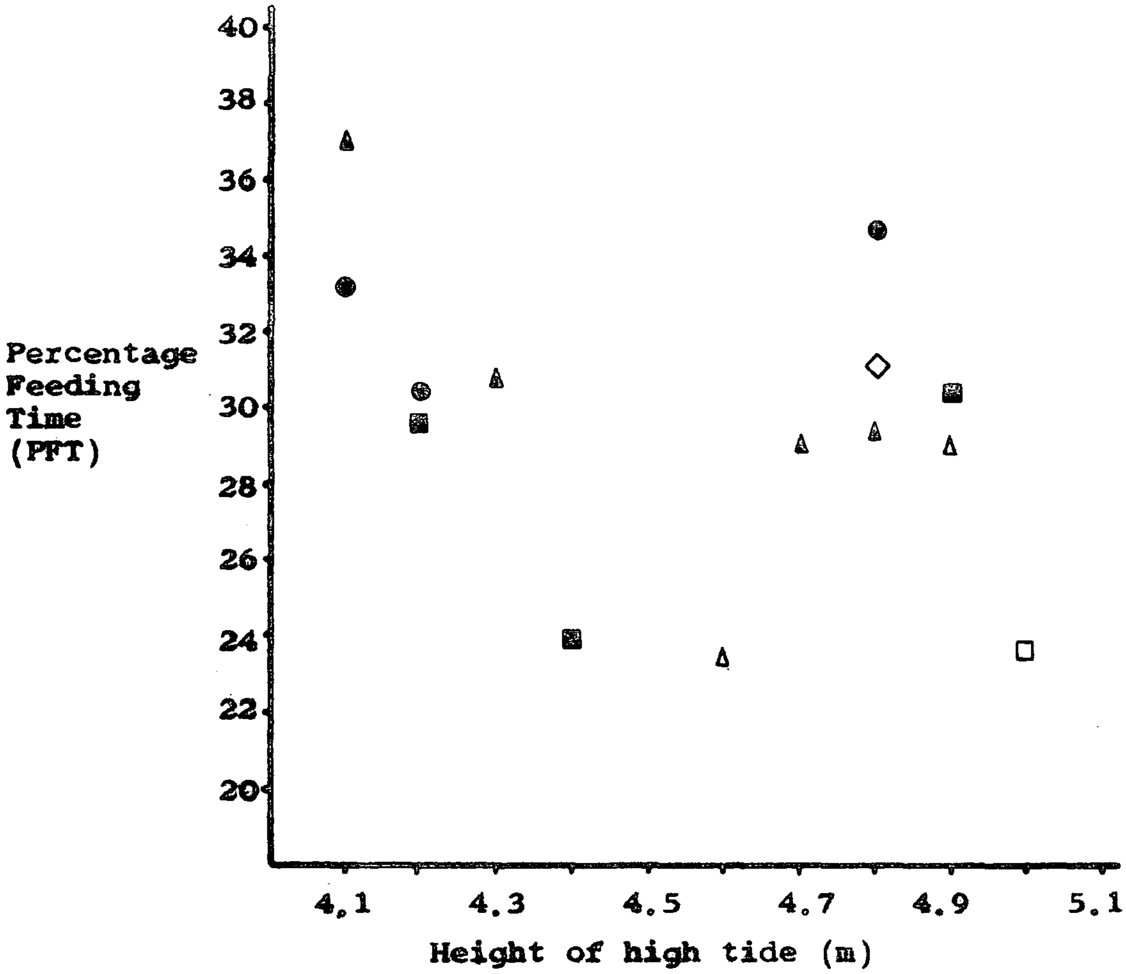


FIGURE 12 Variation in PFT in relation to tide height for all months within the study period.

Explanation of symbols :

Circles - estimates of PFT for May (population size 73-91 birds).

Triangles - estimates of PFT for June (population size 143-160 birds).

Squares - estimates of PFT for July (population size 450-460 birds).

Diamond - estimate of PFT for July 11th (population size 320 birds.

Open Triangles - estimates of PFT for June 18th and 29th.

Open Square - estimate of PFT for July 28th.

exposure of lower shore areas were also the main causes of variation in PFT, or whether this was due to variations in the speed of tidal movements, to variations in the duration of exposure of Seal Sands, or due to some other variable, only indirectly related to tide height. In order to highlight possible causes of variation in PFT, the values of PFT, for each daylight tidal cycle observed, were divided into 3 parts, each representing the feeding carried out between different stages of the tidal cycle (i.e. between 0 and 4 hours after high water (HW+0-4), HW+4-8, and HW+8-12·5) (see Table 4). The duration of the previous (and following) daylight feeding periods, and the time intervals between successive daylight feeding periods (see Table 4) were considered among the possible causes of variation in PFT.

In June and July, PFT (HW+0-4) was positively correlated with tide height ($r=0{\cdot}7$, $n=11$, $p<0{\cdot}05$), presumably because of the faster rate of exposure of feeding areas on spring tides (see Fig. 13a). (N.B. The low value of PFT (HW+0-4) at tide height 4·6m was thought to have been caused by disturbance (see pg.51).). PFT (HW+8-12·5) however, was not significantly correlated with tide height during these months (see Fig. 13b). In Fig. 13b it can be seen that the values of PFT (HW+8-12·5) which differ most from the "expected" values, are those for tide heights 4·3 and 4·4m. At these tide heights the rate at which feeding areas are covered is lower, and the duration of exposure greater than on spring tides. PFT (HW+8-12·5) would therefore be expected to be greater on intermediate tides than on spring tides. On these dates the daylight tidal cycles observed were followed by a further substantial daylight feeding period (longer than 5 hours) on the same day. Other observation days on which

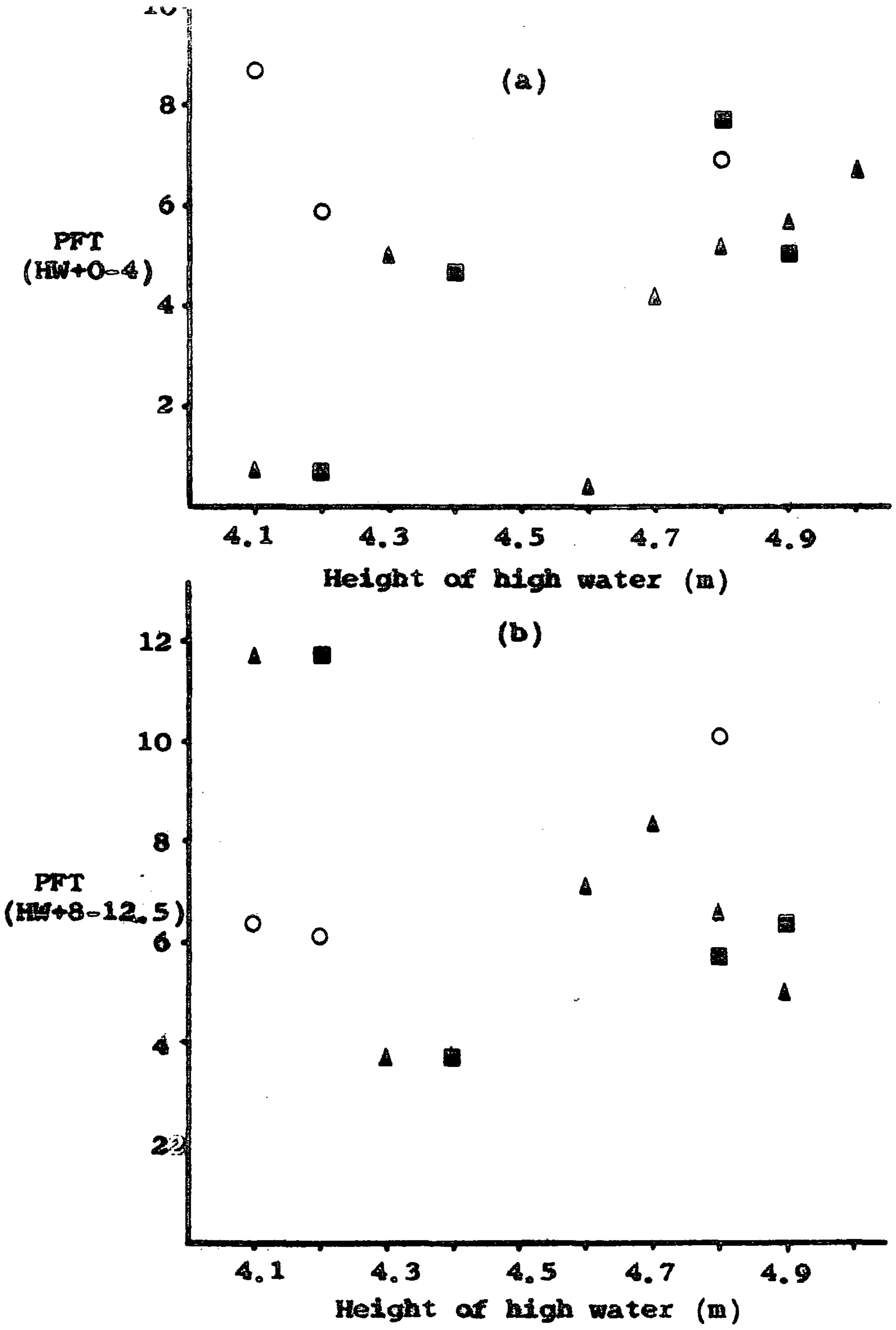
TABLE 4. ESTIMATES OF PFT FOR 3 TIME PERIODS WITHIN THE TIDAL CYCLE.

DATE	PERCENTAGE FEEDING TIME 0-4 HRS. AFTER HIGH WATER	4-8 HRS. AFTER HIGH WATER	8-12½ HRS. AFTER HIGH WATER	HEIGHT OF HIGH TIDE (metres)	TIME OF HIGH-WATER (BST)	TIME SINCE LAST DAYLIGHT FEEDING PERIOD (HRS.)	DURATION OF LAST DAYLIGHT FEEDING PERIOD (HRS.)	TIME TILL NEXT DAYLIGHT FEEDING PERIOD (HRS.)	DURATION OF NEXT DAYLIGHT FEEDING PERIOD (HRS.)
21/5	5.8	18.5	6.1	4.2	0930	4.0	3.5	8.0	(8)
22/5	8.6	18.2	6.3	4.1	1030	4.0	4.5	6.7	(8)
31/5	6.9	17.5	10.1	4.8	0510	9.2	(8)	4.0	2.5
2/6	5.2	17.6	6.5	4.8	0630	10.5	(8)	4.0	1.0
3/6	4.2	16.4	8.3	4.7	0705	4.0	1.0	4.0	0.2
15/6	6.8	N.C.	N.C.	5.0	0550	9.8	(8)	4.0	1.7
18/6	0.4	15.5	7.4	4.6	0800	4.0	2.0	4.0	0.3
21/6	0.8	24.6	11.6	4.1	1040	4.0	4.7	6.5	(8)
25/6	5.0	22.2	3.6	4.3	0210	6.2	(8)	4.0	5.5
29/6	5.7	18.2	5.0	4.9	0445	8.7	(8)	4.0	2.7
11/7	7.7	17.7	5.6	4.8	0330	7.5	(8)	4.0	4.2
20/7	0.8	17.1	11.7	4.2	0945	4.0	3.7	7.5	(8)
25/7	4.7	15.6	3.6	4.4	0220	6.3	(8)	4.0	5.2
2/8	5.0	19.1	6.3	4.9	0815	4.0	2.2	9.0	(8)

N.B. The figures shown are for daylight tidal cycles only.

Brackets indicate the duration of the daylight feeding period on the day following or preceding the day that observations were made.

N.C. indicates data not collected due to disturbance



<u>FIGURE 13</u> Variation in (a) PFT(HW+0-4), and (b) PFT(HW+8-12.5 in relation to the height of the tide. For June and July, PFT(HW+0-4) is positively correlated with tide height (r=0.7, p 0.05). PFT(HW+8-12.5) was not significantly correlated with tide height.

Explanation of symbols: Circles - May estimates
Triangles - June estimates
Squares - July estimates

long (3-4 hour) daylight feeding periods followed the tidal cycles observed (on the same day) include the 29th June and the 11th July (tide heights 4·9 and 4·8m respectively). On these tides PFTs (HW+8-12·5) were slightly lower than on tides (of the same height) which were not followed by a long daylight feeding period on the same day. It seems likely then, that curlew may have fed to a greater extent towards the end of tidal cycles which were not followed by a substantial daylight feeding period on the same day. On the June and July tidal cycles which were not followed by substantial daylight feeding periods on the same day, PFTs (HW+8-12·5) were negatively correlated with tide height ($r=-0{\cdot}8$, $n=8$, $p < 0{\cdot}05$).

From these results, the presence of a similar substantial feeding period, prior to the daylight tidal cycle observed, might be expected to result in a lower PFT (HW+0-4). Unfortunately it is not possible to tell whether this occurred, as the days on which substantial daylight feeding periods occurred in the morning were also the days on which neap tides occurred, and PFTs (HW+0-4) were expected to be low.

When the values of PFT (HW+0-4) and PFT (HW+8-12·5) are added together (see Fig. 14), it is found that, in June and July, significantly higher values are obtained on low neap, and on spring tides, than on "intermediate" (tide height 4·3-4·5m) tides ($t=5{\cdot}5$, $p < 0{\cdot}01$). (The value for tide height 4·6m was ignored in the calculation of t as it was thought that this value was low due to "disturbance" (see pg. 51)). These "intermediate" tides were found on the days during which the highest total daylight feeding time (during 2 consecutive tidal cycles) was available. Long

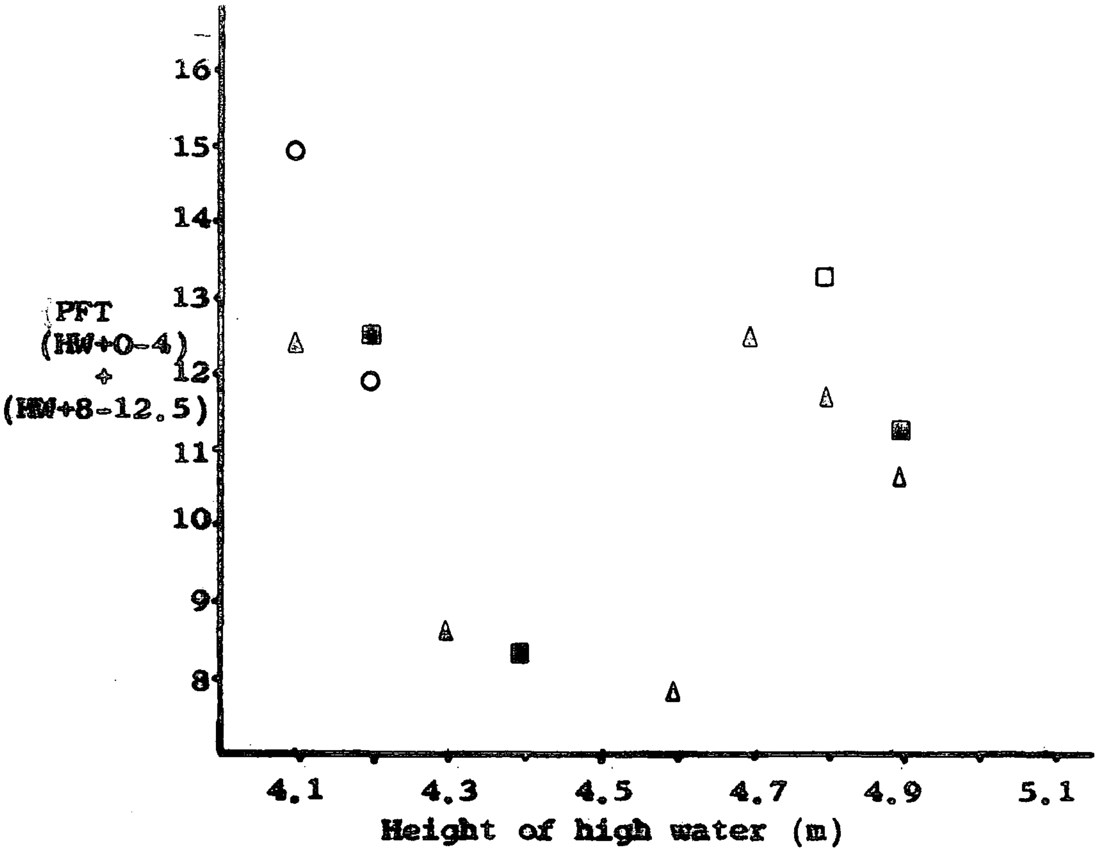


FIGURE 14 Variation in PFT (HW+0-4) + (HW+8-12.5) with tide height

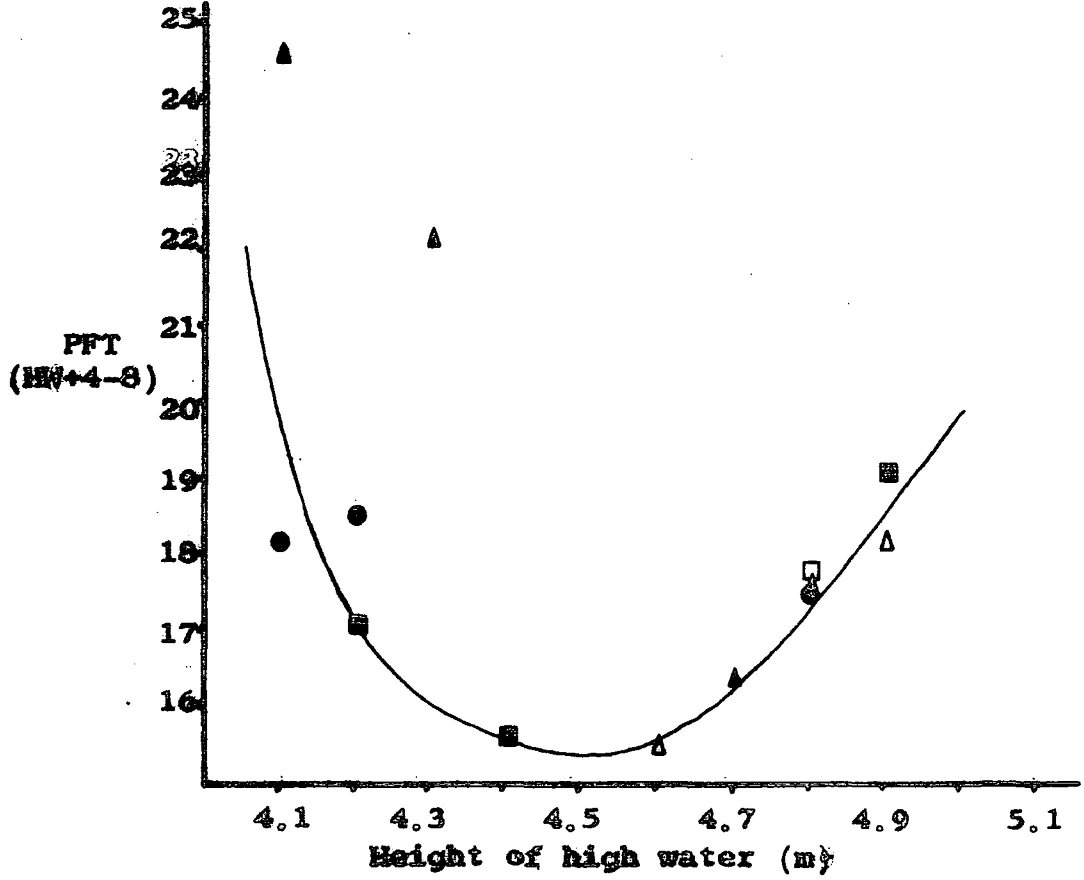


FIGURE 15 Variation in PFT(HW+4-8) with tide height. Line fitted by eye.

Explanation of symbols; Circles - May estimates
Triangles - June estimates
Squares - July estimates

hours of daylight feeding time were also available during the neap tides (though not as long as during intermediate tides). PFT (HW+0-4+8-12·5) may therefore have been higher on neap tides than on spring tides, had the amount of available daylight feeding time been the same.

Variation in the amount of feeding carried out during the low water period (represented by PFT (HW+4-8)) is shown in Fig. 15. These results show that, for all months, PFTs (HW+4-8) were positively correlated with tide height ($r=0{\cdot}94$, $n=6$, $p<0{\cdot}01$) within the tide height range 4·7-4·9m. In June and July, the higher PFTs (HW+4-8) were associated with lower PFTs (HW+0-4+8-12·5) within the tide height range 4·7-4·9m. It seems likely then, that, although curlew fed to a greater extent, during the high spring tides, at low water (presumably on the lower shore feeding areas, which are exposed to their greatest extent on these tides), they fed to a lesser extent at other times, and that, within each month, the overall time spent feeding varied little between tides in the height range 4·7-4·9m.

Within the tide height range 4·4-4·1m, PFTs (HW+4-8) were greater at the lower tide heights. Another interesting point shown in Fig. 15, is that the values of PFT (HW+4-8) for June neap tides are much greater than those for May and July neap tides ($t=5{\cdot}21$, $p<0{\cdot}05$). The significance of these results will be discussed in a later section.

In conclusion, it seems likely that tide height had little effect on total PFT within the tide height range 4·7-4·9m, although it did seem to influence the timing (and positioning) of feeding. At intermediate tide heights, long hours of daylight feeding time were available during the "second" (partial daylight) tidal cycle of the day. This appeared to result in lower PFTs during the "first" (daylight) tidal cycle, presumably because curlew fed to a greater extent on the partial daylight tidal cycles on these dates. During neap tides, long hours of total daylight feeding time were also available, however PFTs were often as high, or even higher (especially on extreme neap tides) than on spring tides.

4.4.2. Non-seasonal variation in PFT between tidal cycles partly covered by darkness.

In this section estimates of PFT for the partial daylight tidal cycles are used to examine a) variation in the combined PFTs for 2 consecutive tidal cycles, and b) variations in the relative use of 2 consecutive tidal cycles. Details of how PFTs for partial daylight tidal cycles were calculated are also given.

Estimates of the proportion of curlew present and the proportion feeding, at dawn or dusk, are listed in Table 5. From these results it was estimated that, in June 18% of the curlew population were present on Seal Sands at night, and that, between the hours of HW+4-8, 11% were feeding. Judging from the variation in feeding intensity (the proportion of curlew feeding at a particular moment in time) with state of tide observed during daylight tidal cycles, and the estimate of percentage feeding at dusk on the 29th June, it was estimated that 5% were feeding between the hours of HW+2-4 and HW+8-10. In July the proportion of curlew using Seal Sands at night was greater (30%), and it was estimated that 20% were feeding between the hours of HW+4-8, and 10% between HW+2-4 and HW+8-10. These estimates were used only for the hours of the low water period (HW+2-10) which were in darkness. During the hours of daylight (0400 hrs. - 2200 hrs.)

TABLE 5. ESTIMATES OF THE PROPORTION OF CURLEW PRESENT AND THE PROPORTION FEEDING AT DAWN OR DUSK.

DATE	PROPORTION OF CURLEW PRESENT	PROPORTION OF CURLEW FEEDING	HEIGHT OF HIGH TIDE (metres)	TIME OF OBSERVATIONS	
				HRS. AFTER HIGH-WATER	B.S.T.
18/6	16.0	12.5	4.5	8.25	0415
21/6	17.5	9.8	4.0	6.00	0420
25/6	19.0	12.0	4.3	7.50	2200
29/6	9.0	5.0	4.8	4.75	2215
11/7	31.0	21.0	4.8	6.00	2200
20/7	30.4	22.6	4.1	7.25	0445
25/7	35.0	20.0	4.4	6.00	2100
28/7	22.0	14.0	5.0	4.25	2130

direct observations provided estimates of the number of curlew present and feeding. Estimates of PFT based on these data are listed in Table 3.

In the previous section it was suggested that the availability of long hours of daylight feeding time during the partial daylight tidal cycle may have resulted in low PFTs during the daylight tidal cycle. In order to show the sep~~e~~arate effects of tide height on PFT, rather than the combined effects of variation in tide height and variation in the relative use of 2 consecutive tidal cycles, the sum of PFTs for 2 consecutive tidal cycles (PFT(2)) were plotted against tide height (see Figs. 16 and 17). Unfortunately, of the 8 estimates of PFT(2) obtained during June and July, only 4 are considered "reliable" for the purposes just mentioned. These "reliable" estimates all lie within the tide height range 4·1-4·4m. In both June and July, PFTs (2) were higher during the extreme low neap tides than at neap/ intermediate tide heights. Although the 4 estimates of PFT(2) lying within the tide height range 4·6-5·0m are thought to be "unreliable", a consideration of the nature and likely extent of their "unreliability" may be helpful when considering the likely effect of tide height on PFT(2) in this range.
For example:

1) On the 18th June (tide height 4·6m) feeding was disturbed during the early half of the daylight tidal cycle. Although it is possible that curlew may have compensated for this disturbance by feeding to a greater extent on the following tidal cycle, the partial daylight tidal cycle observed on this date was the tidal cycle that preceded the daylight tidal cycle. From Figs. 12, 13 and 14, it seems likely that disturbance may have caused a reduction in PFT of at least 6%.

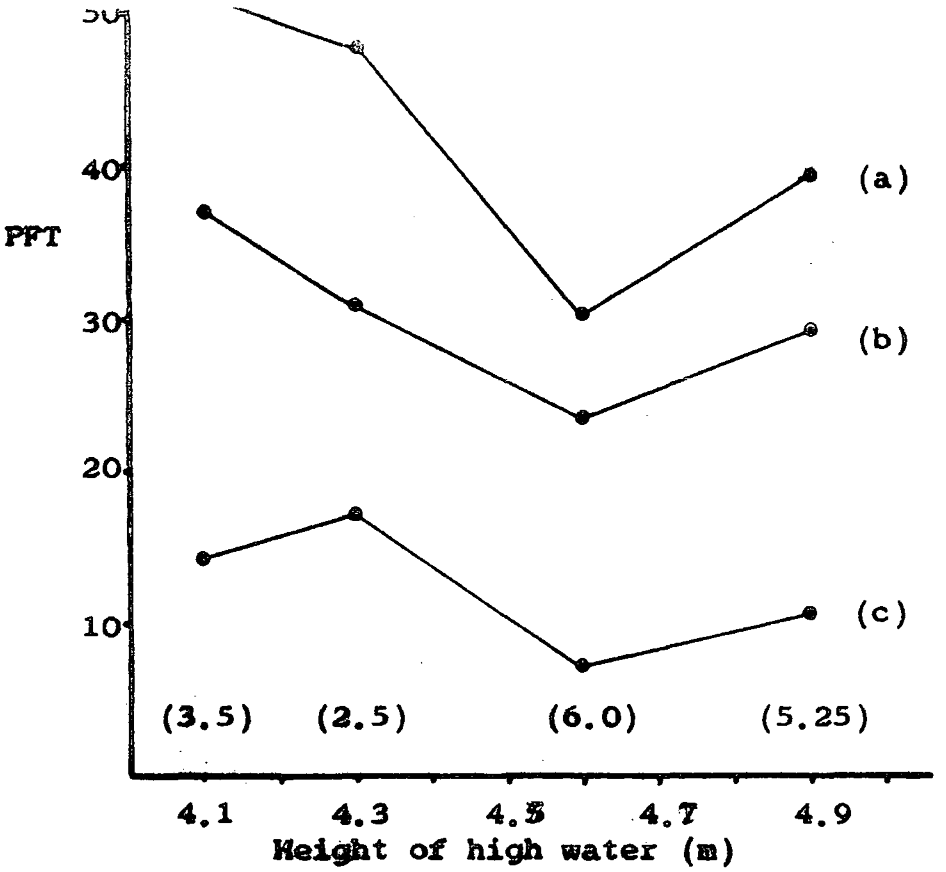


FIGURE 16 Variation in PFT with tide height in June. (a) The sum of PFTs for consecutive tidal cycles. (b) PFTs for daylight tidal cycles. (c) PFTs for partial daylight tidal cycles. Brackets indicate the hours of darkness covering the low-water period.

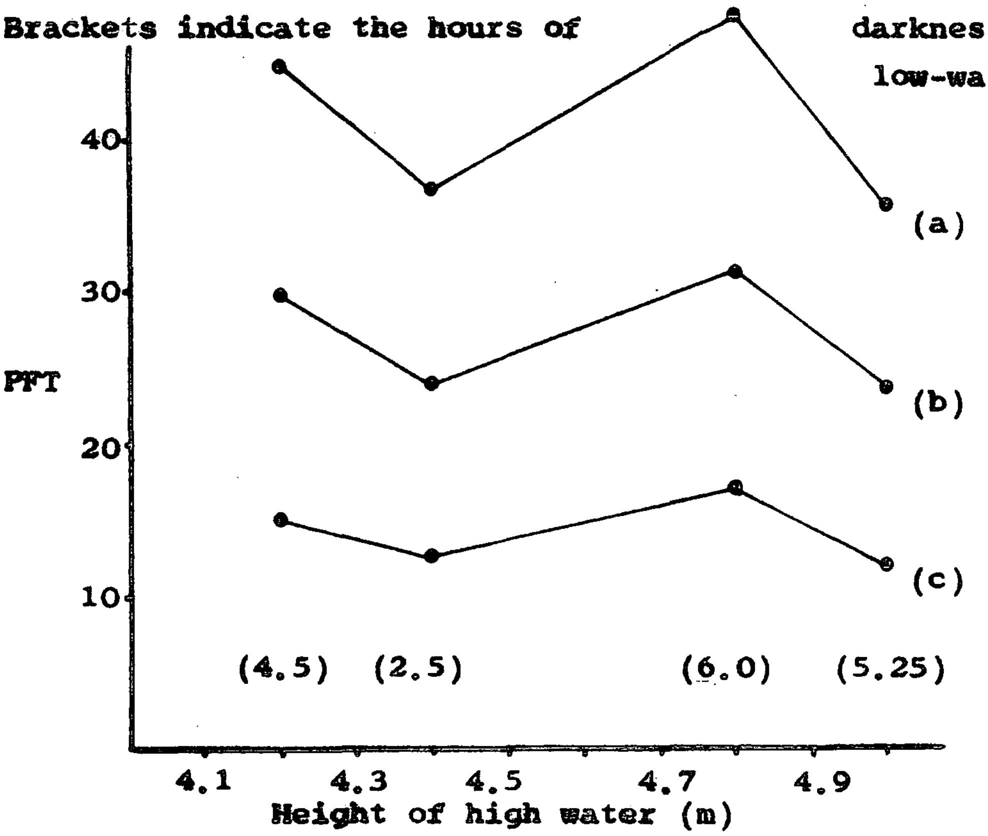


FIGURE 17 Variation in PFT with tide height in July. (a) The sum of PFTs for consecutive tidal cycles. (b) PFTs for daylight tidal cycles. (c) PFTs for partial daylight tidal cycles. Brackets indicate the number of hours of darkness covering the low-water period.

2) On the 29th June (tide height 4·9m) some curlew were observed to fly towards the fields at dusk. It is possible that PFTs(2) may have been slightly greater at this tide height had curlew not used the fields on this date. How much greater, though is not known.

3) On the 28th July (tide height 5·0m) gulls disturbed feeding during the daylight tidal cycle. It is possible, though, that curlew may have compensated for this disturbance by feeding to a greater extent on the following tidal cycle. On this date the partial daylight tidal cycle observed was the one following the "disturbed" one. It is possible, therefore, that the PFT(2) observed may not be greatly different from that expected in the absence of disturbance.

4) On the 11th July (tide height 4·8m) the population size was lower than on other July observation dates. It is possible that the lesser competition for mudflat feeding on this date, resulted in a greater proportion of the daily feeding being carried out on the mudflats rather than on the fields (i.e. a higher PFT(2)) compared with other July observation dates.

In the previous section it was suggested that tide height was likely to have had little effect on PFTs (for daylight tidal cycles) within the tide height range 4·7-4·9m. While strong evidence for a similar relationship between PFT(2) and tide height (within the tide height range 4·6-5·0m) is lacking, the available evidence does not preclude such a relationship.

To show the effects of variation in the amount of available daylight feeding time during the partial daylight tidal cycle on the relative use of 2 consecutive tidal cycles, the proportion of the total daily PFT, carried out on the partial daylight tidal cycle (see Table 6) was plotted against the number of hours of darkness occurring during the low water period of the partial daylight tidal cycle (see Fig. 18).

As with the previous results, however, any conclusions based on the data shown in Fig. 18, must again take into account the reliability of estimates, for example, on the 18th June (6·0 hrs. of darkness) the proportion of the total daily PFT carried out on the partial daylight tidal cycle is likely to be higher than "normal" (for June) as feeding was disturbed on the daylight tidal cycle. The relative use of the two tidal cycles may also have been affected by the use of field areas on the 29th June (5·25 hrs. of darkness). Taking these points into consideration, it seems likely that the slope of the June regression line, shown in Fig. 18, may be less steep than one which only represented variation in the amount of darkness during the low water period. Similar conclusions are also arrived at when the July results are considered.

The main points of this section may be summarised as follows:

1) There is good evidence that the proportion of the total daily PFT carried out on the partial daylight tidal cycle increased as the amount of available daylight feeding time on that tidal cycle increased. Further work is needed for a more precise relationship to be determined.

2) There is evidence that PFTs(2) were higher during the extreme low neap tides than at neap/intermediate tide heights.

3) While it is likely that tide height did not directly affect PFT(2) within the tide height range 4·6-5·0m, and that PFTs(2) within this range were lower than those for neap

TABLE 6 ESTIMATES OF PERCENTAGE OF TOTAL DAILY PFT CARRIED OUT ON THE PARTIAL DAYLIGHT TIDAL CYCLE.

DATE	8/6	18/6	21/6	25/6	29/6	11/7	20/7	25/7	28/7
PFT ON PARTIAL DAYLIGHT TIDAL CYCLE	8.7	6.9	14.1	17.0	10.4	17.0	15.0	12.6	11.8
HEIGHT OF HIGH TIDE (m)	4.2	4.5	4.0	4.3	4.8	4.8	4.1	4.4	5.0
HOURS OF DARKNESS DURING THE LOW-WATER PERIOD	2.0	6.0	3.5	2.5	5.25	3.8	4.5	2.75	5.0
PFT ON THE PRECEDING OR FOLLOWING DAYLIGHT TIDAL CYCLE	——	23.4	37.0	30.8	29.0	31.1	29.6	23.9	23.6
PERCENTAGE OF TOTAL DAILY PFT CARRIED OUT ON THE PARTIAL DAYLIGHT TIDAL CYCLE	——	22.8	27.6	35.6	26.4	35.3	33.6	34.5	33.3

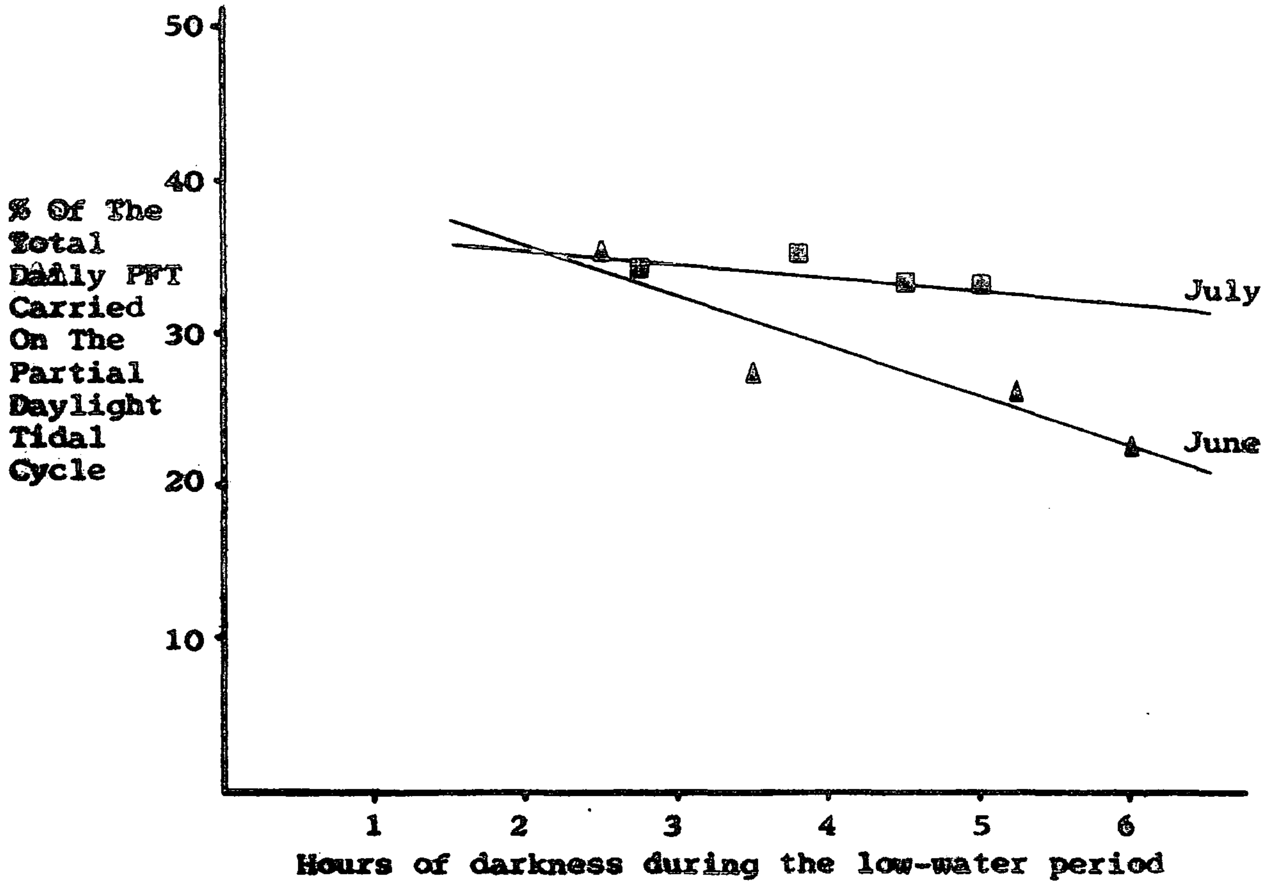


FIGURE 18 The percentage of the total daily PFT carried out on the "partial daylight" tidal cycle in relation to the number of hours of darkness during the low-water period of the partial daylight tidal cycle. June July

The regression lines are shown: $y = -3.1x + 41.4$ (June)

$y = -0.6x + 36.7$ (July)

tides, more work is needed to show conclusively whether this did or did not occur.

4.4.3. Seasonal variation in PFT.

Seasonal variation in PFT can be broadly divided into variation between PFTs in May, early June, late June and July. In early June, PFTs were lower than in May (see Fig. 12, tide height 4·8m). The higher PFTs in May were due mainly to a greater proportion of feeding carried out outside the low water period (see Figs. 14 and 15). In late June PFTs increased. Fig 12 shows that on neap tides PFTs were higher in late June than in May. On the May tidal cycles, however, there was a greater amount of daylight feeding time available on the partial daylight tidal cycles which may account for part of the difference in PFT between these two months. If it is assumed that the relative use of daylight and partial daylight tidal cycles was the same in May as in late June, then the likely PFTs for the May "neap tide" partial daylight tidal cycles may be calculated using the June regression line in Fig. 18. Using these results it is found that in late June PFTs(2) are, on average, 3·5 percentage points above the May values. The increase in PFT in late June was due mainly to an increase in PFT (HW +0-4) (see Fig. 15).

In July PFTs decreased again, to levels just above those for early June. On July neap tides, PFTs(2) were, on average, 6·0 percentage points below the late June values (see Figs. 16 and 17).

4.4.4. Discussion: variations in PFT in relation to variation in the use of different feeding areas.

In this section seasonal and tidal variations in PFT will be discussed in relation to the use of different feeding areas. Although this discussion is based mainly on the results presented in previous results sections, it also draws on some of the results presented in section 4.5, these are:

1) Within each month, calorific intake rates were higher on the "second" major feeding areas than on the Central Bank.
2) Curlew feeding behaviour changed between June and July. In June curlew searched a wider area, took fewer prey per minute, and, on average, took larger prey than in July.
3) On the Central Bank and Greenabella Channel, calorific intake rates were higher in July than in June.

In section 4.2 it was shown that the main tidal variations in the use of different feeding areas, were a reduced use of the "second" major feeding areas (these were mainly lower shore feeding areas) on neap tides. The higher PFTs(2) observed on neap tides may therefore have been the result of curlew having to feed for longer on the less profitable areas in order to obtain the same quantity of food as they did while feeding for a shorter time on more profitable feeding areas. Similar arguments may also be employed to explain the higher PFTs in late June, compared with early June, as a reduction in the use of the MWB and MWC (these were highly profitable lower shore feeding areas) occurred between early and late June. Evidence that this was the main cause of variation in PFT is seen in Fig. 15. In all months, PFTs(HW+4-8) (this represents the feeding carried out during the low water period when lower shore feeding areas are exposed) were higher on extreme low neap tides than at neap/intermediate tide heights. PFTs(HW+4-8) were also much higher during late June (the "reliable" estimates of PFT for late June were made during neap tides) than during May or July. The reduction in use of the highly profitable lower shore feeding areas in late June may also have resulted in an increased use of the partial daylight tidal cycle, as the estimate of PFT for the partial daylight tidal cycle was lower on the 8th June than on the 25th June (see Table 6).

Between late June and July, PFTs decreased. In July population size was much higher than in June, and it seems likely that the increased competition for large food items on the mudflats not only resulted in a change in feeding behaviour (see section 4.5), but also resulted in a greater use of the mudflats at night (the proportion of the population observed feeding at dawn and dusk in July, was greater than in June), and may also have resulted in a greater use of field areas for feeding. On two of the major feeding areas studied (Central Bank and Greenabella Channel), the change in feeding behaviour in July resulted in slightly higher calorific intake rates being recorded for this month. While this may partly explain the lower PFTs in July, another possible explanation is that an increase in field-feeding resulted in the lower PFTs recorded for the mudflats.

The decrease in PFT between May and early June was also associated with an increase in population size. At other times of presumed increased competition for food resour~~s~~ces (between early and late June, and between late June and July), an increase in the use of the partial daylight tidal cycle was thought to have occurred. It is possible, then, that an increased use of the partial daylight tidal cycle may also have occurred at the beginning of June. This may explain why PFTs were lower on the daylight tidal cycles in early June.

4.5. Variations in feeding behaviour and food intake rates.

In this section I will be comparing the biomass and calorific intake rates of curlew feeding on different areas of Seal Sands. I will also be comparing the food intake rates in different months, and at different stages of the tidal cycle. Sex differences and variations in feeding behaviour will also be discussed.

From these results it is hoped to estimate the relative profitability of feeding on different areas and of feeding at different times. Profitability is defined as the net energy gain per unit of feeding time. While it was possible, from the data collected, to estimate the gross rate of energy consumption, the assimilation efficiences of feeding on different prey items are not known, nor was it possible to measure the energy expended during foraging. Estimates of the number of paces and probes made while foraging are given, however the total and relative energy demands of these two activities are not known. In this section differences in pace rates and probe rates will be assumed to have little effect on profitability, however large differences will be noted and their possible effects on estimates of relative profitability considered. Similarly the possible effects of differences in the assimilation efficiences of feeding on crabs or worms will also be considered.

4.5.1. Differences in feeding behaviour and feeding rates between feeding areas.

For each feeding area the mean pace rate, probe rate, prey capture rate, number of paces per food item, and the mean proportion of probes which were successful was calculated (Table 7). The proportion of different types and sizes (relative sizes) of prey taken on each area is shown in Table 8.

TABLE 7. MEAN BIOMASS AND CALORIFIC INTAKE RATES, AND ASPECTS OF THE FEEDING BEHAVIOUR OF CURLEW, ON EACH FEEDING AREA IN MAY AND JUNE.

FEEDING RATES AND BEHAVIOUR	AREA - MWB	MWC	MW	GW	GB	GC	SM	SC	CB	EC
k cals / min.	0.177	0.269	0.469	0.378	0.155	0.103	0.069	0.109	0.110	0.111
S.D.	0.130	0.103	0.296	0.312	0.120	0.049	0.073	0.072	0.089	0.090
k cals / item	0.278	0.234	1.711	0.513	0.162	0.232	0.097	0.142	0.184	0.128
S.D.	0.118	0.086	0.936	0.562	0.066	0.144	0.032	0.058	0.193	0.077
biomass / min.	3.247	5.248	14.29	12.87	3.123	2.687	1.322	2.018	2.469	2.588
S.D. (gms.x10^{-2})	2.363	2.474	8.485	9.058	2.488	1.963	1.386	1.340	2.228	3.227
biomass / item	5.096	4.430	51.19	17.73	3.334	5.732	1.874	2.634	4.369	3.066
S.D.	1.884	1.445	24.42	17.34	2.047	3.897	0.560	1.072	6.281	4.026
items /min.	0.670	1.208	0.293	0.880	0.911	0.492	0.670	0.776	0.663	0.814
S.D.	0.509	0.522	0.135	0.415	0.536	0.213	0.651	0.441	0.443	0.569
paces / min.	51.6	32.8	18.2	65.3	48.5	43.1	48.7	36.2	54.3	52.6
S.D.	16.98	8.66	14.76	13.17	14.37	9.91	12.27	15.89	20.57	23.90
paces / item	118.0	31.5	64.3	82.8	62.2	114.8	110.4	64.9	108.5	99.9
S.D.	77.33	14.92	60.31	30.80	41.42	81.98	82.34	57.11	78.19	80.90
probes / min.	5.51	4.25	2.68	1.20	5.06	3.98	4.12	4.59	2.97	4.09
S.D.	2.34	1.01	0.78	0.98	2.00	5.71	1.61	1.58	3.73	2.46
probes / item	11.62	3.93	10.25	1.24	6.54	9.80	9.25	7.92	4.42	7.02
S.D.	7.30	1.63	5.10	0.73	3.70	12.55	7.99	5.89	4.06	6.11
% success of probing	8.6	24.7	9.7	40.3	14.8	8.6	10.8	12.6	11.9	10.5
sex score	3.1	4.0	3.1	3.4	2.9	2.6	3.0	2.6	3.1	2.6
sample size	18	6	9	5	15	16	6	19	47	11

For details of abbreviations see Table 1. S.D. - Standard deviation

TABLE 8. THE PROPORTIONS OF EACH TYPE AND SIZE (RELATIVE SIZE) OF PREY TAKEN ON EACH AREA OF SEAL SANDS IN MAY AND JUNE.

PREY TYPE / (PREY SIZE) AREA -	MWB	MWC	MW	GW	GB	GC	SM	SC	CB	EC
worms	100.0	97.2	0.0	50.0	97.0	84.2	100.0	100.0	53.0	73.8
(0-¼ bill length)	15.8	50.0	0.0	27.3	50.0	40.7	73.7	56.2	57.5	80.0
(¼-½ bill length)	45.6	32.4	0.0	54.5	40.6	40.7	21.0	31.5	40.0	16.8
(½-¾ bill length)	19.3	8.8	0.0	18.2	4.7	15.6	5.3	6.8	2.5	3.2
(¾-1 bill length)	7.0	5.9	0.0	0.0	1.6	3.1	0.0	0.0	0.0	0.0
(unknown)	12.3	2.9	0.0	0.0	3.1	0.0	0.0	5.5	0.0	0.0
surface items	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	43.0	19.0
crabs	0.0	2.8	100.0	50.0	3.0	15.8	0.0	0.0	4.0	7.1
(x2 bill width)	0.0	100.0	36.4	81.8	50.0	100.0	0.0	0.0	83.4	100.0
(x3 bill width)	0.0	0.0	9.1	9.1	50.0	0.0	0.0	0.0	16.6	0.0
(x4 bill width)	0.0	0.0	27.3	9.1	0.0	0.0	0.0	0.0	0.0	0.0
(unknown)	0.0	0.0	27.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0

For details of abbreviations see Table 1.

These results were obtained directly from observational data. The calculation of mean biomass and calorific intake rates, however required additional information, namely the calorific content and biomass of the different types and sizes of prey. Details of how this information was obtained, and of how biomass and calorific intake rates were calculated, are given in appendix 3.

In May and June data were was collected on all feeding areas used by curlew, however there were was insufficient data to consider the results from the two months sep~~e~~arately. In July data ~~was~~ were collected only on the major feeding areas (Central Bank, Greenabella Bank and Greenabella Channel). These results are compared to those collected on the same areas in May and June, in section 4.5.2.

Estimates of mean biomass and calorific intake rate, for each feeding area, are also listed in Table 7. These are discussed below in relation to how food was obtained (in terms of the area searched, the numbers and types of prey taken etc.). These data may be helpful in providing evidence of the foraging strategies employed, and/or the conditions under which feeding took place. The results for each feeding area are discussed below, and are presented in descending order of "profitability".

1) Mid Tide Wall (MW). On this area crabs were the only prey taken. Pace rates, "probe" rates and capture rates were low, possibly because curlew found it difficult to find crabs among the rocks of the MW, and so had to move slowly and spend a long time looking for movements which might betray a crab's position. However, the high calorific content and biomass of crabs resulted in calorific and biomass intake rates being higher on this area than on any other, despite the low capture rates.

2) Greenabella Wall. On this area crabs comprised 50% of the food items taken. Most of these crabs were small, so although the mean capture rate was more than twice that on the MW, the calorific and biomass intake rates were lower. Most of the crabs caught were taken from among the rocks or were picked up from the mud just to the east of the reclamation wall. The high pace rates observed are likely to have been due to curlew walking long distances along the mud at the base of the reclamation wall in order to find crabs. Although worms were also taken, they were usually taken within a very short distance of each other. Probe rates were very low, but the proportion which were successful was high, suggesting that curlew may have probed for worms only when the chances of successful capture were high.

The Greenabella Wall and MW were the only areas on which crabs were the major food items in the diet. Although the carapace and the tips of the legs and claws were removed from crabs larger than 2·0cm, before their biomass and calorific contents were determined, these crabs contained many other hard parts which are unlikely to be assimilated by curlew. It is possible then, that the "food value" of crabs, and hence the relative profitability of feeding on these areas, may have been overestimated.

3) Mid Tide Wall Channel (MWC). On this area calorific and biomass intake rates were higher than on any of the other feeding areas on which worms comprised the most numerous food items in the diet. This was due to the high proportion of large worms taken, and high capture rates. The high capture rates were due to a high proportion of successful probes rather than a high probe rate. Probe rates were moderate and pace rates low.

4) Mid Tide Wall Bank (MWB). On this area an even greater proportion of large worms were taken than on the MWC. Capture rates, however were lower, due to the high proportion of probes which were unsuccessful. This resulted in lower biomass and calorific intake rates on the MWB than on the MWC. Mean paces per prey, like pace rates and probe rates, were high, indicating that curlew may have had to search a wide area to find suitable prey.

5) Greenabella Bank. On this area the proportion of large worms taken was much lower than on the MWB or MWC. Prey capture rates, however, were the second highest of all feeding areas observed. Pace rates, probe rates and the proportion of probes which were successful were moderately high.

On the following four areas calorific intake rates were similar. These areas are ranked equal in profitability.

6) Greenabella Channel. On this area the proportion of large worms taken was greater than on the Greenabella Bank, but lower than on the MWB or MWC. Prey capture rates, however, were lower than on the Greenabella Bank. This resulted in lower calorific intake rates. The low prey capture rates were due to a high proportion of unsuccessful probes. Probe rates and pace rates were moderate.

7) Scallop Channel. On this area curlew took a greater proportion of small worms than on any of the areas discussed so far. Prey capture rates, however, were moderately high and resulted in calorific intake rates of a similar magnitude to those on the Greenabella Channel. Pace rates and probe rates were moderate.

8) Central Bank. On this area high pace rates, low probe rates and moderate capture rates were observed. This behaviour

is similar, but not as extreme as that observed on the Greenabella Wall. As on the Greenabella Wall, curlew captured prey on this area using 2 methods. These were:

a) Curlew searched the surface of the mud or Entermorpha, picked up and ate invertebrates (mainly worms on Central Bank, but also some crabs).

b) Curlew searched for worms buried in the mud. These were caught after probing.

On the Central Bank about 47% of the prey caught were taken using the first method. On most other areas the second method was the only method used. Most of the worms taken after probing were small worms with low biomass and calorific contents. An average invertebrate taken from the surface had a greater biomass and calorific content than an average worm taken after probing.

9) Eastern Channel. The feeding behaviour observed on this area was similar to that observed on the Central Bank, although the proportion of surface invertebrates taken was lower (about 26%). This resulted in a lower average calorific content of food items. This was "balanced", however, by higher probe and prey capture rates than on the Central Bank.

10) Scalloped Mud. Calorific and biomass intake rates were lower on Scalloped Mud than on any other area. This was due to a high proportion of small worms taken and a low prey capture rate.

To summarise, the results show that the highest biomass and calorific intake rates were observed on the MW and Greenabella Wall. This was due mainly to the high proportion of crabs taken on these areas. As already mentioned, the assimilation efficiences of feeding on crabs and worms may be different, and it is possible that the highest rates of energy assimilation may have occurred on other areas. After the MW and Greenabella Wall, the highest calorific intake rates were observed on the MWC, MWB and the Greenabella Bank, and it seems likely that these were the most profitable of the areas on which worms were the most numerous food items taken. The three areas where the highest pace rates were observed (Greenabella Wall, Central Bank and Eastern Channel) were also the three areas where surface items were taken. These surface invertebrates had a higher average biomass and calorific content than average buried worms taken on the same area. It is possible that curlew actively searched for these larger food items. Whether curlew also selectively preyed upon larger buried items is not clear, as there was insufficient time during this project for extensive sampling of feeding areas.

Clues about the foraging strategies employed by curlew may, however, be obtained by comparing the feeding behaviour and food intake rates, with those observed at other times during the season.

4.5.2. Seasonal variations in feeding behaviour and feeding rates.

The results for July are presented with the corresponding results for May and June in Tables 9 and 10. On the Central Bank, calorific intake rates were significantly higher in July than in May or June ($d=2{\cdot}29$, $p<0{\cdot}05$). On the Greenabella Channel calorific intake rates were also higher in July, but this result was not statistically significant ($t=1{\cdot}71$, $p=0{\cdot}096$). On the Central Bank, probe rates, prey capture rates and the proportion of probes which were successful, were significantly higher in July. On the Greenabella Channel similar results were obtained; however, only the difference

TABLE 9. SEASONAL VARIATION IN FEEDING RATES AND FEEDING BEHAVIOUR.

FEEDING RATES &	AREA -	CENTRAL BANK		GREENABELLA CHANNEL		GREENABELLA BANK	
FEEDING BEHAVIOUR	MONTH -	M & J	JULY	M & J	JULY	M & J	JULY
k cals /minute		0.110	0.155	0.103	0.152	0.155	0.140
S.D.		0.089	0.103	0.049	0.104	0.120	0.105
k cals / item		0.184	0.150	0.232	0.189	0.162	0.180
S.D.		0.193	0.072	0.144	0.094	0.066	0.107
biomass / min. (gms.x10^{-2})		2.469	2.945	2.687	2.917	3.123	2.608
S.D.		2.228	2.182	0.144	2.010	2.488	1.916
biomass / item (gms.x10^{-2})		4.369	2.883	5.732	3.562	3.334	3.367
S.D.		6.281	2.127	3.897	1.643	2.047	1.963
items / min.		0.663	1.028	0.492	0.922	0.911	0.800
S.D.		0.443	0.559	0.213	0.691	0.536	0.458
paces / min.		54.31	44.76	43.10	29.03	48.52	58.81
S.D.		20.57	14.20	9.91	12.17	14.37	11.10
paces / item		108.5	62.5	114.8	41.4	62.2	119.4
S.D.		78.19	56.61	81.98	26.77	41.42	102.96
probes / min.		2.97	3.72	3.98	4.45	5.06	3.69
S.D.		3.73	1.17	5.71	1.71	2.00	0.48
probes / item		4.42	4.88	9.80	6.08	6.54	6.67
S.D.		4.06	3.95	12.55	4.32	3.70	5.51
% success of probing		11.9	19.2	8.6	16.3	14.8	15.0
sex score		3.1	2.6	2.6	2.7	2.9	2.6
sample size		47	50	16	18	15	9

S.D. - Standard deviation M & J - May and June

TABLE 10. SEASONAL VARIATION IN THE PROPORTIONS OF EACH TYPE AND SIZE (RELATIVE SIZE) OF PREY TAKEN.

PREY TYPE /	AREA -	CENTRAL BANK		GREENABELLA CHANNEL		GREENABELLA BANK	
(PREY SIZE)	MONTH -	M & J	JULY	M & J	JULY	M & J	JULY
worms		53.0	98.4	84.2	98.8	97.0	100.0
(0-¼ bill length)		57.5	48.8	40.7	48.2	50.0	54.0
(¼-½ bill length)		40.0	39.7	40.7	39.8	40.6	29.7
(½-¾ bill length)		2.5	6.7	15.6	10.8	4.7	13.5
(¾-1 bill length)		0.0	0.0	3.1	1.2	1.6	2.7
(unknown)		0.0	4.8	0.0	0.0	3.1	0.0
surface items		43.0	1.2	0.0	0.0	0.0	0.0
crabs		4.0	0.4	15.8	1.2	3.0	0.0
(x2 bill width)		83.4	0.0	100.0	100.0	50.0	0.0
(x3 bill width)		16.6	100.0	0.0	0.0	50.0	0.0
(x4 bill width)		0.0	0.0	0.0	0.0	0.0	0.0
(unknown)		0.0	0.0	0.0	0.0	0.0	0.0

M & J - May and June

in prey capture rate was statistically significant.

On the Greenabella Bank calorific intake rates were not significantly different in July to those observed in May and June. Pace rates, probe rates and all those other aspects of curlew feeding behaviour that were quantified, also showed no significant seasonal variation.

On the Greenabella Channel curlew took a greater proportion of small worms, and a lesser proportion of large worms and crabs, in July than in May and June. On the Central Bank the lower average calorific content of food items in July was due mainly to a lesser proportion of surface items in the diet.

Data on the feeding behaviour of curlew were also collected by Knights (1974), who observed curlew feeding on Seal Sands (Greenabella Bank) during the autumn, winter and spring (1973-1974). The pace rates and probe rates he measured were about twice as great, during these seasons, as those measured by myself in the summer. In the autumn, prey capture rates were also about twice as great as those measured, on the same area, in July. Knights also measured the proportion of different sizes of worms taken. His results show that all the worms taken were within the size range < $\frac{1}{4}$-$\frac{1}{2}$ bill length. However, in the summer, about 11% of all worms taken, on the same area, were estimated to be larger than $\frac{1}{2}$ bill length. These differences, however, might have resulted from differences in "estimates" of worm length made by different observers.

Seasonal variations in curlew feeding behaviour are discussed in section 4.5.5.

4.5.3. Variations in feeding rates and feeding behaviour in relation to tidal levels.

Sufficient data to compare the feeding rates of curlew at different stages of the tidal cycle were obtained only from the Central Bank. These results are shown in Table 11 and Figs. 19-21. The results of a similar study by Knights (1975) are also shown (Table 11). These data were collected from the Greenabella Channel during the 1974-1975 winter.

In all months, the lowest prey capture rates occurred between HW+7-9, when prefered feeding areas had been exposed for the longest period and were not yet affected by the flood tide. Peak prey capture rates occurred just before low water. In May and June the HW+7-11 prey capture rates were significantly lower than the HW+4-6 rates. In July the HW+6-7 and the HW+7-8 capture rates were the only capture rates that differed significantly. These results are similar to those of Knights (1975). Knights also reported an increase in feeding success (not statistically significant) towards the end of the tidal cycle, when the flood tide is beginning to cover feeding areas and feeding is concentrated on the tide line. Similar results were found during this study.

No significant variation was found in mean calorific content of food items at different tidal levels, although the lowest values were found between HW+9-11 in all months.

In July no significant variation was found in mean calorific intake rates at different tidal levels. In May and June significantly higher calorific intake rates were achieved at tidal levels HW+4-6 than at HW+7-8 and HW+10-11, and higher rates at HW+3-4 than at HW+7-8. In all months peak calorific intake rates occurred just before low water.

4.5.4. Sex differences.

Using data collected from curlew foraging on the Central Bank, the mean feeding rate of each size class of curlew was calculated. Data on the feeding behaviour of

TABLE 11. VARIATIONS IN FEEDING RATES ON CENTRAL BANK IN RELATION TO TIDAL LEVELS.

HRS. AFTER HIGH WATER ——	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
FEEDING RATES- MAY & JUNE									
k cals / min.	0.112	0.164	0.164	0.209	0.128	0.069	0.120	——	0.071
S.D.	0.072	0.143	0.083	0.098	0.072	0.025	0.115		0.061
k cals / item	0.148	0.164	0.161	0.187	0.172	0.164	0.591	——	0.113
S.D.	0.054	0.035	0.034	0.035	0.050	0.039	0.701		0.057
biomass / min. (gms.x10^{-2})	2.325	3.540	3.619	4.191	2.527	1.595	3.197	——	1.373
S.D.	1.458	2.835	2.312	1.948	1.398	0.696	3.880		1.134
biomass / item (gms.x10^{-2})	3.087	3.649	3.472	3.764	3.371	4.019	17.133	——	2.183
S.D.	1.087	1.257	0.986	0.485	0.899	2.049	23.268		1.010
items / min.	0.717	0.975	1.012	1.111	0.725	0.436	0.342	——	0.567
S.D.	0.337	0.684	0.451	0.521	0.320	0.054	0.305		0.208
sample size	6	15	16	9	8	10	4		3
JULY									
k cals / min.	0.137	0.131	0.116	0.173	0.168	0.142	——	0.126	——
S.D.	0.153	0.110	0.091	0.130	0.093	0.116		0.112	
k cals / item	0.156	0.124	0.157	0.161	0.126	0.199	——	0.104	——
S.D.	0.070	0.043	0.041	0.046	0.024	0.175		0.005	
biomass / min. (gms.x10^{-2})	2.617	2.459	3.090	3.156	3.030	3.295	——	2.370	——
S.D.	2.824	2.108	1.699	2.459	1.628	3.850		2.080	
biomass / item (gms.x10^{-2})	3.100	2.320	2.916	2.795	2.245	4.652	——	1.963	——
S.D.	1.336	0.764	0.777	0.970	0.501	5.841		0.152	
item / min.	0.800	0.925	1.086	1.051	1.275	0.757	——	1.200	——
S.D.	0.600	0.575	0.530	0.692	0.449	0.262		1.039	
sample size	3	8	16	8	6	6		3	
WINTER (P.J.KNIGHTS)									
items / min.	——	2.26	2.20	2.90	2.00	1.40	2.30	——	——
S.D.		0.35	0.27	0.38	0.33	0.25	0.39		
sample size		30	72	21	95	43	48		

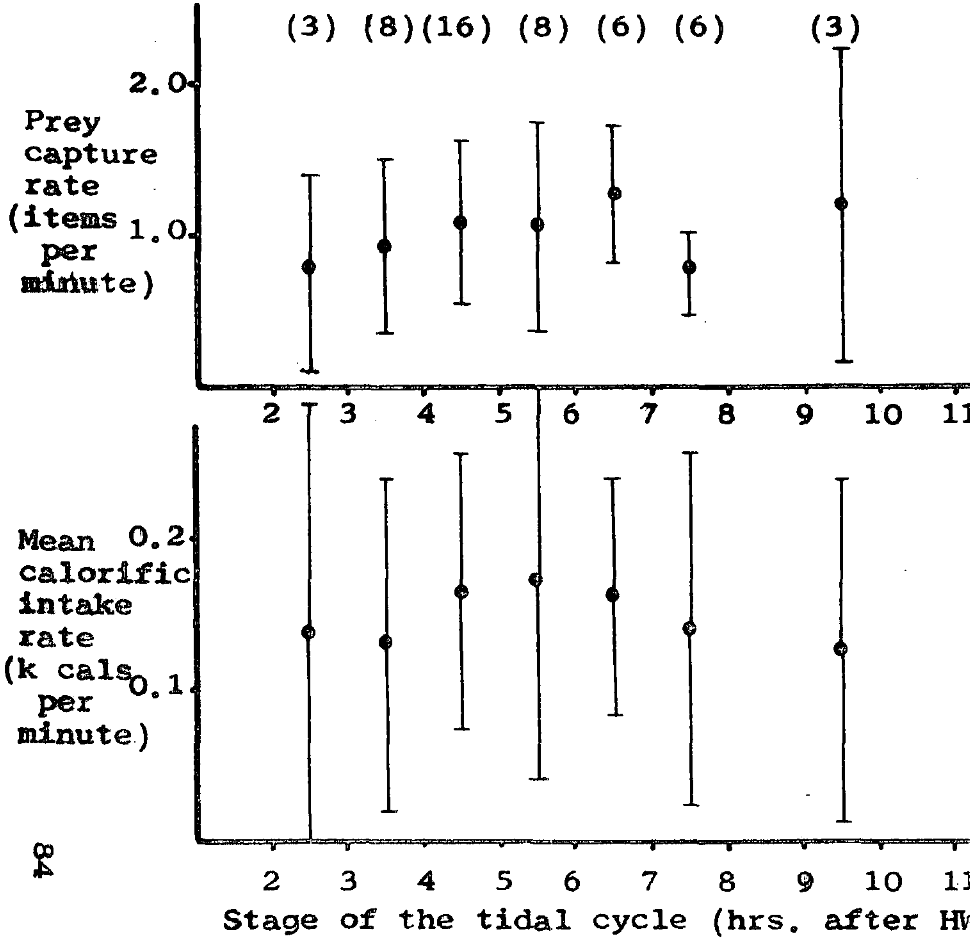


FIGURE 19 Variations in mean prey capture rate and calorific intake rates on the Central Bank in relation to the state of the tide, in July.
Vertical bars show the Standard Deviation, brackets indicate the sample size.

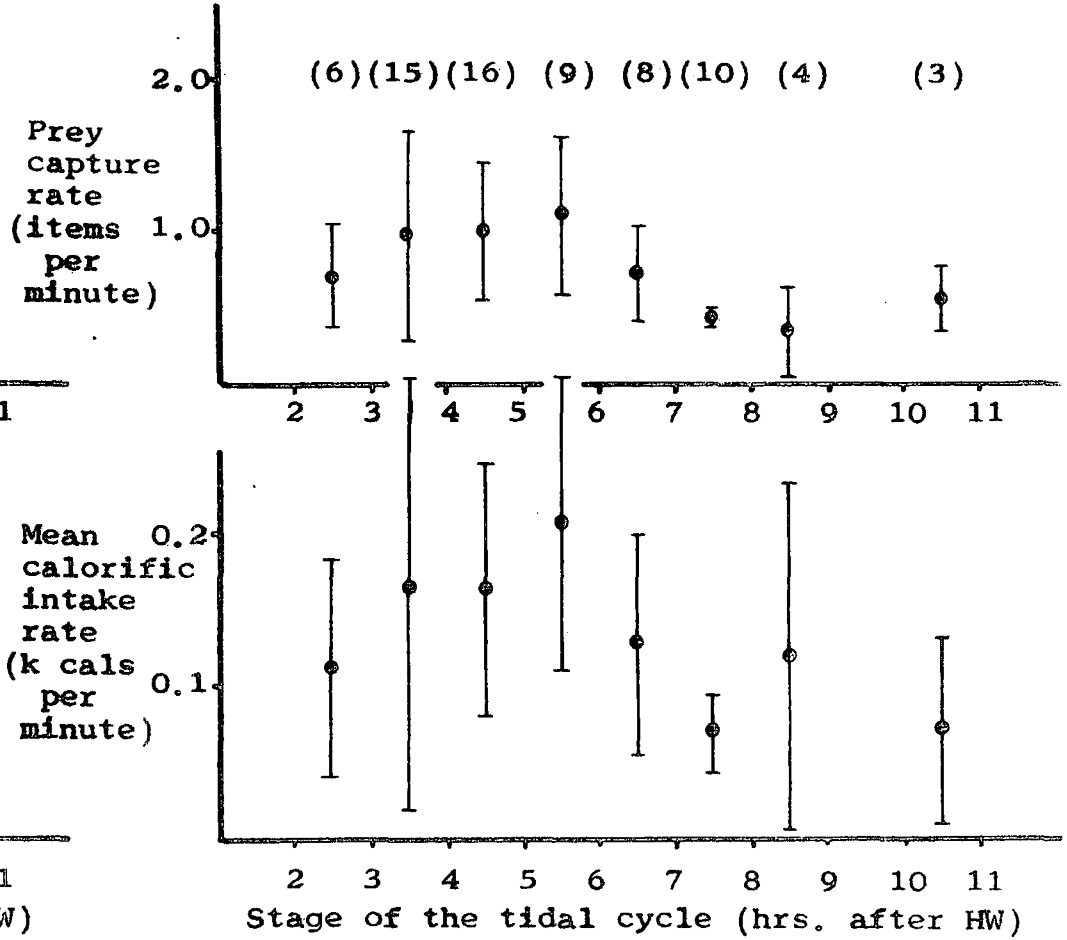


FIGURE 20 Variations in mean prey capture rate and calorific intake rates on Central Bank in relation to the state of the tide in June.
Vertical bars show the Standard Deviation, brackets indicate the sample size.

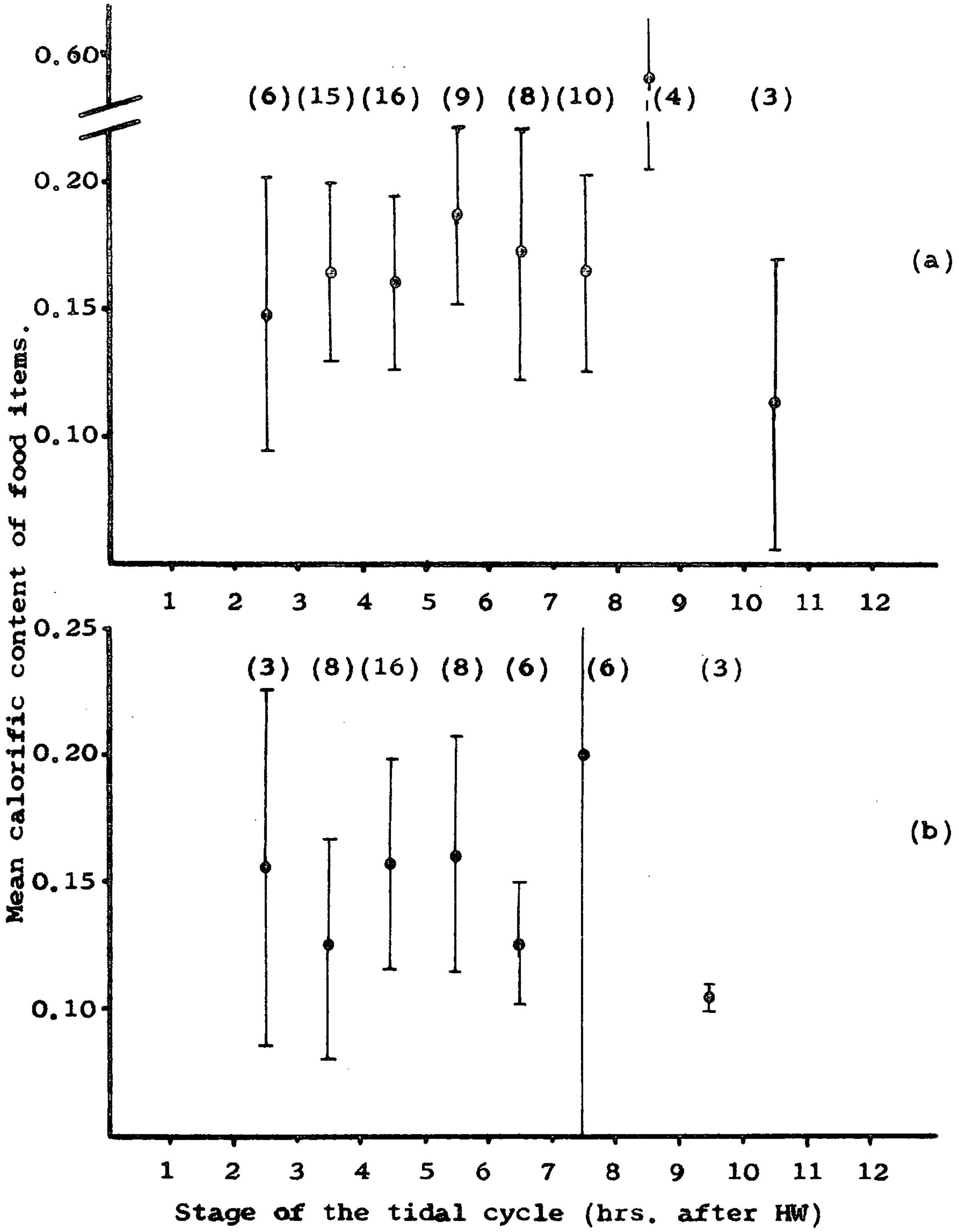


FIGURE 21 Variation in mean calorific content of food items taken on the Central Bank, in relation to the state of the tide, (a) in May and June, and (b) in July.
Vertical bars show the Standard Deviation, brackets indicate the sample size.

curlew were treated in a similar fashion. The results for May and June are presented sep~~e~~arately from those for July (Table 12).

In May and June the feeding rates and feeding behaviour of large males were not significantly different to those of small females. Large females, however, attained significantly higher biomass and calorific intake rates than either large males or small females. Large females also showed significantly higher prey capture rates and made significantly fewer probes per prey than small females, and took prey with significantly higher average calorific contents than large males.

In July biomass and calorific intake rates were also higher for females than for males, but these differences were not statistically significant. In July the prey items taken by small females had a significantly higher average calorific content than those taken by large males.

Sex differences in the feeding rates of curlew have also been reported by Townshend (1980). Townshend found that, except when substrate temperatures were low, males and females achieved similar capture rates, but that biomass intake rates were always higher in females. My results support these conclusions.

In calculating these results I included data obtained from the long observation periods on individual birds (these were all females). These data were not used in the calculation of mean feeding rates for each feeding area, as this would most likely have resulted in the overestimation of mean feeding rates on the Central Bank. In collecting data on the feeding rates on different areas, the curlew observed were chosen at random from those within observational range. The sex of each bird observed was scored in the following

TABLE 12. DIFFERENCES IN FEEDING RATES AND FEEDING BEHAVIOUR BETWEEN SIZE CLASSES OF CURLEW.

FEEDING RATES &	MONTHS -	MAY AND JUNE			JULY		
FEEDING BEHAVIOUR	SIZE CLASS -	LARGE MALE	SMALL FEMALE	LARGE FEMALE	LARGE MALE	SMALL FEMALE	LARGE FEMALE
k cals / min.		0.094	0.084	0.178	0.156	0.222	0.184
S.D.		0.054	0.061	0.109	0.118	0.146	0.117
k cals / item		0.132	0.244	0.176	0.144	0.186	0.168
S.D.		0.042	0.324	0.028	0.094	0.058	0.057
biomass / min. (gms.x10^{-2})		2.209	1.991	3.689	3.048	4.229	3.482
S.D.		1.638	2.003	2.320	2.610	2.692	2.232
biomass / item (gms.x10^{-2})		3.114	6.233	3.654	2.874	3.479	3.170
S.D.		1.601	10.603	0.614	2.905	1.298	1.056
items / min.		0.716	0.432	0.996	1.090	1.168	1.040
S.D.		0.379	0.167	0.544	0.639	0.609	0.573
paces / min.		48.57	58.86	53.88	43.59	40.30	40.62
S.D.		16.18	21.87	22.29	10.94	15.00	22.37
probes / min.		2.561	2.099	2.430	3.840	3.825	2.990
S.D.		2.226	1.886	1.773	1.178	1.406	0.667
probes / item		3.986	5.439	2.998	5.415	3.948	3.642
S.D.		2.411	4.851	3.163	5.044	2.058	2.163
sample size		14	15	42	26	49	5

way; small male (1), large male (2), small female (3), and large female (4). The mean scores for each feeding area are listed in Tables 7 and 9.

4.5.5. Discussion: The foraging strategies of curlew in relation to optimal foraging theory.

Recently much attention has been focussed on the idea that the selection of "efficient" predators has played an important role in the evolution of the feeding behaviour of predators. Efficient foraging may be defined in a number of ways, depending on the particular needs of the predator. An efficient predator may be attempting to maximise its immediate net rate of intake of food (or energy); maximise its immediate net rate of intake of an essential nutrient; or maximise its long-term intake at the expense of short-term efficiency (Krebs and Davies 1978). Much of the recent work on feeding behaviour has been concerned with testing "optimal foraging" models based on the hypothesis that efficient predators make decisions which maximise their net rate of food intake during foraging. Unfortunately the predictions of some optimal foraging models could not be tested with my results, as data on the densities of different types and sizes of prey, in different areas, were not collected. In this section the profitability of (a) feeding on different areas, and (b) of different foraging strategies employed on the same areas, will be discussed in relation to the feeding behaviour of curlew, and with reference to current ideas on optimal foraging.

One of the decisions a predator must make is where to forage. Optimal foraging models predict that optimal predators, feeding on unevenly distributed prey, should forage preferentially on the most profitable patches, and include less profitable patches only when the availability of good places is low (Royama 1970, Hassell and May 1974). If only one prey type is involved, the profitability of a patch should depend on the density of available prey, as predators respond to increases in the density of their prey (up to certain limits) by increasing their rate of feeding (Holling 1965). The tendency to aggregate on the most profitable patches, however, may be counteracted by any mutual interference resulting from high densities of predators (Goss-Custard 1970). This interference may be in the form of; a) less time available for feeding due to increased social interactions; b) reduced availability of prey due to increased disturbance by predators; or c) lower densities of prey due to the increased rate of removal of prey at high predator densities.

Charnov (1976) predicts that an optimal predator should stay in each patch until its rate of intake drops to a level equal to the overall rate of intake for the habitat, and that a predator should not stay in a patch if it could do better by moving to another. This model also predicts that intake rates on all patches should be reduced to the same marginal value.

On Seal Sands the highest densities of curlew occurred on three areas: MW, MWB and MWC, in May and early June. High densities of curlew were obvious on these areas because of the small size of the areas and the high proportion of curlew (30-40%) using them at low water. With the exception of high densities of curlew feeding on the Greenabella Channel in July, variations in the densities of curlew feeding on other areas at low water (when all areas were available), were not obvious. The Mid Tide Wall areas were also among the most profitable feeding areas (the areas on which the greatest net calorific intake rates were attained) in May and June. The other highly profitable feeding areas were the Greenabella Wall and, to a lesser extent, the Greenabella Bank. These areas did not appear to support high densities of curlew.

In May and June the Greenabella Wall was used by no more than 3 curlew at any one time. It is likely that this was due to a particularly low density of preferred prey (crabs), as it appeared that curlew had to search a wide area during foraging (see pg.75). Given the small size of this area and the difficulty curlew had in locating prey, the likely effects of an increase in the number of curlew using this area would be a marked drop in intake rates, as even a small increase in curlew numbers would result in a large increase in competition for preferred prey. On the Mid Tide Wall areas the number of curlew which regularly used these areas was much greater than on the Greenabella Wall, and, unlike the Greenabella Wall, it is probable that an increase in the number of curlew using these areas could have occurred without causing intake rates to fall below the values for other areas.

Although, with the data collected, it was not possible to compare the densities of curlew with the densities of their prey, the results agree with the predictions of optimal foraging models in two respects:

a) Intake rates were of a similar (marginal?) value on four feeding areas in May and June, and on the 3 areas observed in July.

b) Curlew preferred the more profitable Mid Tide Wall areas to other areas.

One aspect of these results does not agree with the predictions of optimal foraging models. If curlew were feeding optimally, a greater density of curlew should have fed on the Mid Tide Wall areas, as predicted by Charnov (1976). Possible reasons why this did not occur include:

1) The intensity of aggresive or other social interactions at high curlew densities prevented other curlew from feeding on the Mid Tide Wall areas.

2) The high estimates of intake rates were due to a bias, in the choice of foraging curlew that were observed, towards the more successful females.

3) The curlew which did not feed on the Mid Tide Wall areas were not able to feed as efficiently as those which did, and would have obtained lower, not higher, intake rates by feeding on those areas.

4) Curlew did not feed optimally.

Each of these possibilities is discussed below.

1) During May and June aggresive interactions between curlew were observed on very few occasions, however, this observation is insufficient to dismiss 1).

2) Although the possibility of a bias towards females, in the choice of foraging curlew observed, cannot be dismissed, it must be noted that mean sex scores (see pg.88) were similar on the MWB, MW and Central Bank, yet estimates of mean intake rate were different. Option 2) thus appears unlikely to be true.

3) The proportion of curlew observed foraging that were female was greater on the Mid Tide Wall areas, the Greenabella Wall, Central Bank and Greenabella Bank than on the other feeding areas. While it is possible that these results were simply due to innadequate sampling, it is also possible that they may represent a true difference in the sex ratios on different

areas. On the MWB, MWC and, to a lesser extent, the Greenabella Bank, a greater proportion of large worms were taken than on other areas. Large worms have deeper burrows than small worms, which may render them less available to the shorter billed males than to the larger females. Similarly the crabs taken on the MW and Greenabella Wall may also have been less available to males than females. If the differences in success between males and females were great enough on these areas, it is possible that males would find feeding less profitable on the Mid Tide Wall areas than on other areas. Although this does not explain why more females did not use the more profitable areas, it must be remembered that, in May and early June, between 30% and 40% of the population were present on these areas at low water. The number of females not feeding on these areas at these times may therefore have been low. The high numbers of females observed foraging on the Central Bank in May and June were mostly observed outside the low water period (HW+4-8) or in late June.

4) Although it is possible that curlew were not feeding optimally in May and June, two aspects of the results, in particular the high densities of curlew on the most profitable areas, are in agreement with the predictions of optimal foraging theory. Further work is therefore needed to show whether or not curlew selected feeding areas in an optimal way.

Other decisions predators make during foraging include how to search for prey and what type of prey to take. Models of optimal diets (MacArthur and Pianka 1966; Emlen 1966; Schoener 1971; Pulliam 1974; Charnov 1976) predict that animals will feed most efficiently if they accept all potential food items encountered when food is scarce, but show greater selectivity towards the more profitable food items as food becomes common. MacArthur and Pianka (1966) define the most profitable prey items as those with the highest E/h values, where E is the energy content of the prey and h is the handling time.

In this study the prey items with the highest energy contents are assumed to be the most profitable food items. The few handling times measured were highly variable, and were dependent upon whether or not curlew washed prey items before swallowing them and therefore on the distance from the capture site to the nearest washing pool, rather than on prey size. In July 30% of all worms taken on the Central Bank and 65% of those taken on the Greenabella Channel were washed before being eaten. On both areas similar values of % of worms washed were obtained for each size class of worms.

On two areas of Seal Sands (Central Bank and Greenabella Channel) curlew took a greater proportion of larger, more profitable prey items, in May and June than they did in July. If it is assumed that curlew fed with the same degree of selectivity in all months, there are 3 possible explanations for the observed differences in prey taken. A fourth explanation, involving differences in selectivity, is also possible. These are:

1) The density of available large prey was greater in May and June than in July.

2) The density of available small prey was lower in May and June.

3) The overall availability of potential prey items was lower in May and June, and the density of large prey items greater.

4) Curlew selectively preyed upon large prey items in May and June.

In discussing these possibilities, the following definitions and assumptions are made:

a) A prey is defined as available when its activity and depth in the mud enables a bird to both detect and capture it (c.f. Goss-Custard 1977a).

b) Probe rates and the proportion of probes which were successful are used as indicators of the availability of prey items.

c) Pace rates and the number of paces per prey are used as indicators of the area searched during foraging and the density of available prey.

The four possible explanations for why curlew may have taken a greater proportion of large prey items in May and June are discussed below.

1) If the density of available large prey decreased in July, without changes in the density or availability of other sizes, a lower overall density of available prey would result, and curlew would be expected to search a greater area during foraging. As pace rates and the number of paces per prey were much lower in July than in May or June, this is unlikely to be the cause of the lesser proportion of large prey taken in July.

2) If the density of available small prey increased in July, a greater overall density of available prey would result. Data on pace rates and the number of paces per prey does not refute this hypothesis.

3) On the Greenabella Channel and the Central Bank probe rates and the proportion that were successful were lower in May and June than in July.

This suggests that the prey items taken in May and June were less easily captured, that is, were less available than the prey items taken in July. While this does not necessarily mean that the overall availability of all potential prey items was lower in May and June (this data could have resulted if large prey items were selectively preyed upon but were less available than small prey items) these data do not refute this hypothesis.

4) If curlew showed greater selectivity towards large prey items in May and June, pace rates and the number of paces per prey would be expected to be high as a result of curlew searching for particular prey types. As already mentioned the seasonal differences in the proportion of probes which were successful might be explained if large prey items were more difficult to capture than small ones. This indeed may occur as large worms have deeper burrows than small worms, and so may be able to escape curlew more easily. Optimal foraging models predict a decrease in selectivity as the density of available prey decreases. The density of available prey items may have been reduced in July due to the increased predation and disturbance resulting from higher curlew densities.

Although it is not possible to determine, from the data collected, which of alternatives 2, 3 or 4 might have occurred, option 4 is considered the most likely. The decrease in the use of two of the preferred feeding areas (MWB and MWC) and of Scallop Channel in June suggests that, overall the densities of available prey may have been greater in May and June than in July. Also the increased disturbance to worms caused by the increased numbers of curlew and other waders using Seal Sands in July would be expected to result in a lower overall availability of prey in July.

If, as seems likely, it is assumed that curlew showed greater selectivity towards large prey items in May and June, then it must be concluded that curlew were not selecting prey in a manner which maximised their net rate of intake of food. On the Greenabella Channel and Central Bank calorific and biomass intake rates were lower in May and June than in July. Judging from the results of Knights (1975) it seems likely that curlew also showed greater selectivity towards large food items in July than they did in autumn.

A preference for large rather than small worms has also been reported for redshank (Goss-Custard 1977a), however, in this case it was demonstrated that redshank varied their responsiveness to small worms in such a way as to maximise biomass ingestion rates. Goss-Custard (1977b) also reported that redshank preferred Corophium volutator to Nereis; however this preference did not maximise calorific or biomass intake rates.

In the early summer months, non-breeding curlew have minimal energy demands, long hours of daylight in which to feed, and carry out very few other activities which might compete with foraging for time. This is in marked contrast to the situations in which the redshank data were collected, or the situations envisaged in optimal foraging models. While it appears unlikely that curlew were selecting prey types which maximised ingestion rates, the high pace rates, the high mean paces per worm, and the low success of probing do suggest an active search for large, difficult to capture prey, in May and June. What then are the reasons for the selection of large prey items? One possibility is that curlew were attempting to maximise their rate of intake of an essential nutrient. For example, large prey items, such as crabs and large worms, may contain greater concentrations of particular nutrients than small worms. Another possibility is that curlew were attempting to minimise the number of prey items ingested to meet their energy demands. This behaviour might be expected if curlew found worms slightly distasteful. The high incidence of washing of worms might also be explained by their distastefulness. These hypothesis are similar to those suggested by Goss-Custard (1977b) to explain why redshank preferred Corophium to Nereis.

4.6. Seasonal variation in the proportion of curlew moulting.

Estimates of the proportion of curlew at different stages of moult, obtained from photographs of 140 curlew taken on the 22nd August, are listed in Table 13. The stage of moult was determined by noting the last primary feather to have dropped (for examples see photographs pp 104-5). Estimates of the approximate dates on which birds, at different stages of moult, had started to moult, are also listed in Table 13. These estimates were based on data on the times taken to reach each stage of moult, obtained from Sach (1968) (see Fig 22).

On the 22nd August the Teesmouth curlew population was estimated to be about 460 birds. Using this estimate, and data on the changes in population size (section 4.1) earlier in the summer, the numbers and proportion of curlew moulting or starting moult, at different dates during the study, were estimated. These results are shown in Table 14 and Figs. 23 and 24.

TABLE 13. ESTIMATES OF THE PROPORTION OF CURLEW AT DIFFERENT STAGES OF MOULT, AND OF THE NUMBER MOULTING AT DIFFERENT DATES DURING THE STUDY.

STAGE OF MOULT REACHED	0	3	4	5	6	7	8	9	10a	10b
NUMBER OF CURLEW PHOTOGRAPHED, AT THIS STAGE OF MOULT	25	3	4	3	9	30	45	17	3	1
PERCENTAGE OF CURLEW PHOTOGRAPHED, AT THIS STAGE OF MOULT	17.9	2.1	2.9	2.1	6.4	21.4	32.1	12.1	2.1	0.7
ESTIMATED NUMBER OF CURLEW IN THE POPULATION AT THIS STAGE OF MOULT	82	10	13	10	30	98	148	56	10	3
TIME TAKEN TO REACH THIS STAGE OF MOULT (DAYS)	—	1	4	10	27	35	41	47	51	72
APPROXIMATE DATE OF THE START OF MOULT (DAY / MONTH)	—	21/8	18/8	12/8	26/7	18/7	12/7	6/7	2/7	11/6
TOTAL NUMBER OF CURLEW MOULTING OR STARTING MOULT AT THIS DATE	378	378	368	355	345	315	217	69	13	3

10a - primary 10 just dropped

10b - primary 10 half-grown

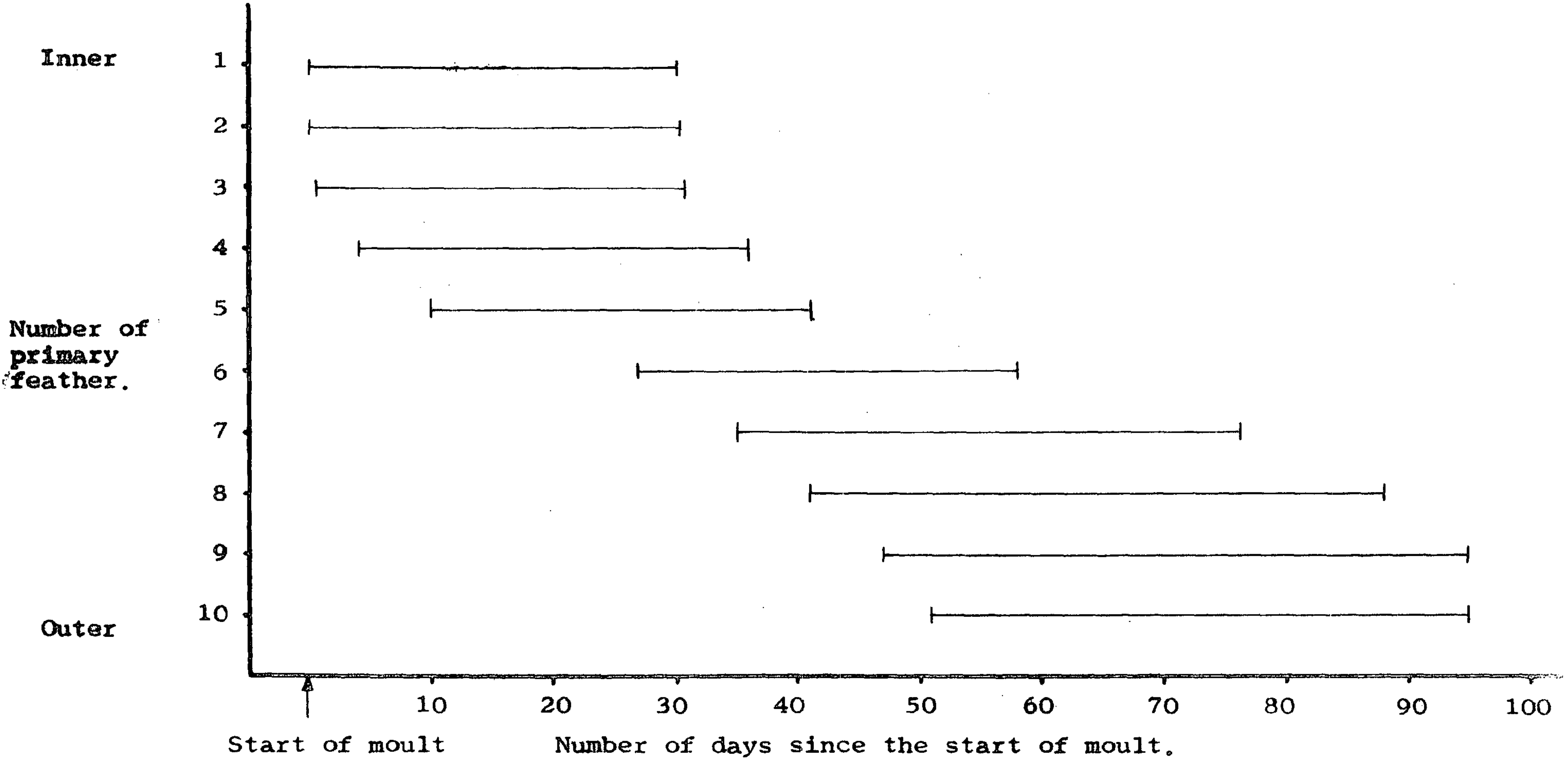


FIGURE 22 The approximate timing of the moult of each curlew primary in relation to the start of moult, after Sach (1968). Vertical bars indicate the timing, in relation to the start of moult, of the dropping of old feathers and the end of growth of new feathers.

TABLE 14. ESTIMATES OF THE PERCENTAGE OF CURLEW MOULTING, OR STARTING MOULT, AT VARIOUS DATES DURING THE STUDY.

DATE	NUMBER OF CURLEW MOULTING	POPULATION SIZE	PERCENTAGE MOULTING
11/6	3	143	2.1
29/6	5	160	3.1
2/7	13	180	7.2
6/7	69	225	30.7
11/7	188	320	58.7
12/7	217	345	62.9
18/7	315	444	70.0
20/7	327	450	72.7
25/7	344	450	76.4
28/7	347	450	77.1
2/8	352	460	76.5
12/8	355	460	77.2

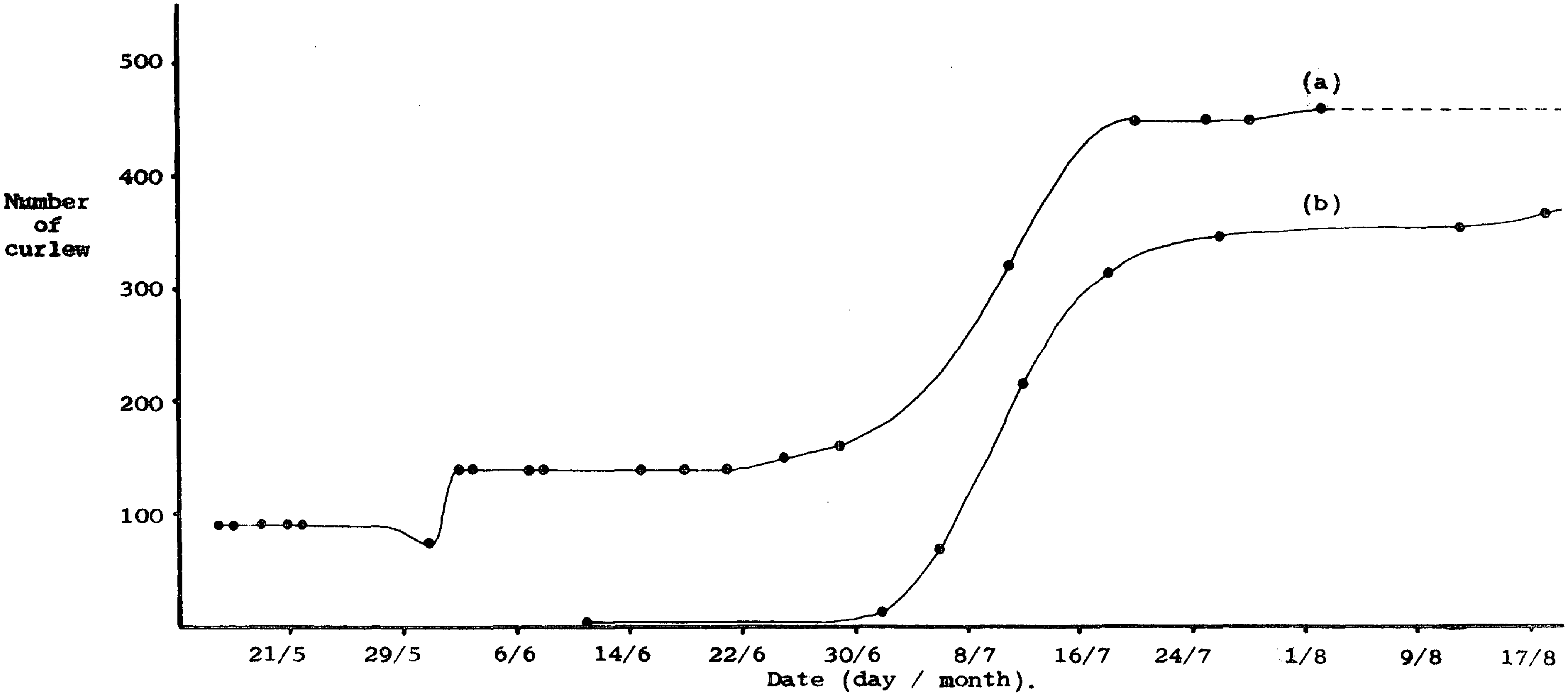


FIGURE 23 Seasonal changes in the number of curlew using Seal Sands (a), and in the number moulting (b).

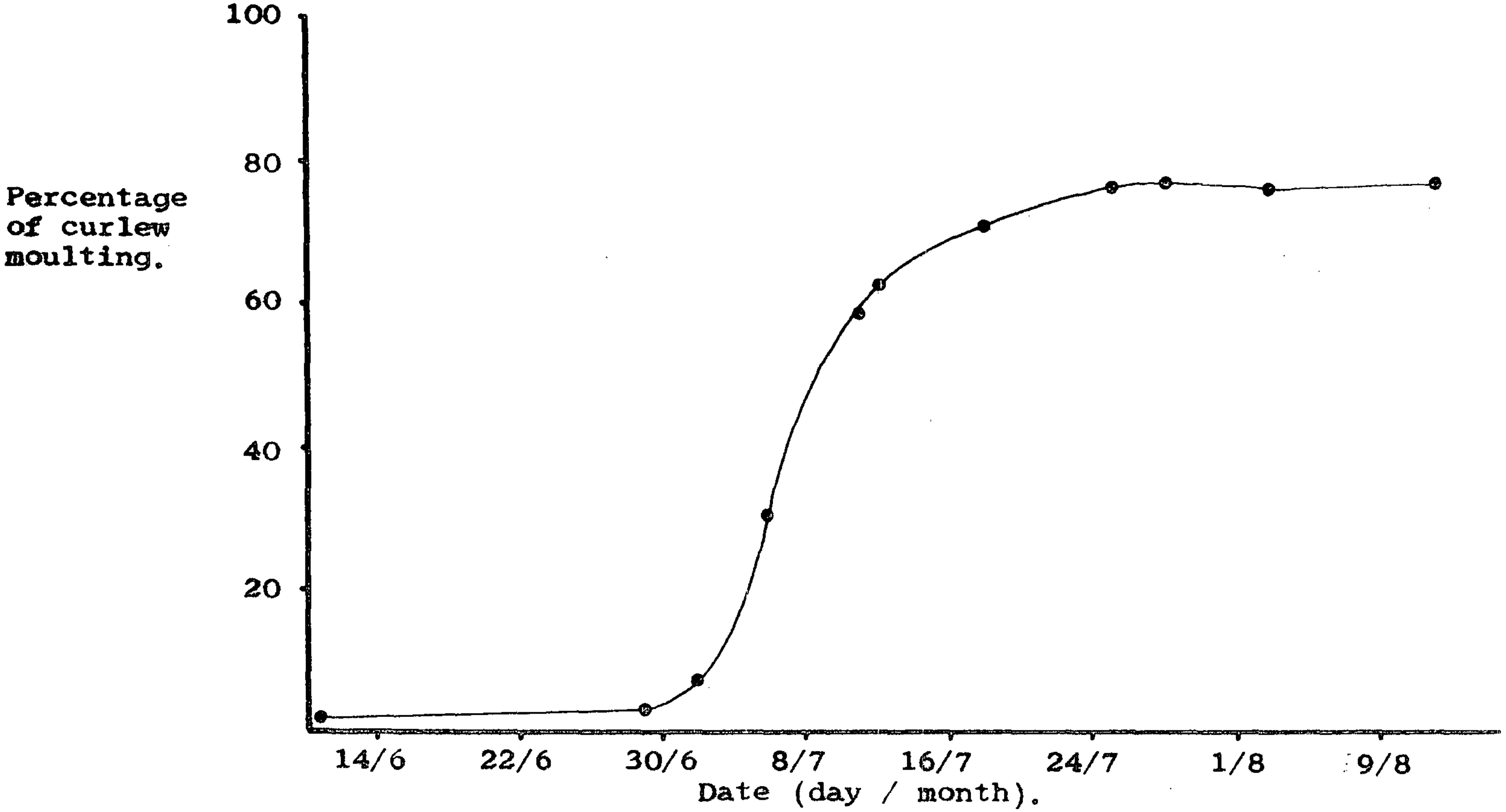
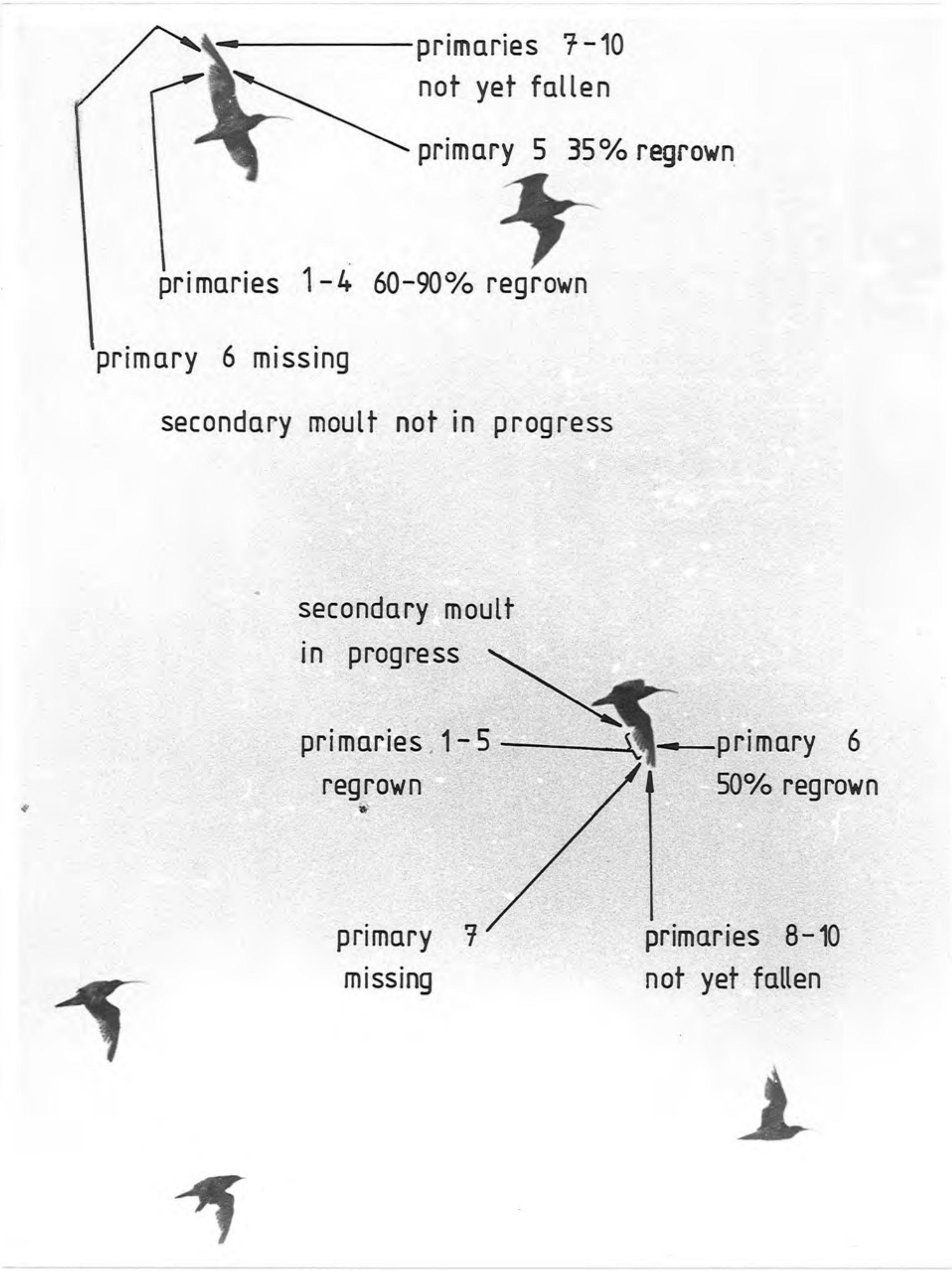
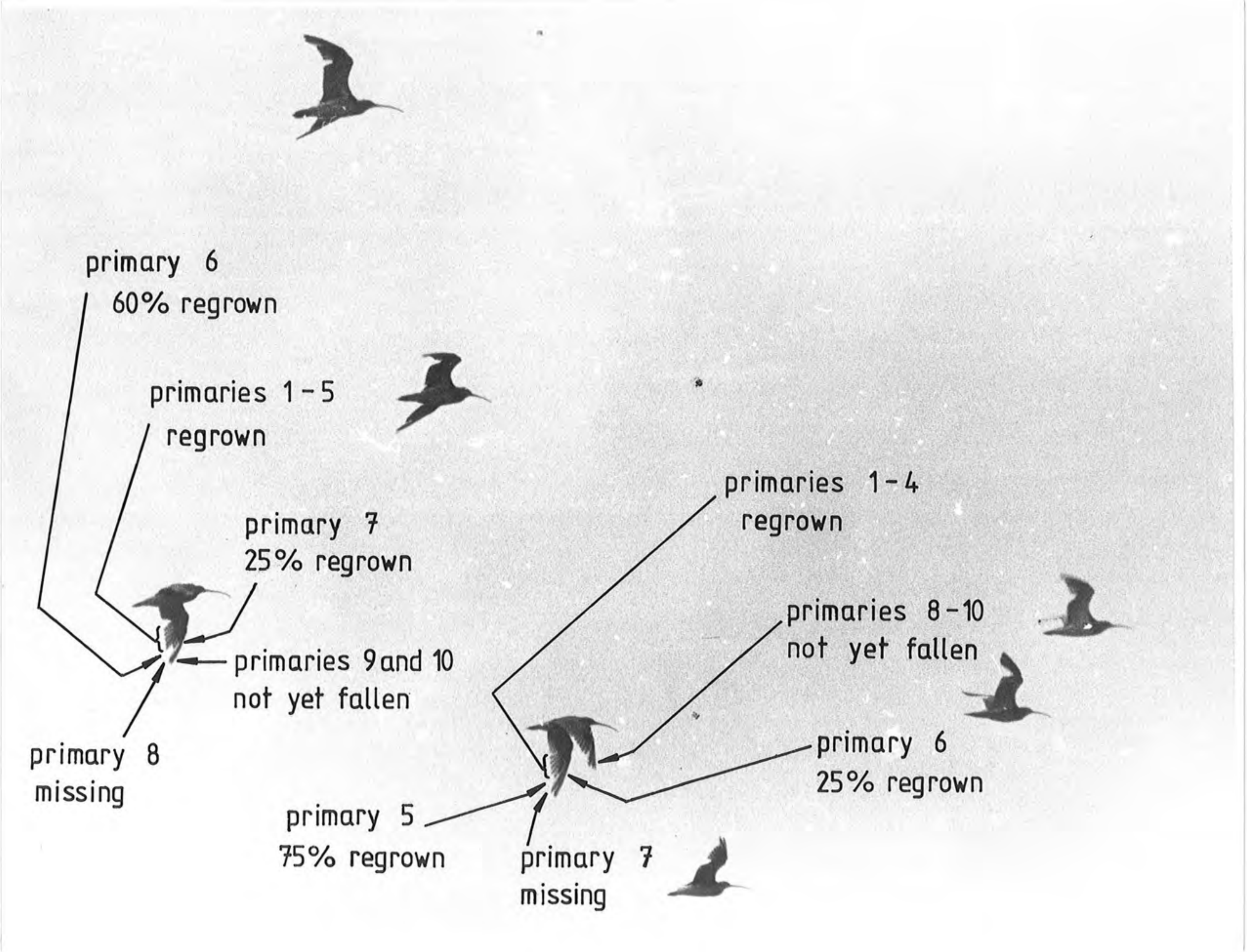


FIGURE 24 Seasonal changes in the proportion of curlew moulting.


primaries 7-10
not yet fallen
primary 5 35% regrown
primaries 1-4 60-90% regrown
primary 6 missing
secondary moult not in progress
secondary moult
in progress
primaries 1-5
regrown
primary 6
50% regrown
primary 7
missing
primaries 8-10
not yet fallen


primary 6
60% regrown
primaries 1 - 5
regrown
primary 7
25% regrown
primaries 9 and 10
not yet fallen
primary 8
missing
primaries 1 - 4
regrown
primaries 8 - 10
not yet fallen
primary 6
25% regrown
primary 5
75% regrown
primary 7
missing

4.7. Estimates Of Daily Food Intake.

4.7.1. Variations in estimates of the food consumed by an "average" curlew.

The number of calories consumed by an "average" curlew during a particular tidal cycle (C/Tc) was calculated using equation (4).

$$(4) \quad C/Tc = \frac{\Sigma \, GFTi \times Ici}{P}$$

GFTi = Gross feeding time on area i: The number of bird hours spent feeding on area i. (see table 1)

Ici = The calorific intake rate (in k cals /hr) measured on area i (see tables 7 and 9)

P = Population size.

As mentioned earlier, a small proportion of the feeding that was thought to have occured on Seal Sands was unobserved. The amount of unobserved feeding was estimated by assuming that those curlew present on the estuary but not observed were either feeding or not feeding in the same proportions as those that were observed (see pg.21). As most of the unobserved feeding was thought to have occured on either the Central Bank or Eastern Channel, the calorific intake rates of "unobserved" foraging curlew were assumed to be equal to the mean of the calorific intake rates on these two areas.

For tidal cycles occuring only in part during the hours of daylight (partial daylight tidal cycles), it was necessary to estimate calorific intake rates for the hours of darkness. Attempts to measure food intake rates at night were unsuccessful during this study. Comparable rates of prey capture at night and during the day, however, have been reported for curlew on Seal Sands by Knights (1974). Calorific and biomass intake rates at night were, therefore, assumed to be of a similar magnitude to those recorded during the daytime. As curlew were not observed to use the Mid Tide Wall areas (the areas of high profitability during the daytime) at night, nightime calorific intake rates were estimated in the same way as those for "unobserved" foraging curlew,

The biomass of food consumed by an "average" curlew during a particular tidal cycle (B/Tc) was calculated by substituting Ibi (The biomass intake rate in grams/hr measured on area i) for Ici, in equation (4).

Estimates of C/Tc and B/Tc for all tidal cycles observed are listed in Table 15. Figs.25-28 show variations in C/Tc and B/Tc in relation to the tide height for all daylight tidal cycles observed. Estimates of C/Tc and B/Tc made in different months are plotted seperately in Figs. 25-27. Estimates of C/Tc for all months are shown together in Fig.28. As with estimates of PFT, it was considered unwise to compare certain estimates of C/Tc and B/Tc because, even within a month, the conditions under which curlew were observed were not always identical. Differences included the degree of disturbance, differences in population size, or variations in the use of field areas (see pages 47-52). These "unreliable" estimates are represented by the same open symbols as used in section 4.4.

Within each month, variations in C/Tc and B/Tc, with tide height, were similar, and were also broadly similar to the variations in PFT reported in section 4.4. Many of the suggested causes of variation in PFT may, therefore, also be applied to variations in C/Tc and B/Tc.

TABLE 15. ESTIMATES OF C/Tc AND B/Tc FOR ALL TIDAL CYCLES OBSERVED

DATE	NUMBER OF CALORIES CONSUMED C/Tc (k cals)	BIOMASS OF FOOD CONSUMED B/Tc (grams)	TIDE HEIGHT (metres) HIGH WATER	TIDE HEIGHT (metres) LOW WATER	HRS OF DARKNESS DURING LOW-WATER PERIOD	POPULATION SIZE	% OF CURLEW MOULTING	MISC. IMFORMATION
16/5	25.58	5.29	5.1	0.5	0.00	91	0.0	(5.5)
17/5	29.69	6.16	5.0	0.6	0.00	91	0.0	(6.0)
19/5	44.89	10.43	4.6	1.2	0.00	91	0.0	(5.75)
21/5	34.84	8.31	4.2	1.8	0.00	91	0.0	(3.8)
22/5	39.21	9.40	4.1	2.0	0.00	91	0.0	(2.75)
31/5	45.36	11.27	4.8	1.0	0.00	73	0.0	(5.5)
2/6	41.33	10.60	4.8	0.9	0.00	143	0.0	(6.0)
3/6	35.75	8.71	4.7	1.1	2.00	143	0.0	(6.0)
8/6	9.09	2.10	4.2	1.2	0.00	143	2.0	
18/6	5.79	1.33	4.5	0.9	6.00	143	2.5	
18/6	25.43	6.25	4.6	1.4	0.00	143	2.5	bulldozer disturbance
21/6	11.57	2.58	4.0	1.5	3.50	143	2.7	
21/6	38.60	9.47	4.1	2.0	0.00	143	2.7	
25/6	28.55	6.71	4.3	1.6	0.00	150	2.9	
25/6	16.73	3.88	4.3	1.4	2.50	150	2.9	curlew 1st observed to fly towards fields
29/6	28.82	6.77	4.9	0.9	0.00	160	3.1	
29/6	8.68	1.92	4.8	0.9	5.25	320	3.1	
11/7	34.33	6.61	4.8	0.9	0.00	320	58.7	
11/7	17.98	3.77	4.8	1.0	3.80	320	58.7	
20/7	11.83	2.34	4.1	1.5	4.50	450	72.7	
20/7	33.61	6.44	4.2	1.8	0.00	450	72.7	
25/7	27.38	5.03	4.4	1.5	0.00	450	76.4	
25/7	10.34	2.06	4.4	1.4	2.75	450	76.4	
28/7	26.59	4.98	5.0	0.7	0.00	450	77.1	large flock of gulls present
28/7	8.76	1.75	5.0	0.8	5.00	450	77.1	
2/8	34.82	6.69	4.9	1.0	0.00	460	76.5	(6.0)

Brackets indicate the number of hours of darkness during the low-water period of the following (not observed) tidal cycle.

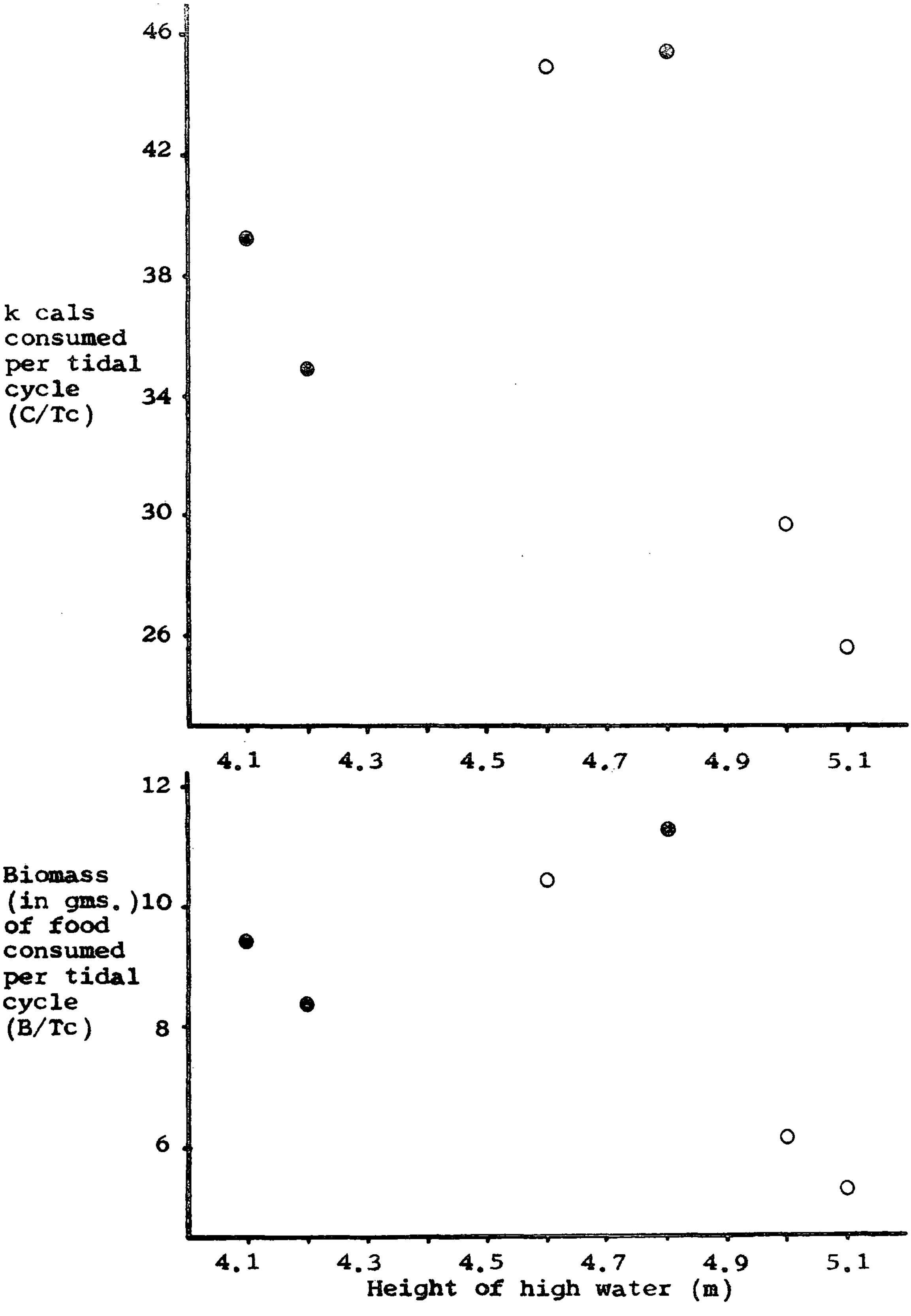


FIGURE 25 Variation in C/Tc and B/Tc in relation to tide height in May (population size 73-91 birds). Open circles indicate the early "unreliable" estimates (see text for details).

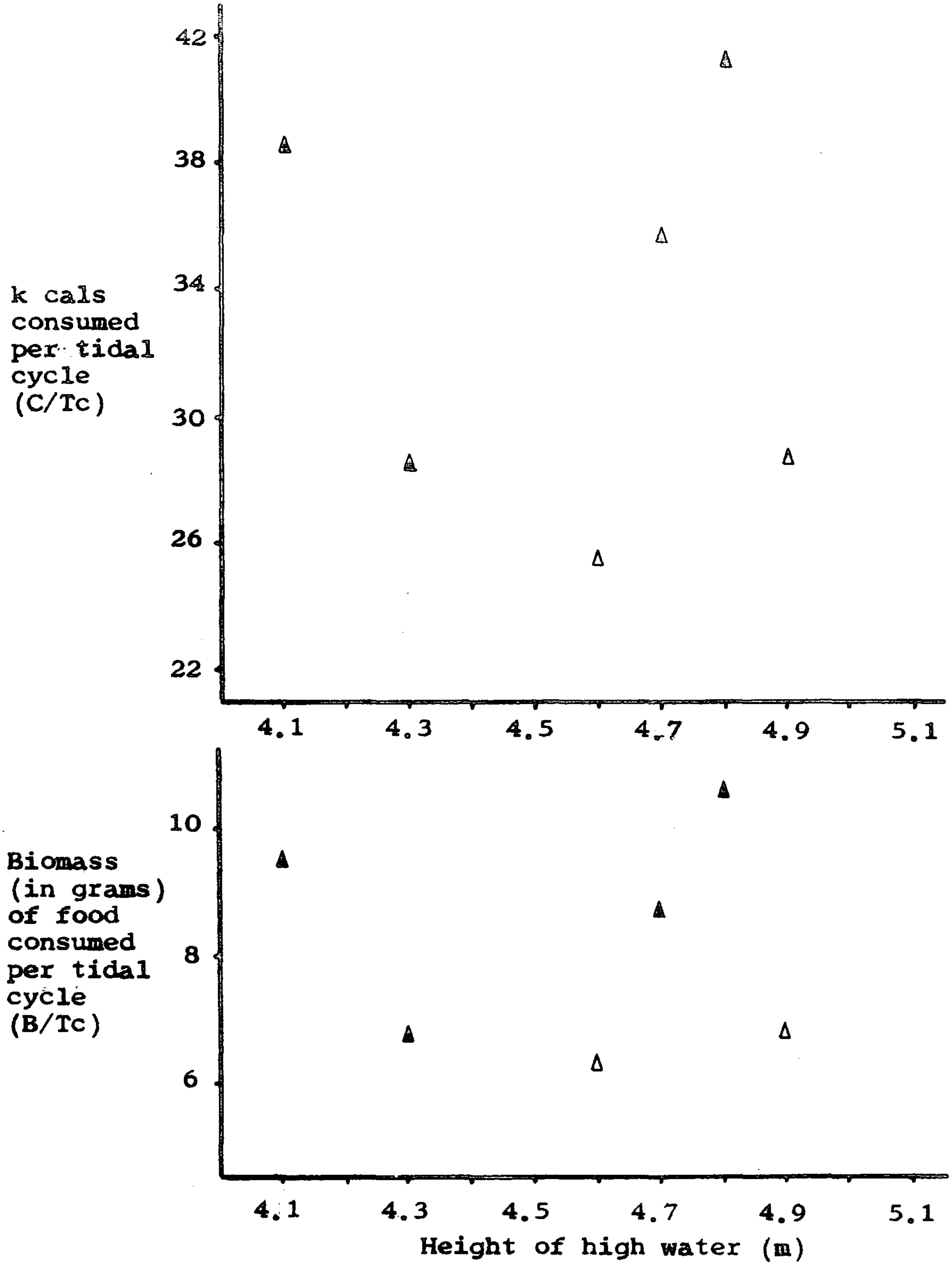


FIGURE 26 Variation in C/Tc and B/Tc in relation to tide height in June (population size 143-160 birds). Open triangles - estimates of C/Tc for June 18th & 29th.

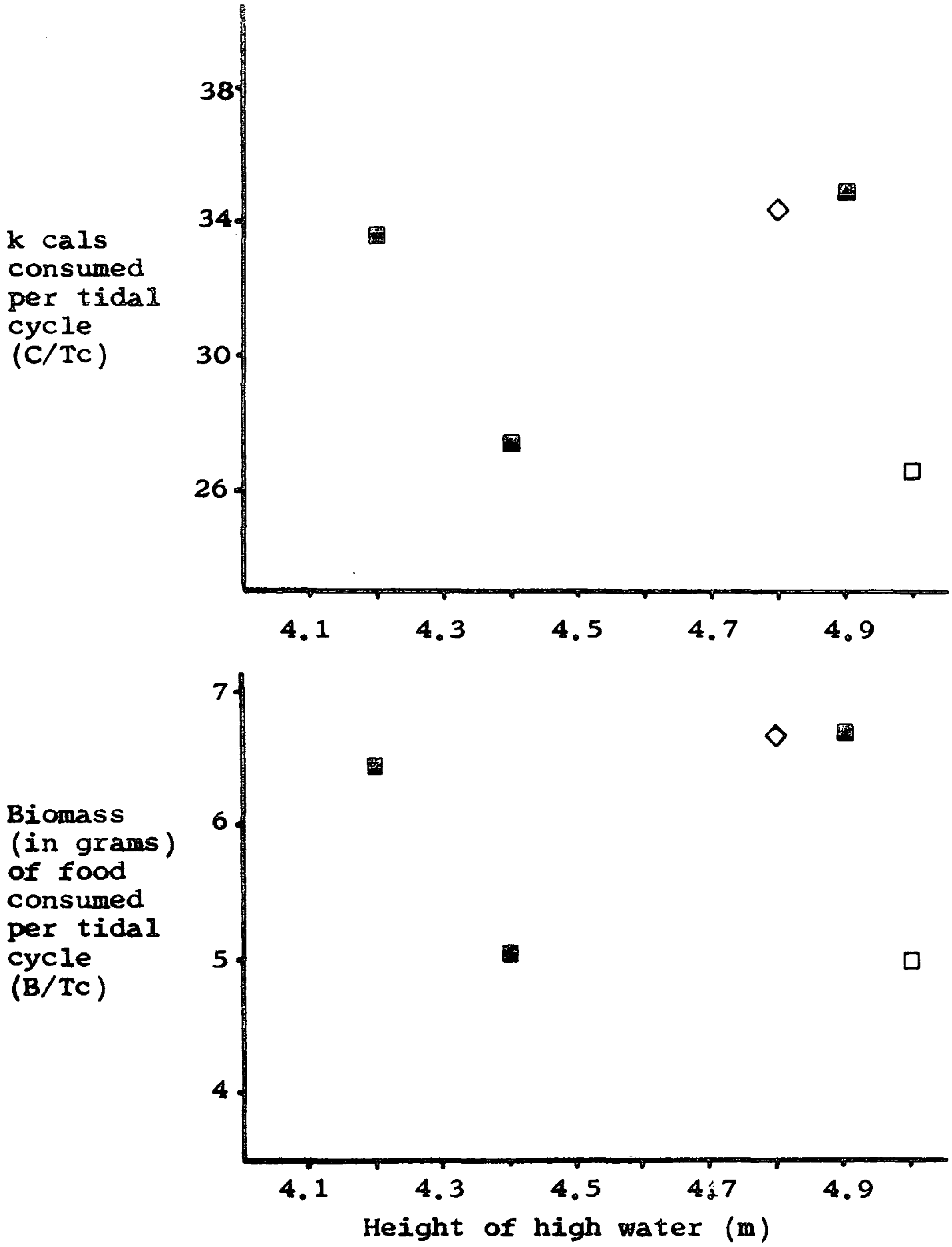


FIGURE 27 Variations in C/Tc and B/Tc in relation to tide height in July (population size 320 (diamond) or 450-460 (squares) birds).
Open square - estimate of C/Tc for July 18th.

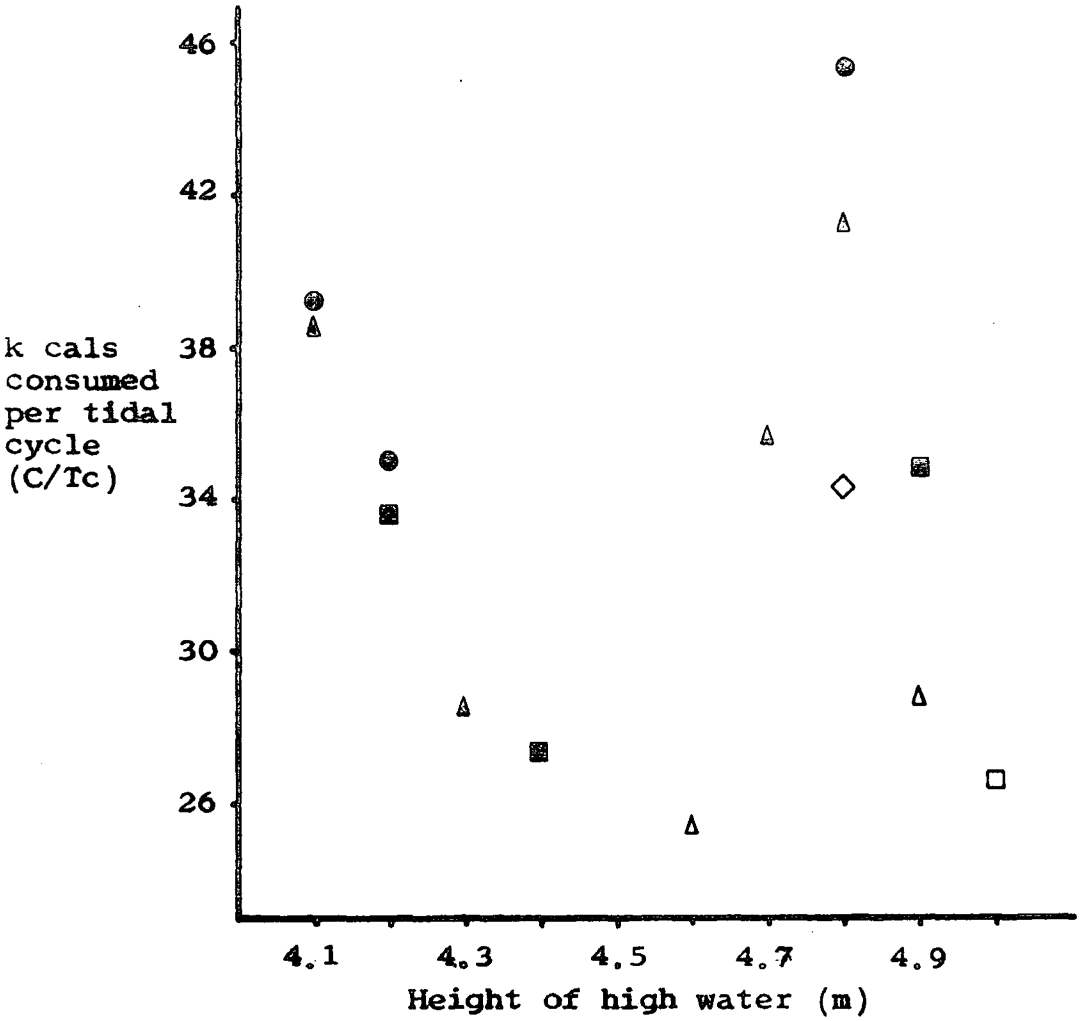


__FIGURE 28__ Variations in C/Tc in relation to tide height for all months within the study period.

Explanation of symbols:

Circles -estimates of C/Tc for May (population size 73-91 birds).

Diamonds -estimates of C/Tc for June (population size 143-160 birds).

Squares - estimates of C/Tc for July (population size 450-460 birds).

Open triangles - estimates of C/Tc for June 18th and 29th.

Open Square - estimate of C/Tc for July 28th.

Seasonal variations in C/Tc and B/Tc, however, were in most cases different to seasonal variations in PFT.

In the following sections, the main conclusions reached in section 4.4., concerning variations in PFT, are discussed again in relation to the corresponding variations in C/Tc. These are:

1) The proportion of the total PFT carried out on the partial daylight tidal cycle increased as the amount of available daylight feeding time increased (see Fig. 18.). Similar results were also obtained when the proportion of the daily calorific intake (the sum of calorific intakes for 2 consecutive tidal cycles) consumed on the partial daylight tidal cycle was considered (Fig.29.). Comments on the reliability of points in Fig. 18. (page 65) also apply to those in Fig.29. In both June and July, the slopes of the regression lines for calorific intakes were steeper than those for PFT.

2) For daylight tidal cycles, PFTs were higher during extremely shallow neap tides than during neap/intermediate tides. It was suggested that this may have been due partly to the increased time needed for curlew to obtain similar quantities of food while feeding at a lower average rate (for example by spending a greater proportion of their feeding time on areas of low profitability) during extreme low neap tides, and partly because curlew spent proportionately more time feeding, and so obtained a greater proportion of their food, during the partial daylight tidal cycles during neap/intermediate tides.

Estimates of PFT were 8.9% higher on extremely shallow neap tides than on neap/intermediate tides in May, and were 20.1% and 23.8% higher respectively in June & July.

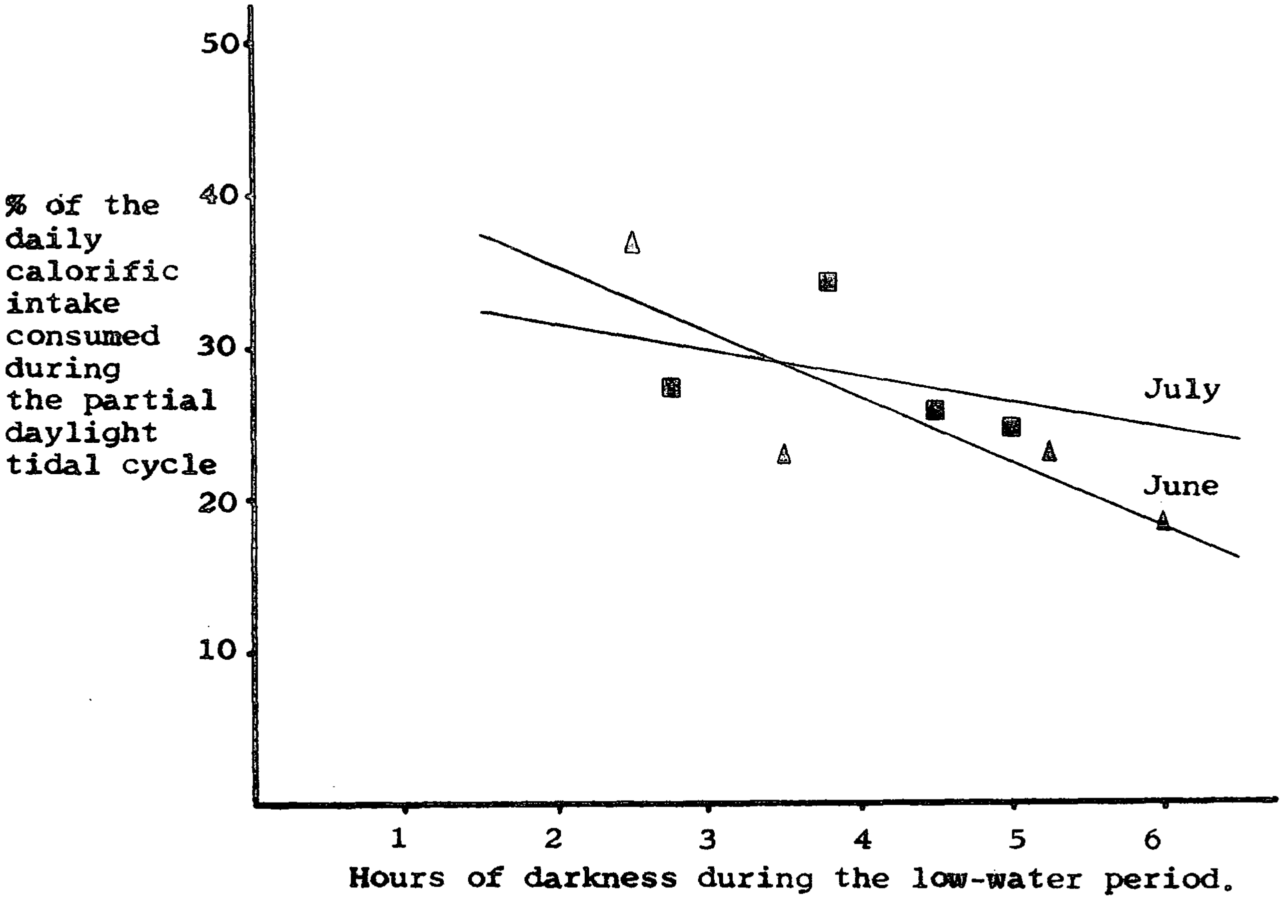


FIGURE 29 The percentage of the daily calorific intake (the number of calories consumed during 2 consecutive tidal cycles) consumed during the partial daylight tidal cycle, in relation to the number of hours of darkness during the low water period of the partial daylight tidal cycle.

June July

The regression lines are shown: $y = -4.27x + 43.85$ (June)

$Y = -1.68x + 34.90$ (July)

For estimates of C/Tc the corresponding values were 12.5% (May), 35.2% (June) and 22.7% (July). When estimates of C/Tc for consecutive tidal cycles were combined, it was found that estimates were only 10.8% (June) and 20.5% (July) higher on extreme low neap tides. Variations in the relative use of consecutive tidal cycles thus accounted for a substantial amount of the variation in C/Tc between neap and neap/intermediate tidal cycles in June, but for only a small proportion of the variation in July. These results also show that, contrary to the general trends reported in section 4.2., curlew apparently spent a greater proportion of their feeding time on more profitable areas during extremely shallow neap tides than they did during neap/intermediate tides, in May and June. It must be remembered, however, that differences in food intake rates at different tide heights, were not studied. Smith (1975) found that bar tailed godwits feeding on Arenicola marina at Lindisfarne attained higher intake rates on spring tides than on neap tides. It is possible that the reduced exposure of feeding areas, and increased interference due to crowding, may also have resulted in curlew feeding at a lower rate on extreme low neap tides than on neap/intermediate tides. Other possible reasons for a "higher than expected" C/Tc on extreme low neap tides include: a) adverse weather condition during the low neap tides, resulting in curlew feeding for longer with a lower intake rate; or b) a greater use of field areas for feeding on the neap/intermediate tides; or c) inaccurate observations.

3) PFTs were higher in late June than in May or early June. (see late June estimates of PFT at neap tides, in

Fig.12). It was suggested that this was due to the reduced use of the highly profitable Mid Tide Wall areas in late June. Fig 28, shows that estimates of C/Tc were slightly lower in late June than in May. It thus seems likely that curlew did increase their feeding times in late June to counter the "loss" of highly profitable feeding areas. Although the estimates of C/Tc for May and late June were similar at tide height 4.1m, a greater amount of daylight feeding time was available on the May date. As suggested in earlier sections, it thus seems likely that an increased use of the partial daylight tidal cycle occurred in late June.

4) PFT(2)s (the combined PFTs for two consecutive tidal cycles) were lower in July than in late June. PFT(2)s were also lower than expected on the 29th June. On the 29th June and throughout July, curlew were observed flying towards the fields in the evening. In July, food intake rates on 2 areas of Seal Sands increased, and the proportion of curlew using the mudflats at night, also increased. It was suggested that, while the higher food intake rates may have partly compensated for the lower feeding times in July, it was likely that field feeding also occured. Estimates of C/Tc(2) (the sum of C/Tcs for consecutive tidal cycles) support this hypothesis. In July the reliable estimates of C/Tc(2) (those for neap tides) were lower than those for June, despite the higher intake rates in July (**see** Figs 30 & 31). It must be remembered, however, that intake rates were measured on only 3 areas in July. On other areas, it was assumed that feeding rates did not vary with season. While this assumption is likely to be invalid, it is unlikely to greatly affect the reliable estimates of

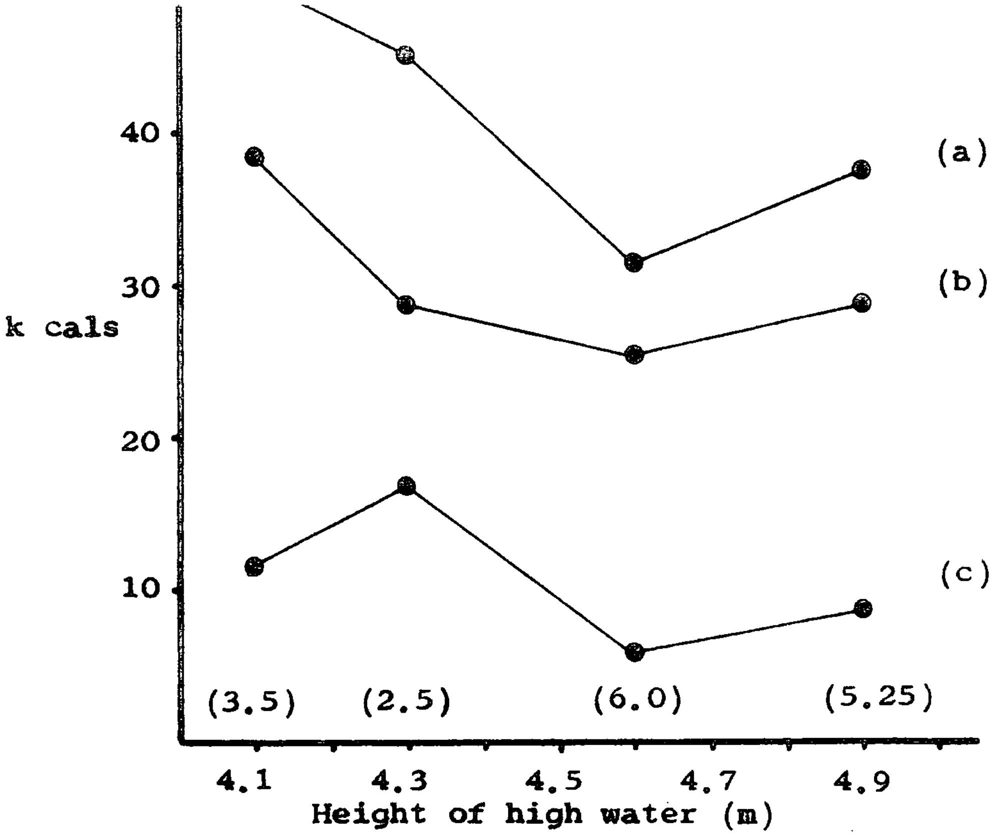


FIGURE 30 Variation in the number of calories consumed in June; (a) the sum of C/Tcs for consecutive tidal cycles; (b) C/Tcs for daylight tidal cycles; (c) C/Tcs for partial daylight tidal cycles. Brackets indicate the number of hours of darkness during the low water period of the partial daylight tidal cycle.

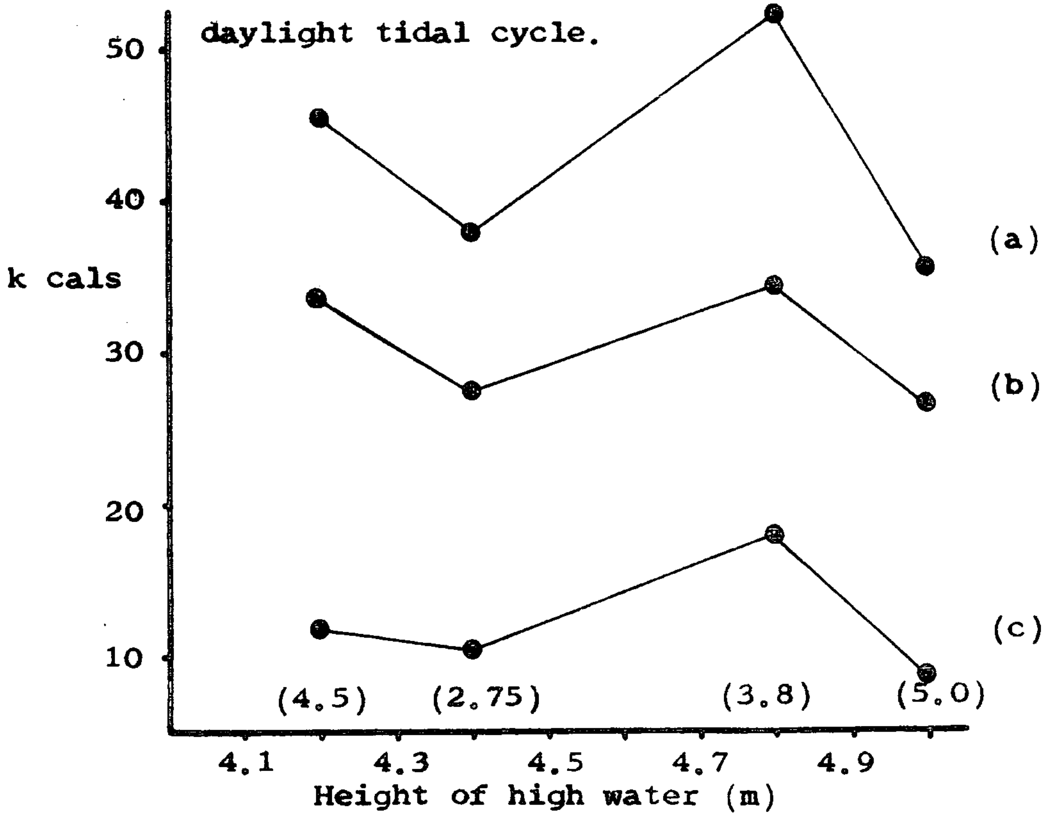


FIGURE 31 Variation in the number of calories consumed, in relation to tide height in July; (a) the sum of C/Tcs for consecutive tidal cycles; (b) C/Tcs for daylight tidal cycles; and (c) C/Tcs for partial daylight tidal cycles. Brackets - hrs. of darkness during the LW period.

C/Tc. On July, neap and neap/intermediate tides, between 85 and 90% of all feeding observed was carried out on the three areas on which feeding rates were measured.

5) An increase in the use of the partial daylight tidal cycle between early and late June is suggested by the low PFT observed on the partial daylight tidal cycle on the 8th June compared with that on the 25th June (Table 6). C/Tcs were also lower on the 8th June than on the 25th June (Table 15). In July the proportion of curlew observed feeding at dawn or dusk, was greater than in June. As already mentioned, it is also likely that curlew used field areas for feeing at night in July. These results suggest that, as the season progressed, and competition for food increased (for example due to an increase in population size, or the reduced use of the prefered Mid Tide Wall areas) curlew obtained a lower proportion of their daily food intake from the daylight tidal cycle. Further evidence for this is seen at the spring tide heights in Fig.28; C/Tcs for daylight tidal cycles were higher in May than in early June, and higher in early June than in July.

In mid-winter, it was estimated that redshank obtained less than 50% of their food requirements from the estuary in daylight, and had to collect the balance from the estuary at night and from the fields at high water (Goss-Custard 1969). Goss-Custard concluded that,"either the daytime ingestion rate on the estuary could not be increased enough to enable the birds to collect all their food during the daylight, or it was advantageous to spread the feeding throughout as much of the day as possible." In this study curlew obtained a lower proportion of their daily intake from the daylight tidal cycle, as the season progressed. As mentioned in point 3), curlew increased their feeding times in late June to counter the "loss" of profitable feeding areas, yet in section 4.5.5. it was shown that curlew were likely to have fed at a lower rate in May and June, than in July, as they fed preferentially on large prey items in May and June. Although prey capture and biomass and calorific intake rates increased in July, prey capture rates were not as high as those recorded by Knights (1974) in autumn. It seems likely, then, that in the summer, curlew prefered to spread their feeding throughout much of the day rather than increase their ingestion (biomass and calorific intake) rates. Whether or not it is possible for waders to increase their mid-winter ingestion rates, however, is not known.

4.7.2. Observations and estimates of the food intake of one individually recognisable curlew.

A single, uniquely marked "small female" curlew was observed during the daylight tidal cycle on the 3rd August. Confirmation that this was a "small female" was obtained from Townshend's (1980) data on curlew captured on Seal Sands. This bird was observed for a total of 405 minutes (HW+3.75 - HW+9.5) while in a feeding territory on the north eastern edge of Central Bank (See Fig.2). During this period, the curlew foraged for 193 minutes. The numbers of different types and sizes of prey consumed during this period are listed in Table 16. Estimates of mean biomass and calorific intake rates, and data on feeding behaviour are listed in Table 17. An estimate of the amount of time spent feeding outside the period HW+3.75 - HW+9.5 (43 minutes) was obtained from observations of the proportion of curlew feeding at different

TABLE 16. THE PROPORTIONS OF DIFFERENT TYPES AND SIZES OF PREY TAKEN BY A SINGLE CURLEW ON THE 3RD AUGUST.

PREY TYPE	WORMS					SURFACE ITEM	CRAB	TOTAL
PREY SIZE	$0-\frac{1}{4}$	$\frac{1}{4}-\frac{1}{2}$	$\frac{1}{2}-\frac{3}{4}$	$\frac{3}{4}-1$	UNKNOWN		x2	
NUMBERS OBSERVED EATEN	103	99	26	5	1	4	1	239
PROPORTION EATEN (%)	43.1	41.4	10.9	2.1	0.4	1.7	0.4	100
CALORIES EATEN (k cals)	8.24	21.09	9.96	3.47	0.19	0.64	0.30	43.89
BIOMASS EATEN (grams)	1.65	3.86	1.87	0.59	0.02	0.14	0.15	8.28

TABLE 17. FEEDING RATES AND FEEDING BEHAVIOUR OF THE CURLEW OBSERVED ON THE 3RD AUGUST.

AVERAGE PREY CAPTURE RATE (items per minute)	1.24
AVERAGE CALORIFIC INTAKE RATE (k cals per min.)	0.227
AVERAGE CALORIFIC CONTENT OF FOOD ITEMS (k cals)	0.184
AVERAGE BIOMASS INTAKE RATE (grams $\times 10^{-2}$ per min.)	3.465
AVERAGE BIOMASS OF FOOD ITEMS (grams $\times 10^{-2}$)	4.297
AVERAGE PACE RATE (paces per min.)	38.76
AVERAGE NUMBER OF PACES PER PREY	28.35
AVERAGE PROBE RATE (probes per min.)	3.97
AVERAGE NUMBER OF PROBES PER PREY	2.87
PERCENTAGE SUCCESS OF PROBING	35

stages of the tidal cycle on the 2nd August. Assuming that the feeding rate of the curlew was not significantly different while feeding outside its territory, the biomass of food consumed was estimated at 10·13 grams, and the number of calories consumed, at 53·68 k cals.

As the flood tide covered the feeding territory at HW+9·5, the curlew was observed to fly to another part of Central Bank. As the curlew left the feeding territory it was noticed that primary moult was in progress.

4.7.3. Discussion: The effects of moult on the daily food intake.

During this study it was possible to estimate the food consumed during feeding only on the estuary. The results presented in section 4.3. show that it is likely that curlew used the estuary exclusively for feeding only in May, and for most of June. Small numbers of curlew were first observed to fly towards the fields at dusk on the 25th June. The most reliable estimate of the amount of food consumed per 25 hrs (the duration of 2 consecutive tidal cycles) is thus that estimated for the 21st June (12·05 grams, 50·17 k cals). On this date it was estimated that only 2·5% of the curlew population were in moult.

In July and August a high proportion of curlew were in moult. On the 29th June, estimates of C/Tc (2) and B/Tc (2) on the estuary were 25% and 28% lower than the equivalent estimates for the 21st June. It is likely that this was due to curlew feeding also on field areas on this date. If it assumed that curlew obtained a similar proportion of their daily food intake from field areas in July, then estimates of the amount of food consumed per 25 hours in July range from 71-51 k cals and 14-9·5 grams, the highest estimates being for early July. As mentioned earlier, however, it is likely that the use of field areas was greater in July than in late June, and probably also greater in late July than in early July.

Variations in the use of field areas has been studied by Townshend (1980). His observations on marked birds revealed that individuals followed different patterns in their use of fields and mudflats. In mid-winter some birds fed exclusively on the adjacent fields; others fed mainly on Seal Sands and used the fields to provide supplementary feeding; and others fed exclusively on the mudflats. The 140-160 birds observed not flying towards field areas on the 20th July (see pg 36), and the similar numbers of curlew observed on Seal Sands at dawn and dusk on other July dates, are thus likely to be curlew which fed exclusively on the mudflats. The marked bird observed on the 3rd August was a bird which fed exclusively on Seal Sands, and in the same feeding territory as that observed on the 3rd August, in past winters (D. Townshend pers. com.). It is thus likely that this bird also fed exclusively on the mudflats on the 3rd August. The amount of food consumed by this bird during the daylight tidal cycle was estimated at 10·13 grams (53·7 k cals). The amount of food consumed during the partial daylight tidal cycle was estimated as follows.

1) The amount of daylight feeding time available during the partial daylight tidal cycle of the 3rd August was only 2 hrs. Much of the feeding on this tidal cycle would thus occur in darkness.

2) The time spent feeding by the individual curlew was assumed to be the same as the average time spent feeding by all curlew which fed exclusively on Seal Sands. July

observations on Seal Sands at dawn and dusk (Table 5) revealed that, of the 30% of the population which were present on Seal Sands (these were assumed to feed exclusively on Seal Sands), $\frac{2}{3}$ were feeding between the hours of HW+4-8, and $\frac{1}{3}$ were feeding between the hours of HW+2-4 and HW+8-10. The average time spent feeding was thus estimated at 240 minutes. This estimate is very close to the 236 minutes estimated for the daylight tidal cycle.

3) As mentioned earlier, Knights (1974) reports that prey capture rates at night were comparable to those recorded during the daytime. Ingestion rates, however may not be as high at night, as during the daytime, if curlew were hunting visually and were selectively preying upon large food items during the daytime. Unfortunately it was not possible to tell whether the individual curlew observed was selecting large prey in preference to small prey during the daytime, so it was assumed that ingestion rates at night were equal to those recorded during the day.

Using these estimates of feeding rate and feeding time, the amount of food consumed during the partial daylight tidal cycle was estimated at 10·31 grams (54·6 kcals). The estimate of the amount of food consumed during 2 consecutive tidal cycles by a moulting female curlew was thus 20·44 grams (108·3 kcals). This is equivalent to 19·62 grams and 104 kcals per 24 hrs.

Before calculating the increased food required by moulting birds a small adjustment was made to the estimate of the food intake of non-moulting birds, to take into account the difference in food requirements of males and females. Female curlew are usually heavier than males, and so have a higher basal metabolic rate. Townshend (1980) calculated that males require 12% less food than females. If it is assumed that the food intake measured on the 21st June represents the average non-moulting food intake of equal numbers of males and females, then this estimate is likely to be 6% below that of an average non-moulting female. The food intake per 25 hrs for an average non-moulting female would thus be 12.82 grams (53.37 k cals), or 12.31 grams and 51.24 k cals per 24 hours.

Estimates of the daily food intake of moulting and non-moulting curlew thus show that moulting birds require an extra 7.57 grams of food, or an extra 52.7 k cals per day. This represents an increase of 63% in the biomass of food consumed per day, or an increase of 103% in the number of calories consumed per day.

It must be remembered, however, that the reliability of these estimates depend, in particular, on two assumptions. These are:

1) That curlew did not feed on areas other than the estuary before the 25th June.

2) That assumptions made about the times spent feeding and the feeding rates during the partial daylight tidal cycles are correct.

CHAPTER 5

SUMMARY

In this study, curlew feeding behaviour was studied in relation to four important variables. The effects of variation in the amount of available daylight feeding time, and the effects of variation in tide height were studied on a day to day basis. The effects of increases in population size, and of moult, were two seasonal variables studied.

In June and July curlew spent a greater proportion of their total daily feeding time feeding during the partial daylight tidal cycle, as the amount of available daylight feeding time during the partial daylight tidal cycle increased. Feeding times were lowest on those daylight tidal cycles which were preceded or followed by partial daylight tidal cycles with the greatest amounts of daylight feeding time available. In June & July these were tidal cycles of neap/intermediate tide height. Long hours of daylight feeding time were also available during the neap tide partial daylight tidal cycles.

The effects of variation in the tide height could be determined over only a narrow range of tidal heights, because variables such as disturbance, population size and the relative use of field areas and mudflats were not constant over a wide range of tidal cycles. During extremely shallow neap tides, feeding times were greater than during neap/intermediate tides. While it is possible that ingestion rates were lower at the lower tidal amplitudes, this aspect of the effects of variation in tidal amplitude was not studied.

The tidal cycle also influenced the areas on which curlew fed. Within a tidal cycle, maximum numbers of feeding birds usually occured on an area shortly after it was exposed. The use of each area varied between tidal cycles. During spring tides, curlew made greater use of lower shore feeding areas than they did during neap tides. The prefered feeding areas were the Mid Tide Wall areas, in May and June, and the Greenabella Channel in July. These were both small, mainly lower shore feeding areas. The Central Bank, howevew, was the largest feeding area, and accomodated the greatest amount of feeding throughout.

Changes in population size occured in two main stages. At the end of May the population size changed from 91 to 73 to 143 birds, and, during the first 2-3 weeks of July, it increased from 160-450 birds. In May, a high proportion of curlew fed on the highly profitable Mid Tide Wall areas at low water. This was true also in early June despite the increase in population size. By the middle of June, though, the use of these areas had decreased dramatically, possibly because the increased intensity of predation in June had significantly reduced the density of available prey. The other possible cause suggested was that the density of available prey was reduced because of the spawning activities of <u>Nereis</u>. During the second half of June, GFTs on the less profitable Central Bank, and the overall times spent feeding on the daylight tidal cycles, were higher than in May or early June. Feeding time on the partial daylight tidal cycle, and the proportion of the total time spent feeding (during two consecutive tidal cycles) spent feeding on the partial daylight tidal cycle, also increased during the second half of June. Curlew thus responded to the "loss" of highly profitable feeding areas by increasing their feeding times rather than by increasing their feeding rates. Indirect evidence suggests that curlew also spent proportionately more time feeding on the partial daylight tidal cycle in early June than in May.

In July, the Greenabella Channel supported a greater proportion of the total feeding carried out on Seal Sands than in June. The proportion of curlew observed feeding on the mudflats at night also increased in July, as did the proportion of curlew observed flying towards field areas in the evening. Calorific and biomass intake rates on two of the three areas on which these were measured in July, were also higher in July than in May and June. Extrapolating from the results of Knights (1974), it seems likely that ingestion rates could have been increased further. Although curlew did increase their ingestion rates in July, it appears that, once again, they preferred to increase their feeding times rather than increase their ingestion rates to levels beyond those observed.

The observed changes in feeding behaviour between June and July cannot be attributed entirely to changes in population size. In June, less than 5% of the curlew population were in moult, whereas, during the second half of July, estimates of the proportion of curlew in moult ranged from 70-77%. The greater food requirements of moulting curlew, as well as the increased interference and greater competition for preferred prey at higher curlew densities, may all have contributed in causing the changes in feeding behaviour observed. A comparison of the estimate of the daily food intake of an "average" curlew in June (12.3 grams , 51.2 k cals), and the estimate of the daily food intake of a single moulting curlew in early August (19.6 grams , 104 k cals), indicate that curlew are likely to require an extra 7.3 grams of food (52.8 k cals) per bird per day during moult. This represents an increase of 60% in the biomass of food consumed, or an increase of 103% in the daily energy intake.

The observed feeding behaviour of curlew does not appear to agree with all the predictions of optimal foraging models. As predicted by these models, greater densities of curlew were found on the more profitable (Mid Tide Wall) feeding areas in May and June; however, these curlew attained greater biomass and calorific intake rates than curlew feeding on the other main feeding areas. According to the models of Charnov (1976), a predator should not stay on a feeding area if it could obtain a greater food intake rate by moving to another. Charnov also predicted that ingestion rates on each feeding area should be reduced to the same (marginal) value. In May and June, calorific intake rates were similar on four of the feeding areas observed (not the Mid Tide Wall areas), and in July, on all three areas on which ingestion rates were measured. The comparison of the proportions of different types and sizes of prey taken in May and June, to those taken in July, and of the seasonal differences in searching behaviour and probing success, on three of the main feeding areas, suggests that curlew showed greater selectivity towards larger, more difficult to catch prey in May and June, than they did in July. Although curlew took a greater proportion of larger, more profitable prey items in May and June, prey were not taken with sufficient frequency for calorific and biomass intake rates to be higher in these months than those attained in July, when the average "size" of prey items was less, and prey capture rates greater, than in May and June. In showing greater selectivity towards larger prey items in May and June, curlew were thus not feeding optimally, in the sense that optimal predators make decisions which maximise their net rate of intake of food. It was suggested that larger prey may have contained greater concentrations of an essential nutrient, and that curlew were attempting to maximise their net rate of intake of this essential nutrient. Alternatively, curlew may have found worms distasteful, and were attempting to minimise the number of prey consumed to meet their food requirements. As mentioned earlier, curlew apparantly preferred to increase their feeding times rather than increase their feeding rates. In doing this, curlew may again have been trying to maximise the proportion of large prey in their diet, as the increase in feeding rate in July resulted in a lesser proportion of large prey taken.

APPENDIX 1

SUPPLEMENTARY DATA

Figure A1 shows the range and frequency of bill lengths in curlew captured on Seal Sands (from Townshend 1980). Mean bill lengths for each size class are as follows:

Small male	10.2cm
Large male	11.5cm
Small female	13.4cm
Large female	15.2cm

In Figures A2 and A3, variations in the estimates of prey capture rate are plotted against the duration of the observation period.

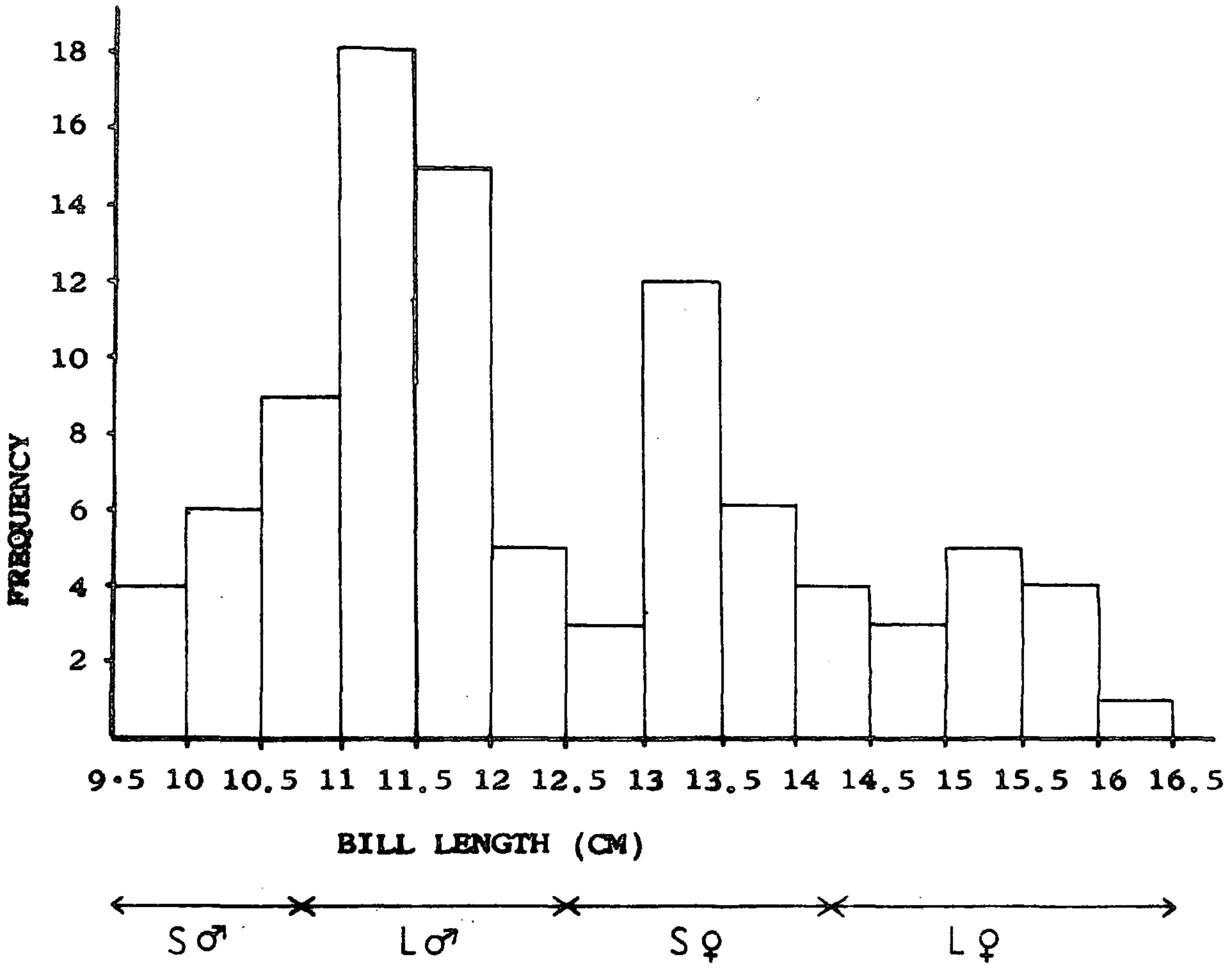


FIGURE A1 The frequency of different bill sizes (length) in curlew captured on Seal Sands. (From Townshend 1980). Arrows indicate the estimated limits of each size of curlew.

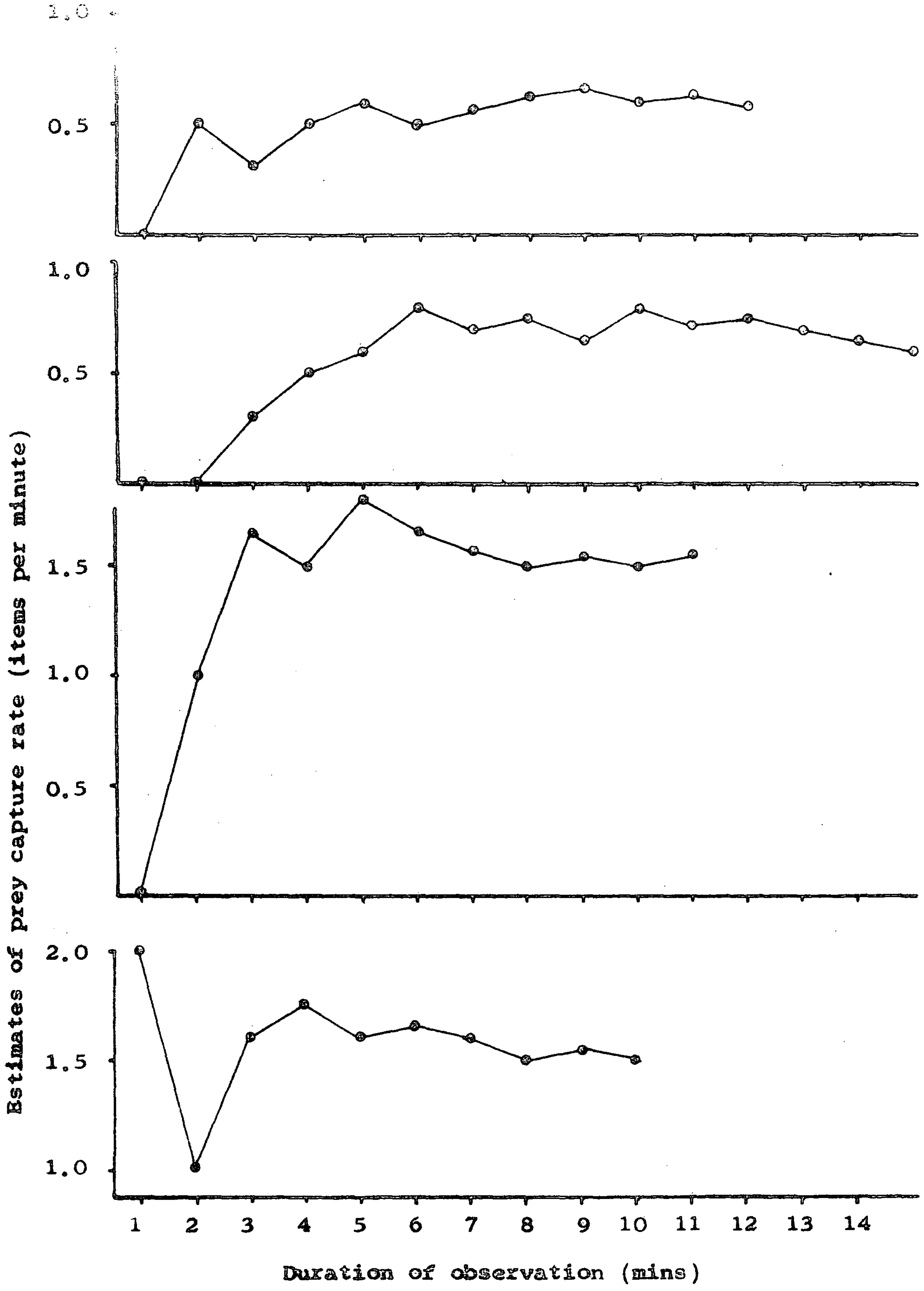


FIGURE A2 Variations in estimates of prey capture rate in relation to the duration of the observation period.

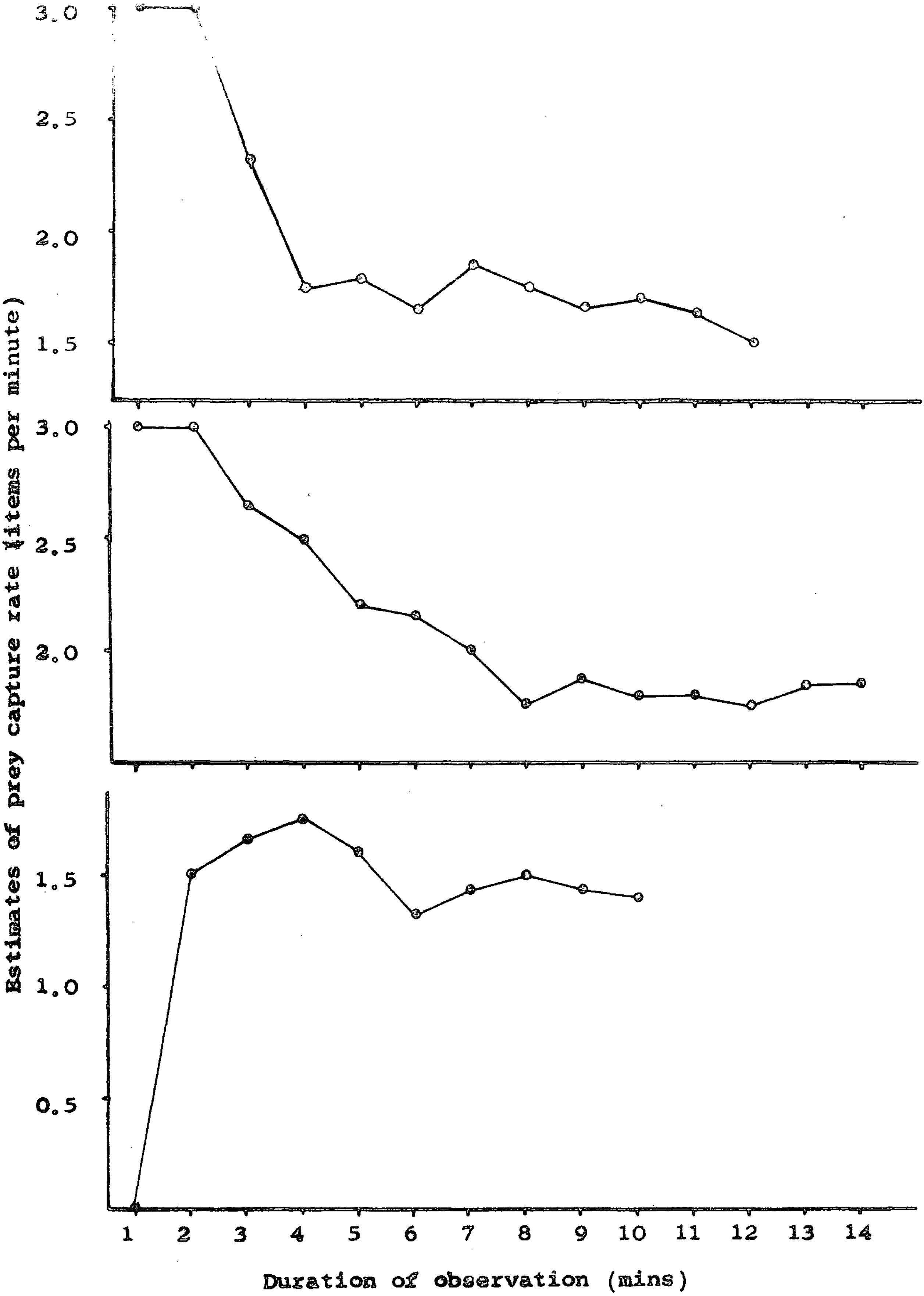


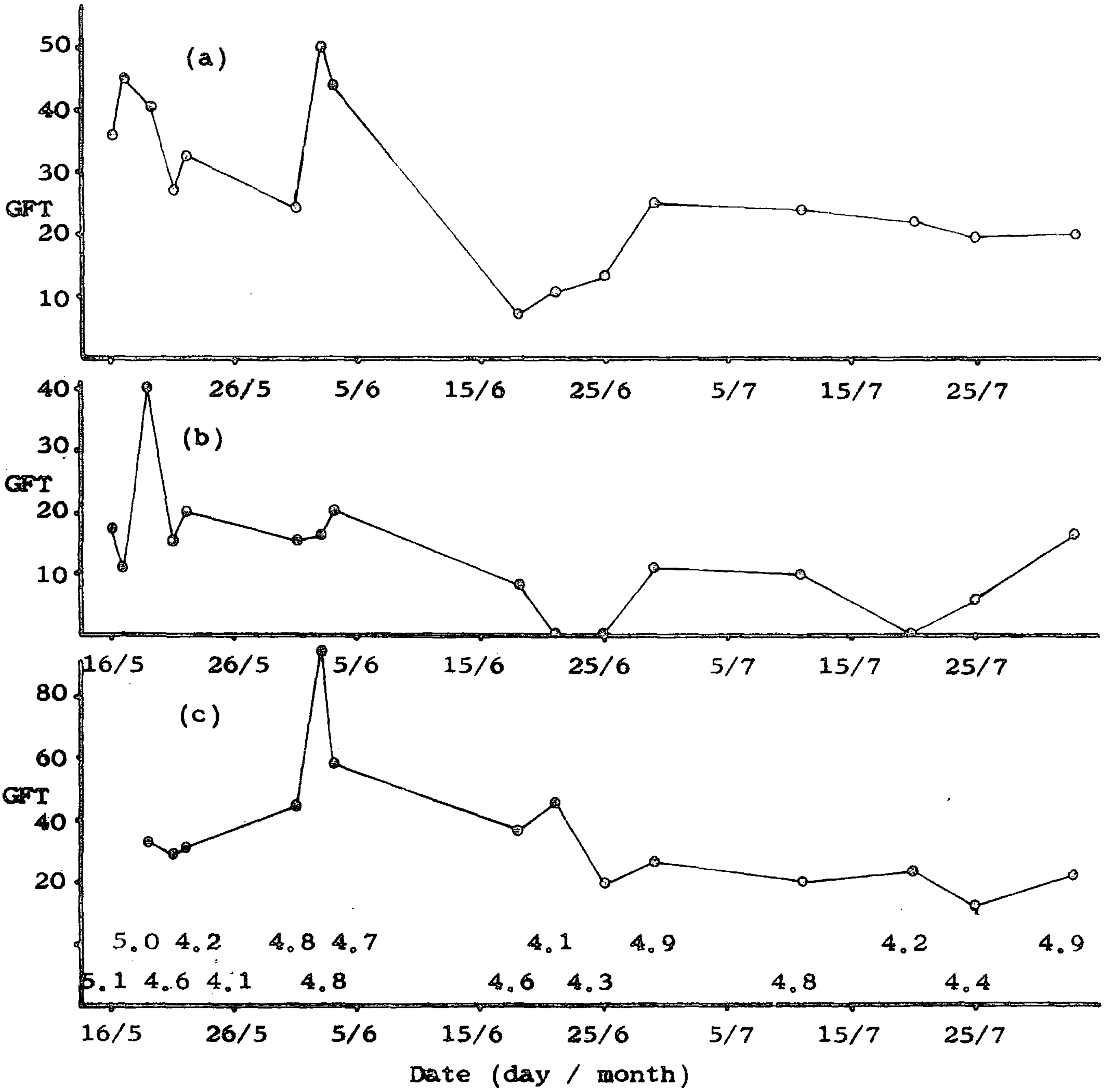
FIGURE A3 Variations in estimates of prey capture rate in relation to the duration of the observation period.

APPENDIX 2

Variations in the use of different areas of Seal Sands

In this appendix, details of the changes in the use of the different feeding areas on Seal Sands, both within and between tidal cycles, will be discussed. The total feeding times (in bird hours) on each feeding area, during each tidal cycle, are represented by the quantities GFT. Another quantity (RFI) was also calculated, to give a measure of the relative use of each area at different population sizes. Estimates of GFT and RFI (Tables 1 & 2), and details of how these two quantities were calculated, are given in section 4.2. Variations in the use of each feeding area are discussed below with reference to how these changes are brought about.

1) Mid Tide Wall Bank (MWB), Mid Tide Wall Channel (MWC) and the Mid Tide Wall (MW). These areas were the second most important feeding areas for curlew after the Central Bank during May and the early part of June. At the beginning of June, when the population size changed from 91 to 73 to 143 birds, the total use of these areas (the combined GFTs for all 3 areas) decreased then increased. These changes were due mainly to changes in GFT on the MW and MWB (see Figures A4 and A5). These changes were in the same proportion as the changes in population size, because the combined RFIs for all 3 areas were of a similar magnitude in May and Early June (see Figure A5). After June 3rd, GFTs were lower on the MWB and the MWC, on the MW a reduction in GFT did not occur until after the 21st June. At the end of June



<u>FIGURE A4</u> Variation in GFT on 3 areas during the study period.

(a) On the Mid Tide Wall Bank.

(b) On the Mid Tide Wall Channel.

(c) On the Mid Tide Wall.

The tide height on each observation day is printed above the base line, for ease of comparison.

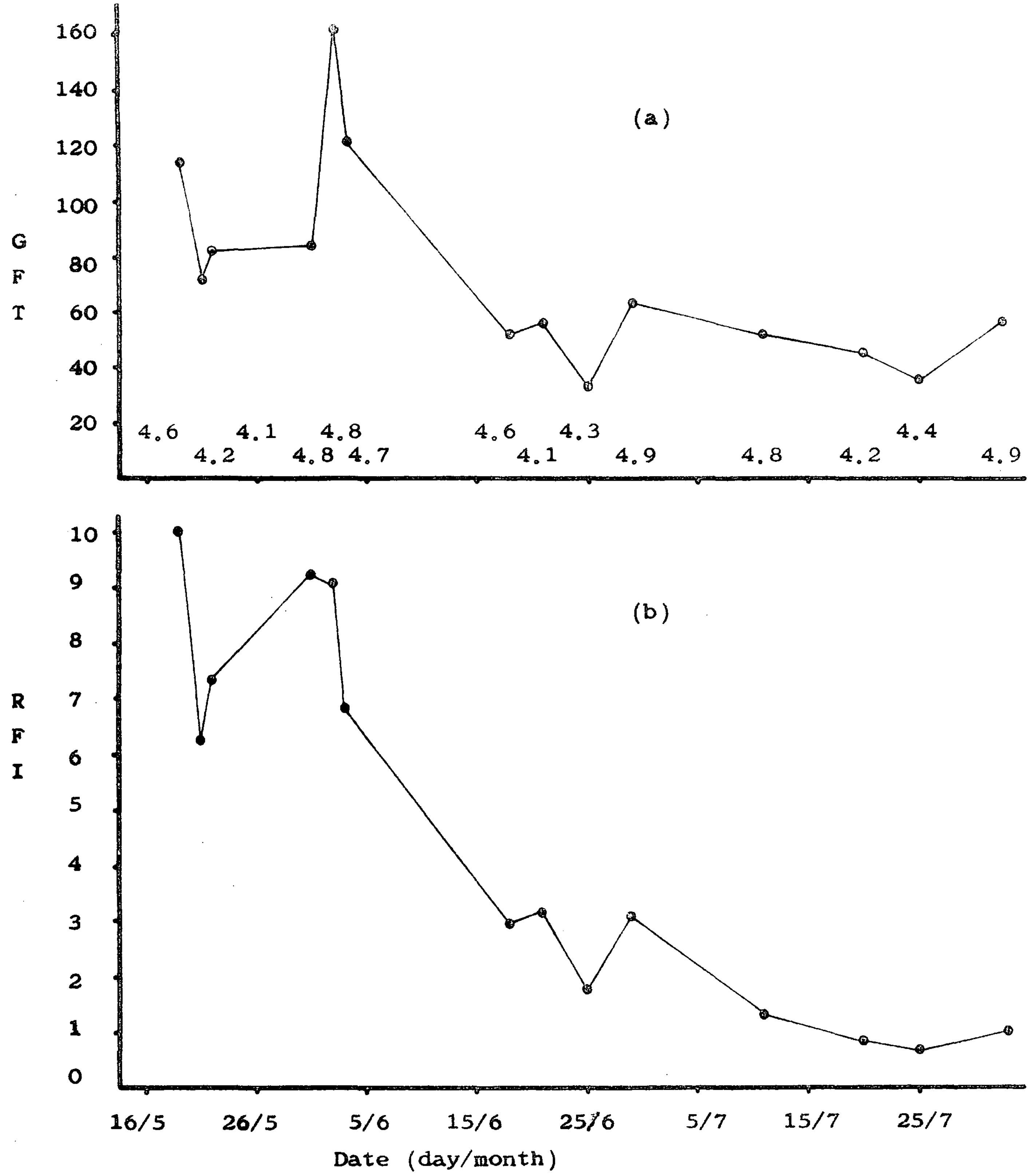


FIGURE A5 Variation in the combined GFTs (a) and RFIs (b) for the three Mid Tide Wall areas (MWB,MWC and MW) during the study period. The tide height on each observation day is printed above the upper base line for ease of comparison.

and during the first two weeks of July, a further increase in population size occured. On the MWB, but not on the MWC or MW, GFTs were higher on the 29th June and during July, than during the middle of June. This increase, however, was not in the same proportion as the increase in population size, because the RFIs for the MWB were lower during July (mean RFI = 0.42 ± 0.06, n=4) than during the second half of June (mean RFI = 0.73 ± 0.18, n=4).

The height of the tide also influenced the use of these areas. The combined GFTs for all three areas were consistently lower at the lower tide heights, than at higher tide heights, but only in the tide height range 5.0 - 4.3m. Within the tide height range 4.0 - 4.2m, GFTs were higher at the lower tide heights. These results were consistent (bearing in mind the seasonal changes in GFT), throughout the study. The individual GFTs for each feeding area, however, did not show consistent variation with tide height.

To help show how these differences in GFT were brought about, the number of birds observed feeding on each area was plotted against the state of the tide, for five different tidal cycles. Figures A6 and A7 (b & c) show that, in May and early June, most of the seasonal and tidal changes in GFT on the MW and MWB were caused by changes in the numbers of curlew feeding rather than by changes in the duration of the feeding period. Although curlew generally started feeding on all areas later on neap tides than they did on spring tides, they also finished later. The overall duration of feeding

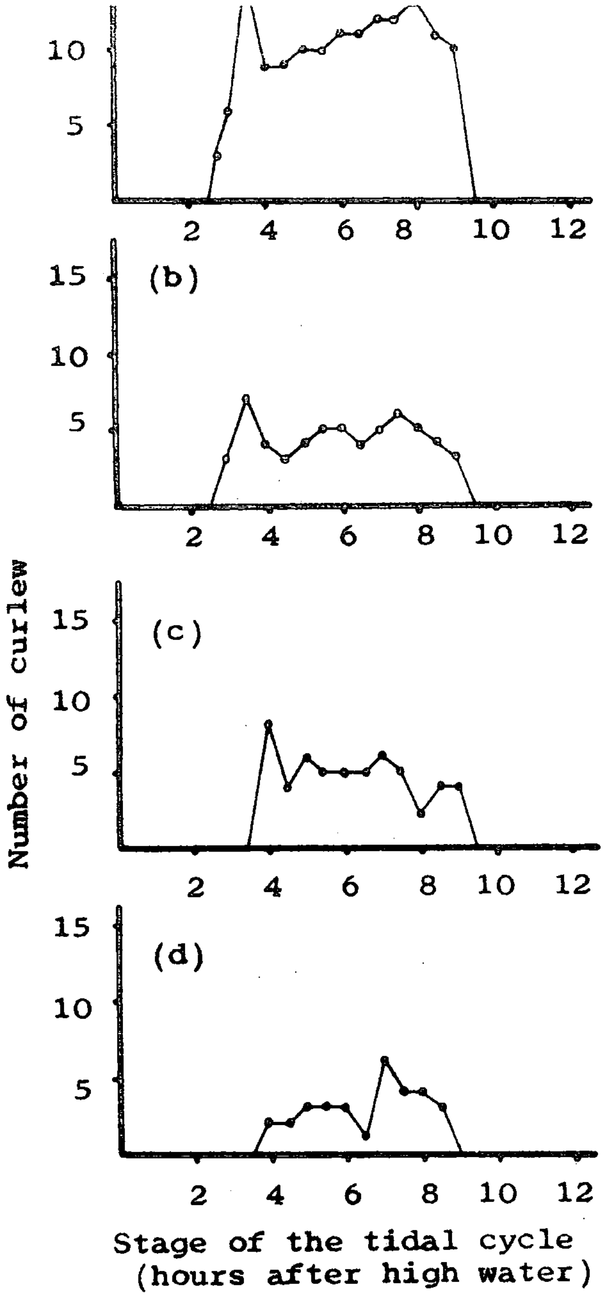


FIGURE A6 Variation in the number of curlew present (a) and feeding (b) on the MW, and in the number feeding on the MWB (c) and MWC (d), in relation to the state of the tide on the 21st May. (tide height 4.2m).

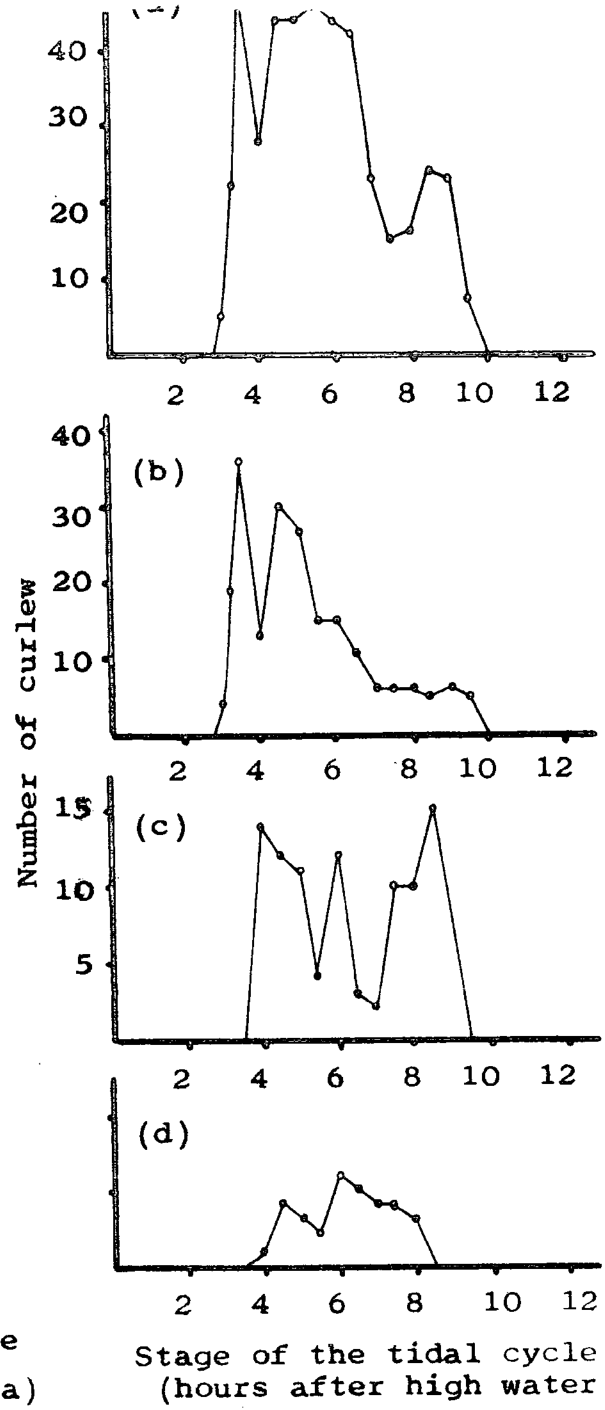


FIGURE A7 Variation in the number of curlew present (a) and feeding (b) on the MW, and in the number feeding on the MWB (c) and MWC (d), in relation to the state of the tide on the 2nd June (tide height 4.8m) did not vary between spring and neap tides.

In May and early June, similar numbers of curlew fed on the MWB (and the MWC) on the ebbing tide, at low water, and on the flowing tide (see Figures A6 and A7, c and d). On the MWB, most of the curlew were observed to feed near the tide edge. Presumably the faster rate, and greater extent of exposure of the MWB during spring tides, allowed more curlew to feed on this area (hence the high GFTs) during these tides. On the MWC, the size, shape and position of this area meant that only a short length of mud was in contact with the tide edge at any one time. In May and early June, it appeared that a lesser proportion of the curlew that fed on this area, fed near the tide edge, than was the case on the MWB (these observations were not quantified). This may have been the reason why variations in the rate and extent of exposure of this area (variations in tide height), had little effect on GFT during May and early June. (The high GFT observed during the intermediate tide (19th June) is difficult to explain, but may have been due to my failure to define clearly the borders between the western edge of the MWC and the northern edge of Greenabella Channel, as this was only the third day of observation and this part of the Greenabella channel had been little used until this date).

During the rest of June, and during July, feeding on the MWB and MWC occured mainly at low water (see Figures A8,A9,A10 and A11). This pattern of activity was particularly obvious on the MWC. On the MWB this activity pattern was seen mainly during June, and on spring tides in July. On both these areas, most of the

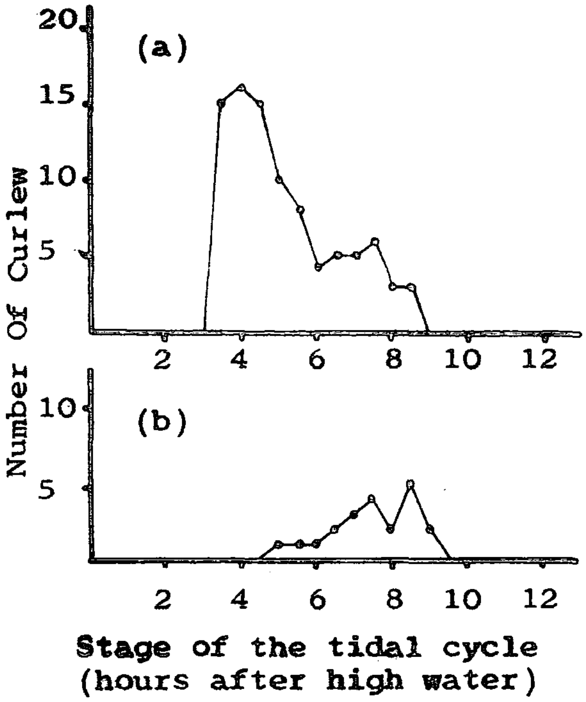


FIGURE A8 Variation in the number of curlew feeding on the MW (a) & MWB (b) in relation to the state of tide on the 21st June (tide ht. 4.1m)

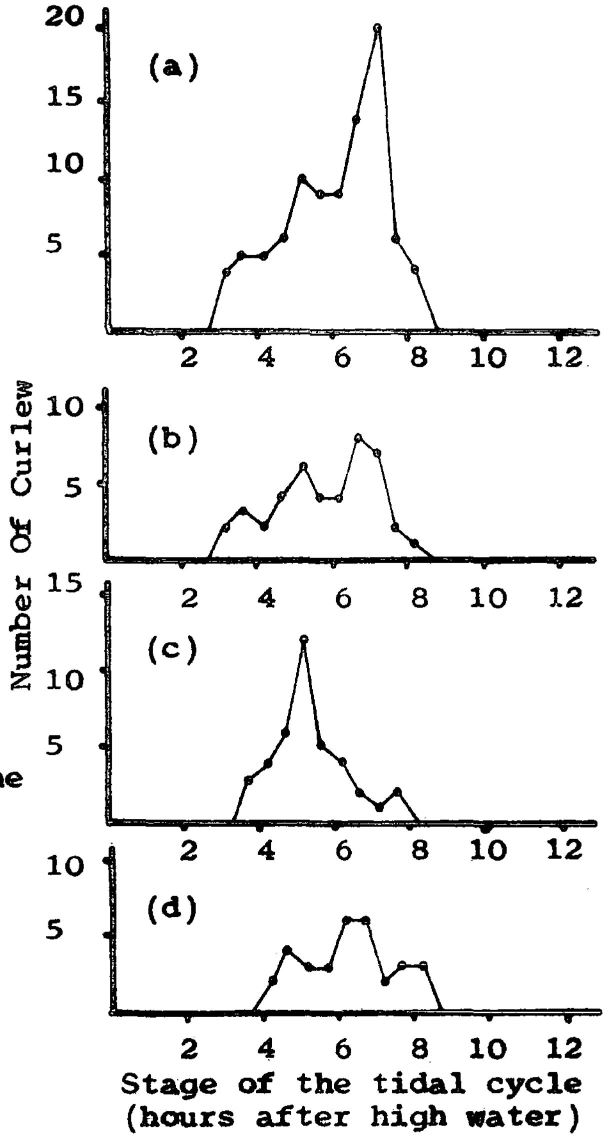


FIGURE A9 Variation in the number of curlew present (a) & feeding (b) on the MW, & in the number feeding on the MWB (c) & MWC (d), in relation to the state of the tide on the 2nd August (tide ht. 4.9m)

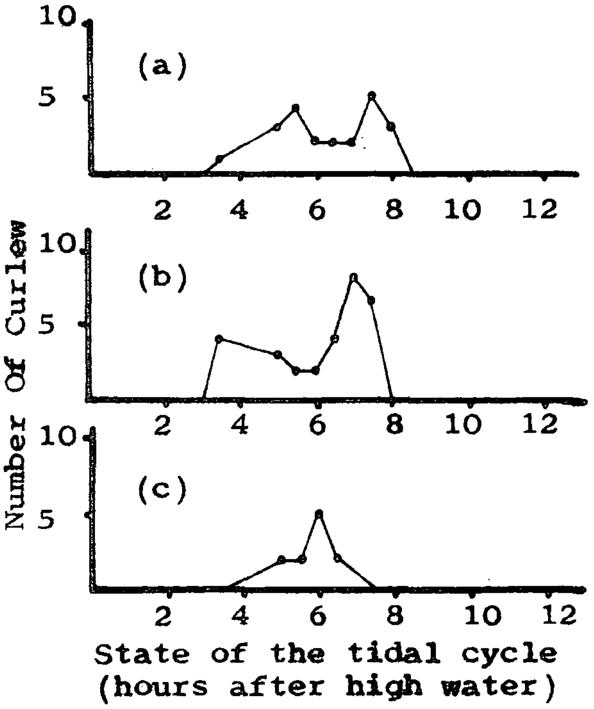


FIGURE A10 Variation in the number of curlew feeding on the MW (a) MWB (b) & MWC (c) in relation to the state of the tide on the 25th July (tide ht. 4.4m)

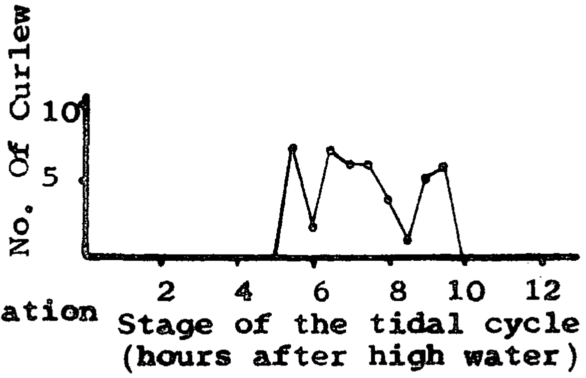


FIGURE A11 Variation in the number of curlew feeding on the MWB in relation to the state of the tide on the 20th July (Tide ht. 4.2m) birds were observed to feed near the tide edge during these times (again this was observed but not quantified). The reduction in GFT on these areas after 3rd June, therefore, appears to have been brought about mainly by a reduction in the use of the middle shore feeding areas. One explanation for this may be that, being small areas, the high predation intensities (GFT) in May and early June significantly reduced the number of prey items available for future predation. The middle shore feeding areas would have been expected to have "suffered" most, as they were exposed on all tides. An alternative explanation is that the density of available prey was reduced for seasonal reasons; for example,it is known (Evans et al, 1979) that Nereis on Seal Sands spawn in the spring and early summer. This may increase their availability to curlew during May and early June, but reduce it thereafter.

The reduction in the use of middle shore feeding areas in mid-June may also explain why the height of the tide greatly influenced the number of curlew feeding on both the MWB and the MWC during the second half of June, and July (GFTs were higher at the higher tide heights) as the height of the tide controls the extent of exposure of lower shore feeding areas. The effects of tide height were more consistent on the MWC than on the MWB. This may have been because some curlew may have compensated for the "loss" of feeding time on the MWC by either changing their feeding sites to include the MWB, or by feeding for a longer time on the MWB during the tidal cycles that the MWC was not used.

(It is difficult to tell which of these alternatives might have occurred because many curlew were observed to move from the MWB and MWC areas to roost, and sometimes to feed, on the MW, between feeding bouts on the MWB and MWC. This makes it difficult to estimate the total number of birds using the individual areas on particular tides). Although the "loss" of feeding time on other lower shore feeding areas may also have resulted in higher GFTs on the MWB, the changes in the use of the MWC are likely to have been the main cause, other than variation in the tide height, of variation in GFT on the MWB. This conclusion was arrived at because, during May, when GFTs did not vary with tide height on the MWC, GFTs on the MWB showed the "expected" variation with tide height, namely a consistently higher GFT at the higher tide heights. During June and July, however, when GFTs on the MWC did vary with tide height, GFTs were higher than expected during neap tides. This effect was most marked in July when, presumably, the greater competition for other lower shore feeding sites resulted in GFTs being even higher than expected on the MWB during neap and intermediate tides. The "extra" feeding carried out on the MWB during neap and intermediate tides in July, may have been the reason why the pattern of feeding activity differed on the MWB between spring and neap tides, namely that to support a greater amount of feeding during neap tides, the middle shore feeding areas of the MWB had to be utilised during the ebbing and flowing tides.

The amount of feeding carried out on the MW is also likely to have been related to the amount of feeding carried out on the other Mid Tide Wall areas (MWB and MWC). In May and June, curlew arrived at the MW at about HW+3, and maximum numbers were present and feeding between HW+3 and HW+4. Curlew began feeding on the MWB and MWC at about HW+4. The start of feeding on these areas was usually associated with a drop in the number of curlew present and feeding on the MW (see Figures A6,A7 and A8). An increase in the number of curlew present on the MW often occured at about HW+9, when curlew were no longer able to feed on the MWB and MWC (see Figure A7). It appears then, that some of the curlew that fed on the MWB and MWC also used the MW for feeding during the period prior to the exposure of the MWB and MWC. As already mentioned, curlew sometimes used the MW for feeding, between feeding bouts on the MWB and MWC. Greater numbers of birds using the MWB and MWC may thus result in a greater use of the MW, during as well as prior to the exposure of the MWB and MWC. (This reasoning assumes that the birds that did not use the MWB and MWC, during the tides when lower numbers of birds used these areas, also did not use the MW, but fed on the other areas). While this seems a likely explanation for the observed differences in GFT on the MW between spring and intermediate tides (GFTs were higher at the higher tide heights, but only within the tide height range 5.0 to 4.3m), it does not explain why GFTs on the MW were greater during the very low neap tides (tides in the height range 4.2 to 4.0m) than during intermediate tides. One possible reason for the increased use of the MW during very low neap tides, is that the feeding areas to which curlew moved from the MWB and MWC at intermediate tide heights, were not used by these curlew (or the other curlew "displaced" from the MWB and MWC at the very low neap tides) to the same extent during the very low neap tides. Instead, the MW was used.

Another interesting feature concerning the use of the MW is that, after the 21st June, curlew no longer used the MW for feeding or resting while "waiting" for the MWB and MWC to be exposed (compare Figures A6, A7 and A8 with A9 and A10), although it was often used for subroosting while the MWB and MWC were being covered by the flood tide (see Figure A10). This was the main cause of the reduction in GFT on the MW after the 21st June.

2) Greenabella Wall. In May and June, feeding by between 1 and 3 birds spanned a time period of between 1 and 3 hours on most tidal cycles. The timing of feeding also varied, and although it always occured between HW+5 and HW+9 on neap tides, on spring tides it often started and finished earlier. The highest GFTs were found during very low neap tides, at other tide heights, however, GFTs were usually higher at the higher tide heights.

In July GFTs were higher than in June. This was due both to a greater number of curlew feeding on this area, and a longer duration of feeding. Maximum numbers of feeding birds were observed just after low water, and on spring tides (see Figure A12). The increase in use of this area in July was proportionately greater than the increase in population size (RFIs were greater in July),

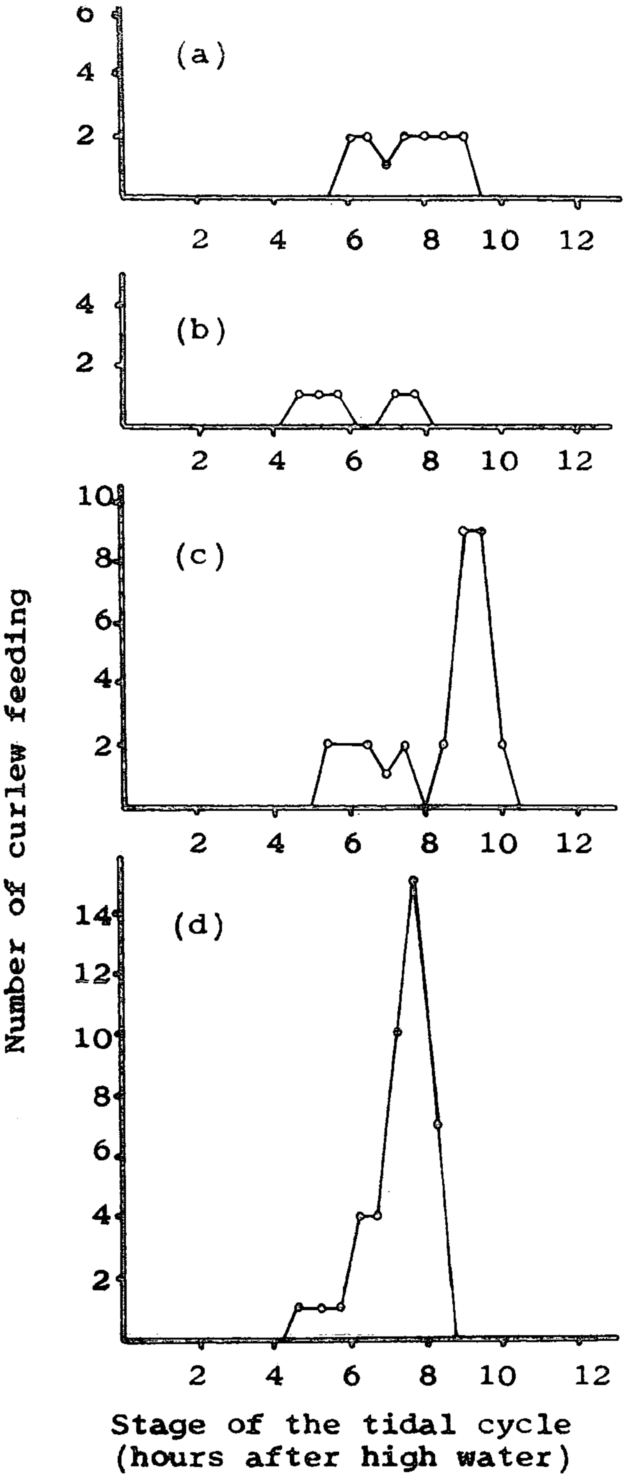


FIGURE A12 Variation in the number of curlew feeding on the Greenabella Wall in relation to the state of the tide.

(a) on the 21st June	(tide height 4.1m)
(b) on the 29th June	(tide height 4.9m)
(c) on the 20th July	(tide height 4.2m)
(d) on the 2nd August	(tide height 4.9m)

but only on spring and intermediate tides. On neap tides, the increase in use of this area was proportionately less than the increase in population size. It is difficult to determine whether an overall change in GFT occured between May and June,as GFTs were so variable in these months.

On the Greenabella Wall, feeding occured mainly near the rocks at the base of the reclamation wall and, at the northern end of this area, near the tide edge. Most of the curlew observed feeding just after low water in July, were birds that had walked northwards from the Greenabella Bank and Greenabella Channel areas, and which fed near the tide edge (lower shore areas) on the Greenabella Wall. The curlew observed feeding at other times during July tidal cycles, and at all times of the tidal cycle in May and June, fed on both the tide edge and the reclamation wall areas, and often changed their feeding sites from one to the other (these observations were not quantified). The greater extent of exposure of the lower shore feeding areas on spring and intermediate tides, may therefore be the reason why higher GFTs were found on these tides during July. In May and June, competition for other lower shore feeding sites, such as the Greenabella Channel, on spring and intermediate tides, would, presumably, have been less than in July, as population size was lower. As curlew appeared to prefer other lower shore feeding areas to the Greenabella Wall (most of the feeding on the Greenabella Wall occured after low water, and after curlew had begun feeding on the other lower shore feeding areas, (see Figures A12d and A14e)), the lower competition for preferred feeding areas may explain why the lower shore feeding areas of the Greenabella Wall were little used on spring tides during May and June. On neap tides, however, most lower shore feeding areas are unavailable and birds have to feed to a greater extent on other, less preferred areas. This may explain why higher GFTs were found on neap tides than on spring or intermediate tides, during May and June.

3) Greenabella Bank On most tides, this area was used for feeding between HW+3 and HW+10. On spring tides feeding often started and finished earlier than on neap tides, however, the timing of feeding did not vary consistently with tide height. During May and June, this area was used by between 1 and 4 birds throughout the feeding period. Maximum numbers of feeding birds were often observed at the end of the feeding period (see Figure A13 a and b) (N.B. the high number of birds recorded feeding at low water (and hence the high GFTs) during the May spring tides, are likely to have been the result of my not having clearly defined the border between the Greenabella Bank and the Greenabella Channel at these times, as these observations were made on the first two days of my study). In May and June the highest GFTs were found on spring tides, however, tide height did not have a consistent effect on GFT during these months.

During observations, movement between the Greenabella Bank and the Greenabella Channel was often observed. During May and the early part of June, This comprised a

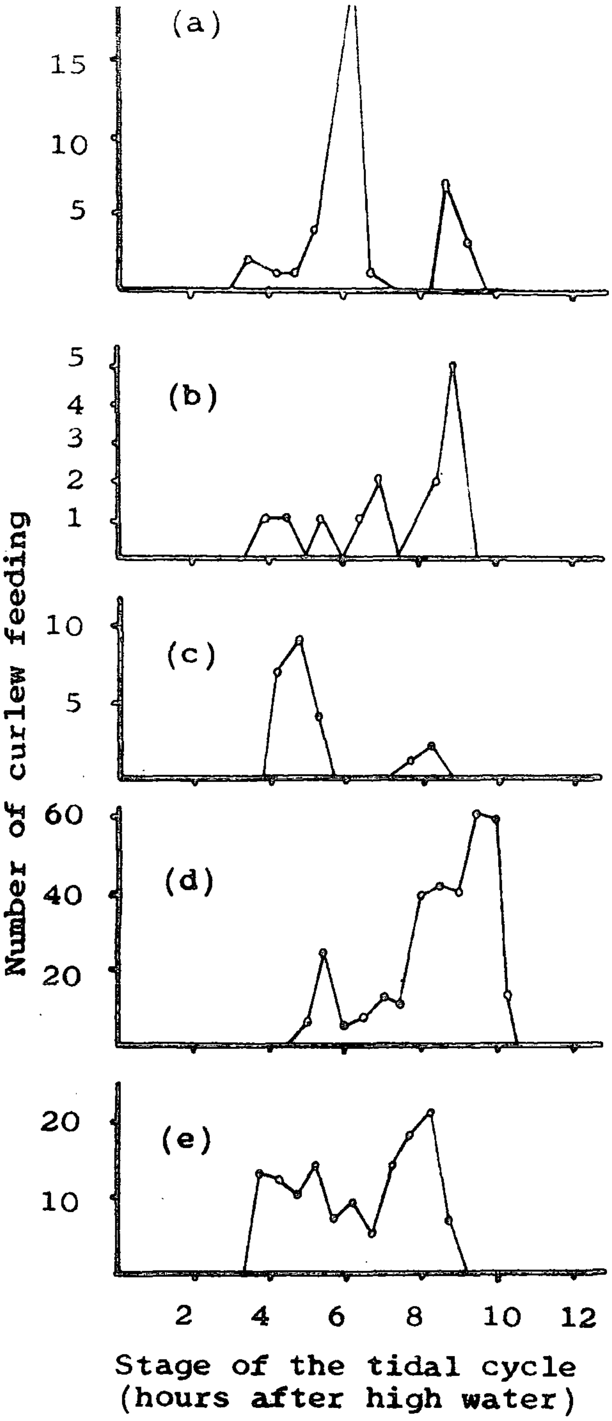


FIGURE A13 Variation in the number of curlew feeding on the Greenabella Bank in relation to the state of the tide.

(a) 17th May	(tide height 5.0m)
(b) 31st May	(tide height 4.8m)
(c) 29th June	(tide height 4.9m)
(d) 20th July	(tide height 4.2m)
(e) 2nd August	(tide height 4.9m)

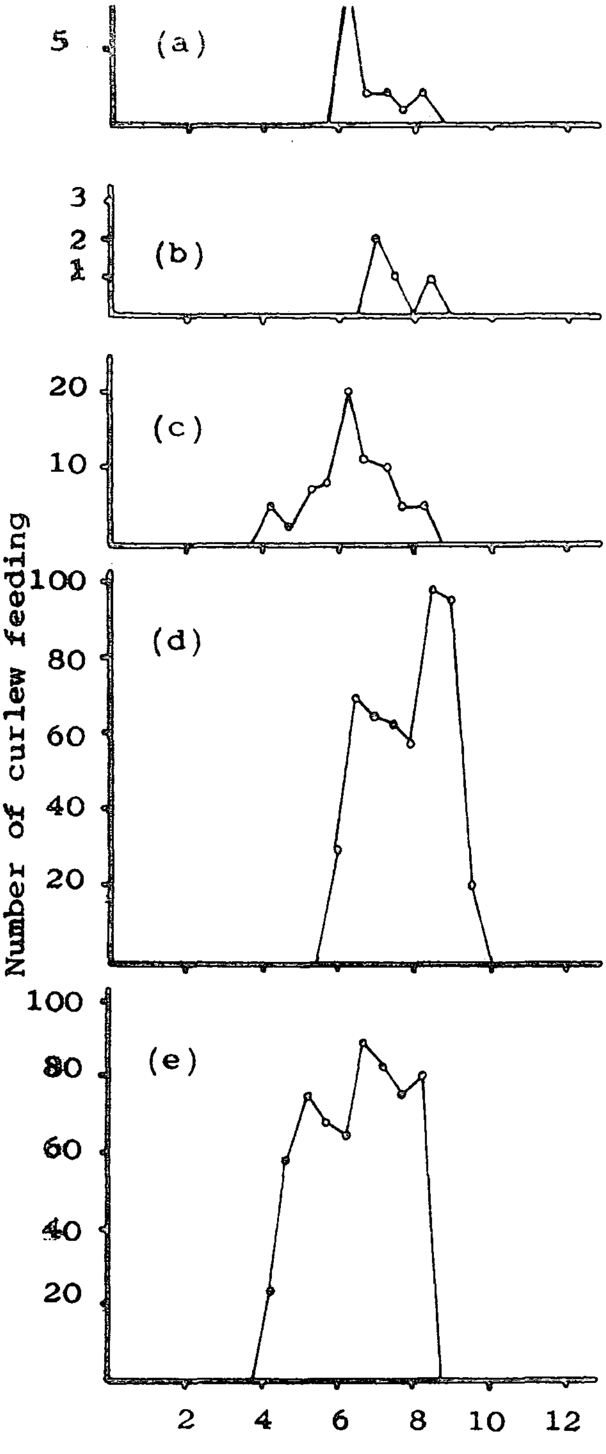


FIGURE A14 Variation in the number of curlew feeding on the Greenabella Channel in relation to the state of the tide.

(a) 17th May	(tide ht 5.0m)
(b) 31st May	(tide ht 4.8m)
(c) 29th June	(tide ht 4.9m)
(d) 20th July	(tide ht 4.2m)
(e) 2nd August	(tide ht 4.9m)

movement on to the Greenabella Bank from the Greenabella Channel as the tide began to rise, there was little movement in the other direction (see Figures A13 and A14 a and b). Variation in the number of birds moving to the Greenabella Bank from the Greenabella Channel, had little effect on GFT. Most of the variation in GFT was due to changes in the intensity (the numbers of birds feeding at any one time) and duration of feeding, during the period prior to this movement. The causes of these changes are unknown.

In July, GFTs were much higher than in May or June. This increase was proportionately greater than the increase in population size (in July RFIs were greater than in May or June). In late June, and throughout July most of the feeding on Greenabella Bank occured during two periods, one just before and the other just after low water. This was probably due to curlew having moved to the lower shore feeding areas, such as the Greenabella Channel, the MWB or the MWC (N.B. the MW was not used by curlew while they were waiting to feed on the MWB and MWC in late June and during July), to feed over the low water period, and to curlew (not necessarily the same ones) having moved from these lower shore feeding areas to the Greenabella Bank as they were covered by the flood tide (see Figures A13 and A14, c,d and e). During July, GFTs were higher on neap tides than on spring or intermediate tides. This was due to a greater intensity and a longer duration of feeding during the second feeding period. The intensity of feeding during the first feeding period was also greater, but the duration was much shorter than was the case on spring tides. Presumably the greater competition for low water feeding areas during neap tides, resulted in a greater number of birds using the Greenabella Bank during the ebbing tide, so that movement on to the lower shore feeding areas could occur as soon as they were exposed (the drop in feeding intensity at the end of the first feeding period, occured when feeding on the lower shore areas started, rather than during the times when maximum numbers of feeding birds occurred on the lower shore areas, as was the case on spring tides (see Figures A13 and A14, c,d and e)). During neap tides in July, the Greenabella Channel was the main lower shore feeding area used by curlew, even though GFTs on this area were lower, during these tides, than during spring tides. When maximum numbers of feeding birds (and, presumably, greatest competition for this area) occured on this area, an increase in the number of curlew using the Greenabella Bank also occured. It seems likely then, that, on neap tides, the higher intensity and longer duration of feeding during this second feeding period on the Greenabella Bank, was brought about by curlew having to feed to a greater extent on this area, because they could not feed for long enough, if at all, on the lower shore feeding areas.

4) Greenabella Channel This area contained the greatest extent of lower shore feeding areas (areas of mud which were only exposed for very short periods of time) of all the areas on Seal Sands. In May and during the early part of June, the Greenabella Channel was, on most occasions, used for feeding at and just after low water, while the

lower shore areas were exposed (see Figure A14 a and b). In May, GFTs were higher than in June. This was due to a greater number of birds using this area, and a slightly longer duration of feeding. Similar differences in the intensity and duration of feeding also occured between tides of different heights. Throughout, GFTs were higher on spring tides than on neap tides, but the highest GFTs were (with one exception) found at intermediate tide heights. In July, GFTs were much higher than in June . This increase was proportionately greater than the increase in population size (in July RFIs were in the order of 10 times greater than the June values), and resulted in this area becoming the second most important feeding area for curlew in July. In late June and during July, feeding occured throughout the period of exposure of this area, the intensity of feeding was also much greater at these times than during the early part of the study. Although the highest feeding intensities were observed on neap tides, on spring and intermediate tides high feeding intensities were supported for longer. This, together with a slightly shorter overall duration of feeding, resulted in lower GFTs on neap tides than on spring or intermediate tides (see Fig A14 c, d, and e).

GFTs were probably lowest on neap tides because the extent of exposure to the lower shore feeding areas were much less than on spring or intermediate tides. This reasoning, however, does not explain why GFTs were higher on intermediate tides than on spring tides. A likely explanation for this is that, during intermediate tides, when fewer birds fed on other lower shore feeding areas, such as the MWB, the MWC or the Scallop Channel, than did on spring tides, the birds "displaced" from these areas fed on the Greenabella Channel.

5) Scalloped Mud and Scallop Channel. In May and June, scalloped mud was usually used for feeding by between 2 and 7 birds throughout much of the period of exposure of this bank. A drop in the number of birds feeding often occured around low water, as birds moved on to the scallop channel to feed (see Fig A15). Scalloped Mud was also often used for feeding and subroosting by large numbers of birds towards the end, and occasionally at the beginning of the period of exposure of this area, as other areas were covered or not yet exposed. This also occured in July. In May and June, most of the variation in GFT was due to variation in the number of birds feeding at the start or end of the period of exposure. This did not vary consistently with tide height or season. (This was also the main cause of variation in GFT between June and July.) The number of birds which used Scalloped Mud and Scallop Channel throughout most of the period of exposure of these areas, however, did vary with both season and the height of tide. In May and June a greater number of birds used Scalloped Mud (during the periods of exposure prior and following the use of the Scallop Channel) on the tides when greatest numbers of birds used Scallop Channel.

In July a greater number of birds used Scalloped Mud (throughout most of its period of exposure) than in May or June (see Figure A16), and a greater proportion did not feed on Scallop Channel. The increase in the number of birds feeding on Scalloped Mud (but not Scallop

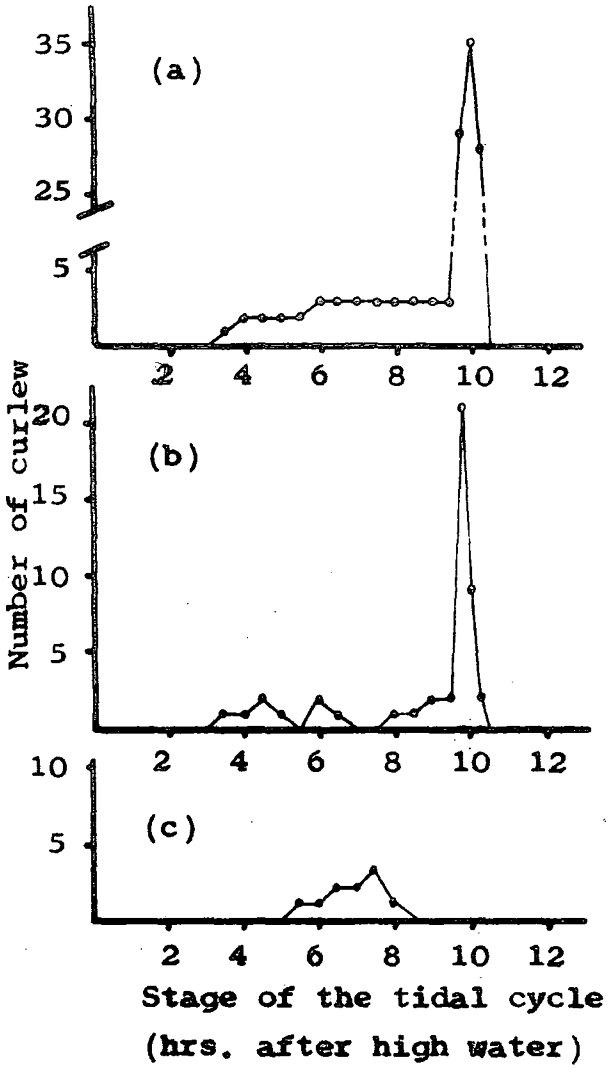


FIGURE A15 Variation in the number of curlew observed on Scalloped Mud and Scallop Channel in relation to the state of the tide on the 3rd June (tide ht. 4.7m).

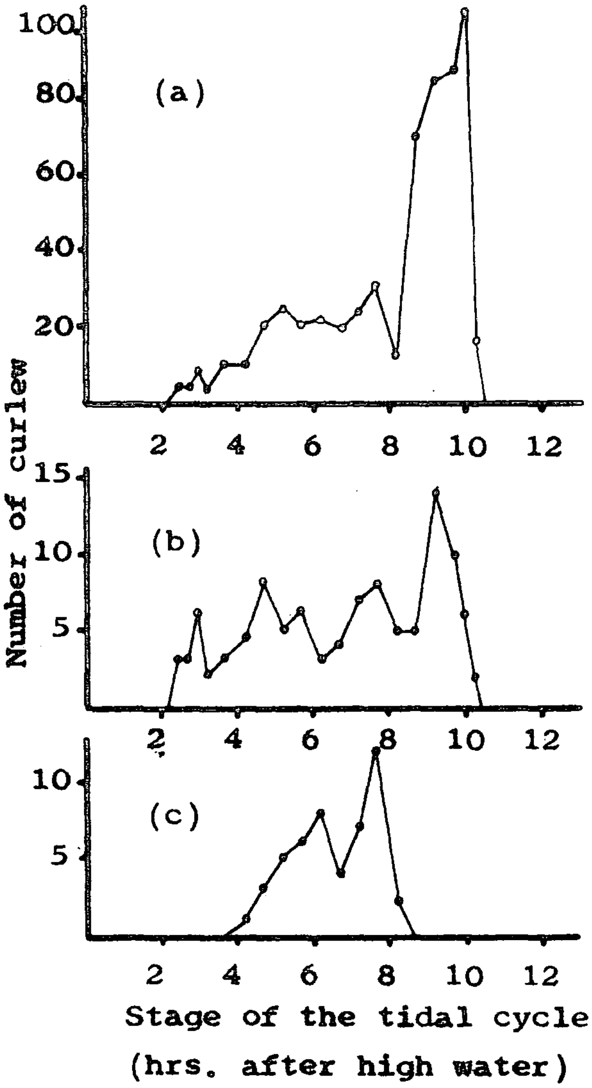


FIGURE A16 Variation in the number of curlew observed on Scalloped Mud and Scallop Channel in relation to the state of the tide on the 2nd August (tide ht. 4.9m).

channel), was the main cause of the increase in GFT between June and July. Seasonal and daily changes in the use of Scallop Channel also affected the number of birds using Scalloped Mud in July (in a similar fashion to that described for May and June), but had little effect on GFT.

On Scallop Channel, feeding occured mainly around low water. GFTs were higher on spring tides than on neap tides, and higher in May than in June. High GFTs were due to a greater number of birds feeding and a slightly longer duration of feeding on the tides when these occured, than on the tides when lower GFTs occured. On spring tides this was probably the result of a greater extent of exposure of the lower shore feeding areas on these tides, than on neap tides. The reduction in GFT between May and June is likely to have been due to a reduction in the use of middle shore feeding areas, as feeding did not occur on neap tides in June (most of the lower shore areas remain covered at low water on neap tides), and the duration of feeding was shorter on spring tides in June, than on spring tides in May.

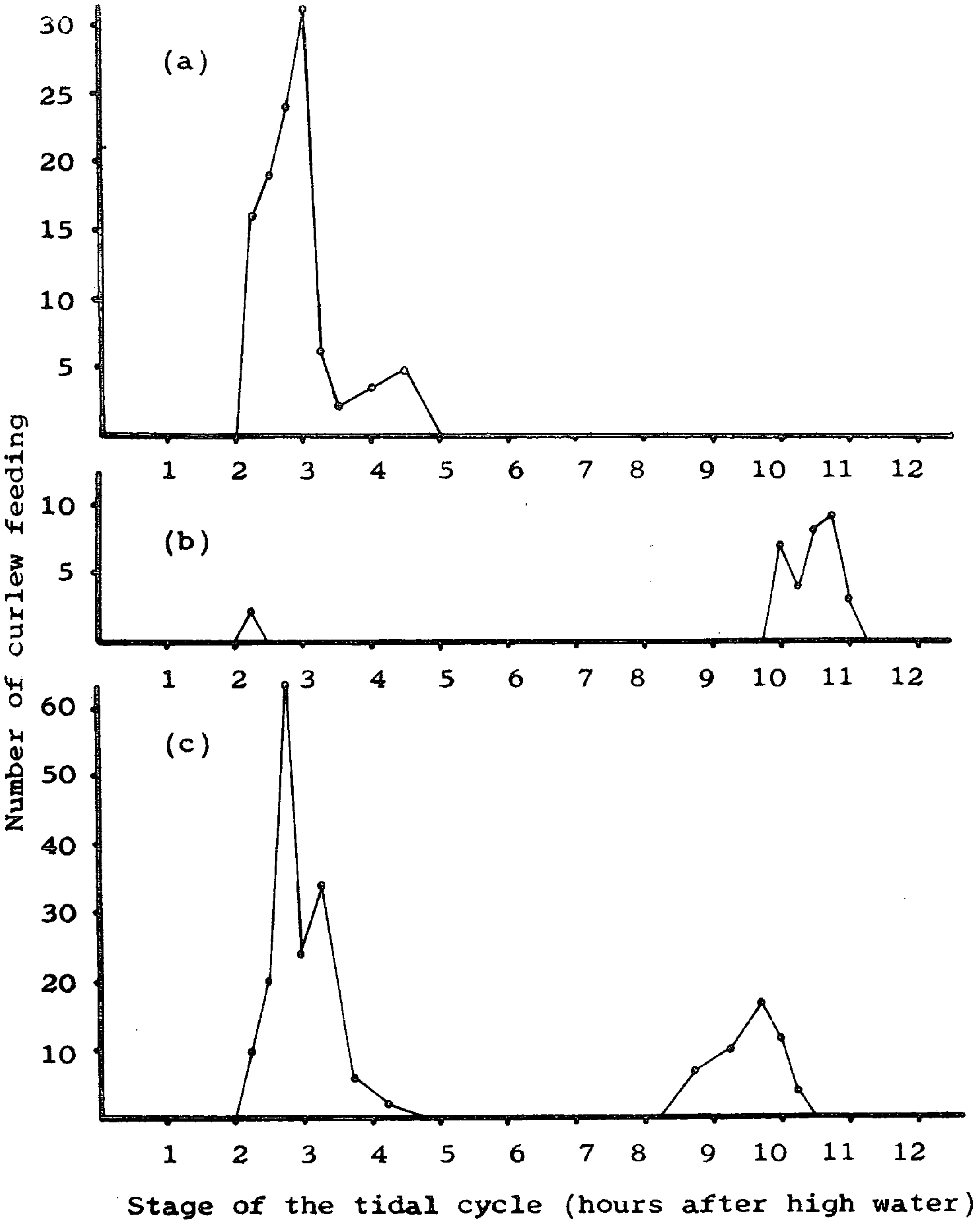
In July GFTs were higher than in June. This was probably due to a greater number of birds feeding on the lower shore feeding areas in July than in June (in July the duration of feeding was longer than in June, but still shorter than in May. Feeding intensities were also higher in July than in June) It is also possible that a greater number of birds fed on the lower shore feeding areas in July than in May, as GFTs were higher on July spring tides than on May spring tides, even though middle shore areas were used in addition to the lower shore areas in May. (The use of middle shore areas on neap tides in May was probably the reason why GFTs were higher on these tides in May than in July.)

6) Eastern Channel. This area was most often used for feeding during the early or later stages of the tidal cycle, as it was one of the first areas to be exposed by the ebbing tide and one of the last to be covered by the flood tides (see Fig A17).

GFTs varied considerable throughout the study but were, on average, higher in July than in May or June. GFTs did not vary consistently with tide height.

7) Central Bank. This remained the most used feeding area throughout the study. Feeding occured throughout the period of exposure of this area. The duration of feeding was longer on neap tides than on spring tides. Maximum numbers of feeding birds were most often found during the early stages of the tidal cycle, before other areas, such as Greenabella and Mid Tide Wall areas were exposed. Feeding intensities usually decreased from this time until low water, presumable because birds moved on to other areas which were being exposed during these times. After low water feeding intensities often increased, as other feeding areas were covered by the flood tide (see Figure A18). The Central Bank was often used for feeding and subroosting by large numbers of curlew, towards the end of its period of exposure.

Variation in the total use of this area were often difficult to discern, as much of the feeding that



<u>FIGURE A17</u> Variation in the number of curlew feeding on Eastern Channel in relation to the state of the tide.

a) 3rd June	(tide height 4.7m)
b) 21st June	(tide height 4.1m)
c) 2nd August	(tide height 4.9m)

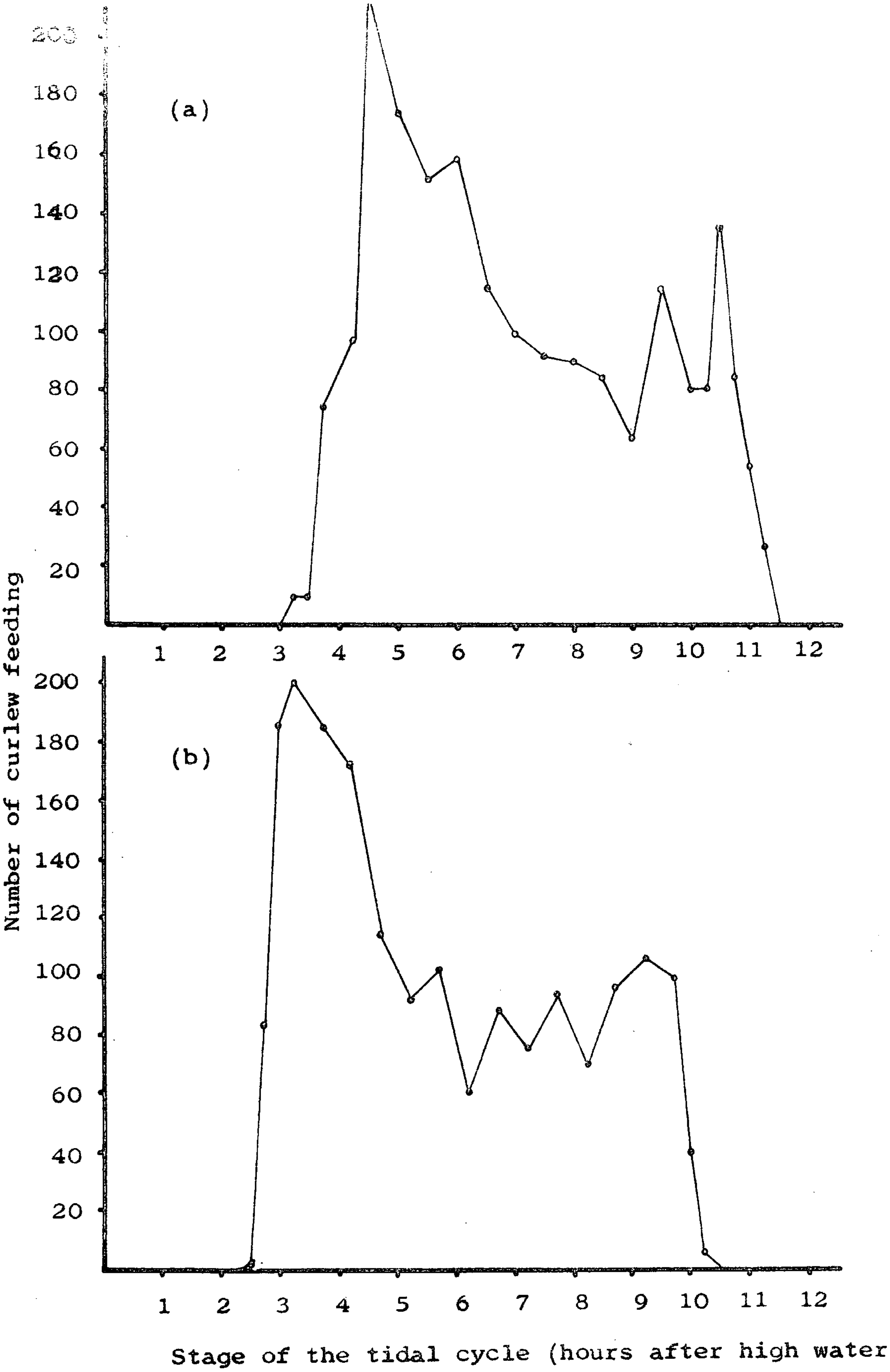


FIGURE A18 Variation in the number of curlew feeding on Central Bank in relation to the state of the tide.

a) 20th July (tide height 4.2m)
b) 2nd August (tide height 4.9m)

was thought to have occured on this area was unobserved, due to bad viewing conditions (see page 21) or due to inexperience at identifying curlew at long distances. GFTs (NO) (ie GFTs estimated but not observed) were particularly high (in relation to GFTs on Central Bank) on four dates (16/5, 17/5, 21/5, 21/6). On the first two dates, a large proportion of this is likely to have been due to my not noticing that curlew were not using the MW. On the latter two dates bad viewing conditions resulted in high GFTs (NO). If it is borne in mind that a greater proportion of feeding on Central Bank is likely to have been unobserved on 21/5 and 21/6, than on other dates, then the following conclusions are arrived at :

a) GFTs on Central Bank increased in early June. This increase was in the same proportion as the increase in population size (RFIs were similar in May and early June).

b) GFTs increased further after the 3rd June.

c) GFTs increased again in July. This increase was not in the same proportion as the increase in population size (RFIs were lower in July than in late June).

d) GFTs were greater on neap tides than on spring tides.

As discussed earlier, changes in the use of Central Bank, within a tidal cycle, appear to be related to changes in the use of other feeding areas. Similarly, variations in the use of Central Bank between tidal cycles may also be related to changes in the use of other areas. The high GFTs on the Central Bank during late June, and during neap tides, both occured at times when GFTs on the preferred lower shore areas were low.

APPENDIX 3

Estimates Of Absolute Size, Calorific Content, And Biomass Of Prey Items.

The range of "dead sizes" (the lengths of worms killed in alcohol) of different "live size" categories of worms (the estimated relative sizes of live worms held against a curlew's bill are shown in Figures A19 and A20 (see also Table A1). From these results, estimates of the median "dead size" of worm in each of four different "live size" classes (0-$\frac{1}{4}$ bill length, $\frac{1}{4}$-$\frac{1}{2}$, $\frac{1}{2}$-$\frac{3}{4}$, $\frac{3}{4}$-1), and for each of two size classes of curlew (large male and large female), were calculated. Equivalent estimates for the other two size classes of curlew (small male and small female) were obtained by plotting the median "dead size", for each "live size" class or worm, against curlew bill length (see Figure A21). These estimates, together with the estimates for "large males" and "large females" are listed in table A2.

When observed clearly, the sizes of crabs taken by curlew were estimated in relation to bill width (x2, x3, or x4 bill width). The range and median size of crabs (measured across the width of the carapace) in each "estimated" size class, are shown in table A3. These results were ontained by estimating, then measuring the sizes of 24 crabs held against a stuffed curlew's bill.

The mean sizes, dry weights and calorific contents of worms and crabs in different "dead size" classes are listed in Table A4. Measurements from worms collected from beneath the surface of the mud on Central Bank

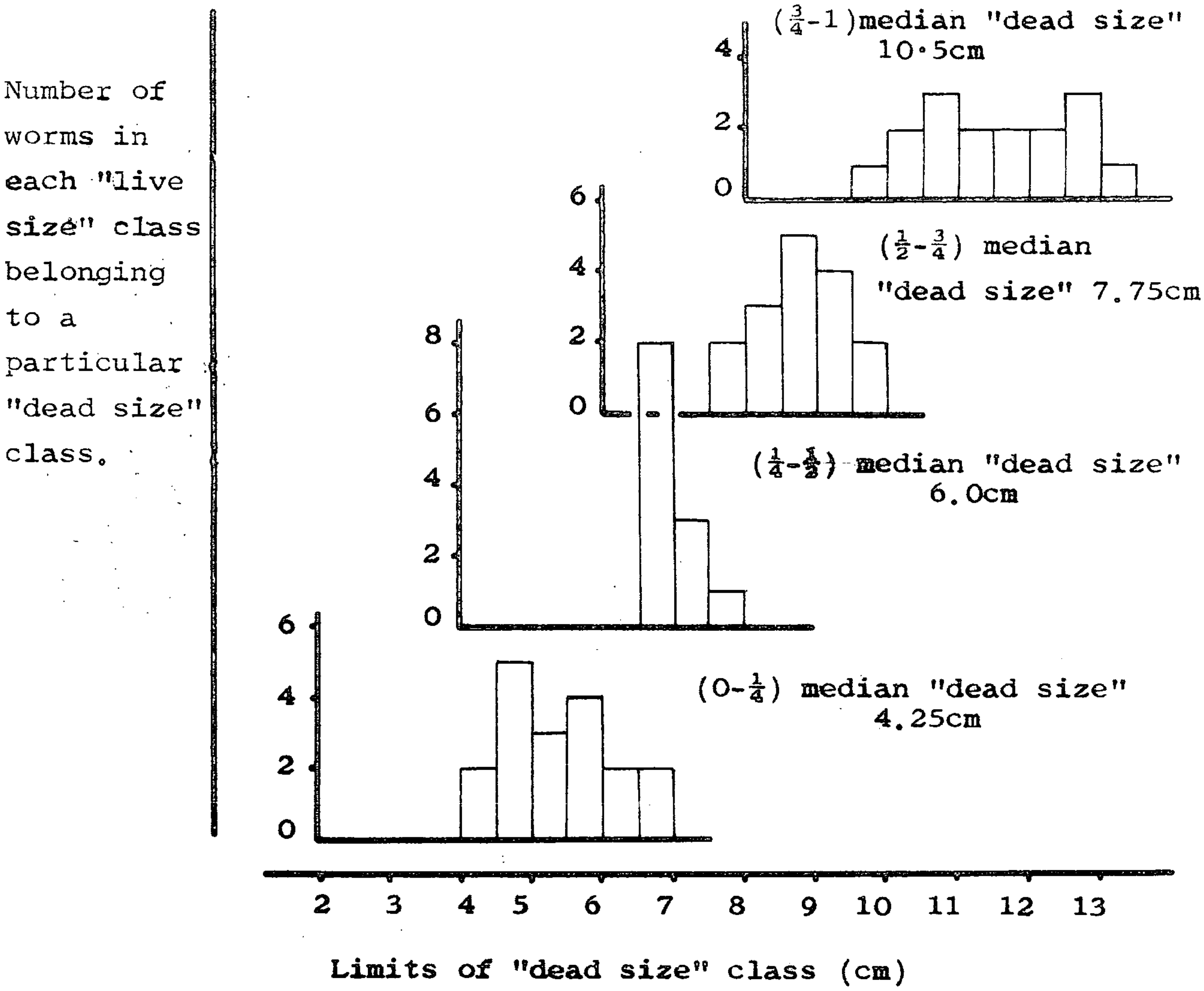


FIGURE A19 The range of "dead sizes" of different "live size" classes of worms, using a "large female" (bill length 15.0cm) stuffed curlew. Brackets indicate the "live size"classes, estimated in relation to the bill size.

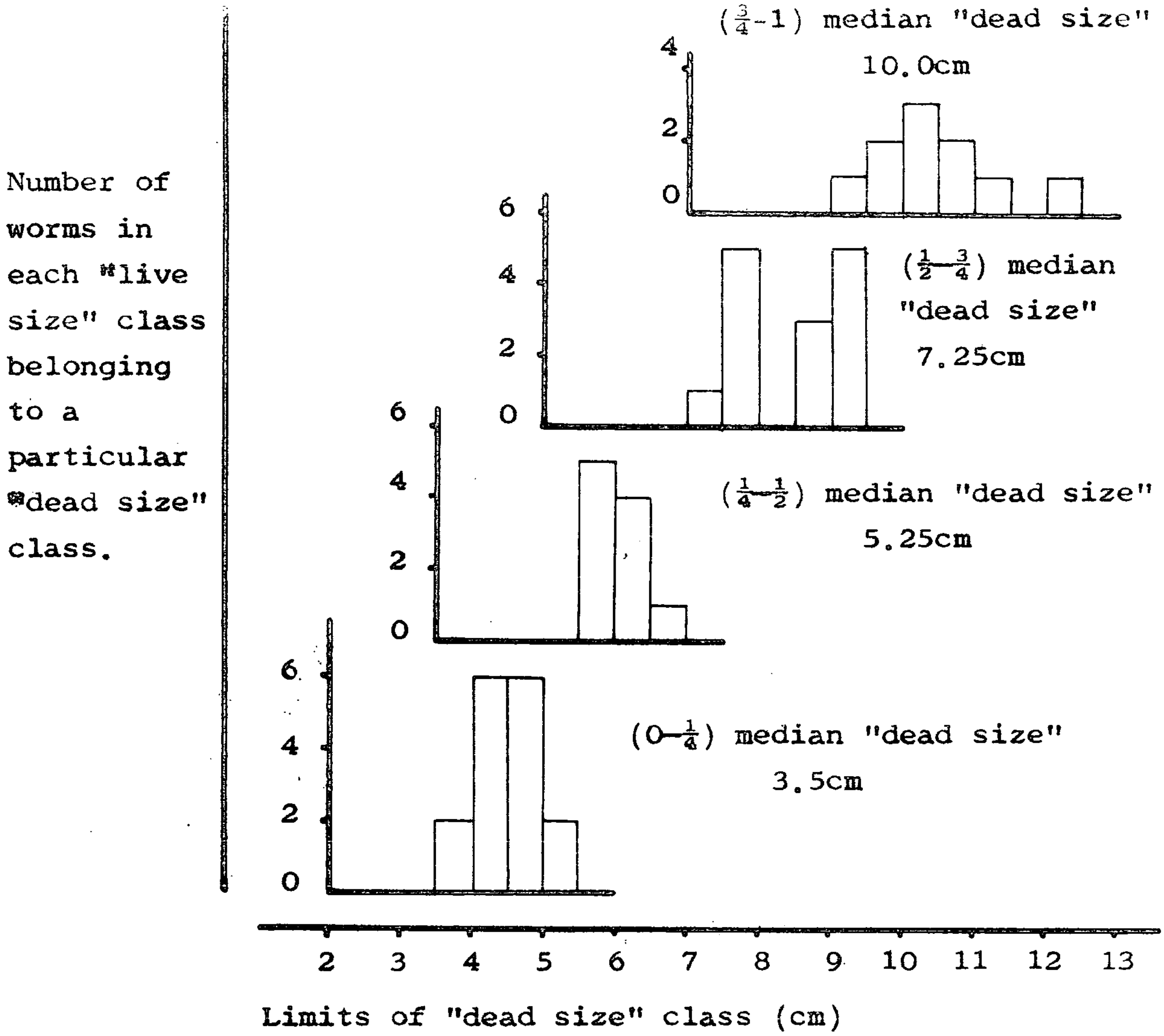


FIGURE A20 The range of dead sizes of different "live size" classes of worms, using a large male (bill length 11.5cm) stuffed curlew. Brackets indicate the "live size" classes, estimated in relation to the bill size.

TABLE A1, MEASUREMENTS OF THE LENGTHS OF WORMS KILLED WITH ALCOHOL (DEAD SIZES) BUT SORTED, WHEN LIVE, INTO SIZES RELATIVE TO THE LENGTH OF A CURLEW'S BILL.

ESTIMATED "LIVE SIZES" OF WORMS	"DEAD SIZES" OF WORMS (IN cm) (a) USING A "LARGE MALE" STUFFED CURLEW - BILL LENGTH 11.5cm.	"DEAD SIZES" OF WORMS (IN cm) (b) USING A "LARGE FEMALE" STUFFE CURLEW - BILL LENGTH 15.0cm.
0-$\frac{1}{4}$ bill length	2.8, 2.9, 3.1, 3.3, 3.3, 3.4, 3.4, 3.4, 3.5, 3.5, 3.7, 3.7, 3.9, 3.9, 4.1, 4.3,	3.3, 3.4, 3.7, 3.7, 3.8, 3.9, 3.9, 4.1, 4.3, 4.4, 4.5, 4.6, 4.8, 4.8, 5.1, 5.2, 5.7, 5.8,
$\frac{1}{4}$-$\frac{1}{2}$ bill length	4.4, 4.5, 4.5, 4.8, 4.9, 5.0, 5.3, 5.3, 5.5, 5.8,	5.5, 5.6, 5.7, 5.8, 5.8, 5.8, 5.9, 5.9, 6.2, 6.3, 6.4, 6.5,
$\frac{1}{2}$-$\frac{3}{4}$ bill length	6.2, 6.5, 6.5, 6.5, 6.7, 6.9, 7.5, 7.5, 7.8, 8.0, 8.1, 8.2, 8.3, 8.5,	6.8, 6.9, 7.2, 7.3, 7.4, 7.5, 7.6, 7.7, 7.7, 7.8, 8.2, 8.3, 8.4, 8.5, 8.6, 8.9,
$\frac{3}{4}$-1 bill length	8.4, 8.6, 8.7, 9.0, 9.2, 9.2, 9.5, 9.7, 10.4, 11.6,	8.9, 9.1, 9.3, 9.7, 9.8, 9.9, 10.4, 10.4, 10.6, 11.3, 11.4, 11.5, 11.6, 12.1.

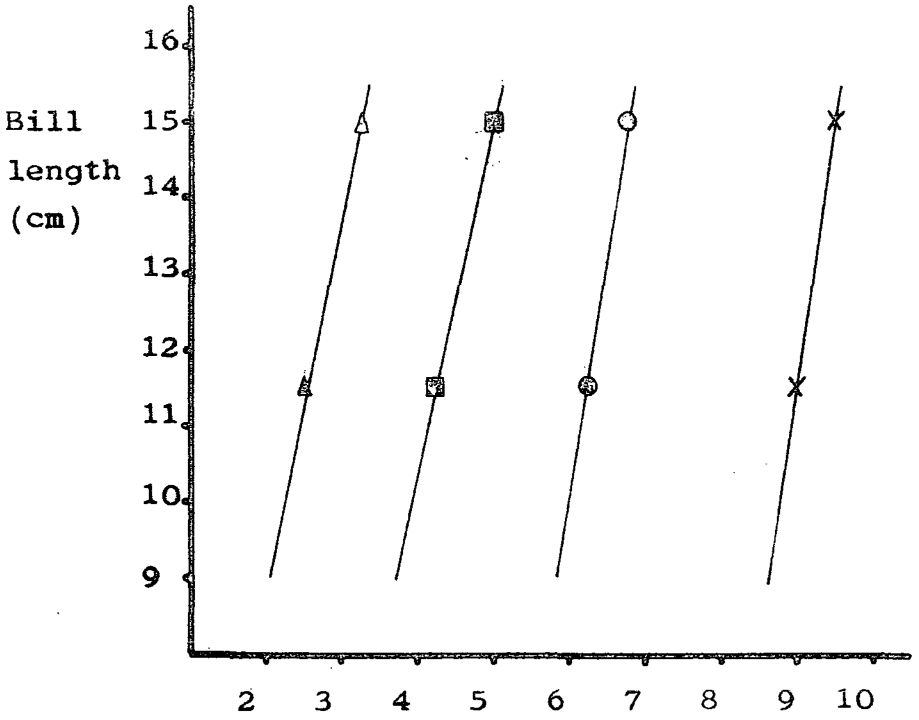


FIGURE A21 Median "dead size" of four different "live size" classes of worm in relation to curlew bill length

▲ $0-\frac{1}{4}$

■ $\frac{1}{4}-\frac{1}{2}$

● $\frac{1}{2}-\frac{3}{4}$

x $\frac{3}{4}-1$

TABLE A2. ESTIMATES OF AVERAGE "DEAD SIZE" OF WORMS IN EACH OF FOUR "LIVE SIZE" CLASSES, FOR EACH OF FOUR SIZE CLASSES OF CURLEW.

ESTIMATED "LIVE SIZES" OF WORMS, IN RELATION TO BILL SIZE	AVERAGE "DEAD SIZE" OF WORMS			
	(A) FOR A SMALL MALE CURLEW BILL LENGTH 10.2 cm	(B) FOR A LARGE MALE CURLEW BILL LENGTH 11.5 cm	(C) FOR A SMALL FEMALE CURLEW BILL LENGTH 13.4 cm	(D) FOR A LARGE FEMALE CURLEW BILL LENGTH 15.2 cm
0-$\frac{1}{4}$	3.24	3.50	3.88	4.25
$\frac{1}{4}$-$\frac{1}{2}$	5.00	5.25	5.63	6.00
$\frac{1}{2}$-$\frac{3}{4}$	7.10	7.25	7.50	7.75
$\frac{3}{4}$-1	9.80	10.00	10.25	10.50

TABLE A3. THE RANGE OF SIZES OF CRABS IN EACH OF THREE "ESTIMATED" SIZE CLASSES.

ESTIMATED SIZE-CLASS OF CRAB (x BILL WIDTH)	RANGE OF CRAB SIZES (WIDTH OF CARAPACE) (cm)	MEDIAN SIZE OF CRAB (cm)
2	1.1 - 1.5	1.3
3	1.6 - 2.2	1.9
4	2.3 - 2.7	2.5

TABLE A4. MEASUREMENTS OF THE CALORIFIC CONTENT AND BIOMASS (DRY WEIGHT) OF DIFFERENT SIZED PREY ITEMS.

"DEAD SIZE" CLASS OF PREY ITEM (cm)	WORMS	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
	CRABS	1-2	2-2.5	2.5-3	3-4	-	-	-	-	-
NUMBER OF ANIMALS IN SAMPLE	BURIED WORMS	-	2	16	18	21	14	10	4	5
	SURFACE WORMS	-	4	8	17	11	9	3	3	-
	CRABS	3	3	3	2					
MEAN "DEAD SIZE" OF PREY ITEMS (cm)	BURIED WORMS	-	2.67	3.53	4.48	5.43	6.58	7.48	8.39	9.68
	SURFACE WORMS	-	2.33	3.46	4.38	5.45	6.53	7.63	8.24	-
	CRABS	1.53	2.13	2.80	3.55	-	-	-	-	-
MEAN CALORIFIC CONTENT OF PREY ITEMS (k cals)	BURIED WORMS	-	-	-	0.127	0.196	0.298	0.383	0.467	0.625
	SURFACE WORMS	-	-	-	0.114	0.237	0.260	0.532	0.415	-
	CRABS	0.397	2.142	3.493	5.588	-	-	-	-	-
MEAN DRY WEIGHT OF PREY ITEMS (grams)	BURIED WORMS	-	0.002	0.010	0.025	0.036	0.056	0.072	0.087	0.113
	SURFACE WORMS	-	0.004	0.011	0.021	0.041	0.047	0.091	0.072	-
	CRABS	0.187	0.573	1.076	2.062	-	-	-	-	-

(buried worms), and from worms collected from the surface of the mud on Central Bank and Eastern Channel (surface worms) are listed seperately. The relationships between size, and calorific content or biomass (dry weight), for each group of invertebrates, are shown in Figs A22-A24. From these graphs and the data in Tables A2 and A3, the average calorific contents and biomass of worms and crabs in each "live size" class were estimated (see Tables A5, A6 & A7).

The results of sampling on the surface of Central Bank, Eastern Channel, and on the Mid Tide Wall are shown in Tables A8 and A9. From these results, and from information obtained from Figures A22-A24, the mean sizes, calorific contents and biomasses of prey items found on the surfaces of the Central Bank, Eastern Channel, and on the Mid Tide Wall, were estimated (see Tables A8 and A9.

Observations of feeding curlew provided data on the number, type and relative size of each prey item consumed in each of 253 observation periods. Estimates of the biomass and calorific content of each prey item observed were obtained from Tables A5-A9, and were used to calculate the total biomass and calorific intake during each observation period. Each of the estimates was then divided by the duration of the observation period and the number of food items eaten, to obtain estimates of biomass and calorific intake rates, and the mean biomass and calorific content of food items.

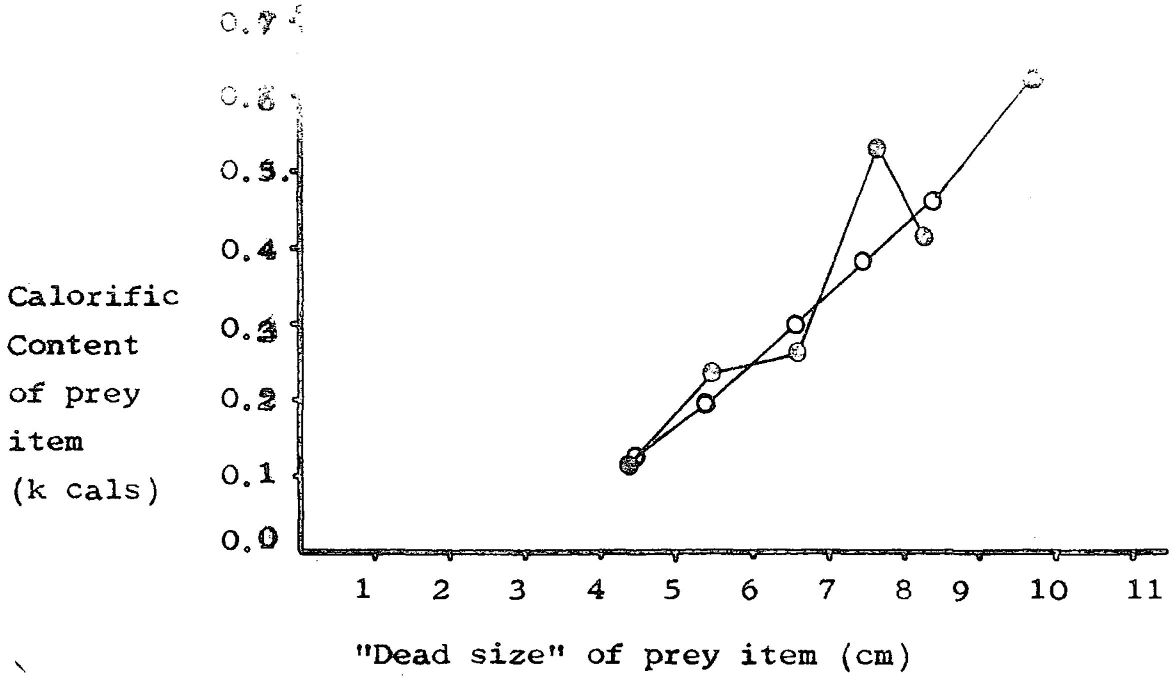


FIGURE A22 Calorific content of *Nereis diversicolor* in relation to the length of worms killed in 70% alcohol.

O - buried worms ● - surface worms

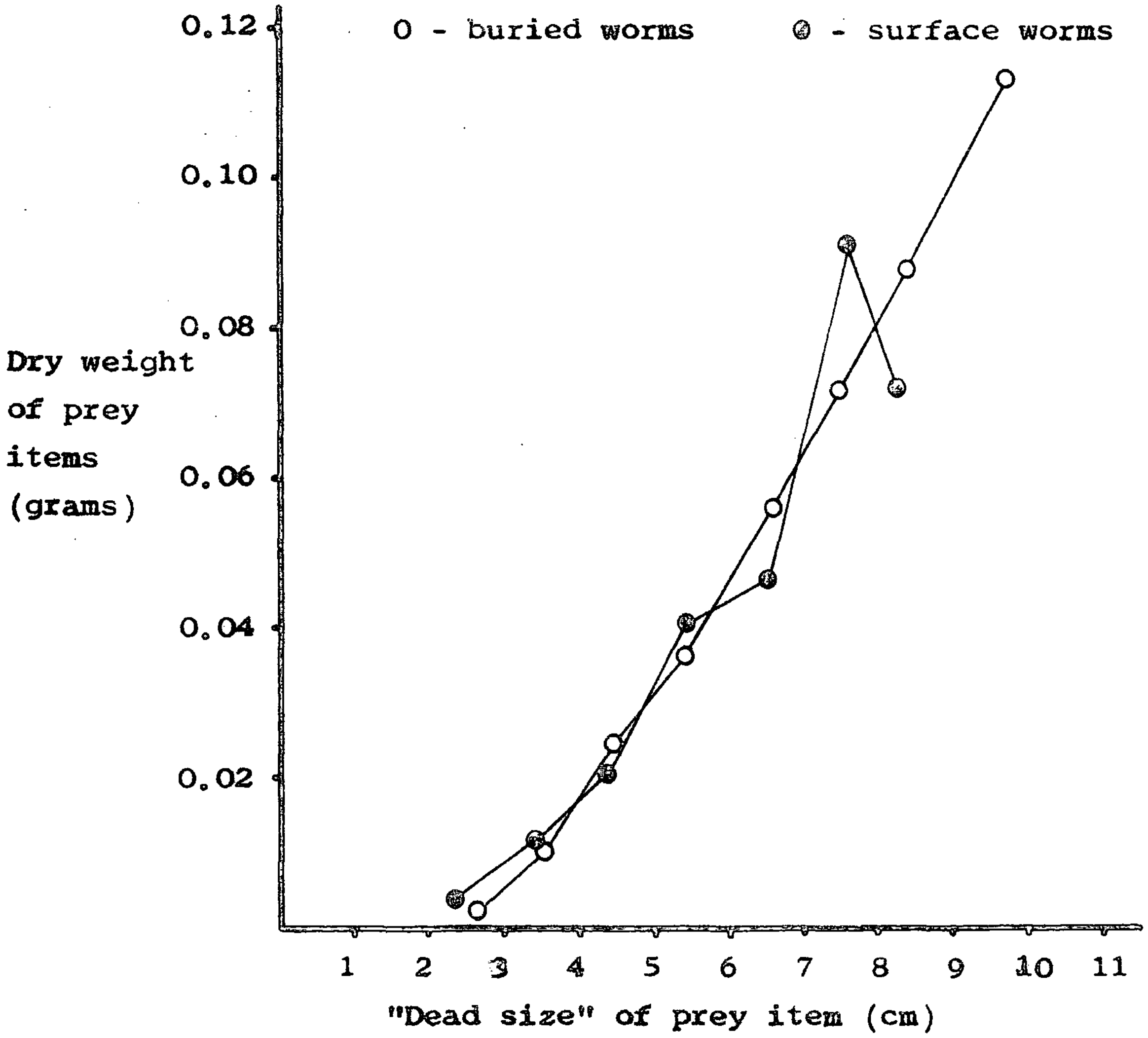


FIGURE A23 Biomass (dry weight) of *Nereis diversicolor* in relation to the length of worms killed in 70% alcohol.

O - buried worms ● - surface worms

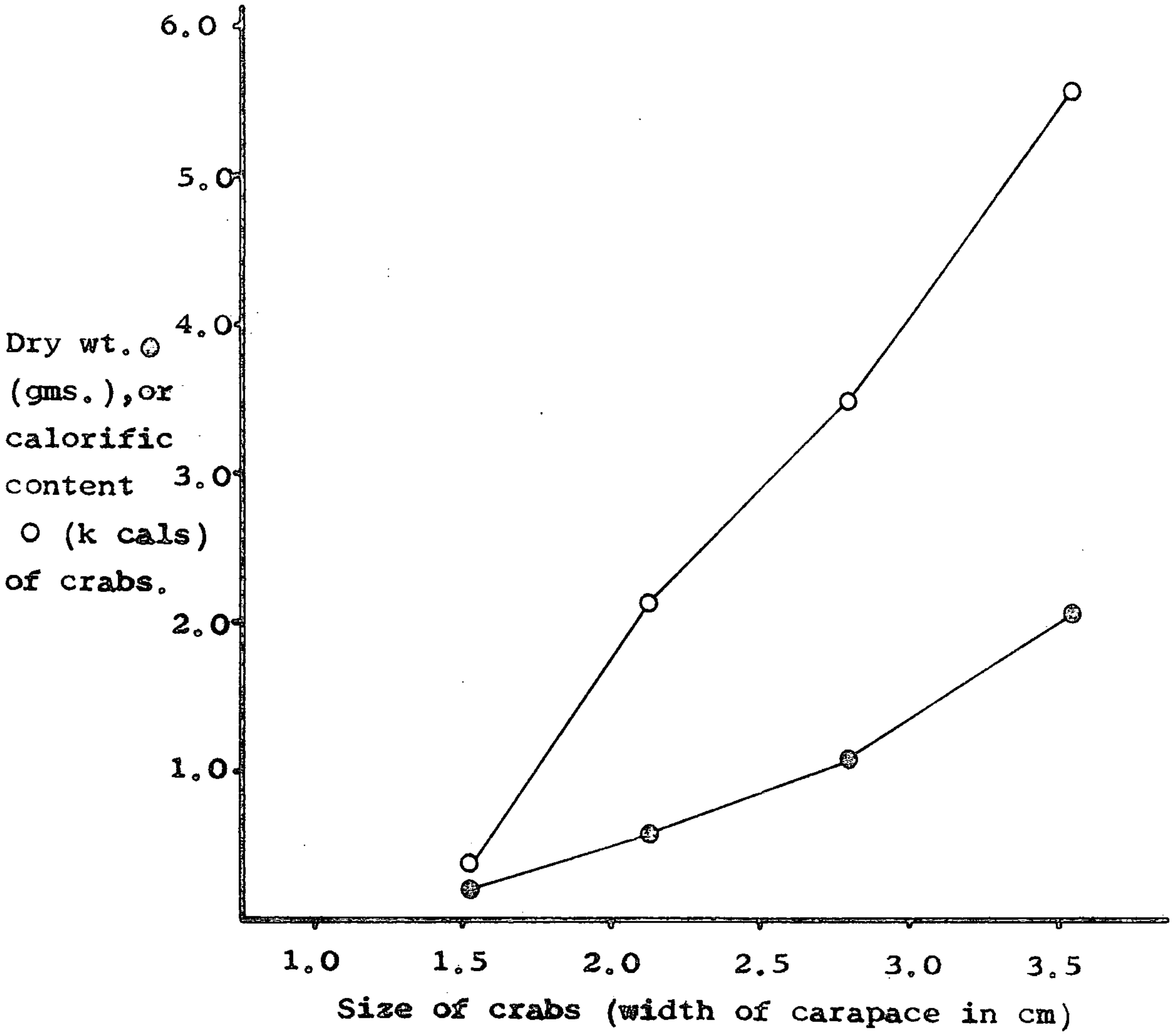


FIGURE A24 Biomass and calorific content of shore crabs (*Carcinus maenus*) in relation to size.

TABLE A5. ESTIMATES OF AVERAGE CALORIFIC CONTENT OF WORMS IN EACH OF FOUR "LIVE SIZE" CLASSES, FOR EACH OF FOUR SIZE CLASSES OF CURLEW.

ESTIMATED "LIVE SIZE" OF WORMS, IN RELATION TO BILL LENGTH	CALORIFIC CONTENT OF CORRESPONDING MEDIAN "DEAD SIZE" OF WORM (IN k cals)			
	(A) FOR A SMALL MALE CURLEW - BILL LENGTH 10.2 cm	(B) FOR A LARGE MALE CURLEW - BILL LENGTH 11.5 cm	(C) FOR A SMALL FEMALE CURLEW BILL LENGTH 13.4 cm	(D) FOR A LARGE FEMALE CURLEW BILL LENGTH 15.2 cm
0-¼	0.035	0.050	0.080	0.110
¼-½	0.165	0.185	0.213	0.246
½-¾	0.345	0.360	0.383	0.407
¾-1	0.640	0.665	0.695	0.730

TABLE A6. ESTIMATES OF AVERAGE BIOMASS (DRY WEIGHT) OF WORMS IN EACH OF FOUR "LIVE SIZE" CLASSES, FOR EACH OF FOUR SIZE CLASSES OF CURLEW.

ESTIMATED "LIVE SIZE" OF WORMS, IN RELATION TO BILL LENGTH	DRY WEIGHT OF CORRESPONDING MEDIAN "DEAD SIZE" OF WORM (IN grams x10)			
	(A) FOR A SMALL MALE CURLEW BILL LENGTH 10.2 cm	(B) FOR A LARGE MALE CURLEW BILL LENGTH 11.5 cm	(C) FOR A SMALL FEMALE CURLEW BILL LENGTH 13.4 cm	(D) FOR A LARGE FEMALE CURLEW BILL LENGTH 15.2 cm
0-¼	0.075	0.105	0.160	0.210
¼-½	0.300	0.330	0.390	0.460
½-¾	0.650	0.680	0.720	0.760
¾-1	1.120	1.135	1.180	1.220

TABLE A7. ESTIMATES OF AVERAGE CALORIFIC CONTENT AND BIOMASS (DRY WEIGHT) OF CRABS IN EACH OF THREE ESTIMATED SIZE CLASSES.

ESTIMATED SIZE CLASS (x BILL WIDTH)	CALORIFIC CONTENT OF THE CORRESPONDING MEDIAN "DEAD SIZE" OF CRAB (IN k cals)	DRY WEIGHT OF THE CORRESPONDING MEDIAN "DEAD SIZE" OF CRAB (IN grams)
2	0.30	0.15
3	1.40	0.44
4	2.85	0.85

TABLE A8. THE RESULTS OF SAMPLING ON THE SURFACE OF THE CENTRAL BANK AND EASTERN CHANNEL.

The results show the "dead size", and estimates of biomass and calorific content of each food item found in each of 3 5x10m^2 sampling areas.

ON CENTRAL BANK SITE A.

DEAD SIZE (cm)	CALORIFIC CONTENT (k cals)	BIOMASS (grams)
4.80	0.160	0.028
2.97	0.030	0.008
3.48	0.050	0.011
5.62	0.240	0.041
4.63	0.140	0.025
4.16	0.100	0.018
7.49	0.500	0.086
4.48	0.125	0.023
3.69	0.065	0.014
2.81	0.029	0.006
7.42	0.475	0.083
6.35	0.260	0.045
3.62	0.064	0.013
5.47	0.235	0.042
2.14	0.022	0.003
2.29	0.025	0.002
1.5 *	0.400	0.180
MEAN -	0.171	0.037

ON CENTRAL BANK SITE B.

DEAD SIZE (cm)	CALORIFIC CONTENT (k cals)	BIOMASS (grams)
4.16	0.100	0.018
4.05	0.095	0.017
8.21	0.425	0.073
6.25	0.255	0.045
1.80	0.020	0.001
2.82	0.030	0.007
5.59	0.235	0.041
2.29	0.025	0.002
6.34	0.260	0.045
5.26	0.215	0.036
4.15	0.100	0.018
3.47	0.050	0.011
3.40	0.046	0.011
3.16	0.034	0.009
1.4 *	0.350	0.150
	0.149	0.032

ON EASTERN CHANNEL

DEAD SIZE (cm)	CALORIFIC CONTENT (k cals)	BIOMASS (grams)
3.17	0.034	0.009
4.87	0.170	0.030
6.54	0.275	0.048
4.15	0.100	0.018
3.05	0.031	0.008
5.79	0.243	0.042
4.24	0.110	0.019
2.82	0.030	0.006
	0.124	0.0226

OVERALL MEAN FOR CENTRAL BANK - 0.160 k cals
0.035 grams

All food items were worms apart from * which crabs

TABLE A9. THE RESULTS OF SAMPLING ON THE MID TIDE WALL.

The results show the mean size of crab found in each of five $1m^2$ sampling areas.

SAMPLING STATION	1	2	3	4	5	OVERALL
MEAN SIZE OF CRAB IN SAMPLE (width of carapace in cm.)	1.87	2.63	1.55	2.37	2.19	2.16
NUMBER OF CRABS IN SAMPLE	17	12	10	18	18	75
STANDARD DEVIATION	0.753	0.688	0.327	0.668	0.710	0.742
CALORIFIC CONTENT OF A "MEAN" CRAB (IN k cals)						2.18
BIOMASS (DRY WEIGHT) OF A "MEAN" CRAB (IN grams)						0.60

BIBLIOGRAPHY

BAILEY, N.T.J. (1964) Statistical Methods In Biology. London: English Universities Press.

BAINBRIDGE, I.P. and MINTON, C.D.T. (1978) The Migration And Mortality of The Curlew In Britain and Ireland. Bird Study 25: 39-50.

BLACKMORE, F.H. (1969) The Effects Of Temperature, Photoperiod And Moult On The Energy Requirements Of The House Sparrow (Passer domesticus). Comp. Biochem. Physiol. 30: 433-444.

BOERE, G.C. (1976) The Significance Of The Dutch Wadenzee In The Annual Life Cycle Of Arctic, Subarctic and Boreal Waders. Part 1. The Junction As A Moulting Area. Ardea 64: 210-291

CHARNOV, E.L. (1976) Optimal Foraging: The Marginal Value Theorem. Theor. Popul. Biol. 9:129-136.

DAVIES, E.A. (1955) Seasonal Changes in The Energy Balance Of The English Sparrow. Auk 72: 385-411

DOLNIK, V.R. and GAVRILOV, V.M. (1979) Bioenergetics of Moult in The Chaffinch (Fringilla coelebs). The Auk 96: 253-264.

EMLEN J.M. (1966) The Role Of Time And Energy in Food Preference. Am.Nat..100: 611-617.

EVANS, P.R. (1966) Autumn Movements, Moult and Measurements Of The Lesser Redpol (Carduelis Flammea Cabaret). Ibis 108: 183-216.

EVANS, P.R., HERDSON, D.M., KNIGHTS P.J., PIENKOWSKI, M.W. (1979). Short Term Effects Of Reclamation Of Part Of

Seal Snads, Teesmouth, On Wintering Waders And Shelducks. I Shorebird Diets, Invertebrate Densities And The Impact Of Predation On The Invertebrates. Oecologia 41;183-206.

EVANS, P.R. (1976) Energy Balance And Optimal Foraging Strategies in Shorebirds; Some Implications of Their Distributions And Movements In The Non-breeding Season. Ardea 64: 117-170.

GOSS-CUSTARD J.D. (1969) The Winter Feeding Ecology Of The Redshank (Tringa totanus). Ibis 111: 338-356.

GOSS-CUSTARD, J.D. (1970) The Response of Redshank (Tringa totanus (L)) To Spatial Variations In The Density Of Their Prey. J. Anim.Ecol.39: 91-113.

GOSS-CUSTARD, J.D. (1977a) Optimal Foraging And The Size Selection Of Worms By Redshank (Tringa totanus) In The Field. Anim.Behav.25: 10-29.

GOSS-CUSTARD, J.D. (1977b) The Energetics Of Prey Selection By Redshank (Tringa totanus (L)) In Relation To Prey Density. J. Anim.Ecol.46: 1-19.

HASSELL, M.P. and MAY, P. (1974) Aggregation of Predators And Insect Parasites And Its Effects On Stability. J. Anim. Ecol. 43: 567-594.

HEPPLESTONE, P.B. (1971) The Feeding Ecology Of Oystercatchers (Haematopus ostralegus (L.)) In Winter in Northern Scotland. J. Anim. Ecol. 40: 651-672.

HOLLING, C.S. (1965) The Functional Responce Of Predators To Prey Density And Its Role In Mimicry And Population Regulation. Mem. Ent. Soc. Can. 45: 1-60.

HULSHER, J.B. (1976) Localisation Of Cockles (Cardium edule (L.)) By The Oystercatcher (Haematopus ostralegus (L.)) In Darkness And Daylight. Ardea 64: 292-310.

KING, J.R., FARNER, D.S. and MORTON, M.L. (1965) The Lipid Reserves Of White-Crowned Sparrows On The Breeding Ground In Central Alaska. Auk 82: 236-252.

KNIGHTS, P.J. (1974) The Effects Of Recent Reclamation Of The Tees Estuary On The Numbers And Feeding Activities Of Overwintering Waders And Shelducks. Unpublished Report To The Coastal Ecology Research Station, Institute Of Terrestrial Ecology.

KNIGHTS, P.J. (1975) Post-reclamation Changes In The Numbers And Feeding Activities Of Overwintering Waders And Shelducks At Teesmouth. Unpublished Report To The Coastal Ecology Research Station, Institute Of Terrestrial Ecology.

KOCH, H.J. and DEBONT, A.F. (1944) Influence De La Mue Sur L'intensite Du Metabolisme Chez Le Pinson (Fringilla coelebs coelebs L.) Annls. Soc. R. Zool. Belg. 75: 81-86.

KREBS, J.R. and DAVIES, N.B. (Ed.) (1978) Behavioural Ecology: An Evolutionary Approach. Sunderland, Mass: Sinauer Assoc.

MACARTHER, R.H. and PIANKA, E.R. (1966) On The Optimal Use Of a Patchy Environment. Am. Nat. 100: 603-609.

MAQSOOD, M. (1952) Thyroid Function In Relation To Reproduction Of Mammals And Birds. Biol. Revs. Cambridge Phil. Soc. 27: 281-319.

NEWTON, I. (1968) The Temperatures, Weights And Body Composition Of Moulting Bullfinches. Condor 70: 323-332.

PEREK, M. and SULMAN F. (1945) The Basal Metabolic Rate In Moulting And Laying Hens. Endocrinology 36: 240-243.

PRATER, A.J. (1972) The Ecology Of Morcambe Bay III. The Food And Feeding Habits Of Knot (Calidris canutus L.), In Morcambe Bay. J. App. Ecol. 9: 179-194.

PULLIAM, H.R. (1974) On The Theory Of Optimal Diets. Amm. Nat. 108: 59-74.

ROYAMA, T. (1970) Factors Governing The Hunting Behaviour And Selection Of Food By The Great Tit (Parus major L.). J. Anim. Ecol. 39: 619-668.

SACH, G. (1968) Die Mauser Von Gossen Brachvogels J. Orn. 109: 485-511.

SCHOENER, T.W. (1971) Theory Of Feeding Strategies. Ann.Rev. Ecol. Syst. 2: 369-404.

SMITH, P.C. (1975) A Study Of The Winter Feeding Ecology And Behaviour Of The Bar Tailed Godwit (Limosa lapponica). Unpublished Ph.D. Thesis. U.Of Durham.

STURKIE, P.D. (1954) Avian Physiology. Ithaca, New York, Comstock.

TOWNSHEND, D.J. (1980) The Use Of Intertidal Habitats By Shorebird Populations, With Special Reference To Grey Plover (Pluvialis squatorala) And Curlew (Numenius arquata). Unpublished Ph.D. Thesis. University Of Durham.

WALLGREN, H. (1954) Energy Metabolism Of Two Species Of The Genus Emberiza As Correlated With Distribution And Migration. Acta. Zool. Fenn. 84: 1-110.

WARD, P. (1964) The Fat Reserves Of Yellow Wagtails (Motacilla flava) Wintering In S.W. Nigeria. Ibis 106: 370-375.