Time and energy budgets of the grey plover (Pluvialis squatarola) at Teesmouth

Wood, Andrew Graham

Wood, Andrew Graham (1984) *Time and energy budgets of the grey plover (Pluvialis squatarola) at Teesmouth*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/7212/

Time and energy budgets of the Grey Plover (*Pluvialis squatarola*) at Teesmouth.

by

Andrew Graham Wood, B.Sc. Hons. (Dunelm)

Department of Zoology, University of Durham

This thesis is presented in candidature for
the degree of Doctor of Philosophy in the
University of Durham, April 1984

To my parents,
George and Barbara

ABSTRACT.

The time and energy budgets of Grey Plovers (Pluvialis squatarola) at Teesmouth were investigated by observation of birds both by day and night, supplemented by additional information from a radio telemetry study and laboratory measurements of metabolic rates.

The radio telemetry study of Grey Plovers confirmed that, on Seal Sands, some birds defended low water feeding territories, whilst others were non-territorial. This behaviour was maintained both diurnally and nocturnally, with territorial birds defending the same areas at night as by day. However territorial birds occasionally vacated their territories to forage on other areas at Teesmouth. Multivariate statistical methods characterised the conditions under which these birds changed foraging locations.

The low-water time budgets of territorial birds were determined for both diurnal and nocturnal periods. No statistical differences could be found between these two budgets. The birds spent an extremely high (in excess of 90%) percentage of time foraging over the low water observation period. The diurnal low water time budget of non-territorial individuals was also determined and compared with that of territorial birds.

The calorific intake rates of territorial birds during the daylight hours showed significant seasonal changes, characterised by a rise to a mid-winter peak, followed by a steady decline to mid March. This pattern may have been influenced by the temperature on the day of measurement.

Respirometric measurements on Grey Plovers produced an estimate of their fasting metabolic rate, together with values for lower critical temperature and the rate of increase of metabolic rate with temperature below lower critical temperature. These measurements were consistent with estimates produced from general allometric equations.

Information on the time budgets of territorial Grey Plovers, and measurements of metabolic parameters, enabled a simple energy budget to be constructed for the birds at Teesmouth.

CONTENTS.

Page

Abstract III
Contents IV
Acknowledgements VI

Chapter 1: General introduction 1
Study area 2
Invertebrate fauna of Seal Sands 3
Use of Seal Sands by Grey Plovers 4

Chapter 2: Foraging and social behaviour of the Grey Plover at Teesmouth.
Introduction 6
Methods 8
Results 11
Discussion 27
Summary 30

Chapter 3: Individual and population time budgets of the Grey Plover.
Introduction 32
Methods 33
Results 35
Discussion 47
Summary 51

Chapter 4: Energy intake rates of territorial Grey Plovers at Teesmouth.
Introduction 52
Methods 53
Results 56
Discussion 64
Summary 67

Chapter 5: Metabolic rate measurements of Grey Plover.
Introduction 68
Methods 69
Results 72
Discussion 76
Summary 78

Chapter 6: Energy budgets of territorial Grey Plovers at Teesmouth.

Introduction 79
Methods 81
Results & Discussion 84
Summary 91

Final conclusions 92

References 97

Appendices 108

ACKNOWLEDGEMENTS.

This study was funded by a Natural Environment Research Council Research Studentship. I am grateful to Professor D. Barker for permission to use facilities in the Department of Zoology, University of Durham.

Throughout this study I have benefited from discussion with, and information supplied by colleagues at the Department of Zoology, University of Durham. I therefore would like to take this opportunity to thank Dr. N.C. Davidson, Dr. P.J. Dugan, Dr. S.A. Goodyer, Dr. M.W. Pienkowski, Dr. D.J. Townshend and R.P. Whitcombe.

I am grateful to the Home Office Special Equipment Unit, Durham Police Headquarters for the initial loan of night viewing equipment. Dr. G. Tobin at the Department of Physiology, University of Leeds provided the necessary equipment and expertise for measurement of gases in a sample, thus allowing recalibration of the diaferometer. I must also thank Dr. D.M. Bryant for providing the possibility of using the heavy water technique on territorial Grey Plovers at Teesmouth. Unfortunately the birds did not foresee the potential in this technique, and remained as elusive as ever.

Dr. P.J. Green of the Department of Mathematics, University of Durham, provided much appreciated statistical advice.

A large proportion of the work presented in this thesis

depended on the past and present effort of bird catchers at Durham. I wish to thank L.R. Goodyer for my introduction to wader catching, and for his efforts in cannon netting birds at Teesmouth; more recently this task was taken over by J. Richardson and Dr. D.J. Townshend. Cannon netting waders is a team effort, and I also would like to thank those persons who gave up their time to help, in what is at times a futile exercise.

Thanks must also go to the Tees and Hartlepool Port Authority, and the British Steel Corporation for access over their land.

Finally I wish to acknowledge the help, advice and encouragement, given throughout this project by my supervisor, Dr. P.R. Evans. To him I offer warmest thanks.

GENERAL INTRODUCTION.

Observations by Pienkowski (1980) and Dugan (1981b) indicated that, in winter, food intake during daylight hours by two species of wader - Ringed and Grey Plovers (<u>Charadrius hiaticula</u> and <u>Pluvialis squatarola</u>) - provided less energy than their basal metabolic rate (BMR) requirements, estimated from the equation of Lasiewski & Dawson (1967). I set out to investigate two major problems raised by these previous studies (i) whether measured BMR´s might be substantially less than those predicted from the non-passerine equation relating BMR to body weight; and (ii) the relative importance of energy intake during diurnal and nocturnal feeding by Grey Plovers under a variety of environmental conditions. The second problem was studied at Seal Sands on the Tees estuary in N.E. England (54´37"N 1´12"W).

Previous studies on waders at Teesmouth have provided limited information on the time budgets of birds by day, and on the possibilities for nocturnal foraging (Knights 1979, Dugan 1981a). Background information on the social organization and foraging of Grey Plovers was well established for birds at Teesmouth by Dugan (1981b) and Townshend (1982), and at Lindisfarne by Pienkowski (1980, 1982, 1983a, 1983b).

Study Area

Grey Plovers were studied on the Tees estuary, particularly on Seal Sands, an area of 140 ha. of mudflats remaining after extensive reclamation of intertidal land during the last 100 years or more.

In the first half of the nineteenth century, the Tees estuary contained about 2,400 ha. of intertidal sand and mudflats. In the late nineteenth century two breakwaters, South and North Gare were constructed either side of the river mouth. Sections of saltmarsh and higher parts of Seal Sands along the north western edge of the estuary were enclosed by slag walls in the 1890's, forming areas of rough grazing land which remain today as Greenabella Marsh and the ICI Brinefields. By 1960 the higher flats on both sides of the river had been reclaimed resulting in the situation shown in figure 1.

During the early 1960's the major part of Bran Sands was totally reclaimed leaving only that small area to the north of Redcar Jetty. Between 1964-66 dredgings from the deepening of the main river channel were pumped onto the eastern edge of Seal Sands. In 1967, 101 ha. of the southern area of Seal Sands were enclosed and progressively infilled with dredgings. In 1970 a slag wall was built across Seal Sands dividing the area of mudflats in half. This area was again gradually reclaimed such that by early 1974 only the north area of 140 ha. was left as a feeding area for shorebirds.

Figure 2 shows the situation throughout the period of this study. The northern parts of Seal Sands and Bran Sands remain as

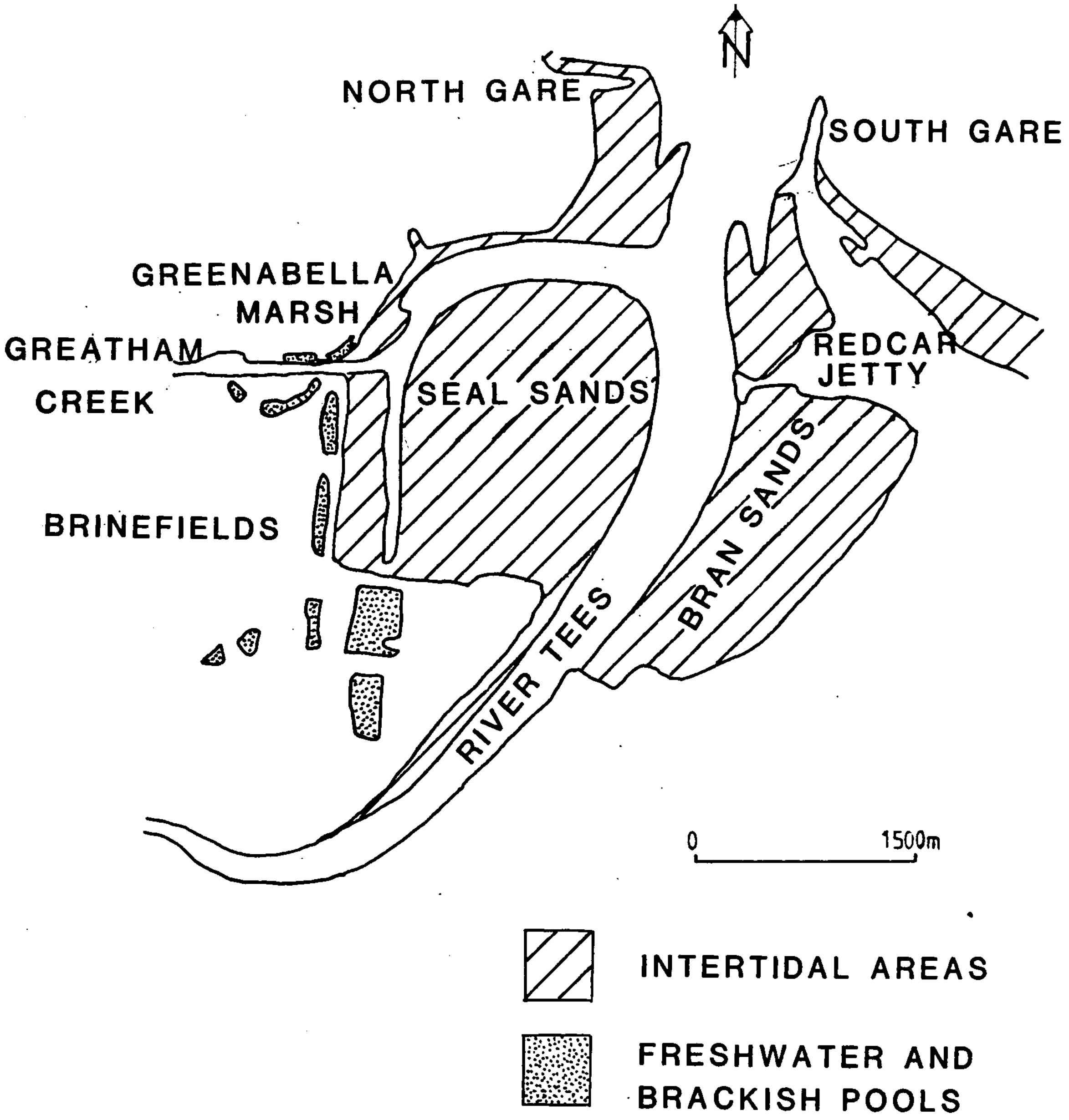


figure 1.1: the Tees estuary in 1960

(redrawn from Knights 1979).

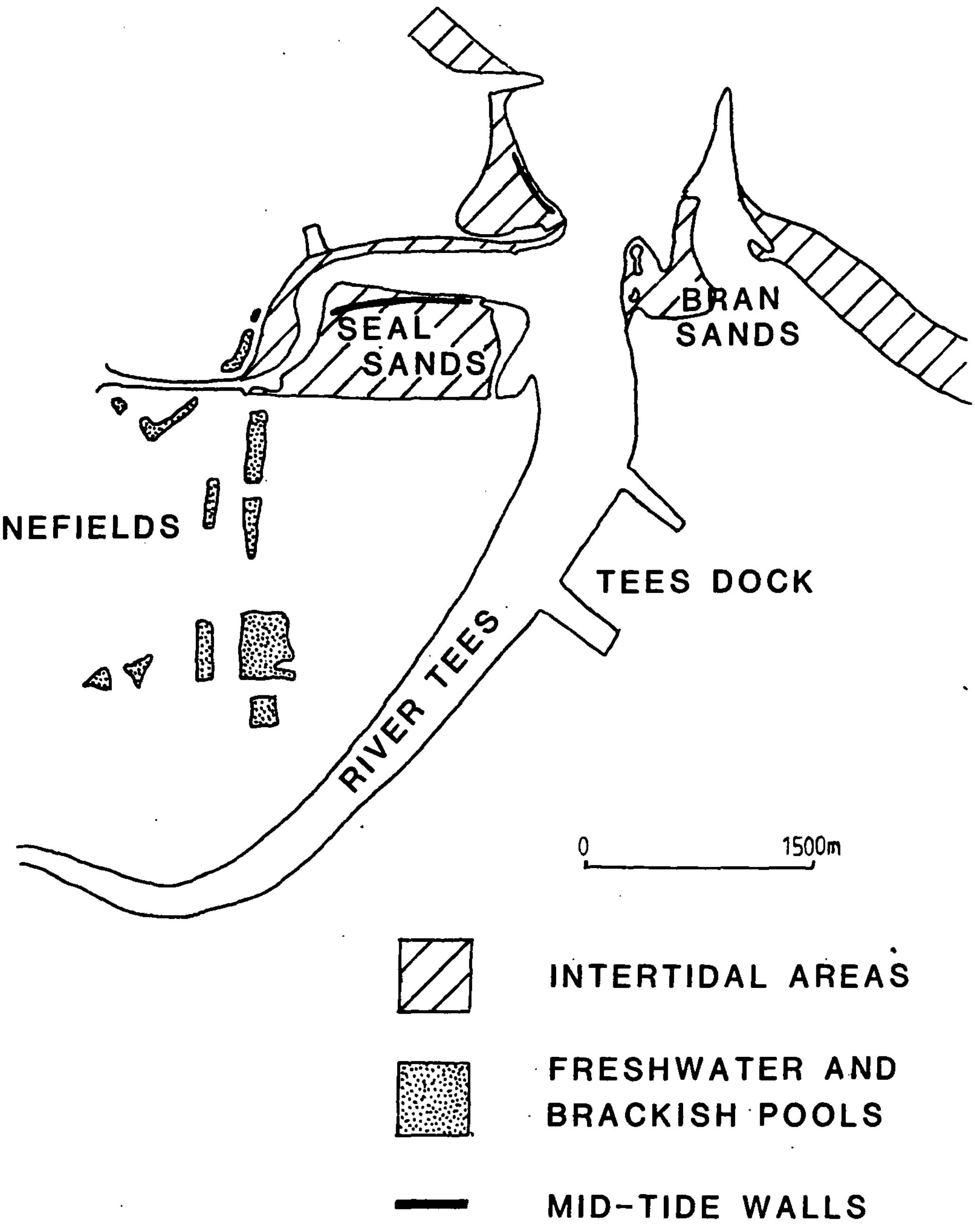


figure 1.2:the Tees estuary in 1980.

the only major areas of intertidal land suitable for foraging shorebirds.

It is clear from this very brief history of reclamation at Teesmouth that the higher tidal level areas were removed first, leaving the lower tidal flats relatively untouched. At present Seal Sands is exposed and available to foraging shorebirds for about seven to eight hours out of each tidal cycle. A consequence of this is that if birds cannot obtain enough food during that period of exposure, then they must move to higher tidal flats on North Gare or the coastal beaches, or (in the case of Curlew Numenius arquata) move to nearby brackish marshes and fields in order to forage (Davidson 1980, Townshend 1982). The feeding opportunities at Teesmouth are thus more restricted than at Lindisfarne, where Pienkowski´s (1980, 1982, 1983a, 1983b) studies of Grey Plover were made.

Invertebrate fauna of Seal Sands

A survey of invertebrates at Teesmouth in 1930 (Alexander et al. 1935) revealed that cockles (Cardium edule L) were present in small numbers and Macoma balthica (L) was considered uncommon. Corophium volutator (Pallas) and Nereis diversicolor O.F. Muller were abundant, but Hydrobia ulvae (Pennant) was not recorded. This survey also indicated that by 1930 the estuary was becoming silted, a feature caused by the restriction of water flow due to reclamation and the construction of breakwaters.

In 1973-74 a further invertebrate survey was made (Evans et al. 1979). From this it was clear that Hydrobia had colonized the estuary and was present in large numbers, whereas cockles were absent and Macoma densties were very low. Nereis diversicolor was the dominant large polychaete, but Corophium was numerous only in small localised patches.

Hydrobia and Nereis diversicolor are the most numerous invertebrates in shorebird diets on Seal Sands, although Dunlin (Calidris alpina), Redshank (Tringa totanus) and Shelduck (Tadorna tadorna) are known to take small oligochaetes and polychaetes (Evans et al. 1979) which are part of a very abundant meiofauna (Gray 1976). Grey Plovers in particular take large numbers of Nereis diversicolor and Hydrobia, and occasionally take Macoma and Carcinus maenas (L); and at the lower tidal levels on Bran Sands, Grey Plover also take Nereis virens (Sars) (Dugan 1981a, 1981b).

Use of Seal Sands by Grey Plovers

On the Tees estuary the number of Grey Plovers present in a winter varies between 100 and 300 birds. Since 1976 a sizable proportion of the birds have been caught and marked with unique combinations of colour rings allowing individual identification. The seasonal pattern of arrival and departure of birds has been well documented by Dugan (1981b) and Townshend (1982). This pattern held throughout the period of this study, and was characterised by an influx in September, particularly of juveniles, with peak numbers in October. After a slight decrease in November due to movement of juveniles, numbers peaked again in December. There are further arrivals of birds on the Tees in February, but then a steady decline to 10-20 birds by mid-April. This is the usual size of the summering population of the Grey

Plover at Teesmouth.

During the winter months, Grey Plover on the Tees exhibit both territorial and non-territorial behaviour on the low water foraging areas, and this social system has been the subject of much recent work (Dugan 1981b, 1982, Townshend 1982, Townshend et al. 1984).

FORAGING AND SOCIAL BEHAVIOUR OF THE GREY PLOVER AT TEESMOUTH.

INTRODUCTION

During the non-breeding season many species of shorebirds have been seen to defend foraging territories (Myers et al. 1979), but a species may not show territorial behaviour in all parts of its wintering range. The decision by an individual as to whether or not it should defend an area, and for how long, is affected by many factors such as prey density, density of conspecifics and habitat type (Myers et al. 1981).

Recent work on shorebirds at Teesmouth during the winter months has revealed that both the Grey Plover (Knights 1979, Dugan 1982, Townshend 1982) and Curlew (Townshend 1982) defend foraging territories. From observations of colour-marked individuals it became clear that the social behaviour of the Grey Plover on Seal Sands is more complex than just a simple territorial/non-territorial system (Townshend 1982); some individuals defend areas for only a single low water period, whilst others defend the same site for many months. These latter have been labelled ´long-term territory holders´ (Townshend et al. 1984).

Direct visual observations provided much information on the use of areas of the mudflats by different individual birds. However two important aspects of Grey Plover social and foraging behaviour remained to be answered. Firstly, and perhaps most importantly, what happens to the birds at night? A number of workers have shown that many wader species continue to forage at night (Knights 1979, Pienkowski 1980, Dugan 1981a, Sutherland 1982), including Grey Plovers. Secondly, do long-term territory holders utilize and defend the same area during the low tide period by night as well as by day, and do they do this throughout the winter? Answers to these two questions have important implications if the time and energy budgets of Grey Plovers at Teesmouth are to be estimated. Preliminary work by Dugan (1981a) suggested that nocturnal feeding may be as important as that during the day.

METHODS

The position and activity of animals were monitored throughout a 24 hour period with the aid of radio-telemetry (Storm 1965, Macdonald et al. 1979). Birds were caught with cannon nets, individually colour ringed, and radio transmitters attached using a harness modified from that used by Brander (1968); the design is shown in figure 1. Bird locations were monitored from the ground using an AVM LA12 receiver and a three element hand-held Yagi antenna. After a bird's release, one to two weeks were allowed to elapse before any serious work was undertaken on that bird, so that any short-term effects of the transmitter on the bird's behaviour would be reduced to a minimum.

To estimate the location of a radio-tagged bird, triangulation was used, i.e. directional fixes of a bird were obtained in quick succession from two (or more) different observation points (figure 2). For each radio fix the direction of maximal signal strength for an individual was determined and drawn as a line on specially prepared field maps. Because data were collected only when the birds were on the mudflat, and hence moving around slowly rather than flying, any errors introduced by the time lag between successive fixes were unimportant when compared to the errors in triangulation itself (Heezen & Tester 1967, Springer 1979). (A check on the accuracy of radio-triangulation estimates of position was provided naturally at Teesmouth because two birds used foraging locations which were close enough for visual as well as radio location to be

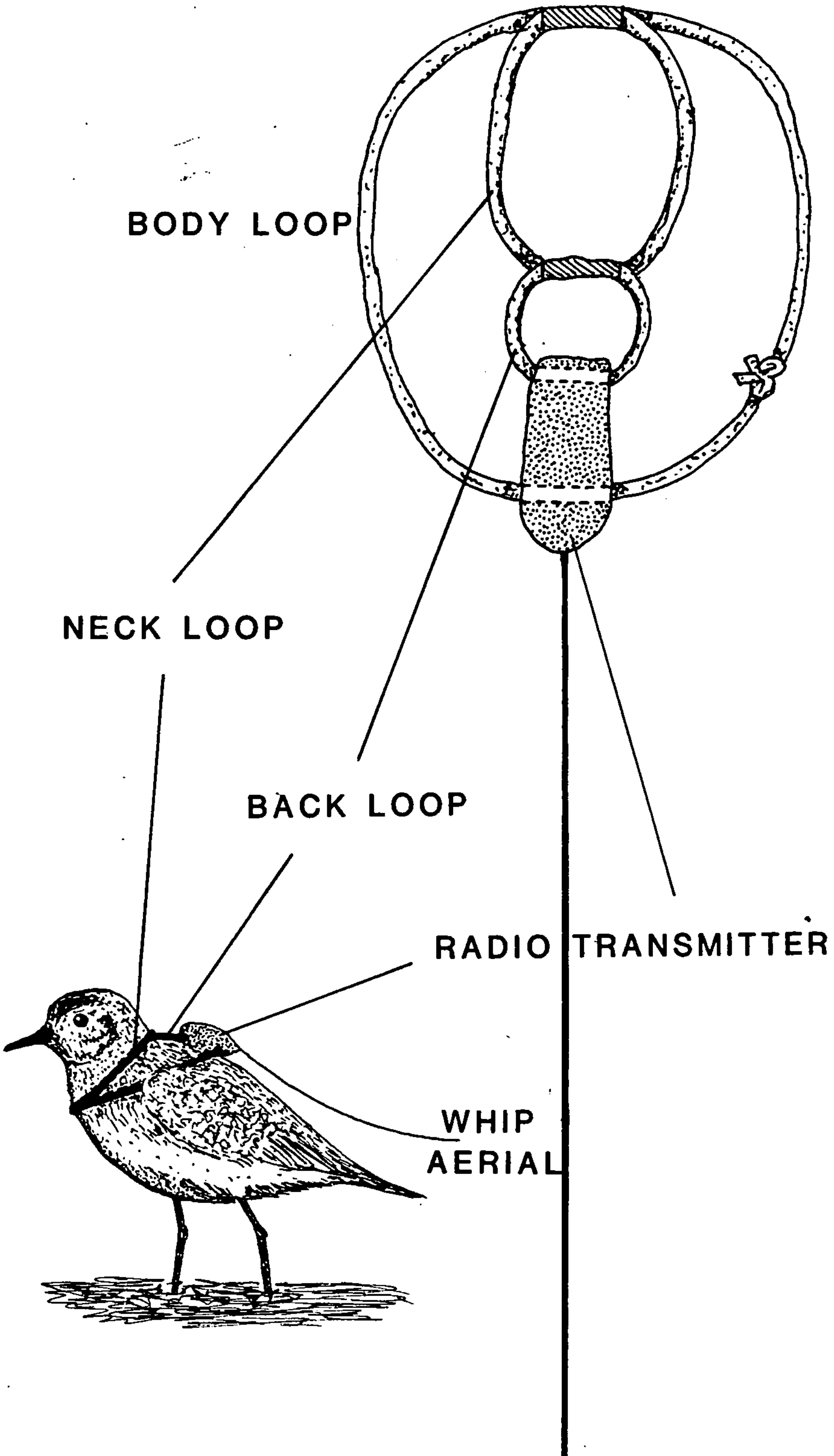


figure 2.1: radio transmitter harness design and position of fitting on a bird.

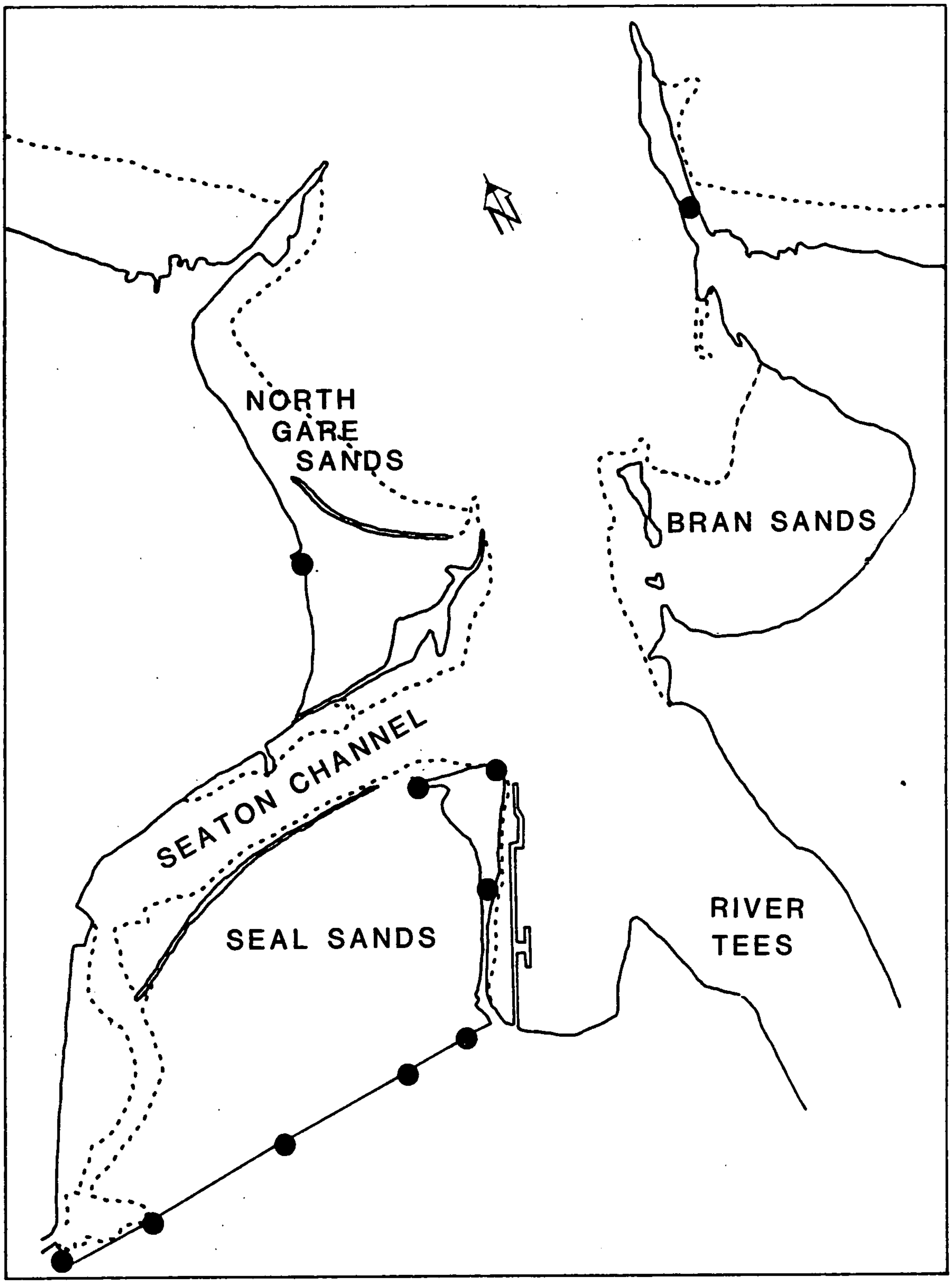


figure 2.2: sites for radio telemetry triangulation around the Teesmouth area.

performed. Within the error limits of the direction finding equipment, no biases in radio location were found.)

To handle the large amount of information which can be collected from a radio-telemetry study, data from the field maps, i.e. the positions of birds obtained by triangulation, were transferred to a computer file in the form of digitised co-ordinates. Additional information on time of day, state of tide and temperature were also recorded for each data case. These data were then used in the analysis programs of GPCIRC, GPCHRON, and GPDATES, written in FORTRAN (appendix 1). Further statistical analysis was performed using SPSS programs (Nie et al. 1975).

Graphical methods of presentation of the data:

Each radio fix has associated with it a certain error arc, within which the actual position of the animal lies (Heezen & Tester 1967). The intersection of two or more such arcs produces an error polygon which surrounds the best estimate of the position of the radio tracked animal (figure 3). The shape and size of the polygon varies with the distance and angle of intersection of the radio fixes. To represent the position of an individual as a point would infer greater accuracy than the triangulation system can produce. Therefore in the following maps I have used a circle to represent the area in which the animal lies. The area assigned to each circle is approximately equal to the area of mud defended as a foraging territory by a Grey Plover carrying a radio transmitter. Radio triangulation on this bird could not distinguish whether it was positioned at one

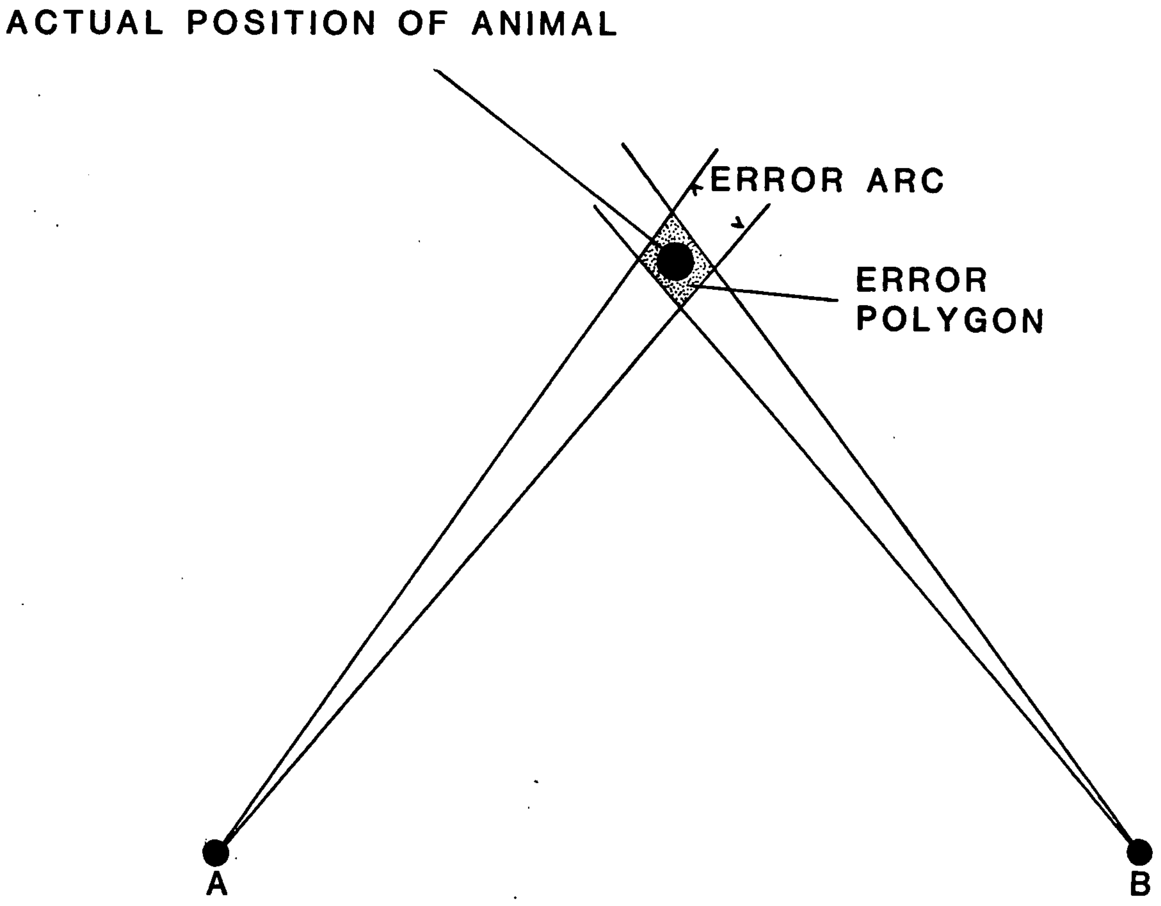


figure 2.3: errors inherent in radio telemetry triangulation, redrawn from Heezen & Tester (1967).

or other extreme edge of its territory, although this could be observed at the time of radio fixes.

Each bird was assigned a three or four digit identifier according to the frequency of its radio transmitter. These identifiers are used to title the plots of the positions of that bird.

RESULTS

Plots of the positions of known territorial Grey Plovers, obtained from the analysis program GPCIRC, for the period January to March 1981, are shown in figures 4 to 8. This period of the year is one during which there is a relatively constant population of territorial individuals (Dugan 1981b, Townshend 1982) which show no month to month variation in their time budgets (chapter 3). The data plotted in figures 4 to 8 refer only to birds´ locations during the period of two hours on either side of low water (when they were known to be spending in excess of 90 percent of their time foraging - see chapter 3).

These maps show clearly that Grey Plovers which were classed as territorial by day from visual observations of their defense of a site, were found in only a single locality by day, on most days, from radio telemetry results. Furthermore, the area defended by day was usually occupied also at night. However on a few days, but rather more nights, birds used ´odd´ foraging locations, for reasons discussed later in this chapter.

For comparison with the diurnal and nocturnal low water foraging locations of long-term territorial individuals, data from a further 7 Grey Plovers are presented in figures 9 to 15. These birds were either non-territorial or defended foraging areas only irregularly.

Figures 4-8: low water foraging locations of long-term territorial Grey Plovers for the period January to March 1981. A line joins two or more different foraging locations used on the same date.

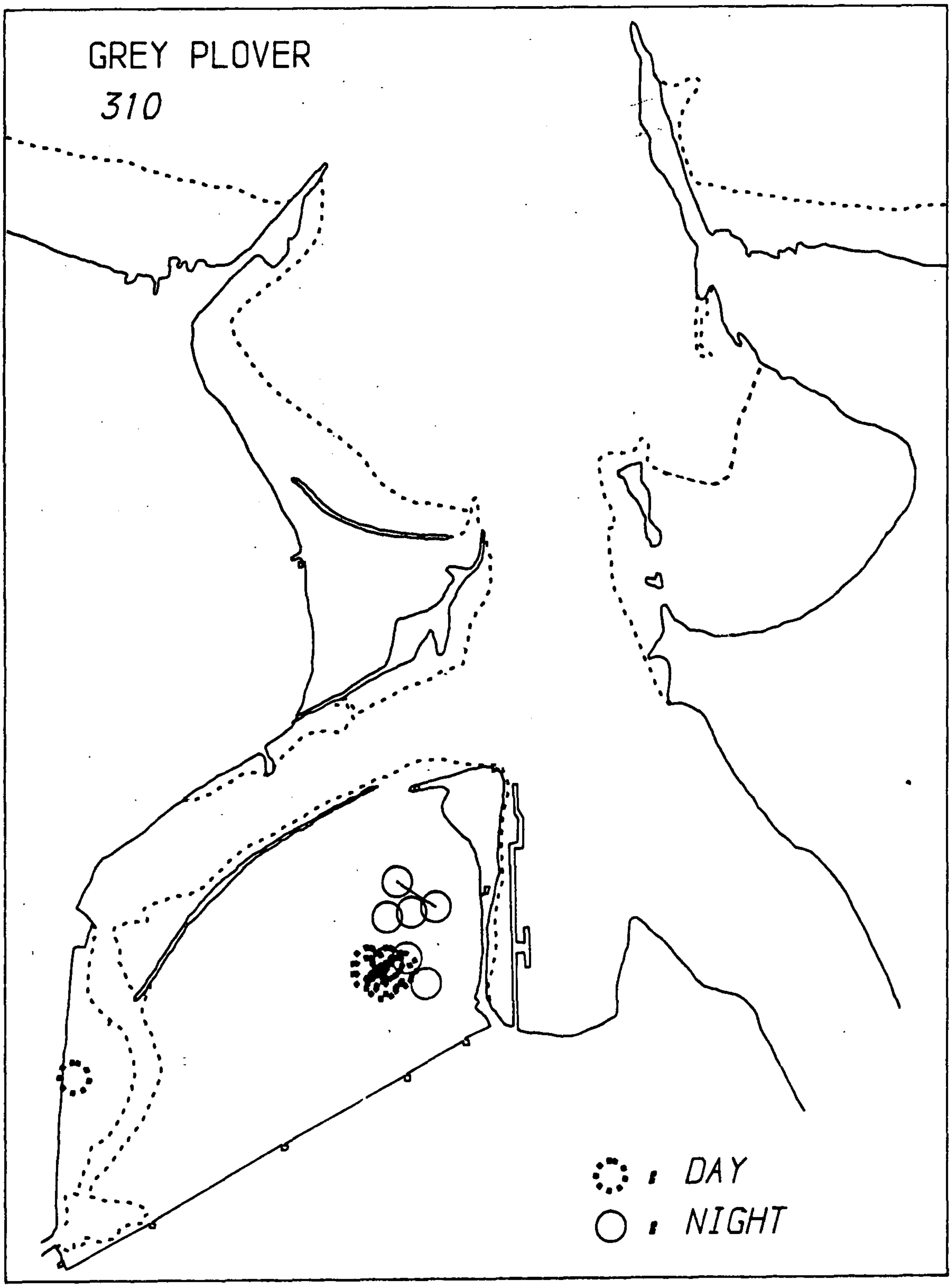


figure 2.4

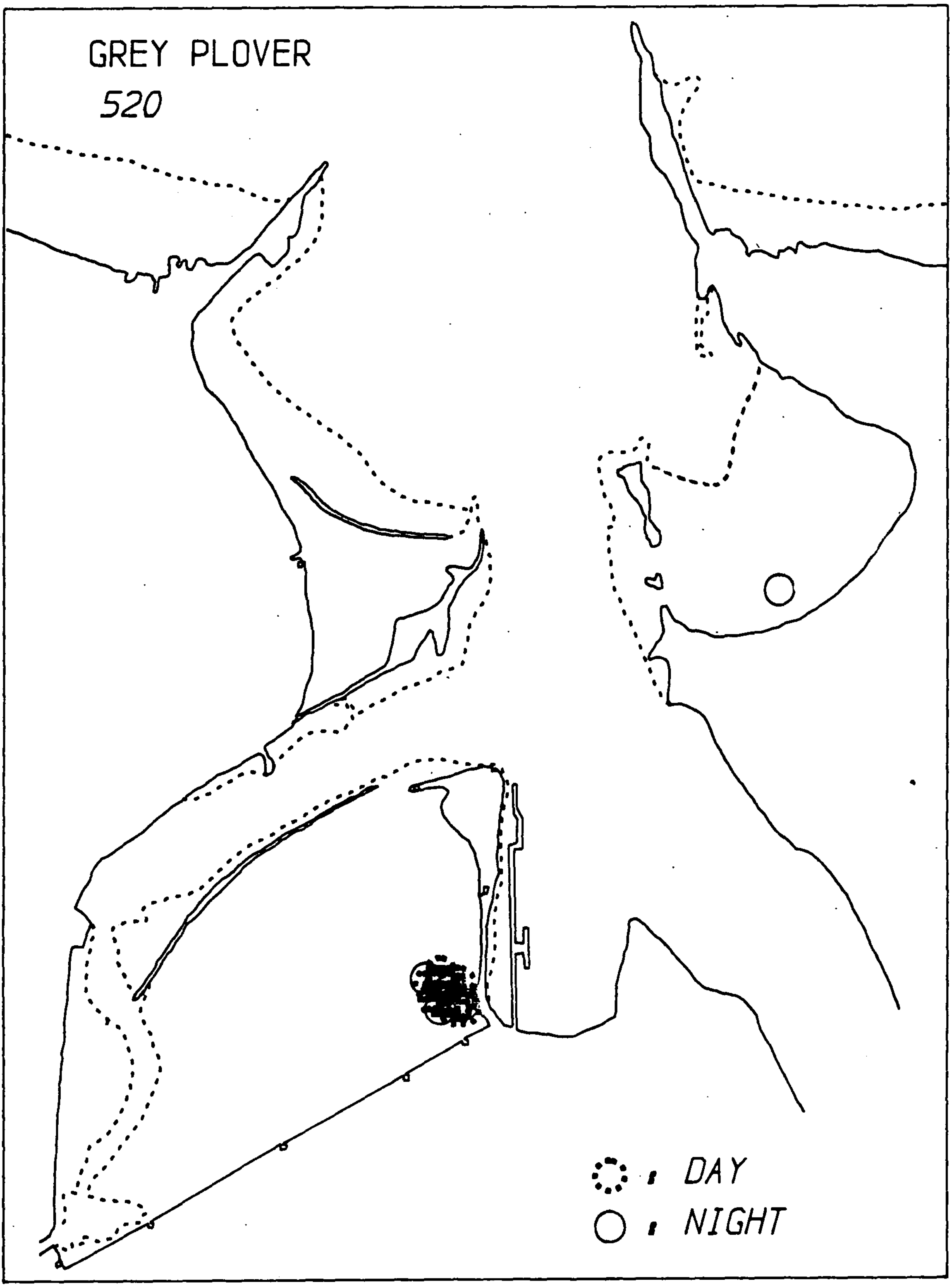


figure 2.5

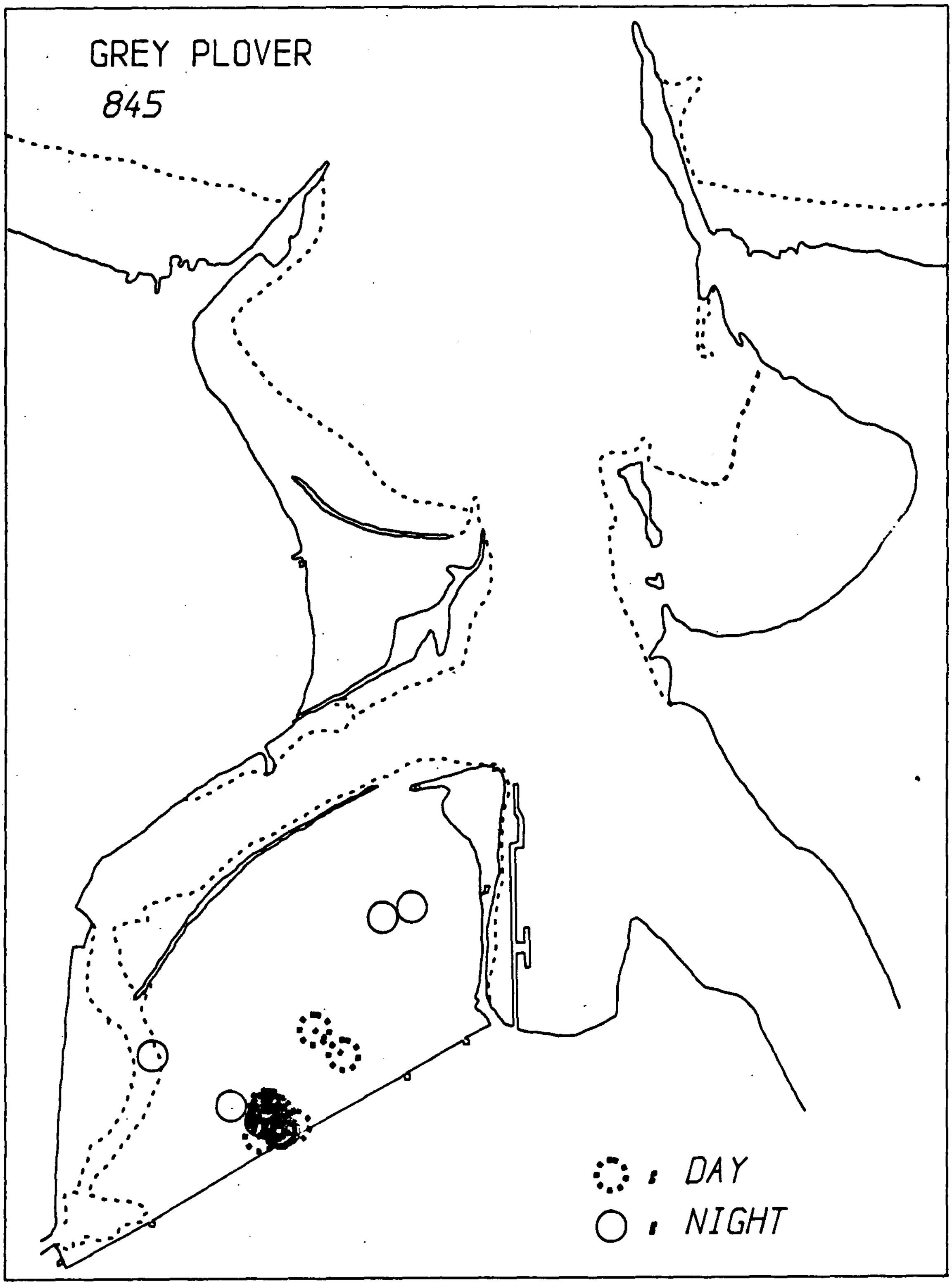


figure 2.6

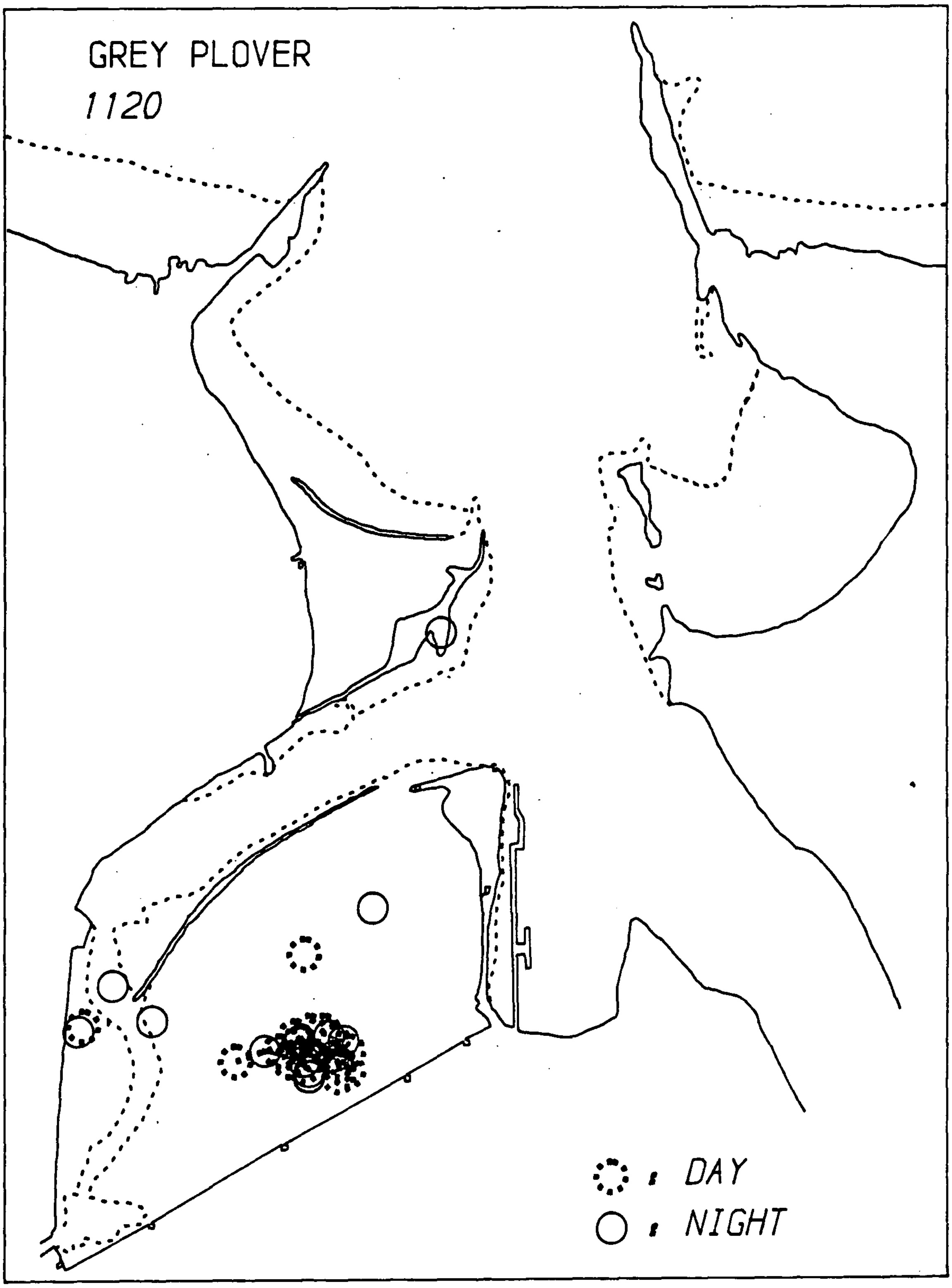


figure 2.7

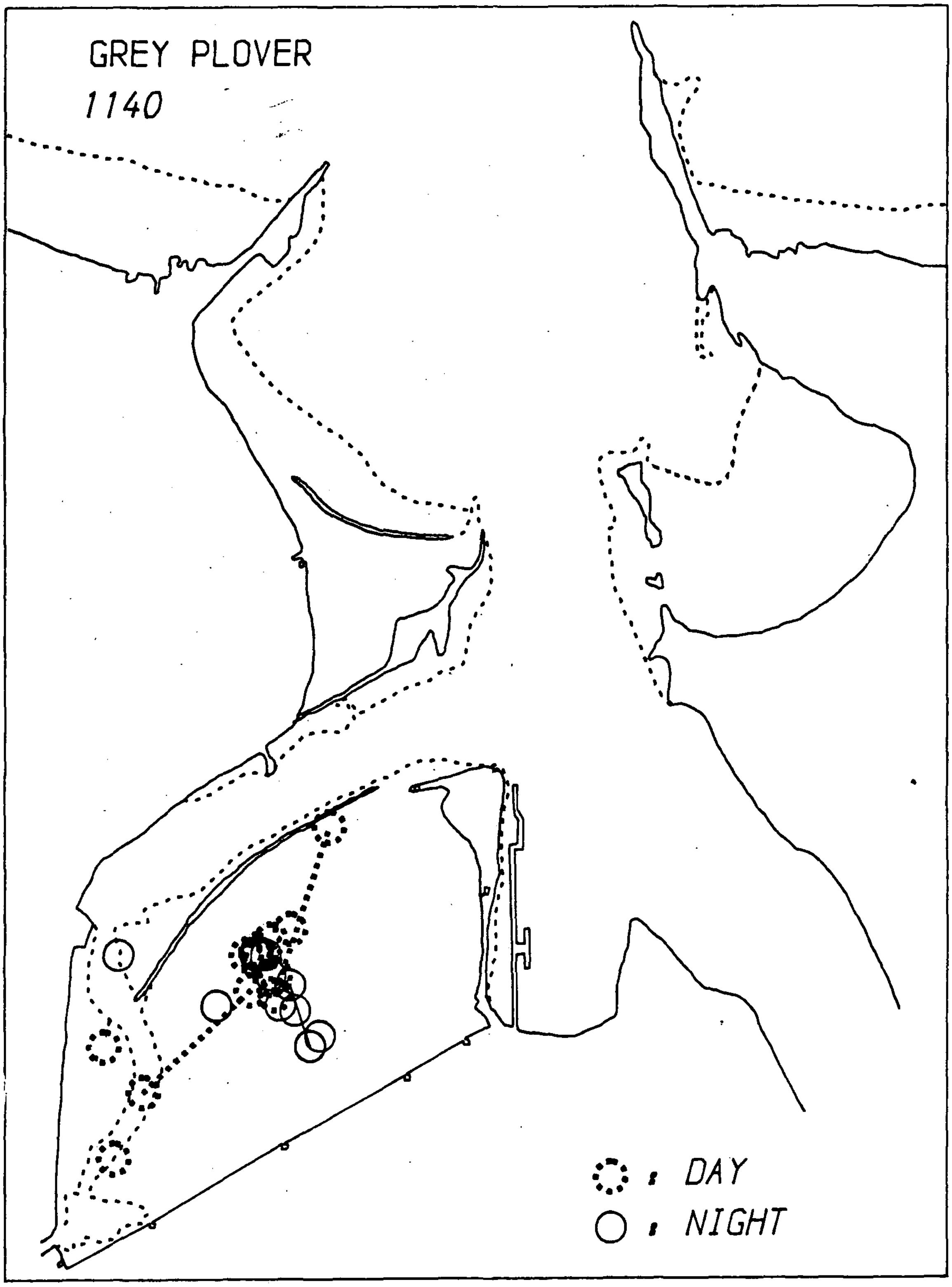


figure 2.8

<u>Figures</u> <u>9-15</u>: low water foraging locations of non-territorial and short term territorial Grey Plovers for the period January to March 1981. A line joins two or more different foraging locations used on the same date.

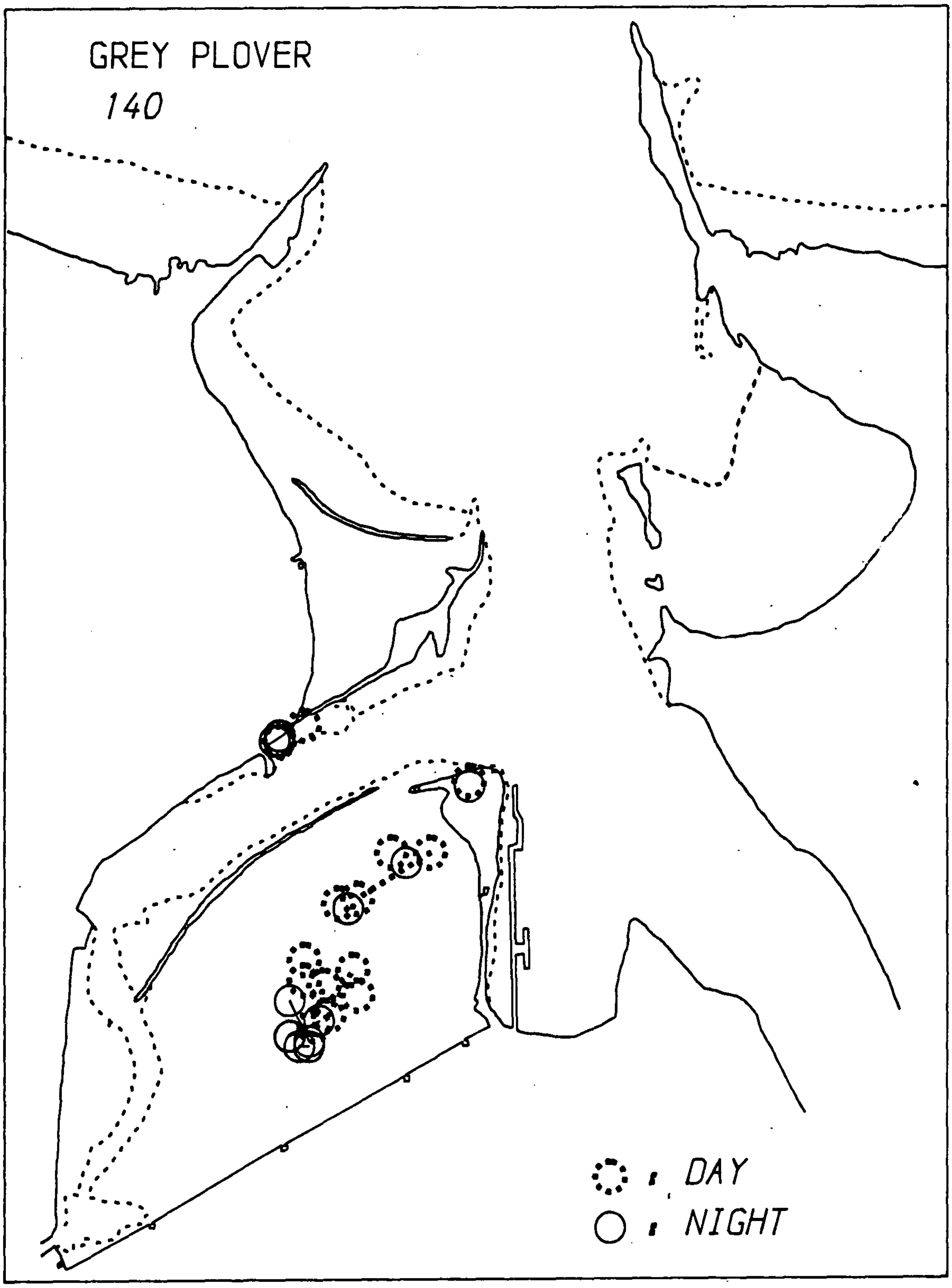


figure 2.9

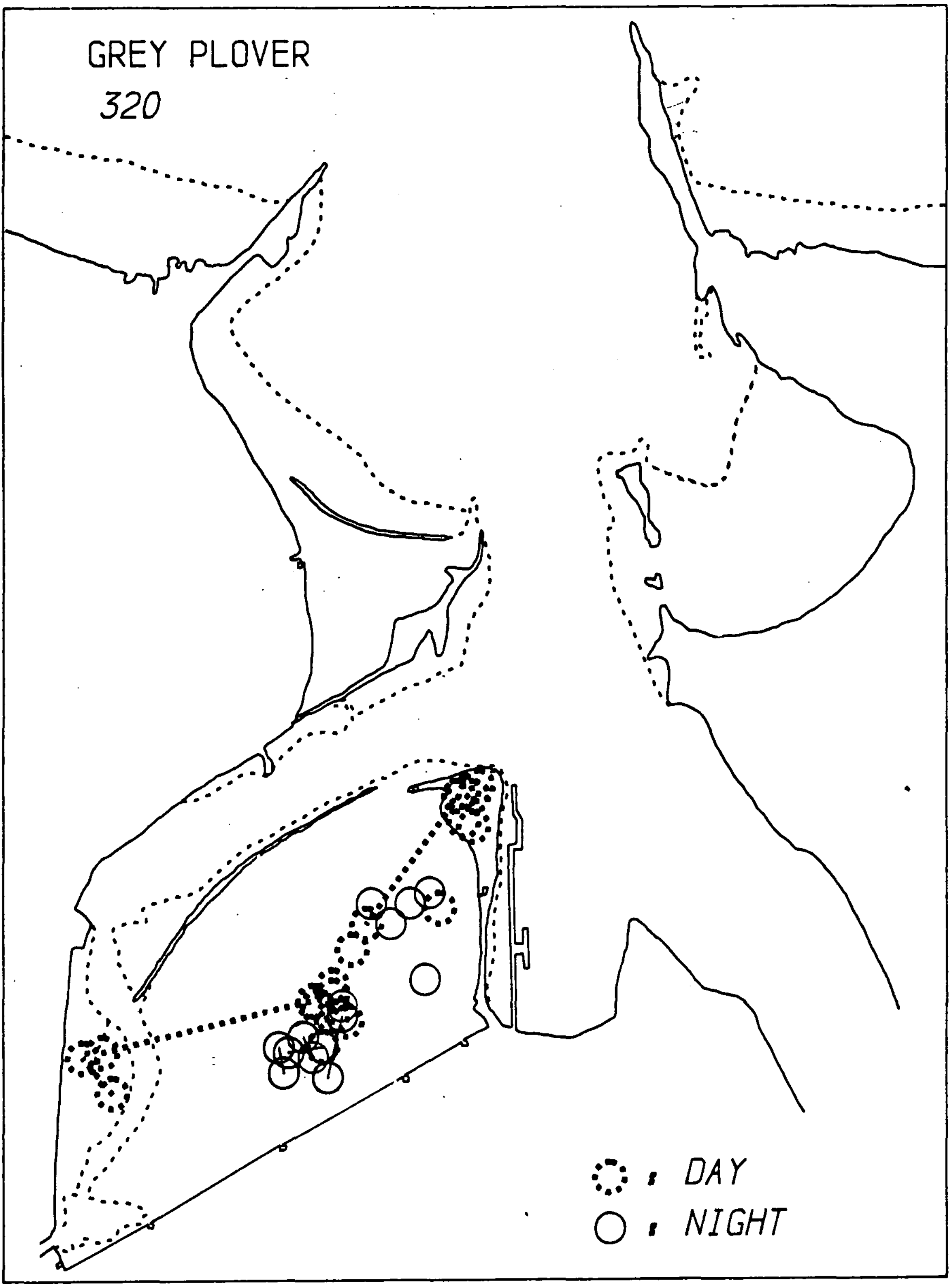


figure 2.10

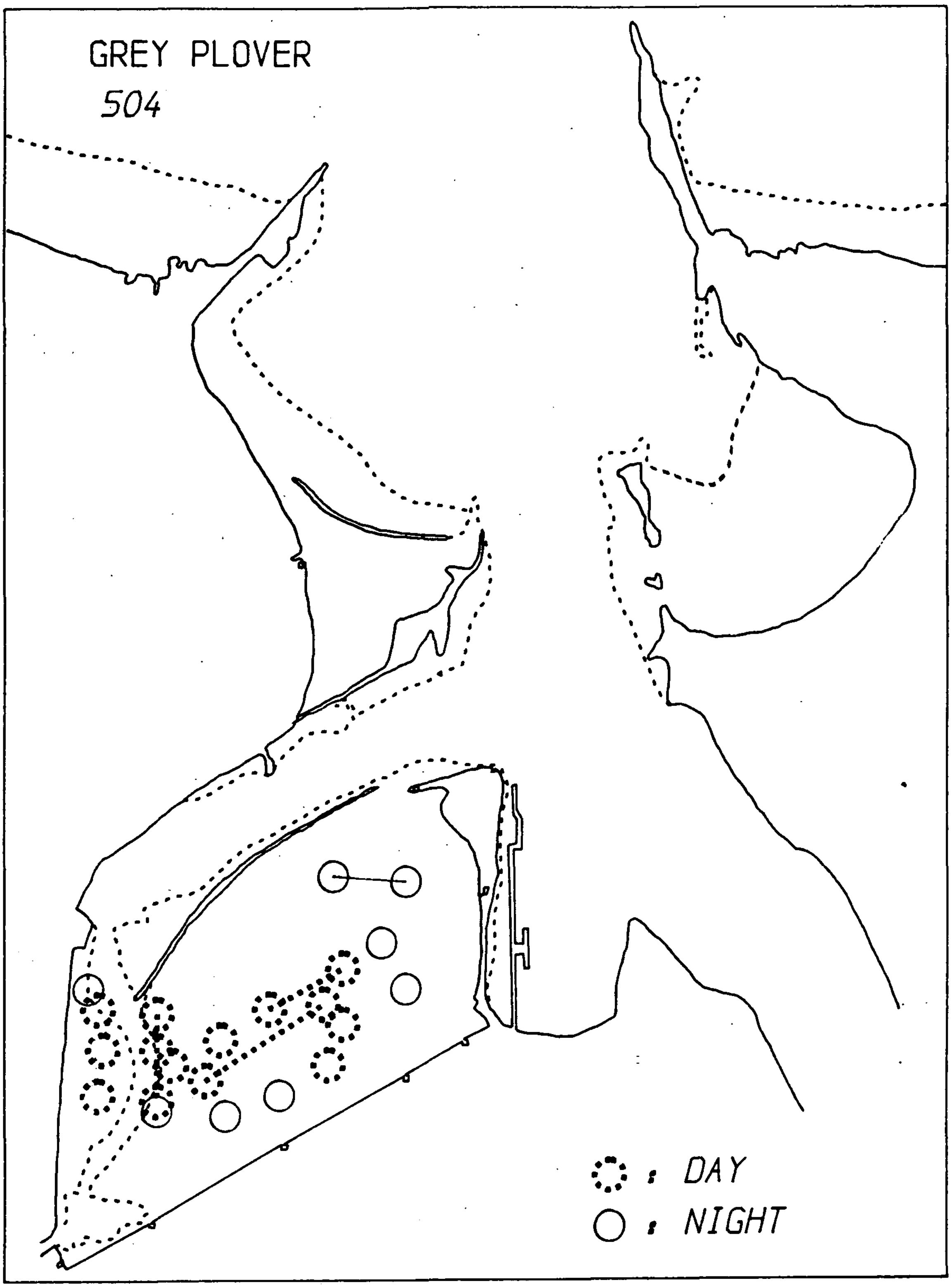


figure 2.11

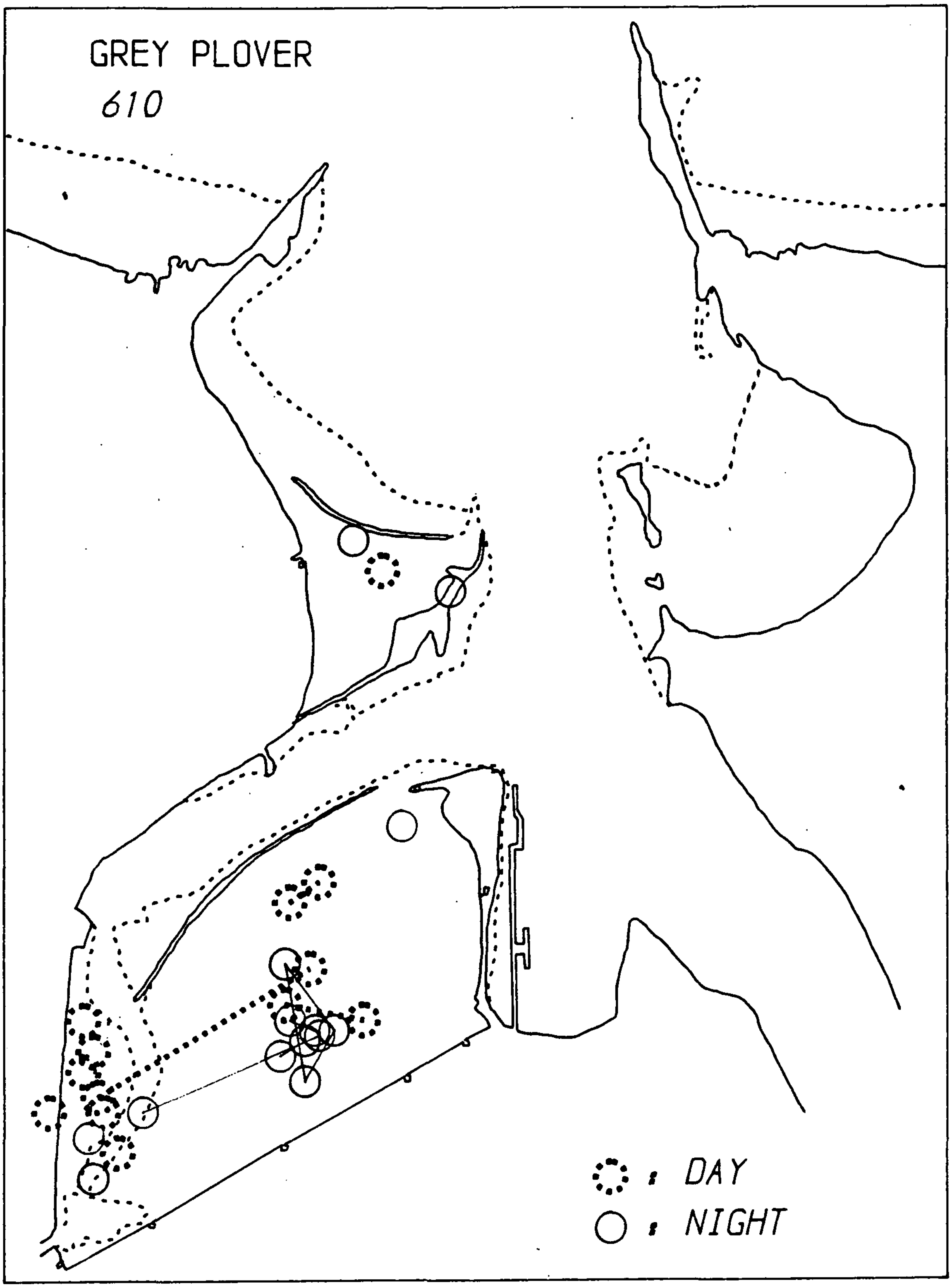


figure 2.12

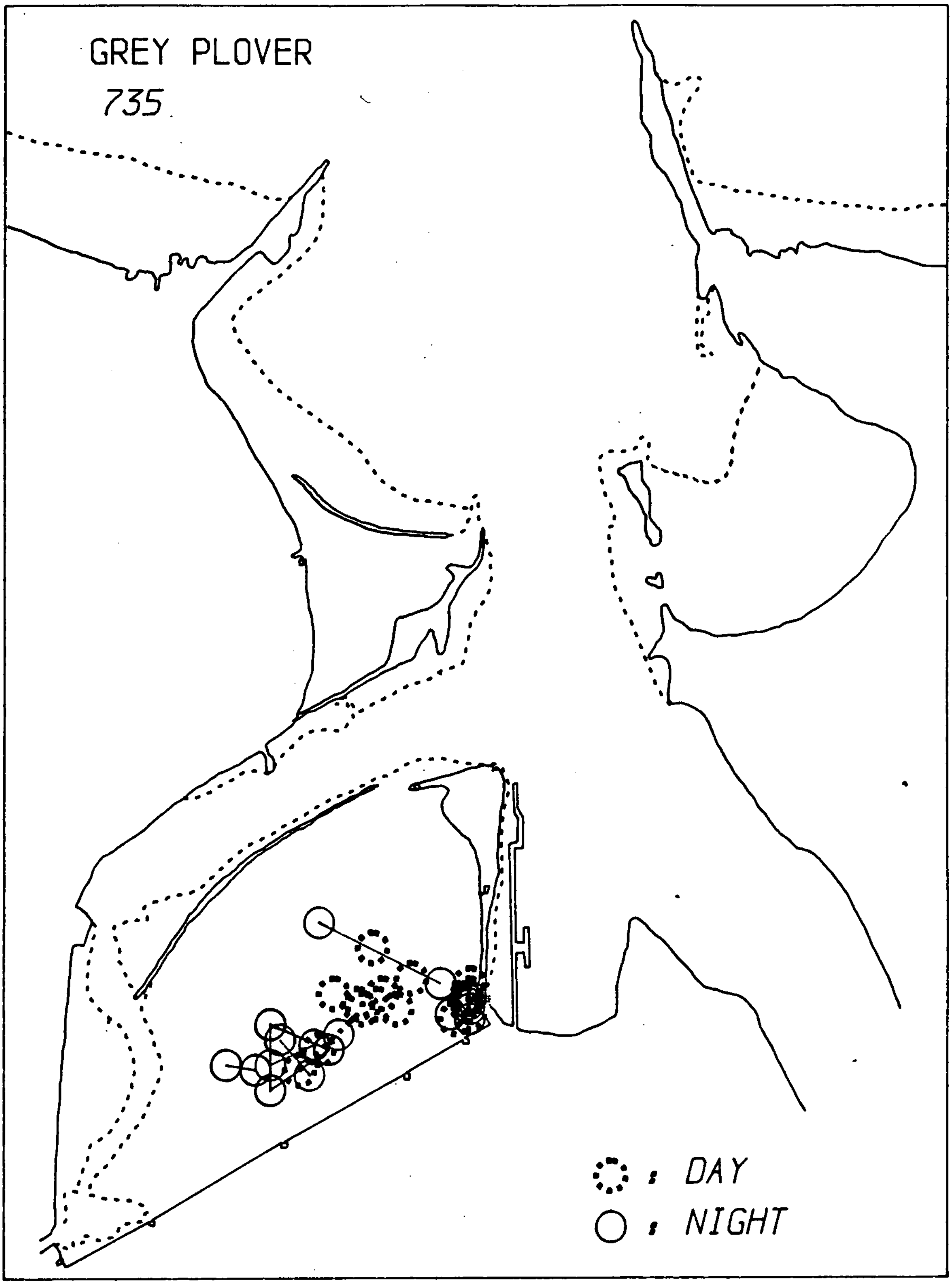


figure 2.13

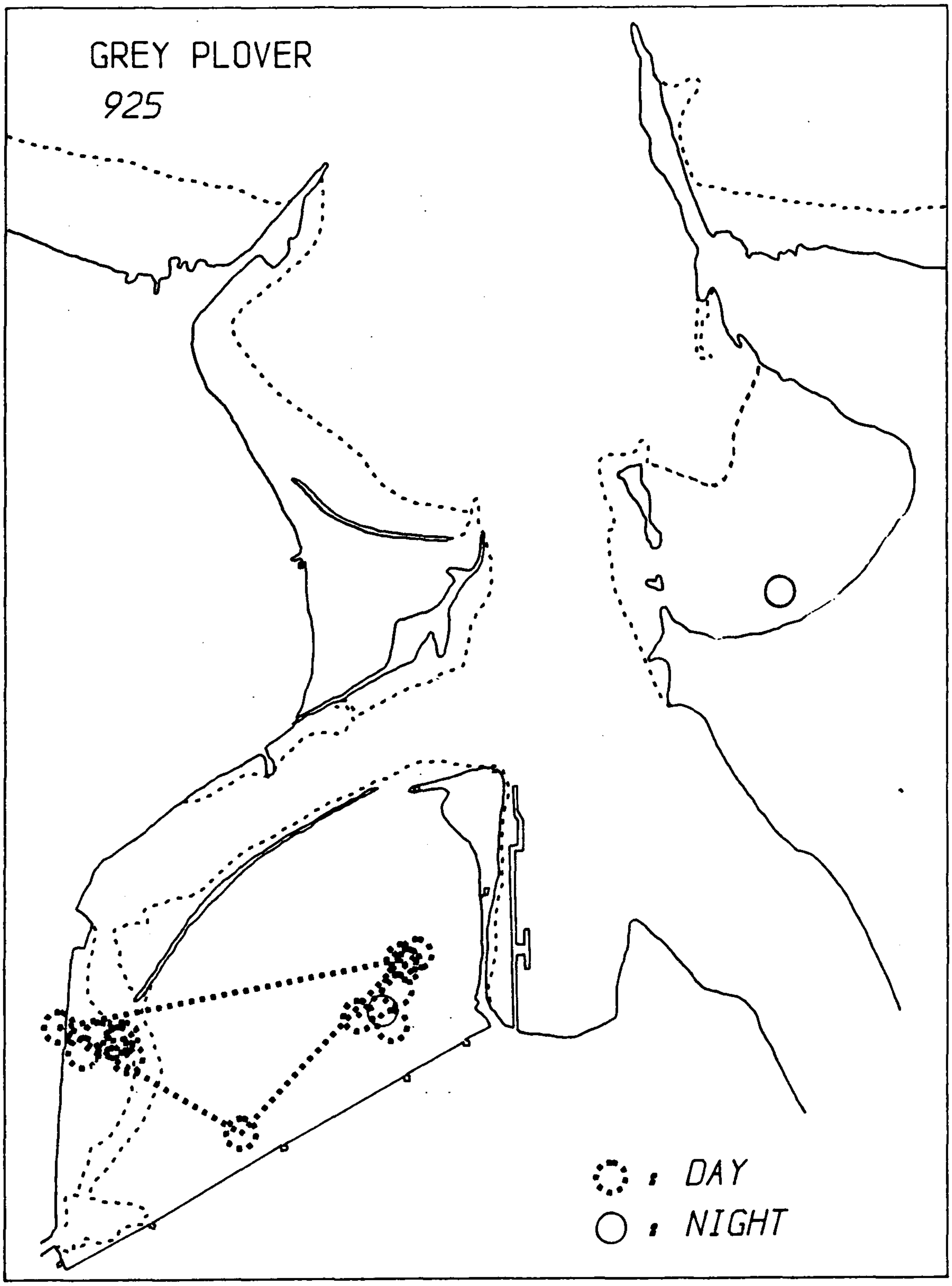


figure 2.14

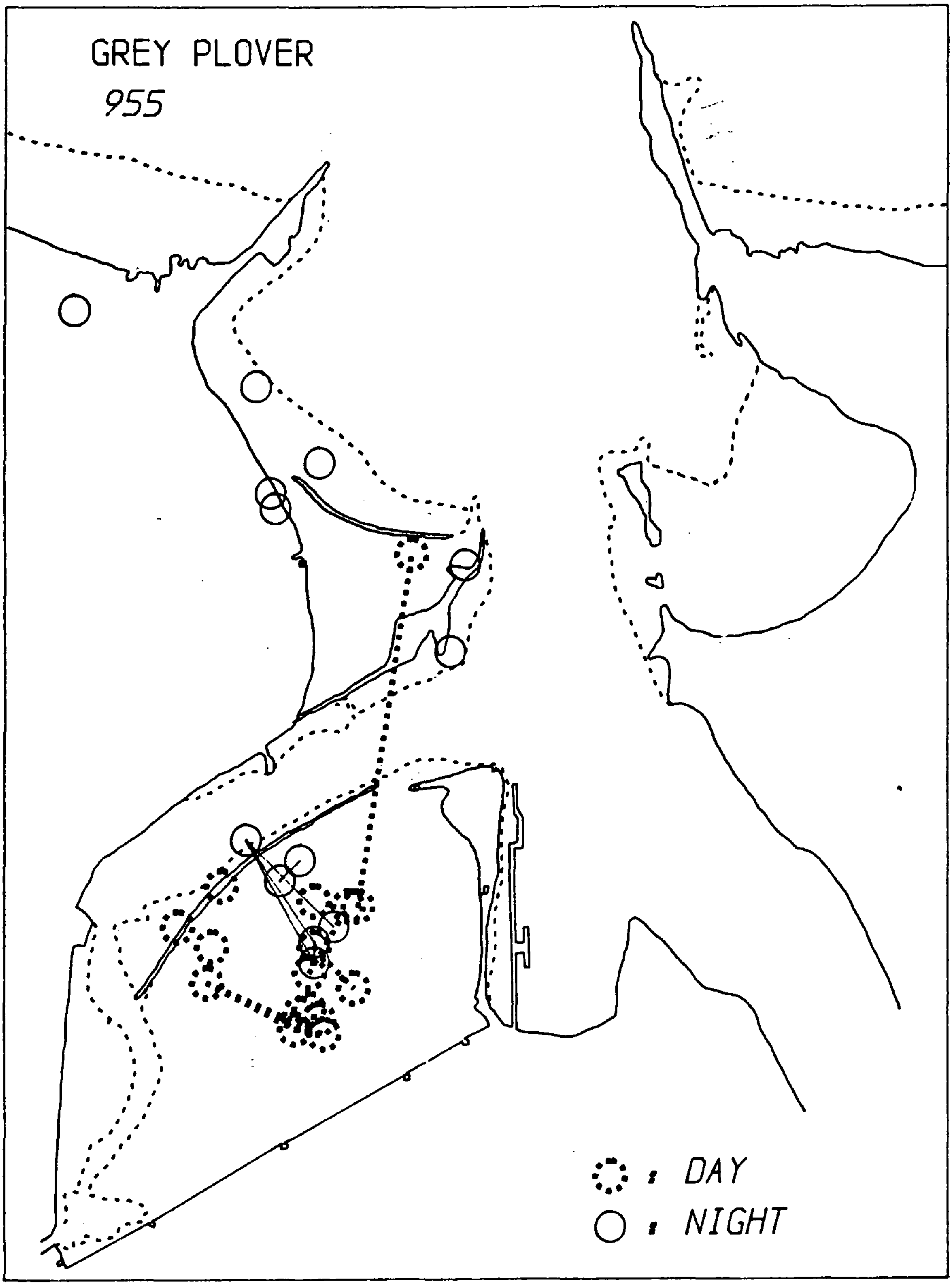


figure 2.15

More specifically, bird 140 (figure 9) was a juvenile that irregularly defended an area of mud to the north of Seaton Channel; bird 320 was also a juvenile which used different areas for foraging by day and night (figure 10). By day it defended an area occasionally in the Peninsula enclosure to the NE of Seal Sands. In contrast, bird 504 (figure 11) was found over almost the whole of Seal Sands, and appeared not to use any specific area at any time. Bird 610 (figure 12) usually used different nocturnal foraging areas from those used by day. Most of its nocturnal foraging was concentrated in one area of Seal Sands, but it was one of the few birds to use the sand flats of North Gare. Bird 735 (figure 13) was another juvenile which sometimes defended an area of mud in the SE corner of Seal Sands close to the territorial bird 520 (figure 5), but often fed elsewhere both by day and night. Bird 925 (figure 14) was one of the few that were found on Bran Sands at night. However, the general lack of information on nocturnal foraging locations arose because the bird was absent from both Seal and Bran Sands on a number of nights, and no radio signal could be detected from it. Bird 955 (figure 15) was one of the most widely ranging of the Teesmouth Grey Plovers, using Seal Sands, North Gare or Seaton Common at night. By day, however it preferred the mudflats of Seal Sands.

The conclusion from these data must be that if the time budget of a Grey Plover without a radio transmitter is obtained from a particular site on Seal Sands at night, this cannot be related to the time budget of a bird seen on the same site by day unless that bird is a known long-term territory holder.

To increase the usefulness of this information we need to know under what conditions long-term territorial Grey Plovers do use low water foraging locations away from their ´normal´ territories. If this were due to depletion, with time, of resources in the defended area, the radio fixes should become more variable later in the study period of January to March. The program GPCHRON plots a line joining the triangulation points in chronological order, and this has been used for the five territorial birds (figures 16 to 20). These maps clearly show that the use of an ´odd´ foraging location by a territorial Grey Plover is a sporadic behaviour, after which the bird returns to its territory. For further analysis I shall define an ´odd´ foraging location for a territorial bird as one which was:

(a) used throughout the whole of a day or night low water period on a date when the territory was not visited;

(b) physically distinct from the collection of radio fixes indicating the bird´s territory, i.e. the error circle of an ´odd´ location did not cross those clustered around the bird´s territory.

When this definition of an ´odd´ foraging location was applied to all five territorial birds, there was remarkable consistency between them in respect of the dates on which ´odd´ foraging locations were used. (These dates were obtained by running program GPDATES, which plots a date within each error circle produced by GPCIRC.)

The influence of the neap/spring tide cycle on the birds´ choice of foraging locations was examined first. On spring tides

Figures 16-20: lines joining low water foraging locations of long-term territorial birds in chronological order. Data are plotted for the period January to March 1981.

	GREY PLOVER				
DATE	310	520	845	1120	1140
20.1	O	X	X	X	X
21.1	X	X	X	X	X
22.1	X	X	X	X	X
25.1	X	X	X	X	X
27.1	X	X	X	X	X
5.2	X	X	O	O	O
7.2	O	X	X	O	X
9.2	X	X	X	X	X
11.2	O	X	X	O	X
19.2	O	O	O	O	O
21.2	O	X	X	X	X
22.2	X	X	X	X	O
23.2	X	X	X	X	O
24.2	O	X	O	O	X
26.2	X	X	X	X	X
27.2	X	X	O	O	X
5.3	X	X	X	O	X
8.3	X	X	X	X	X
18.3	X	X	X	X	X
19.3	X	X	X	X	X
20.3	X	X	X	X	O
23.3	X	X	X	X	X
25.3	X	X	X	O	O
26.3	X	X	X	X	X
29.3	X	X	X	X	X

O - feeding off territory
X - feeding on territory

Table A: Foraging behaviour of territorial Grey Plover on specific dates in 1981.

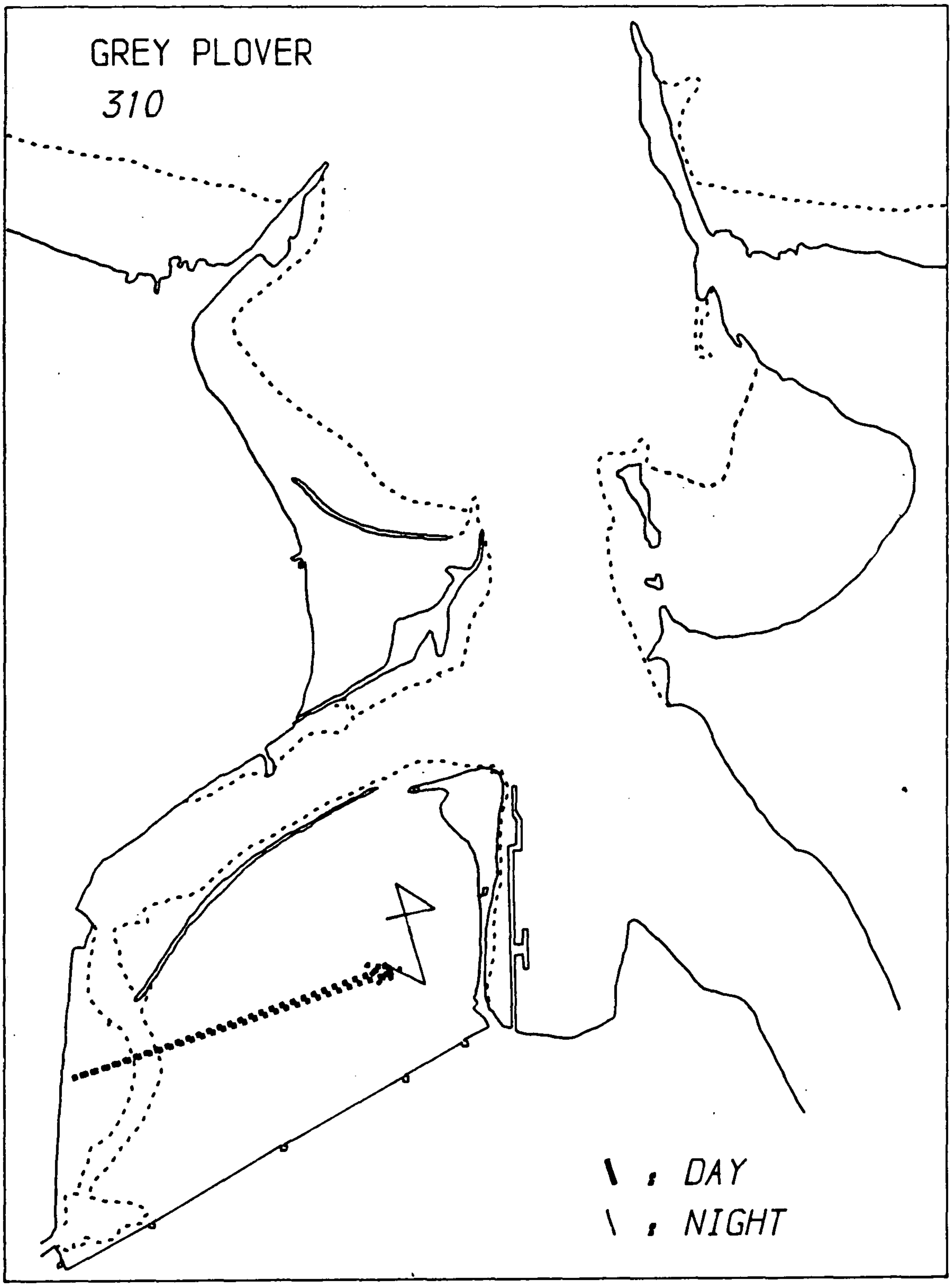


figure 2.16

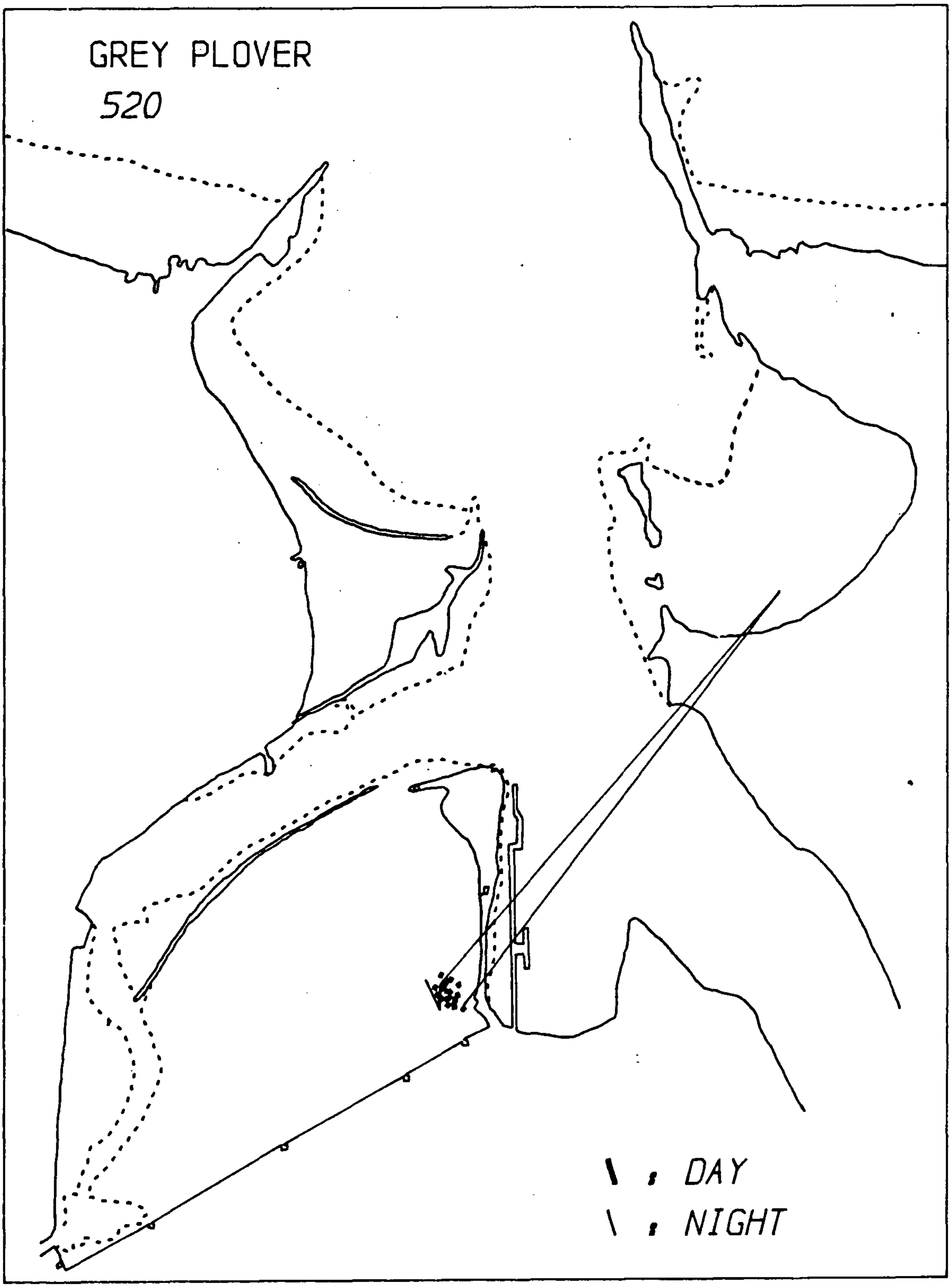


figure 2.17

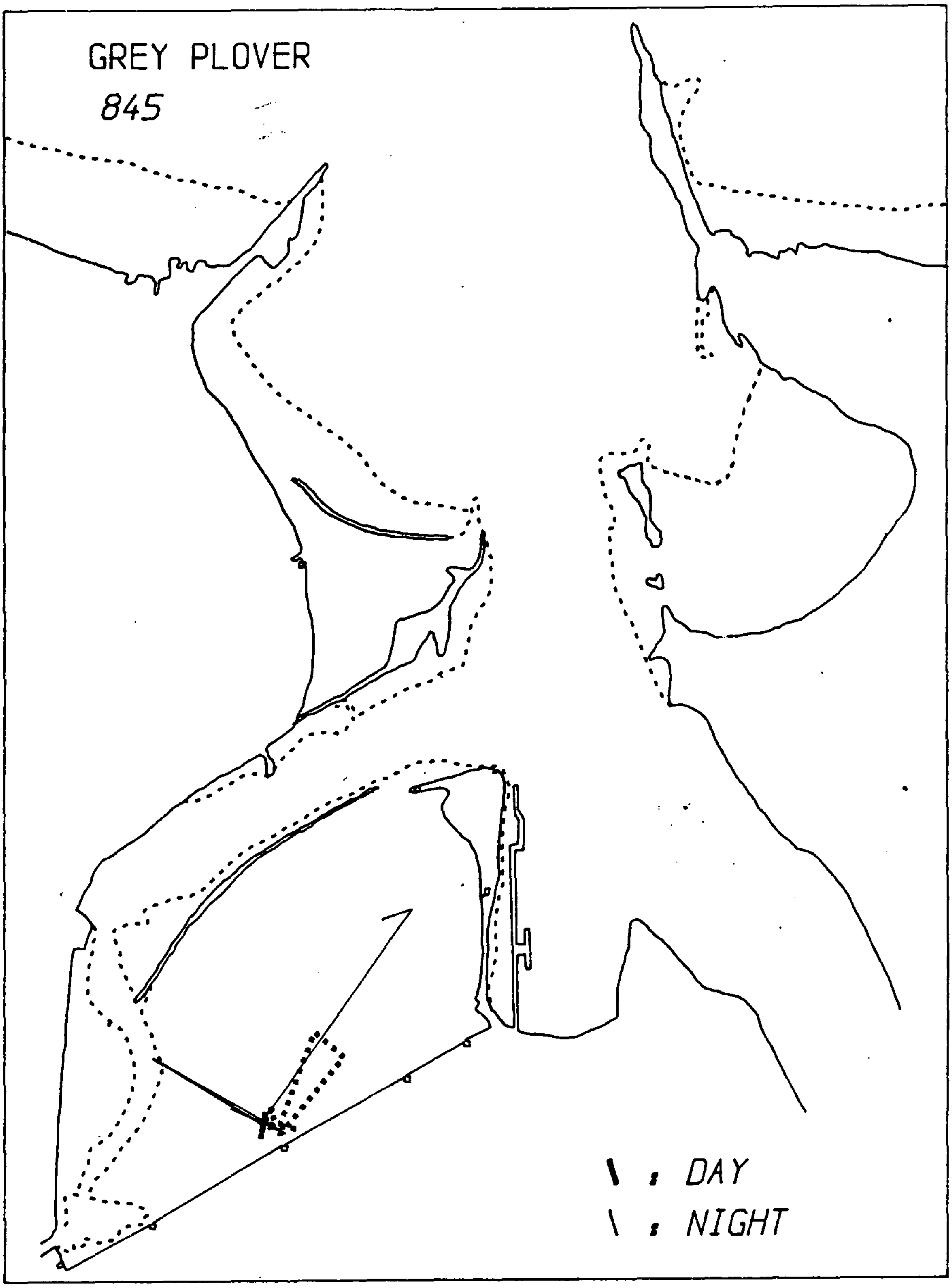


figure 2.18

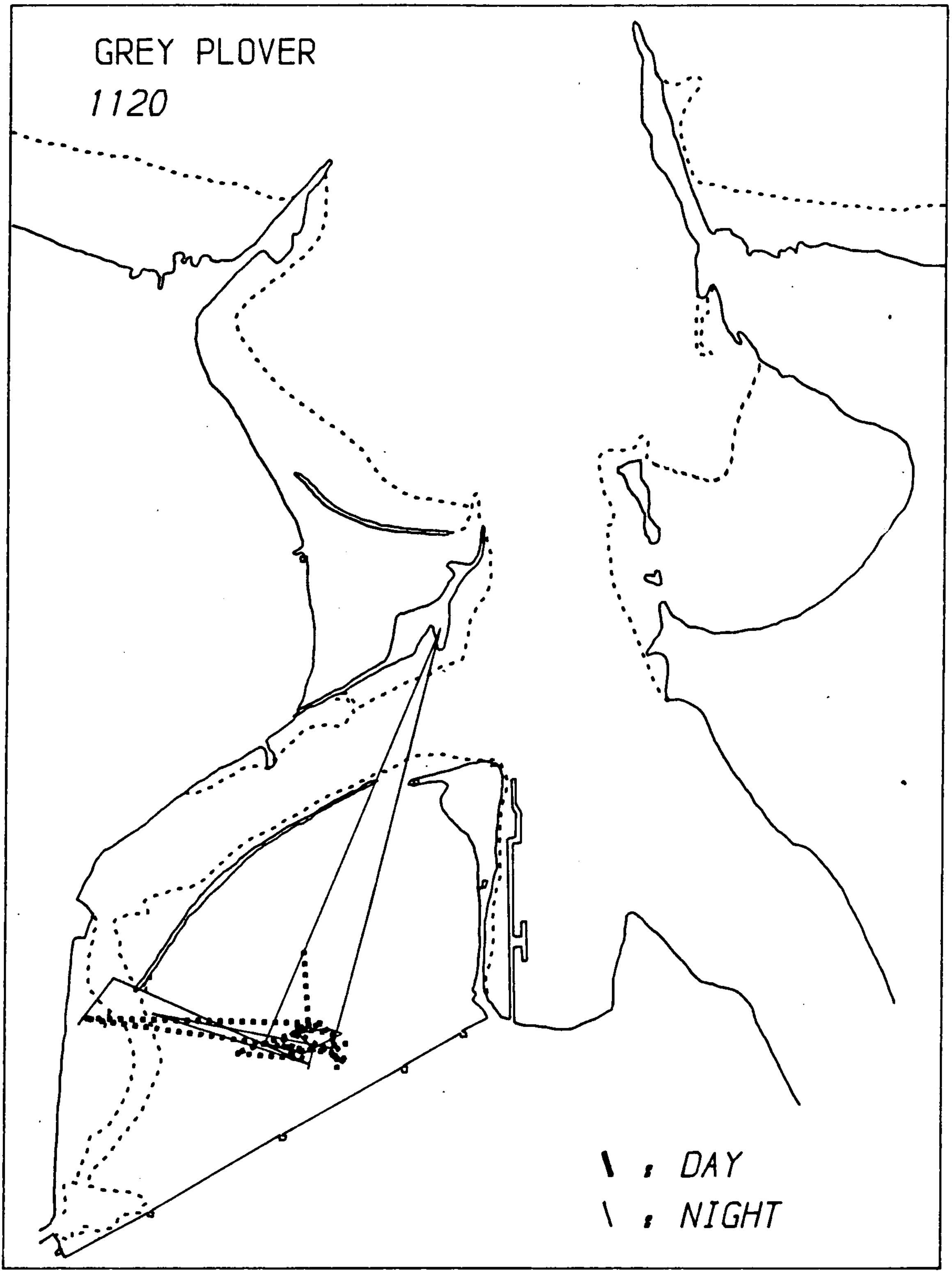


figure 2.19

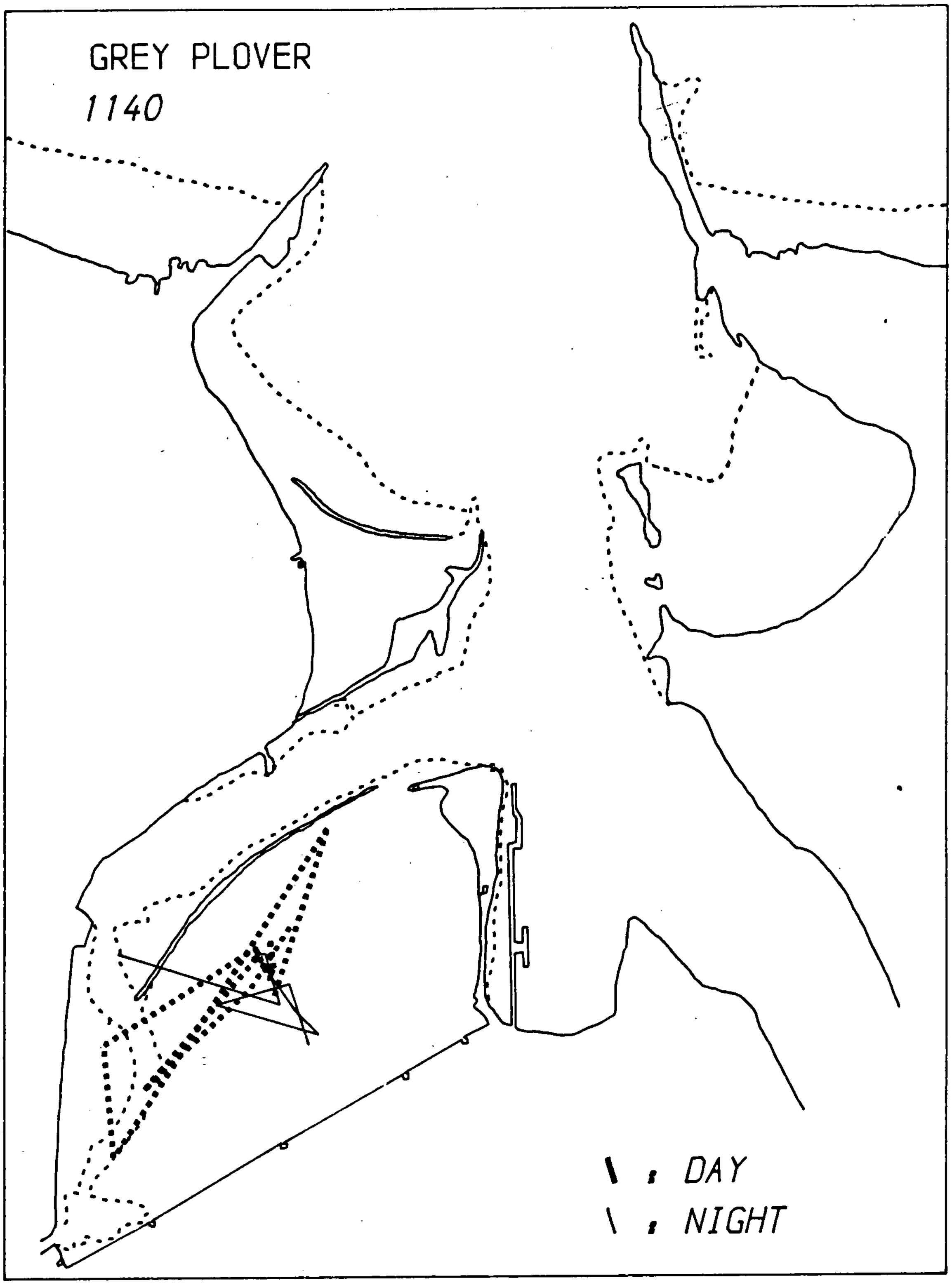


figure 2.20

a larger area of mud is potentially available for use for foraging at Teesmouth, along with an additional food source (Dugan 1981a). However I found no significant difference (t_{23} = 0.793 P>0.4) between the mean height of low water on days on which ´odd´ foraging locations were used ($\bar{H}$ = 1.27m) and days on which normal territorial behaviour was observed ($\bar{H}$ = 1.41m). (The tide height at low water during the night is very similar and directly related to the tide height during the day; hence there was no difference at night either.)

Weather might have influenced foraging locations. Davis (1976) found that Pied Wagtails (Motacilla alba yarrellii) left their feeding territories when weather conditions were poor, and joined others foraging in a flock. The applicability of this hypothesis can be tested also for the Grey Plover, but the difficulty lies in defining what constitutes poor weather conditions. Evans (1976) identified a number of climatic factors which may affect foraging in shorebirds; but there will obviously be an interaction of factors such as temperature, wind and tide to produce effects on a predator and its prey. Dugan et al. (1981) found that one of the weather conditions under which Grey Plover lost weight was associated with higher than normal chill factors. The chill factor is supposedly related to the rate of heat loss by a bird and is derived from the effect of wind strength on metabolic rates of birds at temperatures below thermoneutrality (Gessaman 1973). I found that it is an adequate predictor of the occasions on which territorial Grey Plover move to ´odd´ foraging locations. The mean chill factor on these dates ($\bar{w}$ = 21.42) is significantly higher (t_{23}= 2.336 $P<0.05$) than on those dates ($\bar{w}$ = 12.10) on which normal territorial behaviour was observed. However, there are many more variables than just temperature and windspeed which could affect the foraging locations of normally territorial birds. Because of this, I have used two multivariate techniques to examine which conditions can best explain and predict movement away from the territory. The variables which I considered may have an affect on foraging plovers are:

(1) Height of low water during the day. (HLW)
(2) Minimum daily temperature. (MIT)
(3) 7 day average minimum temperature. (AMIT) (before obsn. date)
(4) Maximum daily temperature. (MAT)
(5) 7 day average maximum temperature. (AMAT) (before obsn. date)
(6) Mean daily windspeed. (DW)
(7) Mean hourly maximum windspeed. (MDW)
(8) Duration of rainfall per 24 hours. (DR)
(9) Number of hours sun per day. (HS)
(10)Mean daily saturation deficit. (SD)
(Daily values refer to those from 00.00 to 24.00 hours each day)

These meteorological variables are intercorrelated as shown by the Pearson product moment correlation matrix in table 1. Values of these variables were taken from the daily records of South Gare weather station, 2 km. NE of Seal Sands, for the period January to March 1981, i.e. that period for which the telemetry data are available.

The hypothesis to be examined using these variables is that

Table 1: Pearson product moment correlation matrix for meteorological variables for the period January to March 1981 (each cell shows the correlation coefficient and its significance).

	MIT	AMIT	MAT	AMAT	DW	MDW	DR	HS	SD
HEIGHT DAYTIME LOW WATER	-0.213 P=0.022	N.S.	-0.224 P=0.017	N.S.	N.S.	N.S.	-0.187 P=0.039	0.186 P=0.039	-0.179 P=0.046
MINIMUM TEMP. (MIT)		0.629 P=0.000	0.671 P=0.000	0.600 P=0.000	0.262 P=0.006	0.251 P=0.008	N.S.	N.S.	0.443 P=0.000
7 DAY AV. MIN. TEMP. (AMIT)			0.673 P=0.000	0.959 P=0.000	N.S.	N.S.	N.S.	N.S.	N.S.
MAXIMUM TEMP. (MAT)				0.706 P=0.000	0.212 P=0.023	N.S.	0.178 P=0.046	N.S.	0.259 P=0.007
7 DAY AV. MAX. TEMP. (AMAT)					N.S.	N.S.	N.S.	N.S.	N.S.
MEAN DAILY WINDSPEED (DW)						0.930 P=0.000	N.S.	N.S.	0.280 P=0.004
MEAN HOURLY MAX. WINDSPEED (MDW)							N.S.	N.S.	0.280 P=0.004
DURATION OF RAINFALL (DR)								-0.260 P=0.007	-0.233 P=0.014
NO. HOURS SUN (HS)									0.199 P=0.030

the meteorological and tidal conditions prevailing at the times that territorial Grey Plover used ´odd´ foraging locations are more extreme in certain ways (as defined by a combination of the variables) than those present during periods of normal territorial behaviour. First I carried out a stepwise discriminant analysis on these variables, as suggested by Richardson (1974). However as pointed out by Williams (1983), intercorrelations between variables produce models which merely describe relationships rather than directly indicate causality, and as such may make interpretation of their results very difficult. What is required is a method of transforming the original data into a set of uncorrelated variables before the discriminant analysis is carried out.

I used principal components analysis to transform the original variables into mutually orthogonal factors (patterns of variation) each accounting for successively smaller proportions of the total variance in the original data set (Cooley & Lohnes 1971, Frey & Pimentel 1978, Chatfield & Collins 1980). This analysis was carried out using the special case of principal components in the factor analysis program of SPSS (Nie et al. 1975); the summary of this first analysis is presented in tables 2 and 3. Using the convention of working with only those factors whose eigenvalues are greater than 1.0 (Huntingford 1976, Frey & Pimentel 1978), four factors were extracted, and the factor scores for each observation date calculated from the factor score coefficient matrix (Nie et al. 1975). Stepwise discriminant analysis was then carried out on these factor scores, using the

Table 2: Eigenvalues, percent variance and cumulative percent variance for the factors extracted in the first run of principal components analysis

FACTOR	EIGENVALUE	% OF VARIANCE ACCOUNTED FOR	CUMULATIVE % OF VARIANCE ACCOUNTED FOR
1	3.42	34.2	34.2
2	2.02	20.2	54.4
3	1.50	15.0	69.4
4	1.09	10.9	80.4
5	0.74	7.4	87.8
.	.	.	.
.	.	.	.
10	0.03	0.3	100.0

Table 3: Factor score coefficients for the first four significant factors

VARIABLE	FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4
HLW	0.03466	0.07271	-0.01096	0.69753
MIT	0.20990	0.03177	0.08350	-0.19804
AMIT	0.32699	-0.08626	-0.06198	0.13446
MAT	0.25928	0.01687	-0.03623	-0.05613
AMAT	0.32393	-0.04701	-0.04735	0.15871
DW	-0.03022	0.48041	-0.04472	0.09843
MDW	-0.03823	0.47505	-0.04354	0.07569
DR	0.05922	0.12657	-0.56100	-0.00645
HS	0.03759	0.07738	0.36291	0.35606
SD	-0.00555	0.06862	0.48922	-0.34424

Table 4: Summary of first discriminant analysis using the factor scores generated from the factor score coefficient matrix (table 3)

```
VARIABLES SELECTED BY THE
STEPWISE ANALYSIS:                        FIRST FACTOR
                                          THIRD FACTOR

CANONICAL DISCRIMINANT FUNCTION

          EIGENVALUE                  0.50446
          CANONICAL CORRELATION       0.5798


          STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS:

          FIRST FACTOR    =  0.97147
          THIRD FACTOR    = -0.70258


          GROUP MEANS (CENTROIDS)

          DATES OF 'ODD' LOCATIONS      -0.65582
          DATES OF NORMAL LOCATIONS      0.71047


   TEST OF EQUALITY OF COVARIANCE MATRIXES USING BOX'S M:

          BOX'S M     = 4.569
          APPROX. F   = 1.379
          DEGREES OF FREEDOM  = 3, 124907.1
          SIGNIFICANCE   = 0.247


   72.0 PERCENT OF CASES CORRECTLY CLASSIFIED BY THIS
          DISCRIMINANT FUNCTION.
```

method of selection of variables with the smallest Wilks´ lambda (equivalent to the largest overall multivariate F). Table 4 summarises this discriminant analysis. The two groups to be discriminated between were: (a) dates on which territorial birds used ´odd´ foraging locations, and (b) dates on which territorial birds exhibited normal territorial behaviour.

If all variables are included via principal components analysis, the resulting discriminant function can correctly classify 72 percent of the original dates into those on which either normal or ´odd´ foraging locations were observed. Because many of the variables used in this first analysis may have been redundant for this classification proceedure, selection of variables was undertaken (see appendix 2) and the analysis re-run. Summaries of analyses for the variables remaining after selection are presented in tables 5 to 7. The final analysis reduced the number of discriminating variables, and increased the discriminating power of the final equation so that 84 percent of cases can now be classified correctly by the discriminant function into normal or ´odd´ foraging behaviour. The final equation relating discriminant score for a particular date to four meteorological variables is:

Discriminant score = 0.2992 x 7 day moving av. min. temp. +
0.2215 x 7 day moving av. max. temp. -
0.2278 x No. hours sun -
0.5493 x Saturation deficit - 1.5847

From the group means in table 7 it is apparent that the more negative is the discriminant score on a particular date, the more

Table 5: Eigenvalues, percent variance and cumulative percent variance for the factors extracted in the final run of principal components analysis

FACTOR	EIGENVALUE	% OF VARIANCE ACCOUNTED FOR	CUMULATIVE % OF VARIANCE ACCOUNTED FOR
1	2.04	50.9	50.9
2	1.13	28.2	79.1
3	0.80	20.0	99.1
4	0.04	0.9	100.0

Table 6: Factor score coefficients for the first two significant factors

VARIABLE	FACTOR 1	FACTOR 2
AMIT	0.51713	-0.08093
AMAT	0.50183	-0.00012
HS	-0.07658	0.67143
SD	-0.02897	0.62750

Table 7: Summary of final discriminant analysis using the factor scores generated from the factor score coefficient matrix (table 6)

```
VARIABLES SELECTED BY THE
STEPWISE ANALYSIS:                         FIRST FACTOR
                                           SECOND FACTOR

CANONICAL DISCRIMINANT FUNCTION

         EIGENVALUE                 0.42697
         CANONICAL CORRELATION      0.547


         STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS:

         FIRST FACTOR    =  1.02001
         SECOND FACTOR   = -0.68711


         GROUP MEANS (CENTROIDS)

         DATES OF 'ODD' LOCATIONS      -0.60216
         DATES OF NORMAL LOCATIONS      0.65234


   TEST OF EQUALITY OF COVARIANCE MATRIXES USING BOX'S M:

         BOX'S M     = 0.187
         APPROX. F   = 0.056
         DEGREES OF FREEDOM  = 3, 124907.1
         SIGNIFICANCE   = 0.982


   84.0 PERCENT OF CASES CORRECTLY CLASSIFIED BY THIS
         DISCRIMINANT FUNCTION.
```

likely that a territorial Grey Plover would be using a foraging location other than that of its territory. Consequently it follows that there is a negative relationship between the first factor (tables 5 and 6) and the incidence of movement from the territory, and a positive relationship between the second factor and the incidence of movement. The loadings of variables in the varimax rotated factor matrix are presented in figure 21. (Orthogonal rotation of the factor matrix was performed to aid interpretation of the results from principal components analysis (Nie et al. 1975, Huntingford 1976).) From this it is clear that the selection of a non-territorial foraging location by a normally territorial bird is more likely to occur if (a) the past seven days have been cold, and (b) there is fast evaporative drying of the mud (as indicated by a high saturation deficit).

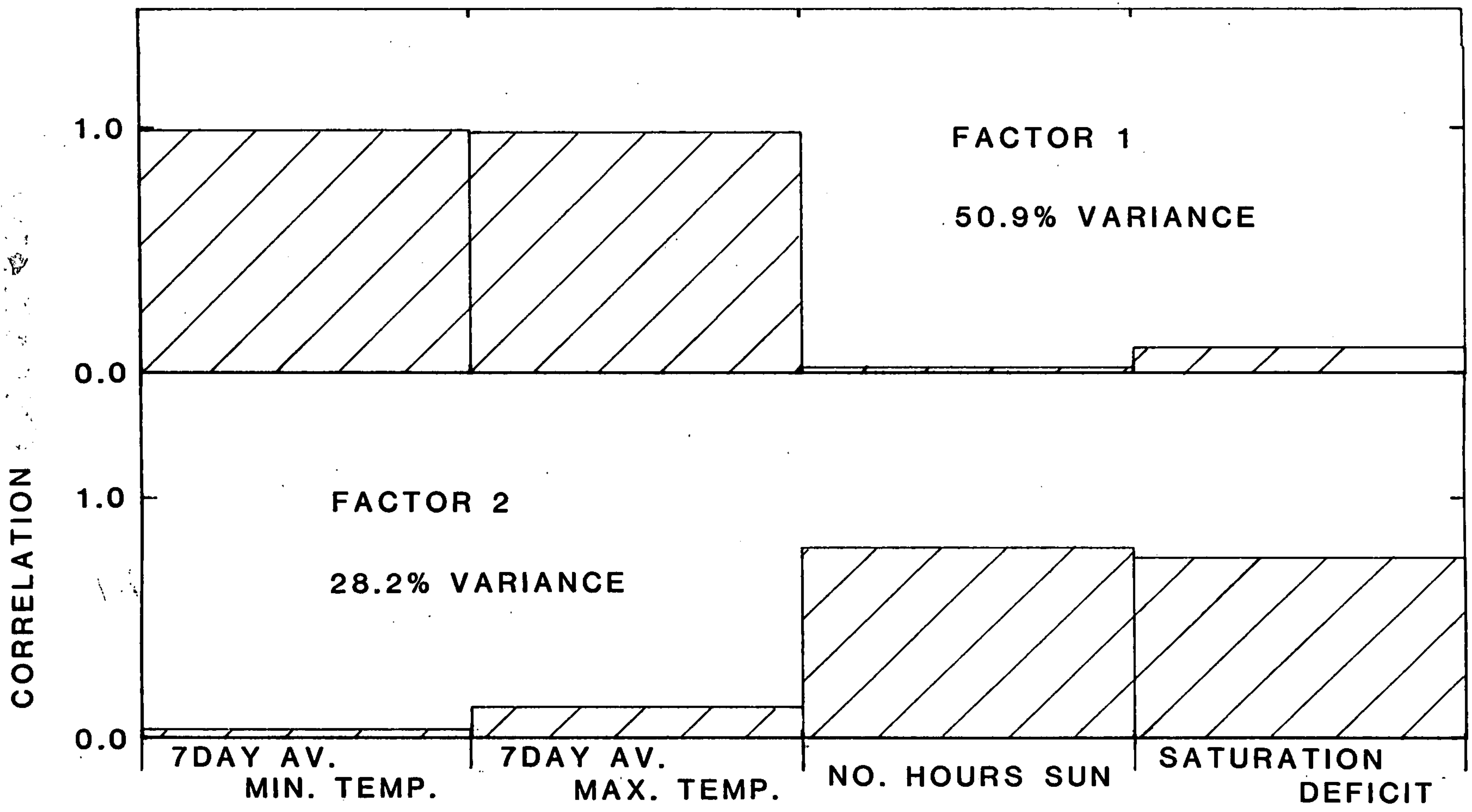


figure 2.21: loading of variables on the two factors produced in the final principal components analysis.

DISCUSSION

The use of radio telemetry to study the foraging and social behaviour of the Grey Plover at Teesmouth enabled a number of previous speculations to be substantiated. Birds which normally defended the same low water foraging territory each day on the mud flats (so called long-term territory holders (Townshend et al. 1984)), usually defended the same area at night. Also, birds which were non-territorial and often moved foraging locations from day to day, exhibited the same behaviour at night.

Radio tagged territorial Grey Plover occasionally used low water foraging locations other than their known territorial sites, as had previously been found for two birds by direct observation by Dugan (1981a, and in Townshend et al. 1984). He proposed that such movement was to take advantage of a more abundant food source at lower tidal levels, particularly at night. The results of my radio telemetry study indicate that the proximate explanation for movements to new foraging locations could be very different, since 84 percent of the dates on which ´odd´ foraging locations were used by territorial birds were associated with more extreme environmental conditions than usual. Movements of foraging location occurred when (a) the birds´ calorific requirements were high (following persistently low temperatures) and (b) prey availability was reduced (during low temperatures and fast drying of the mud (Evans 1976)). When the birds moved under such conditions the new foraging locations were sometimes at lower tidal levels. So the suggestion of Dugan needs to be modified, such that the use of lower tidal areas by territorial Grey Plover is a response to reduced prey availability in their territories (and elsewhere). Under such conditions low tidal level foraging sites presumably become more profitable in terms of the gain in energy intake balanced against the costs of remaining in and defending a territory - a situation very similar to that found by Davis (1976) for territorial Pied Wagtails.

The costs and benefits of territoriality in the Grey Plover have recently been reviewed by Townshend et al. (1984). They concluded that for those birds which defend long-term territories, the benefits of holding a territory must also be measured in the long-term. The results presented in this chapter are consistent with this hypothesis in that it is only the longer term pattern of temperature fluctuations (i.e. 7 day moving averages rather than day to day changes) which influence the behaviour of the birds.

In other work on the Grey Plover (Dugan et al. 1981) high wind strength and chill factors were thought to characterize the conditions under which the birds experienced metabolic stress and foraging difficulties. The wind chill factor they derived from Gessaman (1973) used the daily temperature deficit (from a fixed temperature of 10´C) and daily windspeed, to give an index of the conditions experienced by the birds under consideration. Examination of the chill factors on dates on which territorial Grey Plover used ´odd´ foraging locations revealed that they were significantly more extreme than on dates on which normal territorial behaviour was observed. However, although this index of meteorological conditions appears to provide an explanation for the change in behaviour of territorial birds, care must be exercised in the application of such a hypothetical index. If it is assumed that a change of foraging location by long-term territorial individuals occurs only under very difficult conditions, then the conditions I have characterized in these analyses must be those under which the birds were most stressed. It is significant that changes in foraging location did not occur on dates on which there were high winds, because Dugan (1981b) found that many Grey Plover territories afforded some protection from the wind. Therefore, although chill factors may provide an index of conditions under which Grey Plovers may have difficulties in balancing their energy budgets, the conditions characterized by the multivariate analyses are those under which the birds are forced to find new foraging locations in order to survive.

Although I have restricted the detailed analyses to long-term territorial Grey Plovers, short-term territorial and non-territorial birds showed changes in behaviour that paralleled those of the long-term territorial birds. That is, on dates on which territorial birds used ´odd´ foraging locations, some other birds also tended to move to more peripheral foraging sites such as those on North Gare Sands, Bran Sands and the lower tidal areas (figures 9-15).

SUMMARY

Using radio telemetry on Grey Plovers at Teesmouth has established that long-term territorial birds use the same foraging locations both by day and by night almost continually through the period January to March. On some dates these birds used ´odd´ foraging locations away from their territories. Non-territorial Grey Plover also exhibit consistency in behaviour, night and day throughout this period.

The use of ´odd´ foraging locations by territorial birds was irregular, not related to low tide height and therefore the availability of low tidal areas. Chill factors cannot adequately describe the conditions on which this movement takes place, because Grey Plover territories are known to provide some degree of shelter (Dugan 1981), and hence the conditions that the birds experience cannot be determined from weather station data.

Multivariate methods of principal components analysis coupled with discriminant analysis were used to reduce a set of correlated meteorological and tidal variables, for the period January to March, to those which characterize the conditions under which ´odd´ foraging locations were used. The movement of foraging location by territorial birds occurred when temperatures had been lower than average for a period of at least seven days, on dates with sunshine and a high saturation deficit such that evaporation of surface water led to a rapid drying of intertidal mud. These conditions place a high calorific demand on the birds coupled with a low prey availability. It then becomes more profitable for the birds to move from their territories and

forage elsewhere in the low water period.

INDIVIDUAL AND POPULATION TIME BUDGETS OF THE GREY PLOVER.

INTRODUCTION

In recent years, many attempts have been made to estimate time budgets of various bird species in the field. Some have concentrated on measuring certain aspects of a species' time budget, particularly foraging behaviour (Puttick 1979, Wishart & Sealy 1980, Barnard et al. 1982), while others have provided longer-term estimates of overall time budgets (Wolf & Hainsworth 1971, Utter & LeFebvre 1973, Ashkenazie & Safriel 1979, Maxson & Oring 1980). In this chapter I will present an account of the time budgets of Grey Plovers whilst they are using the intertidal mudflats of the Tees estuary. I have used two methods of estimating the birds' time budgets, that of the overall estimate for the 'population' by observing a group of birds, and individual estimates. Although different observational methods may give different results, there is a particular method which is best for collecting one type of information (Altmann 1974, Jacobsen & Wiggins 1982); however problems arise when more than one measurement of an animal's behaviour is required from the same observation period.

This time budget study was undertaken to collect quantitative information on the diurnal and nocturnal activities of territorial and non-territorial birds, and then to look for differences between these times of activity and categories of social behaviour.

METHODS

The technique of scan sampling (Altmann 1974) was used to estimate the time budgets of territorial and non-territorial Grey Plover on Seal Sands. Birds exhibited only one type of social behaviour on a particular part of Seal Sands (figure 1), hence observations were restricted to Eastern Channel (E.Ch.) and Central Bank South (CB.s.) for territorial birds and to Greenabella Bank (Gb.B.) for non-territorial individuals. In each site a group of individuals was scanned, using a 15-60x60 telescope, every five minutes for forty five minutes out of each hour. Their activities were classified into five behavioural categories, and data either recorded directly on pro-forma sheets or tape-recorded and transcribed later. The categories were as follows:

(1) Foraging activity - this included all subdivisions of plover feeding characteristics (Pienkowski 1980).

(2) Preening and bathing.

(3) Roosting.

(4) Aggressive display.

(5) Flying.

Scan sampling has been used with reasonable success in other observational studies of time budgets of wading birds (Puttick 1979). However estimates of time budgets from this method suffer from a bias against those behaviours which occur infrequently. To help in the quantification of such a bias, and also to obtain information on time budgets of Grey Plovers at night (when, at most, only two individuals can be observed at any one time) the

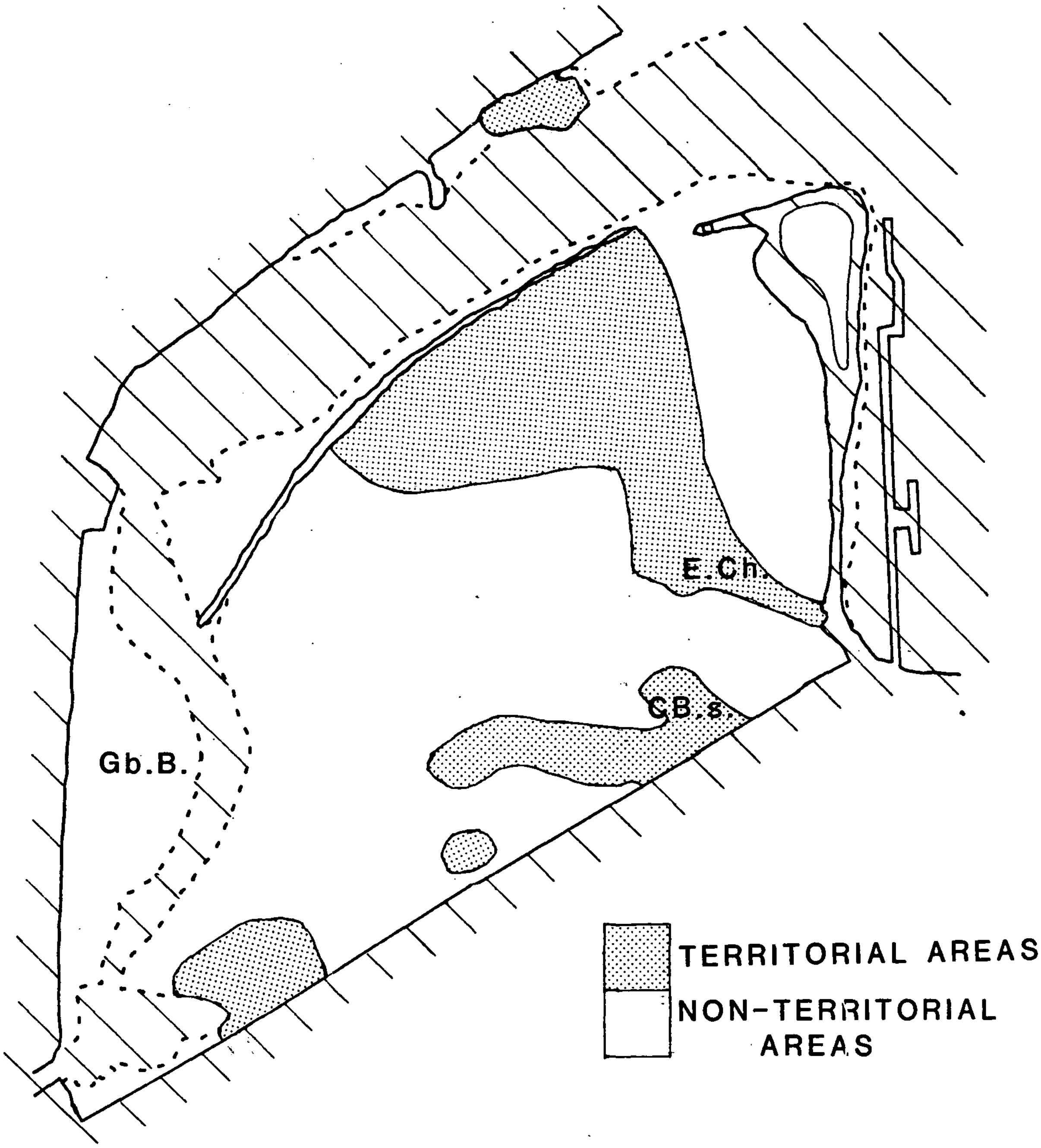


figure 3.1: social behaviour of Grey Plovers on Seal Sands (redrawn from Townshend et al. 1984).

technique of Focal Animal Sampling (Altmann 1974) was used. Observations were made during the day with a 15-60x60 telescope or 10x50 binoculars; at night, with a Modulux 130 image intensifier fitted with a binocular viewer and 600 mm lens. For each bird, the durations of the five behaviours performed in a half hour observation period were recorded, and observations repeated every hour. Activity durations were measured to the nearest second with a stop watch. This technique yielded data on time budgets of individual birds, but because of large hour-to-hour changes in activity, the data are inherently more variable than those obtained from groups of individuals by scan-sampling (Ashkenazie & Safriel 1979).

Data were analysed using the SPSS computer package (Nie et al. 1975, Hull & Nie 1981), particularly the programs for multivariate analysis of variance MANOVA and oneway analysis of variance ONEWAY.

RESULTS

TERRITORIAL BIRDS DURING THE DAY

Data were collected for a total of 109 hours on 22 days between September and March. An initial examination of the data from scan sampling indicated that during the time they were present on the feeding sites, Grey Plovers were engaged in foraging activity for an extremly high percentage of time, and that the rest of the behaviours occurred relatively infrequently. Pooled data, for the whole period that the birds were on the mudflat, could contain two potential sources of variation. Firstly the time budgets could change with time, measured as hours before or after low water, during any one day; and secondly there may be seasonal changes in the birds' time budgets. To test this, a two-way analysis of variance was carried out for date and tidal time (low water minus three hours (LW-3) to low water plus two hours (LW+2)). The time budget data were allocated to the following categories (a) percent time not foraging (100 - percent time foraging) (b) percent time roosting (c) percent time preening/bathing (d) percent time in aggression (e) percent time flying; and data were transformed to $\sqrt{\%\ \text{time} + 0.5}$ (Sokal & Rohlf 1969).

This two-way analysis of variance (table 1) shows that no significant variation with changing tidal time occurs in any behavioral category if seasonal effects are held constant. However, both percent time not foraging and percent time preening show significant variation with date if tidal effects are held constant.

Table 1: Two way analysis of variance for date and tidal time for each time budget behavioural category.

% TIME NOT FORAGING

SOURCE OF VARIATION	D.F.	M.S.	F	
Residual	20	0.137		
Constant	1	165.367		
Date	10	1.160	8.45	***
Tidal time	4	0.155	1.13	N.S.

% TIME ROOSTING

SOURCE OF VARIATION	D.F.	M.S.	F	
Residual	20	0.169		
Constant	1	33.692		
Date	10	0.374	0.17	N.S.
Tidal time	4	0.250	0.25	N.S.

% TIME PREENING

SOURCE OF VARIATION	D.F.	M.S.	F	
Residual	20	0.141		
Constant	1	61.195		
Date	10	1.526	10.87	**
Tidal time	4	0.141	1.00	N.S.

% TIME AGGRESSION

SOURCE OF VARIATION	D.F.	M.S.	F	
Residual	20	0.217		
Constant	1	47.795		
Date	10	0.288	1.33	N.S.
Tidal time	4	0.380	1.75	N.S.

% TIME FLYING

SOURCE OF VARIATION	D.F.	M.S.	F	
Residual	20	0.201		
Constant	1	48.805		
Date	10	0.188	0.934	N.S.
Tidal time	4	0.185	0.923	N.S.

Note: the calculation of an interaction term was suppressed.

** - P<0.01 * - P<0.05 N.S. - not significant

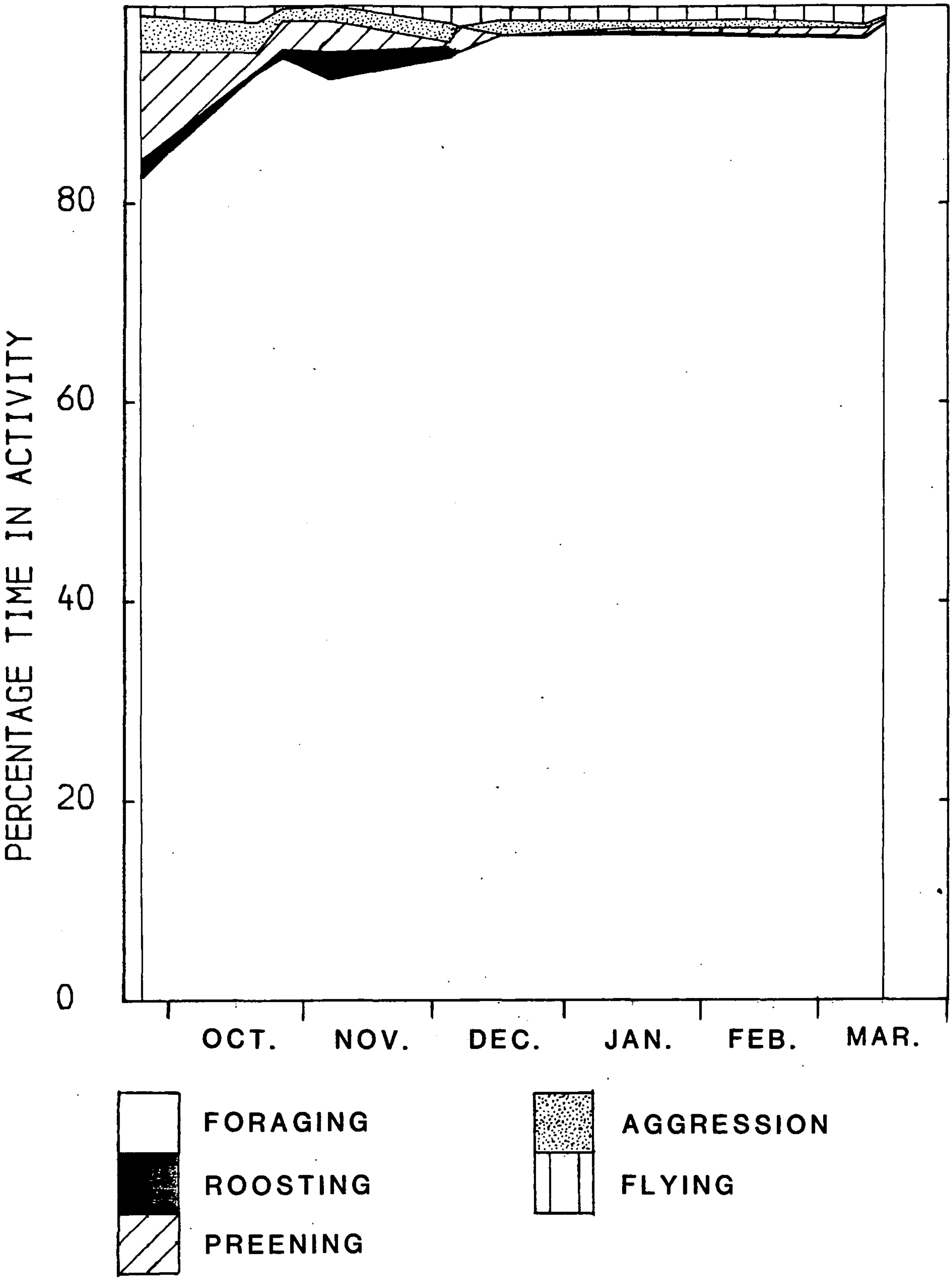
Thus data for the five hour period around low water can legitimately be pooled to produce time budget estimates for each date. These are shown in figure 2. The most striking feature is the large amount of time that territorial Grey Plovers spend foraging, and further inspection suggests that there may be three periods of differing time budgets during the period that the territorial birds are present at Teesmouth:

(1) September - October.

(2) November - early December.

(3) Mid December - March.

Table 2 shows the results of a one-way analysis of variance of time budgets for the three date periods; the data transformation of $\sqrt{\%\ \text{time} + 0.5}$ was used as before. Again significant seasonal trends in the data for the behavioural categories of ´percent time not foraging´ and ´percent time preening´ were confirmed, and that for ´percent time in aggression´ was significant at P=0.07. These seasonal changes in time budgets of territorial Grey Plover (figure 3) are interpreted easily if the timings of moult and territory uptake are considered. Post-nuptual moult in Grey Plovers occurs between late July and early December (Branson & Minton 1976, Ginn & Melville 1983), and a higher incidence of preening might be expected then than in the mid to late winter period. This is exactly what was found. Any rise in preening activity for the spring pre-nuptual moult would not have occurred until after the end of March, by which time most of the Grey Plovers have left the Tees, and are outside the



igure 3.2: seasonal changes in Grey Plover time budgets during the low water observation period.

An estimate of the daily % time allocated to each activity was calculated, rather than a mean of the five minute observation periods.

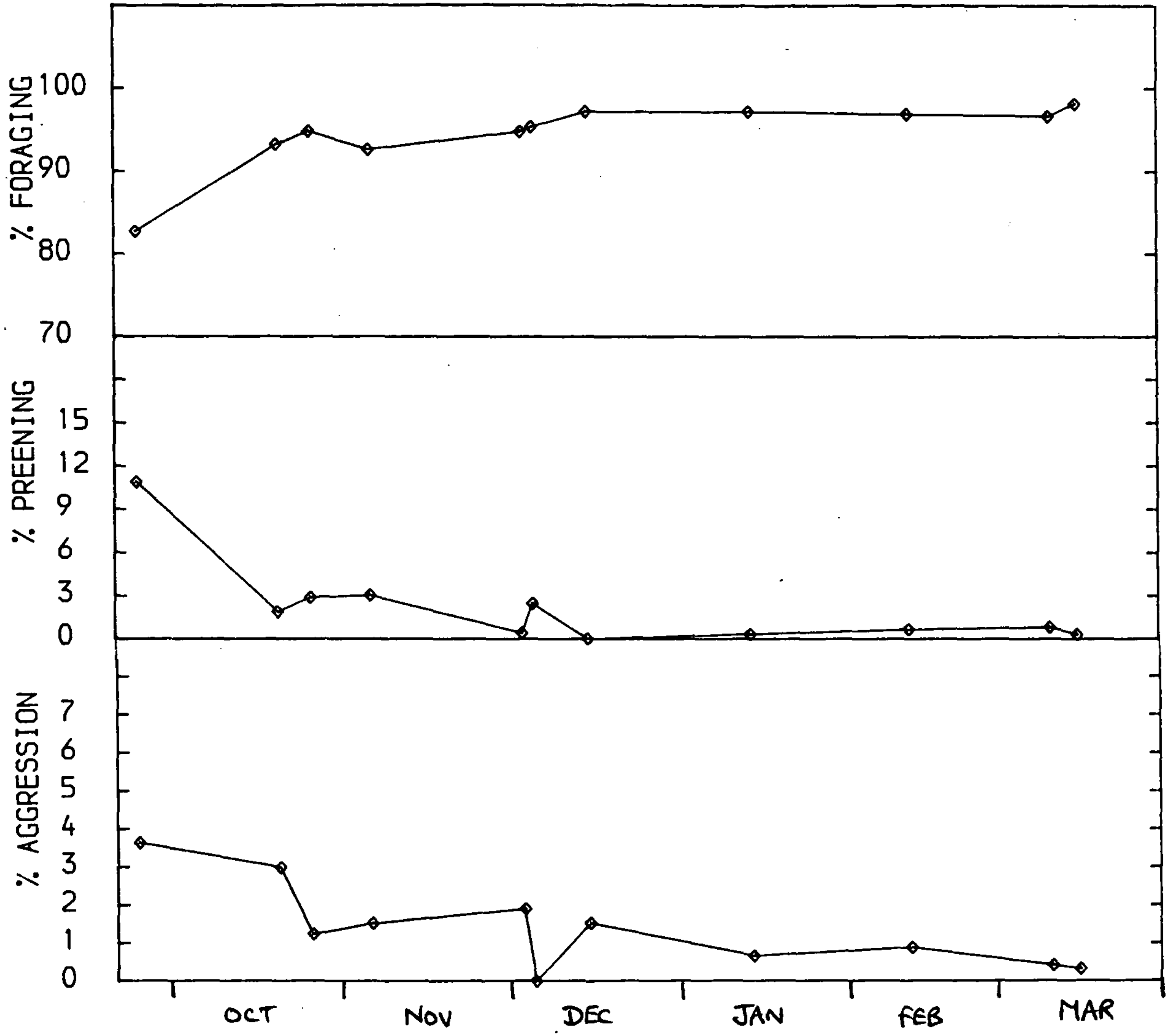


figure 3.3: seasonal changes in some behavioural categories of Grey Plover time budgets at Teesmouth.

Table 2: One way analysis of variance: seasonal trends in the five time budget behaviour categories.

% TIME NOT FORAGING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between date periods	2	1.630	5.92	*
Within date periods	8	0.275		
Total	10			

% TIME ROOSTING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between date periods	2	0.253	2.69	N.S.
Within date periods	8	0.094		
Total	10			

% TIME PREENING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between date periods	2	1.603	5.05	*
Within date periods	8	0.318		
Total	10			

% TIME AGGRESSION

SOURCE OF VARIATION	D.F.	M.S.	F	P
Between date periods	2	0.394	3.67	0.074
Within date periods	8	0.108		
Total	10			

% TIME FLYING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between date periods	2	0.033	0.36	N.S.
Within date periods	8	0.093		
Total	10			

* - $P<0.05$

An estimate of the ´daily´ percentage time allocated to each activity in the total observation time was calculated, rather than a mean of the five minute observation periods.

time span of the data presented here. Most territories are taken up by adult Plovers between late September and November (Townshend 1982, Townshend et al. 1984) so a higher incidence of aggression would be predicted in this period, as was found (figure 3). The percentage of time that birds spent in aggression decreased as the winter progressed and birds became more firmly established in their low water feeding territories (Dugan 1981b, Townshend 1982, and chapter 2).

It has been pointed out that scan sampling may underestimate activities that occur infrequently. The differences between estimates of time budgets from scan and focal animal samples of territorial Grey Plovers have been examined and are presented in table 3. For this bird species, no consistent differences between the time budget estimates produced by these two techniques can be established.

TERRITORIAL BIRDS AT NIGHT

Because of the obvious difficulties in direct observation of animals at night, and due to limitations of the image intensifier, night observations had to be confined to focal animal sampling. From the radio telemetry results it was clear that territorial Grey Plover use the same low water foraging locations both by day and by night. The inference from this is that any territorial bird found at night in the same area as that defended by a diurnal territory holder, would be almost certainly the same bird. Observations made on the same sites by night and again during the next day thus enable comparisons to be made between the nocturnal and diurnal time budgets of the same

Table 3: Difference between the time budget estimates derived from focal animal and scan sampling.

Time Budget Factor	No. Cases	Estimate Derived From	Mean	t Value
% Time Foraging	5	Focal animal sampling	93.46	1.38 N.S.
		Scan sampling	95.92	
% Time Roosting	5	Focal animal sampling	0.48	-0.33 N.S.
		Scan sampling	0.74	
% Time Preening	5	Focal animal sampling	1.68	0.87 N.S.
		Scan sampling	0.73	
% Time Aggression	5	Focal animal sampling	1.60	0.42 N.S.
		Scan sampling	1.27	
% Time Flying	5	Focal animal sampling	0.34	-1.52 N.S.
		Scan sampling	1.08	

Note: Comparisons have been made by paired t-tests.

individual territorial Grey Plovers.

Nocturnal observations revealed firstly that Grey Plovers at Teesmouth did in fact forage extensively during the hours of darkness, a result consistent with observations and inference of other workers (Knights 1979, Pienkowski 1980, Dugan 1981b). Observations of nocturnal time budgets were confined to dates during the late winter period (mid December to March) when no seasonal changes in diurnal budgets were apparent. The average time budget for the five night-time hours around low water is compared with that of the following day in table 4.

The extremely high percentage of observation time in which the birds were foraging is again an important result, very similar to the general diurnal situation. These two time budgets have been compared in a one-way analysis of variance in table 5. There are no differences significant at the 5% level between the diurnal and nocturnal time budgets of territorial Grey Plovers in this part of the winter, although there is a suggestion that the bird spent slightly more of its time foraging at night.

NON-TERRITORIAL GREY PLOVERS

Non-territorial birds were more difficult to observe because of the physical position of the areas which they used in relation to observation positions (figure 1). Nocturnal observations on these birds were not possible because of the limitations of range of the night viewing equipment.

From scan sampling, an average five hourly (low water) time budget of non-territorial Grey Plover was constructed for the

Table 4: Nocturnal and diurnal time budgets of the same individual territorial Grey Plover between December and March.

	NOCTURNAL TIME BUDGET	DIURNAL TIME BUDGET
	Mean percentage time in activity	Mean percentage time in activity
% TIME FORAGING	98.04	92.22
% TIME ROOSTING	1.09	0.88
% TIME PREENING	0.37	1.33
% TIME AGGRESSION	0.16	1.83
% TIME FLYING	0.12	0.10
N	2	3

Note: Percentages are for the five hour observation period around low water; all calculations are performed on $\sqrt{\%\ \text{time} + 0.5}$ data transformation.

Table 5: One way analysis of variance: difference between diurnal and nocturnal time budgets of territorial Grey Plover.

% TIME NOT FORAGING

SOURCE OF VARIATION	D.F.	M.S.	F	P
Between night and day	1	2.049	6.46	0.085
Within nights and days	3	0.317		
Total	4			

% TIME ROOSTING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between night and day	1	0.009	0.014	N.S.
Within nights and days	3	0.631		
Total	4			

% TIME PREENING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between night and day	1	0.210	0.633	N.S.
Within nights and days	3	0.332		
Total	4			

% TIME AGGRESSION

SOURCE OF VARIATION	D.F.	M.S.	F	
Between night and day	1	0.608	1.557	N.S.
Within nights and days	3	0.390		
Total	4			

% TIME FLYING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between night and day	1	0.0001	0.009	N.S.
Within nights and days	3	0.009		
Total	4			

late winter period only, because of the uncertainty in earlier months that the ´population´ of individuals present may have changed in composition. (The transitory nature of foraging locations used by non-territorial birds was emphasised in chapter 2.) The time budget for non-territorial birds can be compared with that of territorial birds by day, again using the observations for the late winter period (tables 6 & 7).

Territorial birds spent significantly (P=0.05) more time in aggressive behaviour than did non-territorial birds. This is hardly surprising since territorial birds must spend some time in actually defending areas, particularly during the influx of birds in January and February (Dugan 1981b, Townshend 1982); however non-territorial birds also defend an ´individual´ distance around themselves. The increased time allocated to aggressive behaviour by territorial Grey Plovers is not to the detriment of time spent foraging, which is similar whether the birds are territorial or not. Rather, territorial birds reduce the level of other non-foraging, non-aggressive activities.

Table 6: One way analysis of variance: differences between time budgets of territorial and non-territorial Grey Plover.

% TIME NOT FORAGING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between social behaviours	1	0.048	0.5	N.S.
Within a social behaviour	6	0.096		
Total	7			

% TIME ROOSTING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between social behaviours	1	0.019	1.06	N.S.
Within a social behaviour	6	0.018		
Total	7			

% TIME PREENING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between social behaviours	1	0.002	0.04	N.S.
Within a social behaviour	6	0.043		
Total	7			

% TIME AGGRESSION

SOURCE OF VARIATION	D.F.	M.S.	F	
Between social behaviours	1	0.218	5.89	*
Within a social behaviour	6	0.037		
Total	7			

% TIME FLYING

SOURCE OF VARIATION	D.F.	M.S.	F	
Between social behaviours	1	0.00	0.0	N.S.
Within a social behaviour	6	0.071		
Total	7			

* - $P<0.05$

Table 7: Time budgets of territorial and non-territorial Grey Plover by day.

	NON-TERRITORIAL BIRDS Mean percentage time in activity	TERRITORIAL BIRDS Mean percentage time in activity
% TIME FORAGING	97.57	97.01
% TIME ROOSTING	0.36	0.19
% TIME PREENING	0.37	0.43
% TIME AGGRESSION	0.19	0.84
% TIME FLYING	1.50	1.49
N	4	4

Note: Percentages are for the five hour observation period around low water; all calculations are performed on $\sqrt{\%\ \text{time} + 0.5}$ data transformation.

DISCUSSION

The results of this time budget study of Grey Plovers at Teesmouth show that the birds use a very high percentage of the time for which they are on the mudflats, for foraging activities. Seal Sands is available for foraging waders for around seven to eight hours in each tidal cycle, and although there are other high water feeding sites within the estuary, Grey Plovers normally fly to roost when Seal Sands is covered. So although the birds appear to spend an extremely high percentage of observation time in foraging activities, this time accounts for only approximately 63 percent of any tidal period. The average time budget for the diurnal low water period (ie that time when the physical influence of the tide has a negligible influence on foraging plovers) is 97 percent time foraging; and if the average time budget for the additional three hours during tidal ebb and flow is taken as 60 percent time foraging (estimated from a few hours observation), then a result of 83.1 % time foraging is produced for the eight hour diurnal low water period.

Quantification of the Grey Plover nocturnal time budget provides an interesting result, in that even for a predator foraging visually (a factor which may be an advantage or a disadvantage to nocturnal foraging (Pienkowski 1980)) nocturnal activities are at least as important as those by day. There are two questions to be considered , firstly how long do the birds spend foraging at night (what is their nocturnal time budget), and secondly what is their feeding efficiency at night? In this chapter I have considered the first question and will return to the second in the next chapter.

With such a high percentage of the time spent on the mudflats used for foraging, an interesting question is what determines the time spent foraging by Grey Plovers? Some insight into this problem was obtained in one session of nocturnal and diurnal observations on the 15/16th February 1983. During the afternoon high water on the 15th a large number of dead small fish were washed over Seal Sands. As the tide receeded, these fish were left in the creeks of the mudflat within the territorial areas of many Grey Plovers. Nocturnal observations on one territorial bird revealed that it used this super-abundant food source, and changed its time budget to that shown in table 8.

Table 8: Time budget of territorial Grey Plover on 15/16th February.

	NOCTURNAL TIME BUDGET	SIG.	DIURNAL TIME BUDGET	SIG.
% TIME FORAGING	28.08	**	72.44	***
% TIME ROOSTING	65.77	**	8.0	N.S.
% TIME PREENING	5.77	N.S.	18.67	**
% TIME AGGRESSION	0.0	N.S.	0.22	N.S.
% TIME FLYING	0.38	N.S.	0.67	N.S.

*** - P<0.001 ** - P<0.01

The significance values are those for the t-test comparison of these values with the seasonal population means (Sokal & Rohlf 1969).

After the next high tide and in the following diurnal observation period a number of fish remained in the bird's territory and it continued to use this food source. However, because of food stealing by Black-headed Gulls (*Larus ridibundus*) (which were not present during the night) the bird returned to foraging for ragworms before it left its territory three hours after it had been uncovered by the tide.

From the nocturnal observations on this Grey Plover it is clear that the time allocated to foraging was very much reduced when the bird had an alternative supply of large food items; it spent a much higher percentage of observation time roosting on its territory. This suggests that the high percentage time normally used for foraging is a result of the problems in balancing the individual's energy budget when it is foraging for worms.

The data of Kersten et al. (1983) provide an interesting comparison between the time budgets of my Grey Plovers at Teesmouth and of birds using an intertidal area in Morocco. They found that , on average, the time budget comprised:

Mean seasonal time budget: 90.0% time foraging
5.5% time in aggression
4.3% time preening
0.1% time roosting
0.1% time flying

The birds in Morocco were foraging in very similar conditions to the Tees birds, in that they were territorial and foraging for ragworms (*Nereis divorsicolor*) and shorecrabs (*Carcinus maenas*).

The similarity of these time budgets is very striking, but further comparisons cannot be made because little is known of the calorific intake rates of the Moroccan birds. Also, at the time of year when observations were made (March), the Grey Plover may have been increasing fat reserves in preparation for a northward migration, and so foraging for longer or more intensively than in winter.

As a final comment, it is worth noting that many of the statistical tests on these time budget studies of the Grey Plover produced at best differences significant at the five percent probability level. This is not surprising if consideration is given to the magnitude of the numbers involved. Sokal & Rohlf (1969) give a formula for estimating the number of replicates required to investigate a difference between the means of two samples to obtain a result significant at the five percent level. The result for the Grey Plover situation is in excess of four thousand replicates. Clearly this is only a theoretical result, but it is a consequence of the very small percentages of time used for non-foraging activities, and the high coefficient of variation in the data. So although some differences between the time budgets of territorial and non-territorial birds were suggested, the amount of fieldwork needed to make an adequate comparison between the two time budgets was prohibitively high.

SUMMARY

Scan sampling estimates of Grey Plover time budgets for the five hours around low water indicate an extremely high (in excess of ninety percent) proportion of time spent in foraging activities throughout the winter months. No tidal effects are evident in the time budgets of territorial birds during the restricted observation period when the physical presence of the tide did not affect the foraging plovers. Seasonal decreases in the percentage time spent in preening and in aggression are apparent for territorial birds; and these trends can be explained by the timing of moult and of territory establishment.

Comparisons of territorial Grey Plover time budgets estimated by scan and focal animal sampling did not reveal any consistent biases of the two observational methods.

Territorial birds by night exhibited very similar time budgets to those observed by day, with a very high incidence of nocturnal foraging activity.

Non-territorial Grey Plovers in the same period of the year spent significantly (P=0.05) less time in aggressive behaviour than did the territorial birds; this being a reflection of the obvious need for territorial individuals to spend more energy defending their exclusive space rather than an ´individual´ distance.

ENERGY INTAKE RATES OF TERRITORIAL GREY PLOVERS AT TEESMOUTH.

INTRODUCTION

The foraging behaviour of plovers has been investigated by Pienkowski (1980, 1982, 1983a, 1983b) at Lindisfarne and by Dugan (1981a, 1981b) and Townshend (1982) at Teesmouth. Their characteristic foraging methods are well documented. Estimation of the energy intake of any animal in the field is a difficult problem, but for visually foraging plovers it is easier because the vast majority of prey items they take can be identified directly by a human observer (Dugan 1981b, Townshend 1982).

In this chapter I will consider patterns in a number of foraging parameters measured in the field, leading up to estimation of the calorific intake rate of the Grey Plover. This information will be used in subsequent chapters for constructing a time and energy budget for territorial birds using Seal Sands at Teesmouth. Data on energy intake is available for the time period during which the territorial areas of Grey Plover are uncovered by the tide. Very little information was collected over the time period when the ebbing and flooding tide restricted the birds to a small area of mud because of the difficulty in locating particular individuals.

METHODS

Observations on prey intake rates and foraging behaviour of Grey Plovers on Seal Sands were carried out in conjunction with observations on the birds' time budgets during the 15 minutes of every hour in which scan-sampling was suspended (see previous chapter). Information collected whilst using a 15-60x60 telescope was dictated into a tape recorder and then transcribed and analysed later. A stop watch was used to time foraging bouts, peck rates, etc.. Because of the limited variety of macrofauna in Seal Sands (Evans et al. 1979) each prey item taken by a plover was normally identifiable in the field with confidence. The sizes of prey taken were estimated by comparison with the bill length of the bird. Grey Plovers show little variation in bill size; measurements of individuals gave an average of 29.0 ± 0.1(S.E.) mm (n=194). Errors resulting from this method of estimation of prey size were corrected for by the methods of Dugan (1981b) before the data were analysed. In the analysis of plover food intake rates, only observation periods of at least five minutes were included to reduce variability in the data. Justification for this time interval was given by Dugan (1981b) and Townshend (1982).

Meteorological variables used in the analysis of seasonal variation in energy intake were obtained from South Gare weather station, 3km NE of Seal Sands.

QUANTIFICATION OF ENERGY INTAKE

(a) Intake of Nereis divorsicolor:

Body lengths of Nereis taken by birds were estimated in the field, corrected for the part of the worm concealed in the bill, and biomasses then estimated from the regression of body weight on body length obtained by Dugan (1981b):

$$\log(\text{dry flesh weight (mg)}) = a + b \times \log(\text{body length (cm)})$$

values of 'a' and 'b' were taken as:

$a = -0.462 \pm 0.039$ (S.E.) $n=22$

$b = 2.47 \pm 0.037$ (S.E.) $n=22$

(The dry flesh weights of <u>Nereis</u> ranging from 1/4 bill length to 3 bill lengths in size are given in appendix 3). Calorific contents of the different worm sizes were estimated by using a calorific value of 4.8 calories (20.1 J) per mg..

(b) Intake of <u>Hydrobia</u> <u>ulvae</u>:

Grey Plovers are known to take only the larger size classes of <u>Hydrobia</u> (Evans et al. 1979). The average calorific content of an individual of these size classes was taken as 3.2 cals.(13.4 J) (Dugan 1981b).

(c) Intake of <u>Macoma</u> <u>balthica</u>:

Two size classes of <u>Macoma</u> were taken by Grey Plovers at Teesmouth, those smaller than 1/4 bill length, and those greater than 1/3 bill length (Dugan 1981b). The calorific contents of these were taken as 10 cals.(41.9 J) and 54 cals.(226.1 J) respectively.

(d) Intake of small items:

Pienkowski (1973) estimated that 99.4% of pecks made by Grey Plovers at Teesmouth were successful when they were feeding on <u>Nereis</u>. Where birds were taking some smaller prey, cine-film indicated that the success rate was around 90% (Pienkowski

1983a). Although my direct observations suggested a lower overall peck success rate, swallowing of small prey items must have been overlooked. Consequently I have adjusted the peck success rate of the birds to ninety percent by adding 6 cals.(25.1 J) for each seemingly unsuccessful peck. In practice this has little effect on the calorific intake rates which are heavily dependent on the number of large worms taken.

(e) Variables used in the analysis:

Data transformations were applied (Sokal & Rohlf 1969) before analyses were carried out using the SPSS package (Nie et al. 1975). Each data case was produced for a five minute observation period using the following variables:

(1) Number of paces per five minutes.

(2) $\sqrt{(\text{Number of worms} > 1 \text{ bill length}) + 0.5}$.

(3) Number of pecks per five minutes.

(4) Log calorific intake per five minutes.

The analysis was carried out at two levels. Firstly, information for a single colour-marked territorial bird was examined, and then data on all territorial individuals were pooled.

RESULTS

(a) Energy intake and foraging behaviour of a single territorial bird.

Data were available from a total of 42 hour periods during which foraging was quantified, covering 6 days between October and March. A two-way analysis of variance was carried out for date and time around low water(LW-3 hours to LW+3 hours), for each of the four foraging parameters. (Calculation of the date/tidal time interaction term was suppressed as this was not thought to be important.) None of the four parameters showed any significant variation with either time around low water or with date. Therefore a mean daily value for each foraging variable was calculated and used in a one-way analysis of variance to look for a seasonal pattern in these parameters (table 1). Again none of the parameters showed any significant seasonal pattern for this single bird; this perhaps is a surprising result as it might be expected that if any trends in the data are present they should be more apparent here, as population trends may be masked by individual variation when data from a number of individuals are pooled.

(b) Energy intake and foraging behaviour of all territorial birds.

A two-way analysis of variance was carried out to examine the data for seasonal and tidal (6 hours around low water) patterns in the foraging parameters (calculation of the date/tidal time interaction term was again suppressed in the analysis). No foraging parameter showed any significant

Table 1: One way analysis of variance: seasonal pattern in foraging parameters for a single territorial Grey Plover.

PACING RATE PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Between dates	4	20145.49	1.64	N.S.
Within each date	11	12277.06		
Total	15			

NUMBER OF LARGE WORMS TAKEN PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Between dates	4	0.417	1.01	N.S.
Within each date	11	0.413		
Total	15			

PECK RATE PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Between dates	4	32.58	0.65	N.S.
Within each date	11	50.42		
Total	15			

CALORIFIC INTAKE PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Between dates	4	0.028	0.84	N.S.
Within each date	11	0.034		
Total	15			

N.S. - not significant

Table 2: One way analysis of variance: seasonal pattern in foraging parameters for all territorial Grey Plover.

PACING RATE PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Between dates	5	9575.07	1.32	N.S.
Within each date	33	7257.18		
Total	38			

NUMBER OF LARGE WORMS TAKEN PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Between dates	5	1.185	3.64	**
Within each date	33	0.325		
Total	38			

PECK RATE PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Between dates	5	383.12	2.08	N.S.
Within each date	33	184.22		
Total	38			

CALORIFIC INTAKE PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	P
Between dates	5	0.137	2.42	0.056
Within each date	33	0.056		
Total	38			

** - P<0.01

variation either with date or with time around low water, so a mean daily value was calculated and used in a one-way analysis of variance to look for a seasonal pattern in the foraging parameters (table 2).

This examination of the data set for all territorial individuals indicates a significant (P<0.01) seasonal pattern only in the number of large worms taken by Grey Plover (figure 1). However there is also a suggestion of a seasonal pattern in the birds calorific intake (P=0.056). The correlation matrix for these four foraging parameters (table 3) reveals that the birds calorific intake is significantly correlated with both the number of large worms it takes and its peck rate.

Table 3: Pearson product-moment correlations between the four foraging parameters measured for territorial Grey Plovers at Teesmouth.

VARIABLE	PACING RATE	NO. LARGE WORMS	PECK RATE	CALORIFIC INTAKE
PACING RATE		N.S.	N.S.	N.S
NO.LARGE WORMS			N.S.	r=0.82 ***
PECK RATE				r=0.39 **

N.S. - not significant
** - P<0.01
*** - P<0.001

A multiple regression analysis of the best predictor variables for calorific intake (table 4) indicates that both the number of large worms (those greater than one bill length) taken and the peck rate are the variables needed to best explain the

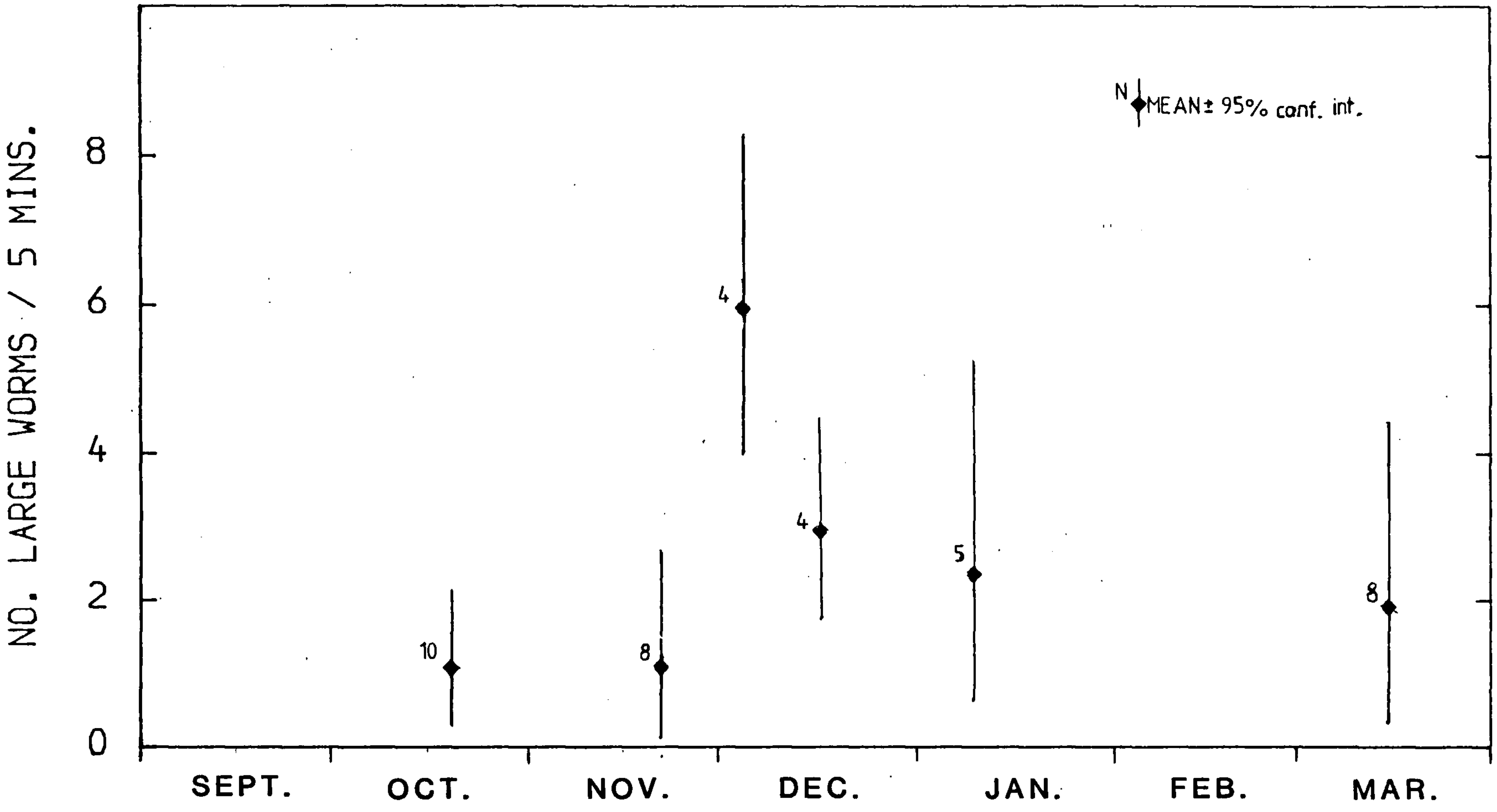


figure 4.1: seasonal changes in the rate of intake of large worms (>1 bill length) by territorial Grey Plover.

Table 4: Summary of stepwise multiple regression using backwards removal:

dependent variable - calorific intake,

independent variables - pacing rate, number of large worms, peck rate.

Step No.	Multiple R	R squared	R squared change	Variable	F
1				IN: PECK RATE	
2				IN: NO. LARGE WORMS	
3	0.9056	0.8201	0.8201	IN: PACING RATE	53.19 ***
4	0.9056	0.8201	-0.0000	OUT: PACING RATE	82.06 ***

VARIABLES IN THE FINAL EQUATION:

$$\text{LOG CAL. INTAKE} = 1.783 + 0.007(+0.001) \times \text{PECK RATE} + 0.32(+0.028) \times \sqrt{\text{NO. LARGE WORMS} + 0.5}$$

*** - P<0.001

birds´ observed calorific intake. In fact these are the only variables which need be measured in a further study, if all that is required is to estimate the calorific intake of Grey Plover.

A possible source of the seasonal variation in energy intake is that weather conditions differed from one observation period to another. Although the information analysed above was obtained from territorial birds within their territories, so the weather extremes examined in chapter 2 had no direct effect on the foraging locations, the factors of temperature, windspeed and time after high water are other possible influences on foraging birds that need to be examined (Pienkowski 1983a).

I have eliminated the possibility of tidal effects in the low water observation period (LW-3 hours to LW+3 hours), and no observations were taken (or possible) in high winds, so temperature is the only measured variable which might be expected to have any influence on the foraging data. The influence of season and temperature on rate of calorific intake can be examined in a two way analysis of variance; temperature for each day of observation was classified as high (>10´C), medium (9-6´C), or low (<5´C). Table 5 shows that if the seasonal effects are held constant, then there was no significant pattern in any of the foraging parameters with a change in temperature. However, if the effects of temperature are held constant, the only variable which showed a significant seasonal pattern was that of the number of large worms taken per five minutes. The important conclusion from this is that over the range of

Table 5: Two way analysis of variance: seasonal and temperature effects of the four foraging parameters of territorial Grey Plover.

PACING RATE PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Within cells	30	6524.63		
Constant	1	2727127.41	417.98	
Date	5	9574.86	1.47	N.S.
Temperature	2	5992.75	0.92	N.S.

NUMBER OF LARGE WORMS TAKEN PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Within cells	30	0.329		
Constant	1	95.974	291.98	
Date	5	1.185	3.61	*
Temperature	2	0.338	1.03	N.S.

PECK RATE PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Within cells	30	199.04		
Constant	1	35642.08	179.07	
Date	5	383.12	1.93	N.S.
Temperature	2	4.71	0.02	N.S.

CALORIFIC INTAKE PER FIVE MINUTES

SOURCE OF VARIATION	D.F.	M.S.	F	
Within cells	30	0.060		
Constant	1	243.385	4057.88	
Date	5	0.137	2.28	N.S.
Temperature	2	0.030	0.51	N.S.

Note: calculation of an interaction term was suppressed.

* - $P<0.05$

temperatures examined, the apparent seasonal pattern of calorific intake in the Grey Plover was not statistically significant when the variation in temperatures under which the observations were made were taken into account.

(b) Nocturnal foraging

Use of an image intensifier enabled observations to be made on foraging Grey Plovers, and as mentioned in chapter 3, it provided a means of estimating their nocturnal time budgets. However, quantification of the birds' food intake by night proved very much more difficult. Because of the distances over which observations had to be made it was not possible to distinguish the capture of anything other than large worms; this occurred very infrequently. It was possible to count the birds' peck and pacing rates, again for five minute observation periods, and these are presented in table 6. There were no significant differences between the diurnal and nocturnal values of either foraging parameter during the same mid-winter period.

Table 6: Comparison of day and night peck and pacing rates (per 5 minutes) of territorial Grey Plover for the mid winter period (December - January).

DIURNAL PECK RATE MEAN(±S.E.)= 29.3± 1.92 (n=14)
t = 1.01 N.S.
NOCTURNAL PECK RATE MEAN(±S.E.)= 33.0± 3.13 (n=8)

DIURNAL PACING RATE MEAN(±S.E.)= 252.1± 14.1 (n=13)
t = 0.35 N.S.
NOCTURNAL PACING RATE MEAN(±S.E.)= 237.3± 37.3 (n=8)

DISCUSSION

The results obtained from observations on territorial Grey Plover indicate that if seasonal influences are removed, the calorific intake of the birds does not change from hour to hour during the period of exposure of their territories. This implies that any effects on the plovers' prey of daily patterns of drying and heating or cooling of the mud to air temperature, has no measurable effect on Grey Plover energy intake at Teesmouth. This may be a phenomenon which is peculiar to the Tees mudflats, in that only the lower tidal levels are used for long-term territories, and these areas suffer less from variation in environmental conditions.

Seasonal patterns in foraging behaviour are important complicating factors which should be allowed for in any examination of the affects of environmental conditions. The apparent seasonal pattern in calorific intake by day of Grey Plovers at Lindisfarne (Pienkowski 1980,1982) and that reported here (figure 2) seem at first sight to be in total disagreement. Pienkowski suggests a mid winter decrease in total intake, whereas I found a mid winter increase in the rate of calorific intake of the birds. This apparent discrepancy may be resolved if the temperatures on observation days are taken into consideration, for there is no statistically significant pattern in calorific intake on the Tees if temperature influences are removed. Clearly there will be a seasonal pattern in temperatures over a winter period. Furthermore, the seasonal pattern in the intake rate of large worms by Grey Plover on the

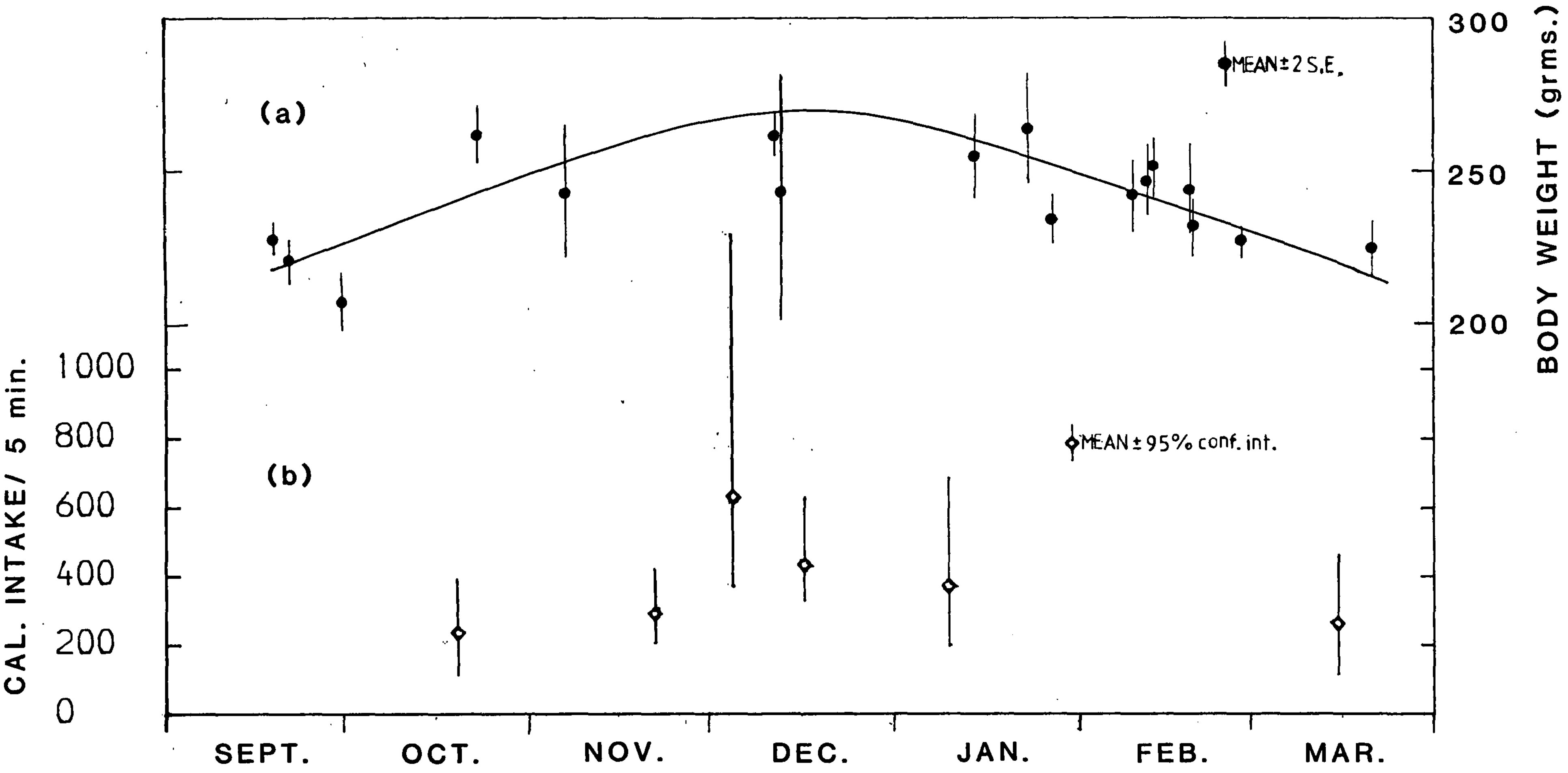


figure 4.2: seasonal weight pattern and calorific intake rate of Grey Plovers at Teesmouth.

Tees, both reported here and by Dugan (1981b) indicate that if there is a seasonal pattern of calorific intake (independent of environmental influences, and one whose statistical confirmation is masked by individual variation) this would take the form of an increase during the mid winter period.

If the relationship between date and total body weight is examined for the Tees Grey Plover (figure 2a, data for all Tees birds up to 1982), there is an obvious peak in mid winter. This corresponds to that found for Grey Plover elsewhere (Minton 1975). This body weight increase is due to a rapid build up of fat reserves in November and December (Davidson 1981); the rate of increase of fat reserves being highest in this period. This is directly correlated with the calorific intake of the Grey Plover, which is highest in the period from late November to mid December.

The birds achieve the increased rate of calorific intake in November and December by increasing the rate of intake of large worms (figure 1). It is not achieved by an increase in foraging time whilst the birds are on their territories (chapter 3), however the effects of foraging off-territory during the high water period cannot be discounted. The implications of this result are that if the Grey Plovers are seeking to increase their overall calorific intake to build up body condition, then they must change their ´optimal diet´ (Goss Custard 1977b) to include a higher proportion of the larger size classes of worms. This may be achieved by an increased use of different foraging locations as outlined in chapter 2. The results of Dugan et al.

(1981) support this idea, because in the late winter period when foraging time of territorial birds is maintained at above 90 percent of the time for which they are using their territories, they showed that these birds can still recover normal body condition after a period of severe weather.

Data from my nocturnal observations of Grey Plover show that foraging by night is an activity which is carried out at a similar rate and for a similar time to that found by day; and as such, may contribute a significant proportion of the birds calorific intake per 24 hours. Unfortunately it was not possible to ascertain whether nocturnal or diurnal foraging contributed most to the birds´ overall energy budget. This is a common problem due to the difficulties in watching foraging birds at night; previous workers have observed or assumed values for the intake rate at night for waders to be between 50 and 100 percent of that observed diurnally (Drinnan 1957, Davidson 1967, Heppleston 1971, Prater 1972, Hulscher 1974, 1976, Schramm 1978, Pienkowski 1980, Sutherland 1982). From the observations in chapter 3 and those presented here, I suggest that nocturnal and diurnal foraging in the Grey Plover be considered indistinguishable in terms of the birds´ calorific intake.

SUMMARY

Calorific intake rates of Grey Plovers on their territories show a significant (P=0.056) seasonal pattern if the tidal effects are held constant on each day. However if the effects of environmental temperature are also allowed for then there is no significant seasonal pattern apparent. This result is most likely due to individual variation masking any population trend in calorific intake rate, because a seasonal pattern of intake of large worms (greater than one bill length) is present even when tidal and temperature effects are removed. This seasonal trend in foraging parameters of Grey Plovers is characterised by a mid winter peak with lower values early an late in the season; a pattern which is closely followed by total body weight and lipid index of the birds at Teesmouth.

METABOLIC RATE MEASUREMENTS OF GREY PLOVER.

INTRODUCTION

Accurate energy budget estimates from time budget studies depend on accurate estimates of the energy cost of each activity. These are usually expressed as multiples of basal metabolic rate (BMR) (Wolf & Hainsworth 1971, Utter & LeFebvre 1973, Schartz & Zimmerman 1974, Ashkenazie & Safriel 1979, Maxson & Oring 1980, Puttick 1980). Measurement of the BMR for a particular species (rather than extrapolation of its value from an allometric equation) will therefore increase the accuracy of such an energy budget estimate.

When aspects of an animals metabolic rate are to be examined, it is important that the energy relationships are measured in a natural context. Results from studies of birds in the laboratory are difficult to interpret, because they represent the interaction of an animal with an artificial environment. Such studies have direct ecological relevance only when that artificial environment is similar to the animal's natural environment (Walsberg 1983).

An attempt was made to make this study more ecologically relevant by using wild caught birds held in an outdoor aviary at all times except when used for metabolic rate measurement.

Calculations in this chapter have been produced in Kcals for ease of comparison with previous work; for conversion to SI units, 1 calorie = 4.187 joules.

METHODS

Birds were caught at Teesmouth using cannon nets, and their weight and biometrics measured soon after capture. They were then held (under licence from the Nature Conservancy Council) in an outdoor aviary. In captivity the birds were not provided with food but had an ample fresh water supply. Their total body weight was measured at intervals throughout the period of captivity, and the birds were released back into the wild after the period of experimentation.

Measurements of the birds´ metabolism were made with a Kipp and Zonen diaferometer (Romijn & Lokhorst 1961, Westerterp 1973) using the apparatus shown in figure 1. The metabolic rate of the bird is estimated from concurrent measurement of carbon dioxide output and oxygen uptake in an open-flow system. Changes in ambient carbon dioxide and oxygen concentrations are monitored by periodic reference to ´normal´ air.

The bird was placed in a respiration chamber which itself was inside a constant temperature cabinet. The environmental temperature at which the birds´ metabolism was measured could be changed several times during a four hour session.

Birds were immediately made familiar with the apparatus and measurement proceedure, but a period of two to three days elapsed before results were collected. A bird was placed into the metabolism chamber and left at constant temperature for one hour before the start of a session. When the temperature at which the birds metabolism was measured was changed, a further one hour was allowed to elapse before measurements were attempted. These

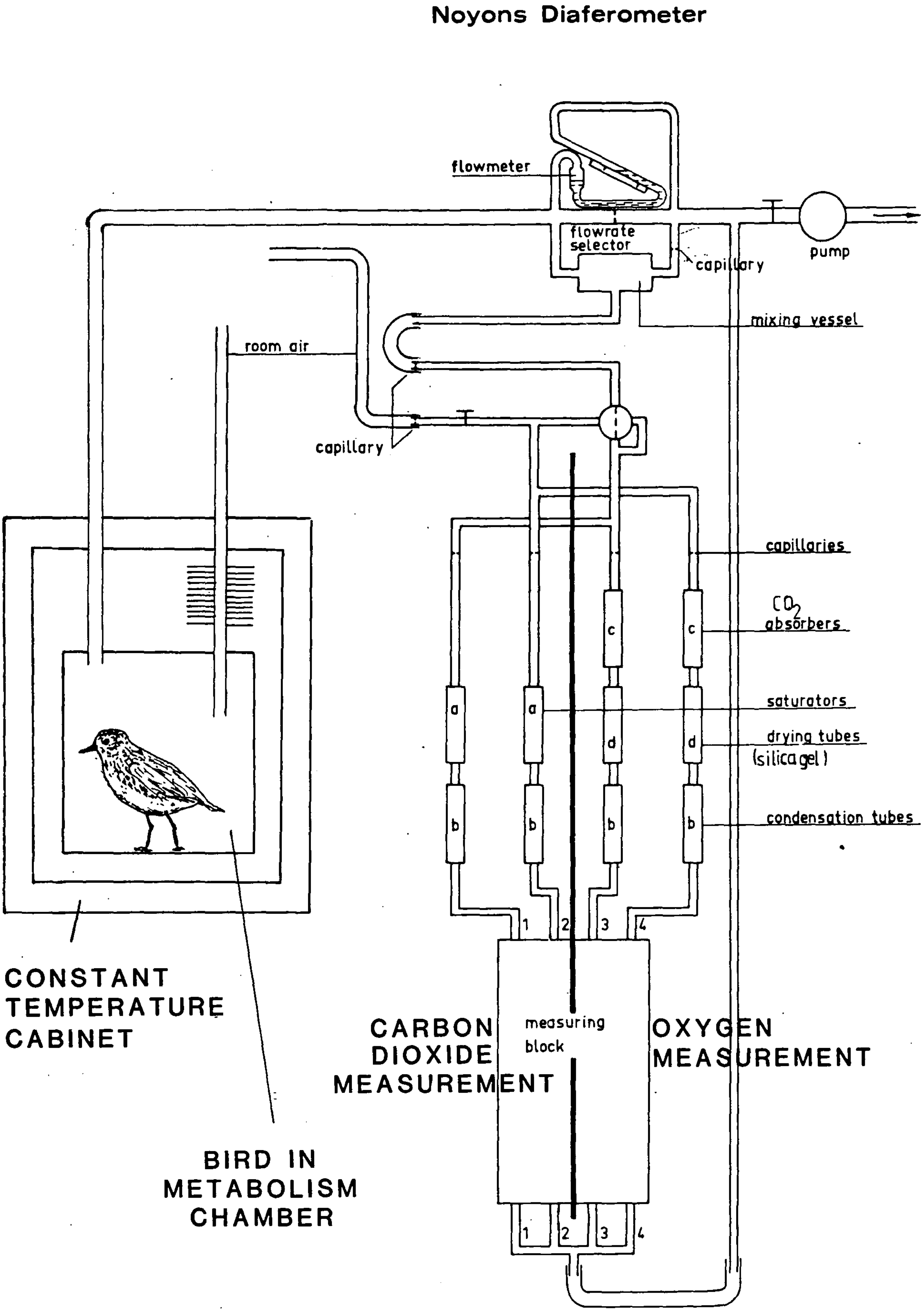


figure 5.1: metabolic rate measurement apparatus.

timings were deduced from a preliminary study of the time needed for a steady state of metabolic rate to be achieved.

The apparatus allowed simultaneous monitoring of oxygen uptake and carbon dioxide output of a bird. This has the advantage of being able to directly measure the respiratory quotient (RQ) of a bird, and so give an indication of the substrate being metabolised. In many analyses oxygen uptake only has been measured and an assumption made about the probable RQ.

My measurement of basal level metabolic rates refer to a quiescent bird in a post absorptive state, measured during the day at a temperature in its thermoneutral zone. Such conditions, described by King (1974), lead to a measurement of a fasting metabolic rate (FMR), which includes energy expenditure over and above that measured for a bird resting without food at night in a thermoneutral environment - the basal metabolic rate (BMR) (the difference is probably about 25%). Measurement of the birds' metabolic rate at different temperatures was undertaken to determine the level of basal FMR, lower critical temperature (LCT), and the linear rate of increase in metabolic rate at temperatures below the thermoneutral range (figure 2). These values are used later to estimate the energy budget of Grey Plovers at Teesmouth during the winter months (chapter 6).

Calculations

The metabolic rate of a bird was calculated from the equations given below. Calibration of the diaferometer system was performed using a sample of air run through a separate measurement system.

figure 5.2: Theoretical metabolic rate temperature relationship for a 'typical' bird (Calder & King 1974).

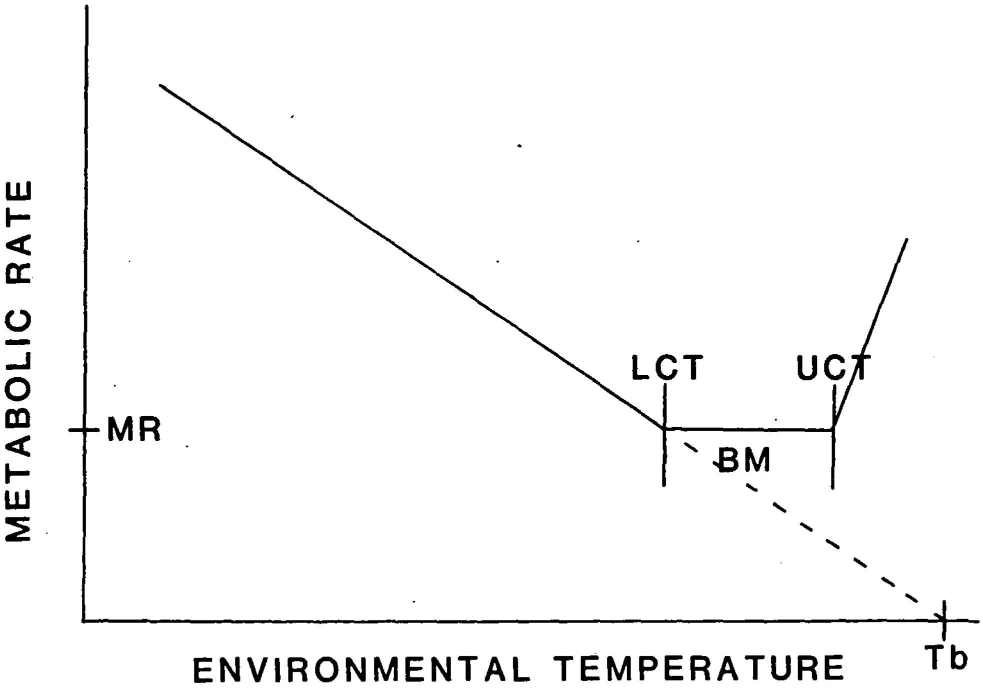
LCT - lower critical temperature

UCT - upper critical temperature

BM - zone of thermoneutrality

Tb - body temperature

MR - basal level of metabolic rate



Change in oxygen conc. (%) (#O_2) = O_2 reading x 0.00955

Change in carbon dioxide conc. (%) (#CO_2) =

(CO_2 reading x 0.00929) - 0.1 x #O_2

Air flow rate through apparatus = 0.8 litres per minute

RQ = #CO_2 / #O_2

Metabolic rate (Kcal/day) = (#O_2 x cc x 3.871 x 0.8 x 24 x 0.6)+

(#CO_2 x cc x 1.194 x 0.8 x 24 x 0.6)

(from Romijn & Lokhorst 1961)

cc - correction factor to reduce gas to standard temperature (0°C) and pressure (760 mm Hg).

RESULTS

Although it was intended that the results of this metabolism study should be applicable to the field situation, the use of wild birds posed a number of problems. But by not feeding them during the experiments, the influence of unknown quantities such as an unnatural food supply in captivity were removed. However, measurements of metabolic rates are usually made on animals which maintain a constant body weight, but during measurements on Grey Plovers, the birds were progressively losing weight (figure 3). Le Maho et al. (1981) showed that the basal metabolic rate of fasting geese decreased with decreasing body weight; a similar result was found by Westerterp (1976) for rats. Measurements were carried out to determine the nature of the metabolic rate - temperature relationship, and Grey Plovers of different weights were measured at different sets of temperatures. What is required is to produce a general relationship for a constant body weight individual. The raw data in figure 4 indicates that as expected, there is a general increase in metabolic rate with a decrease in temperature below LCT - estimated to be 17´C; and above LCT metabolic rate remains constant with increasing temperature. If regression lines are drawn through the points from each measurement session (during which the bird´s body weight remained relatively constant), there is close similarity amongst the gradients of the metabolic rate - temperature relationships.

The mean value for this gradient (h) is:

h (± 1 S.E.) = 1.34 (± 0.12) Kcal/day/´C

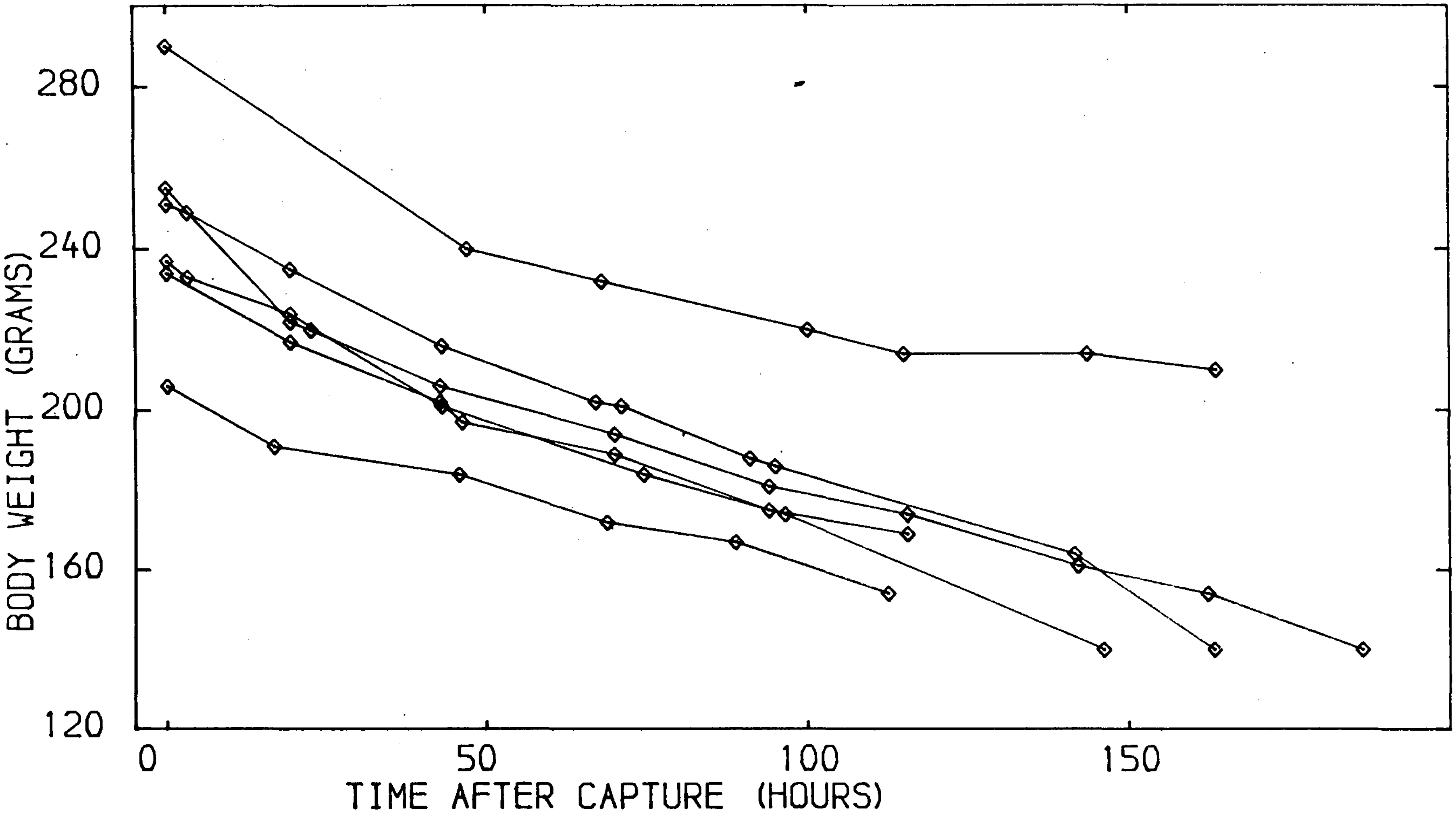


figure 5.3: weight loss of Grey Plovers in captivity.

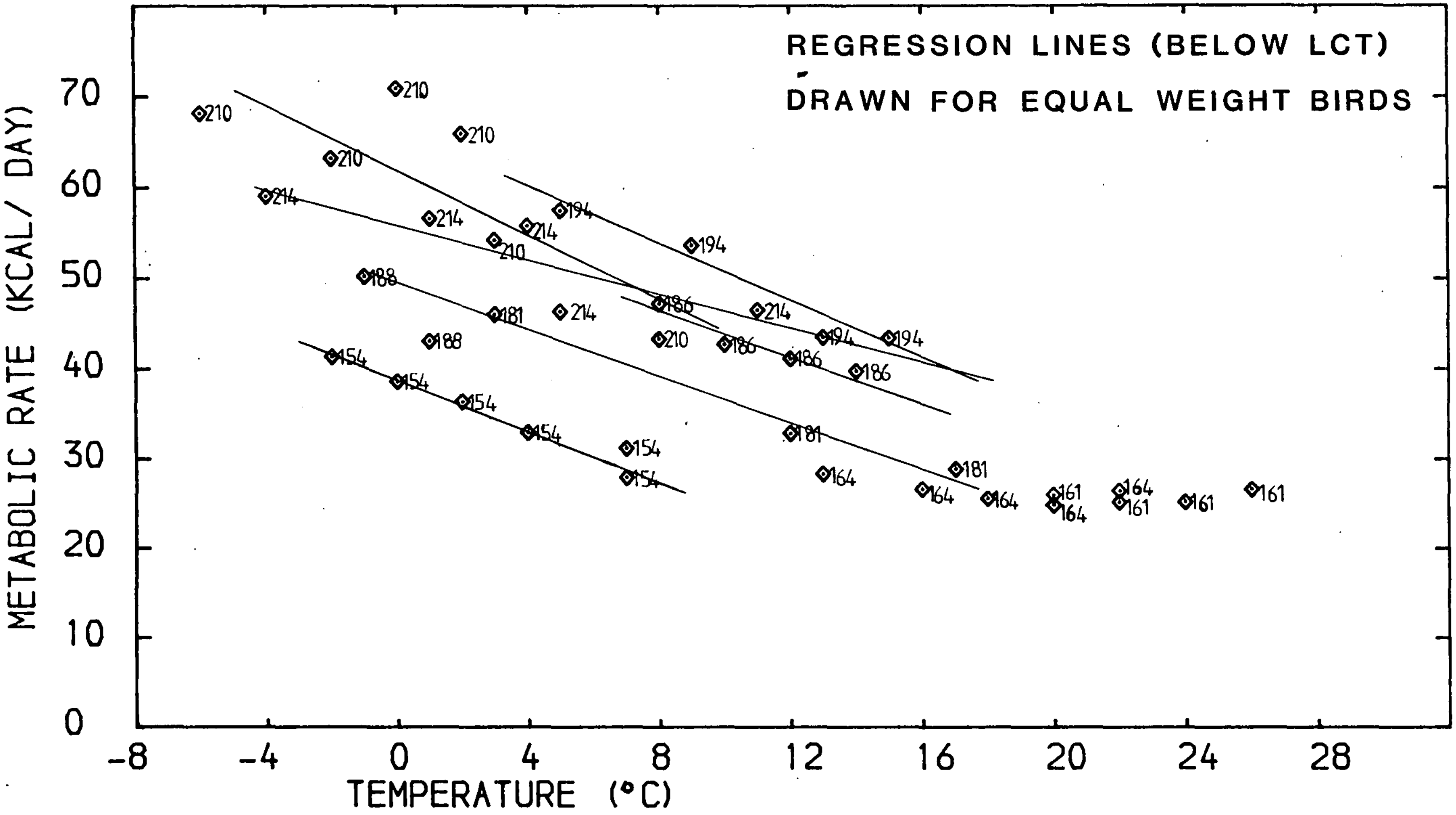


figure 5.4: metabolic rate/temperature relationship for GreyPlovers

(body weight at measurement is placed against each point).

The value of the metabolic rate at the LCT (basal level) was estimated from each of these regressions, and converted to a gram specific metabolic rate (to remove the influence of decreasing body weight leading to decreasing total metabolic rate).

The resulting basal FMR was 0.1662 (±0.014)S.E. Kcal/gram/day, and the mean value of the respiratory quotient throughout the measurements was 0.77 (±0.01)S.E..

There has been much discussion of the metabolic rate, weight relationship in birds (Lasiewski & Dawson 1967, Aschoff & Pohl 1970, King 1974, Calder & King 1974, Kendeigh et al. 1977), and the allometric equations for this and many other features of avian physiology appear to be well established. However in these papers it is frequently stated that ´body weight´ of a bird should be used in the equations. This is an ambiguous term as it could mean lean weight or total body weight (lean weight + fat). As lean weights and, more noticeably, total body weights of many birds in natural conditions exhibit marked seasonal fluctuations (Johnston & McFarlane 1967, Davidson 1981, Dugan et al. 1981) this must be taken into account when estimating a parameter from an allometric equation. The average lean weight for a particular season would seem to be the best measure for use in these equations, as this shows least seasonal fluctuation, and the fat load is metabolicaly inactive (Wallgren 1954).

The average lean weight of Grey Plovers at Teesmouth does not change significantly over the period November to March (Davidson 1981); the mean value (±1 S.E.) is 210.4 ± 4.0 grams (N.C. Davidson pers. comm.). Thus the basal FMR in the thermoneutral zone for Grey Plover at Teesmouth is 34.9 Kcal/day.

The value of BMR for a 210 gram bird from the general, non-passerine equation of Kendeigh et al. (1977) is 26.55 Kcal/day (this equation is very similar to that of Lasiewski & Dawson (1967) and Aschoff & Pohl (1970) but uses a greater range of species). My measured value of basal FMR is 1.32 x BMR, and falls in the range of results summarized by King (1974) of 1.2 - 1.8 x BMR for quiescent birds during the day in their thermoneutral zone.

A further comparison can be made between the general allometric equations and the results from this study. Lasiewski et al. (1967) give an equation for the heat transfer coefficient (h) ie. the rate of increase of metabolic rate per degree decrease in temperature below LCT:

$$h = 4.08 \times m^{-0.51}$$

h - heat transfer coefficient (cal/gram/hour/´C)

m - body mass in grams

For a Grey Plover of average lean mass 210 grams, the estimated value from this equation is therefore 1.35 Kcal/gram/day/´C. This compares very well with the value of 1.34 Kcal/gram/day/´C obtained in this study.

In October 1982 I succeeded in catching a moulting Grey Plover at Teesmouth. Measurements of its basal FMR in the thermoneutral zone gave the following results:

basal FMR = 30.76 Kcal/day; total weight = 165.0 grams.

Mean RQ = 0.68

Mean weight specific MR (± 1 S.E.) = 0.188 (±0.001) Kcal/day/grm

For a hypothetical 210 gram bird the value for the basal FMR of a moulting bird is 39.48 Kcal/day. This gives a minimal estimate for the energetic costs of moulting in the Grey Plover, which is an increase of 13% in basal FMR above what was measured for a non-moulting bird. This value is again very similar to the minimal cost of moulting summarized from numerous sources in King (1974), and more recently by Walsberg (1983).

DISCUSSION

This study of metabolic rates is different from many other comparable studies in that measurements were made on birds which had lived in their natural environment until a few days before measurements were made (most metabolic measurements have been made on birds which have been in captivity for some time, and hence may not be maintaining their natural pattern of body weight (see for example Goss-Custard et al. 1981)). The main problem with my study was that birds were starving and hence losing weight throughout the measurement period. This resulted in a decrease in metabolic rate with decreasing body weight. This must be due at least in part to the reduction of lean weight of an individual, but there may also be a slight reduction in body temperature with fasting (Westerterp 1976, Walsberg 1983).

The calculations involving weight specific basal FMR estimation from figure 4, may not be correct if the total body weights used were not lean weights. From the biometrics at capture, the lean weight of a Grey Plover can be estimated from the formula of Davidson (1983). Then using the rates of tissue loss by starving geese given by Le Maho et al. (1981), a minimal rate of decrease of lean weight and weight of fat can be estimated. This gives the result that after 50 - 100 hours in captivity, total lean weight equalled total body weight ie. the fat store was totally depleted. As all measurements of metabolic rate were possible only after such a period in captivity, it is assumed that the measured body weights of birds when used for metabolic rate determination, were very close to lean weights, and the capture stress problems described by Davidson (in press) would be minimised.

It was important that the respirometer could monitor both oxygen uptake and carbon dioxide output of fasting birds, so that RQ was known, since a simple measurement of oxygen uptake and an assumption of a constant RQ would be unsatisfactory. It is known that RQ decreases with time in fasting birds (Romijn & Lokhorst 1961, 1964).

After corrections were applied to the data, the results obtained for the Grey Plover were compared with that predicted from allometric equations. The metabolic rates measured were fasting and not basal rates, and therefore were expected to be higher than BMR estimates. In fact the measured FMR was well within the expected range of values for the increase above BMR, BMR being calculated from the equation of Kendeigh et al. (1977). The slope of the measured increase in metabolic rate with decreasing temperature below LCT again produced good agreement with the allometric equation of Lasiewski el al. (1967).

It therefore seems reasonable to asssume that Grey Plovers conform to the body weight - BMR non-passerine equation of Kendeigh et al. (1977). This, together with results summarized in Pinowski & Kendeigh (1977), suggest that for plovers at least, general allometric equations provide reasonable estimates of metabolic parameters. The very limited data I have for the sandpiper group indicate that this conclusion could be extended to waders in general.

SUMMARY

Measurements were made on the metabolic rates of quiescent, fasting Grey Plover during the day (fasting metabolic rate). After correction for body weight change through the period of measurement, the metabolism - temperature relationship was determined for this species.

Lower critical temperature was estimated to be 17°C; the basal FMR for a 210 gram (average lean weight) bird in its thermoneutral zone was 34.9 Kcal/day. The change in FMR below LCT was a linear increase at a rate of 1.34 Kcal/day/°C.

Measurement of basal FMR for a moulting bird gave the result of 39.48 Kcal/day, giving the estimate of a 13% increase in metabolic rate due to moult.

ENERGY BUDGETS OF TERRITORIAL GREY PLOVERS AT TEESMOUTH.

INTRODUCTION

Estimation of the energy budget of an animal in the field can be made directly by the heavy water (D_2O^{18}) technique (Utter & LeFebvre 1973, Hails & Bryant 1979, Weathers & Nagy 1980, Bryant & Westerterp 1983), or indirectly from a time budget study using multipliers of BMR to provide the caloric equivalents for each activity (Wolf & Hainsworth 1971, Schartz & Zimmerman 1974, Ashkenazie & Safriel 1979, Maxson & Oring 1980, Puttick 1980).

An attempt was made in the final year of my study to use the heavy water technique to measure the daily energy expenditure of a wild bird, but this failed because of difficulties of capturing and recapturing the same bird on successive days. For this reason the results presented in this chapter are confined to estimates based on time spent in each type of activity. The accuracy of this method partly depends on the accuracy of measurement (or estimate) of the caloric equivalents of each activity; in this study these are based on the laboratory measurements of metabolic rate of Grey Plovers presented in chapter 5.

An energy budget has been calculated for territorial Grey Plovers using Seal Sands as the sole foraging area. Because no difference could be found between nocturnal and diurnal time budgets and feeding rates of these birds, no distinction is made as to the time of day at which the foraging activity takes place, except that it must occur during the low water period.

Calculations in this chapter have been produced in Kcals for ease of comparison with previous work; for conversion to SI units, 1 calorie = 4.187 joules.

METHODS

Two methods were used to estimate the energy budget of the Grey Plover (Ashkenazie & Safriel 1979). Firstly the time budget of territorial birds was converted into an estimate of energy requirements by using estimates for the energetic costs of activities, and measurements of various aspects of the bird's metabolism. Secondly, total energy uptake was estimated from observations of feeding rates and calorific intake.

(i) Estimation of energy cost:

The daily energy cost of existence (DCE) is given by:

$$DCE = DCPT + DCM$$

where DCPT is the daily cost of production and thermoregulation, and DCM is the daily energy cost of maintenance plus other activities. DCPT is equivalent to the fasting metabolic rate (FMR) (King 1974) of the bird at a particular temperature (measured in chapter 5) minus the energetic cost of maintenance. The energetic cost of maintenance is taken as the basal level of FMR, and is higher than the basal metabolic rate (BMR), because it is measured on a quiescent bird in its thermoneutral temperature range (King 1974). The BMR of a Grey Plover can be estimated from the non-passerine equation of Kendeigh et al. (1977):

$$BMR = 0.5224 \times W^{0.7347} \quad \text{(Kcal/24 hours)}$$

where W is the bird's weight in grams.

The value of DCPT equals (FMR - basal level of FMR); however this value does not include a correction for body weight changes, as discussed later. A further modification is required when time spent in flight is considered. Since flight produces enough heat to maintain body temperature (Berger & Hart 1974), expenditure on thermoregulation should not be included; the correct equation therefore is:

DCPT = (FMR - basal FMR)(1 - (flight time in hours/24))

DCM is obtained by totalling the energy costs of all activity types, three levels of activity being recognised: roosting, flight and non-flight activity (Utter & LeFebvre 1973). The daily energy costs of each activity category were estimated from the following functions, each multiplied by the proportion of that activity in each 24 hours (this was obtained from the time budget study, chapter 3).

(a) Daily energy cost of roosting (DECR):

DECR = basal FMR x hrs. roosting/24 (Kcal/day)

(b) Daily energy cost of flight (DECF):

DECF = 12 x BMR x hrs. flying/24 (Kcal/day)

(King 1974, Ashkenazie & Safriel 1979)

(c) Daily energy cost of non-flight activity (DECNFA): (includes foraging preening and aggression)

DECNFA = 0.239 x BMR(1.94 - 0.021 x T) x

hrs. non-flight activity/24 (Kcal/day)

where T is the ambient temperature (Ashkenazie & Safriel 1979).

(ii) Estimation of energy uptake:

The daily energy uptake DEU was calculated from:

DEU = Average calorific intake per five minutes (ACI) x
No. minutes foraging (NMF)/5

Since most birds assimilate only 80-90 percent of the energy content of the food they ingest (Ashkenazie & Safriel 1979, Evans et al. 1979) this value for DEU needs a correction factor:

DEU = 0.85 x ACI x NMF/5

The average number of minutes spent per day each month, is calculated from the time budget information for the five hour low water observation period, plus an estimate for the foraging time during tidal ebb and flow across Seal Sands. This involves making two assumptions about Grey Plover time budgets; firstly, that the time spent foraging outside my low water observation period (ie. approx. three hours per tide) does not change seasonally; and secondly, that territorial birds do not forage during the high water period. Limited observations on the Tees birds suggest that these assumptions are reasonable, except when weather condition deteriorate (Davidson 1980).

RESULTS AND DISCUSSION

The average daily energy budgets of Grey Plover in each month at Teesmouth can be calculated using the following values for metabolic rates:

basal FMR (chapter 5) = 34.9 Kcal/day

BMR (Kendeigh et al. 1977) = 26.55 Kcal/day

and the metabolism and time budget data summarized in appendix 4. The daily energy requirements and energy intake in each month are summarized in tables 1 and 2, and it is clear that only in the month of December did estimated intake exceed expenditure. As mentioned earlier, this energy budget is calculated for a bird maintaining a constant body weight. From chapter 4 the seasonal pattern of body weight of Grey Plovers at Teesmouth was characterised as a steady increase to a peak in late December, followed by a steady decrease to the end of March. Therefore birds must be achieving a positive energy balance in the months of October to December, but a negative energy balance in January to March. The average increase represents storage of 0.62 grams of fat per day, implying an extra energy requirement of 5.59 Kcals/day in October to December.

The potential errors induced by the various terms in the energy budget equations can be investigated using sensitivity analysis (see, e.g. Furness 1978). This calculates the percentage change in the final result caused by a one percent change in the value of each input parameter. Those parameters with large sensitivity values will be most important in determining the precision of the final results.

Table 1: Energy requirements (DCE) of Grey Plovers at Teesmouth (Kcals/day)

MONTH	FMR (1)	COST OF THERMOREG. (DCPT)	COST OF ROOSTING (DECR)	COST OF FLYING (DECF)	COST OF NON-FLIGHT ACTIVITY (DECNFA)	TOTAL ENERGY REQ. (DCE)
OCT	45.49	9.97	10.90	18.59	6.98	46.44
NOV	47.36	11.73	11.11	18.59	7.03	48.46
DEC	52.99	16.98	10.83	19.65	7.44	54.90
JAN	51.25	15.36	10.86	19.38	7.33	52.93
FEB	52.32	16.38	10.85	19.12	7.41	53.76
MAR	48.70	12.97	10.85	19.12	7.18	50.12

(1) calculated from the average monthly temperatures and the FMR - temperature relationship from chapter 5.

Table 2: Energy uptake (DEU) of Grey Plover at Teesmouth.

MONTH	CAL. INTAKE PER 5 MINS. (cal)	NO. MINS. SPENT FORAGING PER 24 HRS.	DEU (Kcal/day)
OCT	235.9	780	31.29
NOV	292.0	780	38.72
DEC	424.1	792	57.11
JAN	371.7	798	50.43
FEB	371.7	798	50.43
MAR	264.1	804	36.09

Table 3: Analysis of energy budget parameters: sensitivity is the percentage change in the final result due to a 1% change in input parameter value. Data for October only.

PARAMETER	MEAN	SENSITIVITY
(a) Energy expenditure equation:		
lean weight	210.4	0.24
basal FMR/gram weight	0.1662	0.26
environmental temperature	9.1	0.26
heat transfer coefficient	1.34	0.15
no. hours roosting	7.5	0.26
no. hours flying	1.4	0.39
no. hours non-flight activity	15.1	0.15
multiplicator - cost flight	12.0	0.39
multiplicator - cost non-flight activity	0.418	0.15
multiplicator - BMR	0.5224	0.54
exponent - BMR	0.7347	2.20
(b) Energy uptake equation:		
assimilation efficiency	0.85	0.97
calorific intake/5 mins.	235.9	0.97
no. feeding minutes/day	780.0	0.97

The results of such an analysis are presented in table 3, using each parameter of the energy expenditure and uptake equations. The energy expenditure equation (DCE) is affected most by a change in the estimate of BMR. However the allometric equation for this estimate has been established by a number of authors (Lasiewski & Dawson 1967, Aschoff & Pohl 1970, Kendeigh et al. 1977), all obtaining broadly similar results. The parameters which have the next largest influence on the precision of the energy expenditure estimate is the caloric equivalent of, and the time spent in, flight activity. The time spent flying by territorial birds is only a minor part of their total activity; but the estimate for the caloric equivalent of flight activity is a simplified mean value (Schartz & Zimmerman 1971, Berger & Hart 1974 and Kendeigh et al. 1977). In reality the energetic cost of flight activity has no simple relationship with BMR (Hails 1979). The rest of the parameters in the energy expenditure equation have low sensitivity values and therefore have a minor effect on its precision.

The sensitivity values for each parameter in the daily energy uptake equation (DEU) are all the same because it is a simple multiplicative equation, but the parameter which shows greatest variation within a month is the calorific intake rate. The assimilation efficiency is a relatively constant value at between 0.8 and 0.9, and the number of minutes spent foraging per day during the low water observation period, is maintained at a constantly high value. This and previous studies (Dugan 1981b, Townshend 1982) have shown that the calorific intake rates of

Grey Plovers are extremely variable. The monthly average calorific intake rates are used in the energy budget calculations, and some insight into the effects of this parameter can be gained by recalculating the DEU using the upper 95% confidence limit of the mean monthly calorific intake rates:

MONTH	CAL. INTAKE/5 MINS. (UPPER 95% CONF. LIM.)	NEW ESTIMATE OF DEU (Kcal/day)	DCE FROM TABLE 1 (Kcal/day)
OCT	395.91	52.50	46.44
NOV	405.32	53.75	48.46
DEC	632.32	85.14	54.90
JAN	633.72	85.97	52.93
FEB	633.72	85.97	53.76
MAR	443.81	60.66	50.12

Using these values for the calorific intake rate can adequately balance the Grey Plover energy budget throughout the season, and produce the excess of intake over expenditure needed early in the season to model the natural situation.

Increasing the percent time foraging per 24 hours to that observed during the low water observation period produces a 15-17% increase in DEU which is insufficient to balance the overall energy budget.

The calculated monthly values for DCE of territorial Grey Plovers are for birds under average conditions. There are many factors which have not been taken into account in this simple model. Whitlock (1979) gives some data for additional factors which will affect the energy budgets of birds in their natural environment. He found that windspeeds of 9 m/sec produced an increase of 1.23 times in the metabolic rate of Oystercatchers

(Haematopus ostralegus). Windy conditions will therefore increase the metabolic requirement of Grey Plovers at Teesmouth, but the costs may be overcome by seeking shelter in creeks and by seeking shelter within a flock of birds at a roost. (Both strategies are used by Grey Plovers, see e.g. Dugan 1981b.) Whitlock predicts that under conditions of a 9 m/sec wind, Oystercatchers could save between 14 and 26 percent of the predicted energy cost at that windspeed, by seeking a sheltered roost with other individuals.

Thus a more accurate model of Grey Plover energy budgets would need to include a component for windspeed, as this both increases energy expenditure (Whitlock 1979) and may reduce foraging time (Dugan 1981b). However such a model would also require more detailed time budget observations to take account of the various micro-climates used by the birds in different weather conditions.

One further comparison is worth making, namely, between the calculated DCEs and the allometric equation for total energy expenditure for a free living bird given by Walsberg (1983); for a 210 gram Grey Plover it is estimated as 80.08 Kcal/day (from the equation for all birds other than aerial feeders). This is an extremely high value when compared to the DCEs in table 1, but as I have subsequently made clear, the average monthly DCEs are minimum values. It is also possible that the foraging strategy used by plovers is much less energy demanding compared to those of other bird species, in that the sit-and-wait strategy of plovers should be energetically less expensive than the active foraging of sandpipers.

SUMMARY

Using assumptions from the time budget study of chapter 3, that no distinction can be made between nocturnal and diurnal time budgets and foraging behaviour, I have produced a time budget estimate for Grey Plovers using Seal Sands on two low water periods per 24 hours.

A simple model to calculate the energetic costs of each category of Grey Plover activity (flying, roosting and non-flight activity) produced a minimal estimate for the average daily energy expenditure of territorial birds in the months in which they are present at Teesmouth. Average monthly calorific intake rates were also calculated using time budget information on the mean time per day spent foraging.

Using the calculated average daily energy expenditures and intakes, and with knowledge of the pattern of total body weight change at Teesmouth, a simple energy budget model for Grey Plovers can be constructed. Results of a sensitivity analysis suggest that this energy budget can adequately model the natural situation if higher than average calorific intake rates are assumed.

FINAL CONCLUSIONS.

The aim of this study was to provide an answer to two important questions which arose out of previous attempts to balance the energy budgets of foraging plovers (Pienkowski 1980, Dugan 1981b).

Firstly, are the basal metabolic rates of these birds less than those predicted from an equation relating metabolic rate to body weight? Measurements of the metabolic rates of Grey Plovers provided the answer, as well as providing measured (rather than estimated) metabolic parameters for use in an energy budget calculation. The measured fasting metabolic rates (FMRs) for this species indicated that allometric equations provide reasonable estimates of a number of metabolic parameters (including BMR), and therefore that the metabolic rates used in previous calculations of energy budgets were correct.

The second question was related to the relative importance of nocturnal and diurnal foraging to these birds. To answer this, a number of simple observations had to be carried out before a realistic comparison could be made. The radio telemetry study at Teesmouth revealed that all Grey Plovers regularly foraged both by day and night; and that, more importantly, territorial birds used their observed diurnal territory at night. This meant that diurnal observations on a territorial individual were directly comparable with nocturnal observations, as the same individual was involved. (With a lack of any visual individual identification usable both at night and during the day, this was an important factor to determine.) Time budget information on territorial individuals revealed that Grey Plovers spent an extremely high percentage of time (during the five hours around low water) foraging, both by day, and also by night. In fact there was no statistical difference apparent between nocturnal and diurnal time budgets of territorial birds. Furthermore, limited data on peck and pacing rates did not suggest any difference between diurnal and nocturnal intake.

Answering these two questions provided data for a revised but simple energy budget for the territorial Grey Plovers at Teesmouth. Averaged data produced an estimate for the minimum daily energy requirement of a Grey Plover to be in the region of 2 times their basal metabolic rate - an estimate lower than that for other bird species (Utter & LeFebvre 1973, Ebbing et al. 1975, Hails & Bryant 1979, Drent & Daan 1980).

Comparison of the Grey Plover energy budget from this study with those of other species supports the conclusion of Walsberg (1983) that the survival of an animal in its natural environment appears to be governed by the problem of energy acquisition rather than that of energy expenditure. It is known that the calorific intake rates of Grey Plovers are extremely variable. However, why it should be that average intake rates produce estimates of overall energy intake that are lower than those needed to balance the birds average energy expenditure is a major problem. This could be solved by postulating an even higher percent time allocation to foraging, and/or higher calorific intake rates. The foraging time budget estimate for the time of tidal ebb and flow across the mudflats of Seal Sands is the most inaccurate, and requires further work; it is possible that there is a seasonal pattern in the use of this time period (Pienkowski 1973, Knights 1979).

With regards to the Grey Plover, there is also the possibility that calorific intake rates observed during the day are lower than those at night, and taking an average based on the diurnal estimate may produce an artificially low value. Obtaining information on calorific intake rates of birds during the night is an extremely difficult task, and one which suffers from the limitations of the night vision equipment. It has been suggested that Grey Plovers may use an alternative food source at night (Dugan 1981a), but for the majority of territorial birds on Seal Sands this cannot be the case, as they use the same low water feeding territory both by day and by night. However this does not exclude the possibility of increased invertebrate activity and therefore prey availability for the birds during the night.

The major problem with all time-energy budget studies is the extensive use of averaged data, with no account being taken of changes in activity and activity costs under different environmental conditions. This problem was touched upon briefly in this study by looking at the responses of territorial birds on different dates, and by examining the apparent seasonal pattern of foraging parameters for the influence of temperature. Predictive foraging models of Evans (1976) and Norberg (1977), and data on House Martins (Delichon urbica) from Bryant & Westerterp (1980) all suggest that there is a positive relationship between food abundance and foraging effort; therefore on days of low prey availability the birds' average daily energy expenditure should be reduced. Examining the costs of the various activities in the Grey Plover energy budget (chapter 6, table 1) indicates that flight is the most energy expensive activity, and therefore if reduced, would produce the most effective reduction in the overall daily energy requirement. This raises the possibility that Grey Plovers reduce the distance they fly to a high water roost, or remove flight totally from the low water time budget, during periods of extreme environmental conditions. There are other possible strategies open to Grey Plovers in addition to reducing energy expenditure in extreme conditions. They could try to increase their overall calorific intake by exploiting a different food source (Dugan 1981a); or they could remain in their 'normal' foraging location and rely on stored energy reserves to balance their energy budget. Each of these three strategies may be favoured at different times of year, depending on whether the birds were trying to increase or decrease body condition (Davidson 1981).

This study of Grey Plovers at Teesmouth highlights some of the problems of a time-energy budget study, and indicates the direction for future research in the absence of a more direct measure of daily energy requirements, such as can theoretically be obtained by the heavy water technique. Future investigations must provide information on the nocturnal situation, as well as more detail on diurnal intake rates in response to seasonal and environmental influences such as temperature, windspeed and humidity. Subsequent energy budget calculations will need to be averaged over much smaller time intervals, and require detailed information on the birds overall time budgets, taking into account the micro-climates selected under particular environmental conditions.

REFERENCES.

Alexander, W.B., B.A. Southgate and R. Bassingdale 1935 Survey of the River Tees, Part 2 - The Estuary - Chemical and Biological. Dept. of Science an Industrial Research, Water Pollution Technical Paper No. 5, pp. 171

Altmann, J. 1974 Observational study of behaviour: sampling methods. Behaviour 49: 227-265

Aschoff, J. and H. Pohl 1970 Rhythmic variations in energy metabolism. Fed. Proc. 29: 1541-1552

Ashkenazie, S. and U.N. Safriel 1979 Time-energy budget of the Semipalmated Sandpiper Calidris pusilla at Barrow, Alaska. Ecology 60: 783-799

Barnard, C.J., D.B.A. Thompson and H.Stephens 1982 Time budgets, feeding efficiency and flock dynamics in mixed species flocks of Lapwings, Golden Plovers and Gulls. Behaviour 80: 44-69

Berger, M. and J.S. Hart 1974 Physiology and energetics of flight. In Farner, D.S., J.R. King and K.C. Parkes (Eds.) Avian Biology, Vol. 4, pp 415-477. Academic Press, New York

Brander, R.B. 1968 A radio-package harness for game birds. J. Wildl. Manage. 32: 630-632

Branson, N.J.B.A. and C.D.T. Minton 1976 Moult, measurements and migration of the Grey Plover. Bird Study 23: 257-266

Bryant, D.M. and K.R. Westerterp 1980 The energy budget of the house martin (Delichon urbica). Ardea 68: 91-102

Bryant, D.M. and K.R. Westerterp 1983 Short-term variability in energy turnover by breeding House Martins Delichon urbica a study using doubly-labelled water (D_2O^{18}). J. Anim. Ecol. 52: 525-543

Calder, W.A. and J.R. King 1974 Thermal and caloric relations of birds. In Farner, D.S., J.R. King and K.C. Parkes (Eds.) Avian Biology, Vol. 4, pp. 259-413. Academic Press, New York

Chatfield, C. and A.J. Collins 1980 Introduction to multivariate analysis. Chapman and Hall, London

Cooley, W.W. and P.R. Lohnes 1971 Multivariate data analysis. John Wiley & Sons, New York

Davidson, N.C. 1980 Seal Sands Feasability Study. Unpbl. report to Cleveland County Council and the Nature Conservancy Council. pp. 144

Davidson, N.C. 1981 Seasonal changes in nutritional condition of shorebirds during the non-breeding season. Ph.D. thesis, University of Durham

Davidson, N.C. 1983 Formulae for estimating the lean weight and fat reserves of live shorebirds. Ringing & Migration 4: 159-166

Davidson, N.C. (in press) Changes in the condition of Dunlins and Knots during short-term captivity. Can. J. Zool.

Davidson, P.E. 1967 A study of the Oystercatcher (Haematopus ostralegus L.) in relation to the fishery for Cockles (Cardium edule L.) in the Burry Inlet, South Wales. Fishery Invest., Lond. (Ser. II) 25: 1-28

Davis, N.B. 1976 Food, flocking and territorial behaviour in the Pied Wagtail Motacilla alba yarrellii, in winter. J Anim. Ecol. 45: 235-254

Drent, R.M. and S. Daan 1980 The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252

Drinnan, R.E. 1957 The winter feeding of the Oystercatcher (Haematopus ostralegus) on the edible cockle (Cardium edule). J. Anim. Ecol. 26: 441-469

Dugan, P.J. 1981a The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. In Jones, N.V. and W.J. Wolff (Eds.) Feeding and survival strategies of estuarine organisms, pp. 251-260. Plenum publishing Co. Ltd., London

Dugan, P.J. 1981b Seasonal movements of shorebirds in relation to prey availability and spacing behaviour. Ph.D. thesis, University of Durham

Dugan, P.J. 1982 Seasonal changes in patch use by a territorial Grey Plover: weather-dependent adjustments in foraging behaviour. J. Anim. Ecol. 51: 849-857

Dugan, P.J., P.R. Evans, L.R. Goodyer and N.C. Davidson 1981 Winter fat reserves in shorebirds: disturbance of regulated levels by severe weather conditions. Ibis 123: 359-363

Ebbinge, B., K. Canters and R.M. Drent 1975 Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. Wildfowl 26: 5-19

Evans, P.R. 1976 Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. Ardea 64: 117-139

Evans, P.R., D.M. Herdson, P.J. Knights and M.W. Pienkowski 1979 Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. I. Shorebird diets, invertebrate densities, and the impact of predation on invertebrates. Oecologia 41: 183-206

Frey, D.F. and R.A. Pimentel 1978 Principal component analysis and factor analysis. In Colgan, P.W. (Ed.) Quantitative ethology, pp. 219-245 John Wiley, New York

Furness, R.W. 1978 Energy requirements of seabird communities: a bio-energetics model. J. Anim. Ecol. 47: 39-53

Gessaman, J.A. 1973 Ecological energetics of homeotherms. Logan: Utah State University Press

Ginn, H.B. and D.S. Melville 1983 Moult in birds. British Trust for Ornithology, Field Guide No. 19. B.T.O. Tring

Goss-Custard, J.D. 1977a The energetics of prey selection by Redshank (Tringa totanus L.) in relation to prey density. J. Anim. Ecol. 46: 1-19

Goss-Custard, J.D. 1977b Optimal foraging and size selection of worms by Redshank, (Tringa totanus) in the field. Anim. Behav. 25: 10-29

Goss-Custard, J.D., R.E. Jones and L. Harrison 1981 Weights of Knot in captivity. Wader Study Group Bull. 32: 34-35

Gray, J.S. 1976 The fauna of the polluted River Tees estuary. Estuarine and Coastal Marine Science 4: 653-676

Hails, C.J. 1979 A comparison of flight energetics in hirundines and other birds. Comp. Biochem. Physiol. 63: 581-585

Hails, C.J. and D.M. Bryant 1979 Reproductive energetics of a free-living bird. J. Anim. Ecol. 48: 471-482

Heezen, K.L. and J.R. Tester 1967 Evaluation of radio-tracking by triangulation with special reference to deer movements. J. Wildl. Manage. 31: 124-141

Heppleston, P.B. 1971 The feeding ecology of Oystercatchers (Haematopus ostralegus L.) in winter in northern Scotland. J. Anim. Ecol. 40: 651-672

Hull, C.H. and N.H. Nie 1981 SPSS: Statistical package for the social sciences, update 7-9. New proceedures and facilities for releases 7-9. McGraw-Hill, New York

Hulscher, J.B. 1974 An experimental study of the food intake of the Oystercatcher Heamatopus ostralegus L. in captivity during the summer. Ardea 62: 155-171

Hulscher, J.B. 1976 Localisation of cockles (Cardium edule L.) by the Oystercatcher (Haematopus ostralegus L.) in darkness and daylight. Ardea 64: 292-310

Huntingford, F.A. 1976 An investigation of the territorial behaviour of the Three-spined Stickleback (Gasterosteus aculeatus) using principal components analysis. Anim. Behav. 24: 822-834

Jacobsen, N.K. and A.D. Wiggins 1982 Temporal and procedural influences on activity estimated by time-sampling. J. Wildl. Manage. 46: 313-324

Johnston, D.W. and R.W. McFarlane 1967 Migration and bioenergetics of flight in the Pacific Golden Plover. Condor 69: 156-168

Kersten, M., T. Piersma, C. Smit and P. Zegers 1983 Wader migration along the Atlantic coast of Morocco, March 1981; report of the Netherlands Morocco Expedition 1981. Research Institute for Nature Management, Texel, The Netherlands

Kendeigh, S.C., V.R. Dolnik and V.M. Gavrilov 1977 In Pinowski, J. and S.C. Kendeigh (Eds.) Granivorous Birds in Ecosystems, pp. 127-204. Cambridge Uni. Press, London

Knights, P.J. 1979 Effects of changes in land use on some animal populations. Ph.D. thesis, University of Durham

King, J.R. 1974 Seasonal allocation of time and energy resources in birds. In Paynter, R.A. (Ed.) Avian Energetics, pp. 4-85. Pub. of Nuttall Ornithological Club No. 15

Lasiewski, R.C., W.W. Weathers and M.H. Bernstein 1967 Physiological responses of the Giant Hummingbird Patagona gigas. Comp. Biochem. Physiol. 23: 797-813

Lasiewski, R.C. and W.R. Dawson 1967 A re-examination of the relation between SMR and body weight in birds. Condor 69: 13-23

Le Maho, Y., H. Vu Van Kha, H. Koubi, G. Dewasmes, J. Girard, P. Ferre and M. Cagnard 1981 Body composition, energy expenditure, and plasma metabolites in long-term fasting geese. Am. J. Physiol. 241: E242-E354

Minton, C.D.T. 1975 Waders of the wash - Ringing and biometric studies. Contribution to Wash feasability study report

Macdonald, D.W., F.G. Ball and N.G. Hough 1979 The evaluation of home range size and configuration using radio tracking data. In Amlander C.J. and D.W. Macdonald (Eds.) A handbook on biotelemetry and radio tracking, pp. 405-424. Pergamon Press, Oxford

Maxson, S.J. and L.W. Oring 1980 Breeding season time and energy budgets of the polyandrous Spotted Sandpiper. Behaviour 74: 200-263

Myers, J.P., P.G. Connors and F.A. Pitelka 1979 Territoriality in non-breeding shorebirds. Studies in Avian Biology No. 2: 231-246

Myers, J.P., P.G. Connors and F.A. Pitelka 1981 Optimal territory size and the Sanderling: compromises in a variable environment. In Kamil, A.C. and T.D. Sargent (Eds.) Foraging behaviour - ecological, ethological, and psychological approaches, pp. 135-158. Garland series in ethology. New York

Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner and D.H. Bent 1975 SPSS: Statistical package for the social sciences. 2nd ed. McGraw-Hill, New York

Norberg, R.A. 1977 An ecological theory on foraging time and energetics and choice of optimal food searching method. J. Anim. Ecol. 46: 511-530

Pienkowski, M.W. 1973 Feeding activities of wading birds and Shelducks at Teesmouth and some possible effects of further loss of habitat. Unpublished report to Coastal Ecology Research Station, Institute of Terrestrial Ecology

Pienkowski, M.W. 1980 Aspects of the ecology and behaviour of Ringed and Grey Plovers, Charadrius hiaticula and Pluvialis squatarola. Ph.D. thesis, University of Durham

Pienkowski, M.W. 1982 Diet and energy intake of Grey and Ringed Plovers, Pluvialis squatarola and Charadrius hiaticula, in the non-breeding season. J. Zool., Lond. 197: 511-549

Pienkowski, M.W. 1983a The effects of environmental conditions on feeding rates and prey selection of shore plovers. Ornis Scand. 14: 227-238

Pienkowski, M.W. 1983b Changes in the foraging pattern of plovers in relation to environmental factors. Anim. Behav. 31: 244-264

Prater, A.J. 1972 The ecology of Morecambe Bay. The food and feeding habits of Knot (Calidris canutus L.) in Morecambe Bay. J. Appl. Ecol. 9: 179-194

Puttick, G.M. 1979 Foraging behaviour and activity budgets of Curlew Sandpipers. Ardea 67: 111-122

Puttick, G.M. 1980 Energy budgets of Curlew Sandpipers at Langebaan Lagoon, South Africa. Estuarine and Coastal Marine Science 11: 207-215

Richardson, W.J. 1974 Multivariate approaches to forecasting day-to-day variations in the amount of bird migration. From proceedings of a conference on the biological aspects of the bird/aircraft collision problem. S.A. Gauthreaux, (Ed.) Clemson University, South Carolina, U.S.A.

Romijn, C. and W. Lokhorst 1961 Some aspects of energy metabolism in birds. Proc. 2nd. Symp. Energy Metabolism Wageningen: 49-58

Romijn, C. and W. Lokhorst 1964 Some aspects of poultry metabolism. Zentralblatt Vet. Med. 11: 297- 314

Schartz, R.L. and J.L. Zimmerman 1971 The time and energy budget of the male dickcissel (Spiza americana). Condor 73: 65-76

Schramm, M. 1978 The feeding ecology of Grey Plover on the Swartkops estuary. B.Sc. thesis, University of Port Elizabeth, South Africa

Sokal, P.R. and F.J. Rohlf 1969 Biometry. Freeman, San Francisco

Springer, J.T. 1979 Some sources of bias and sampling error in radio triangulation. J. Wildl. Manage. 43: 926-935

Storm, G.L. 1965 Movement and activities of foxes as determined by radio-tracking. J. Wildl. Manage. 29: 1-13

Sutherland, W.J. 1982 Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality. J. Anim. Ecol. 51: 491-501

Townshend, D.J. 1982 The use of intertidal habitats by shorebird populations, with special reference to Grey Plover (Pluvialis squatarola) and Curlew (Numenius arquata). Ph.D. thesis, University of Durham

Townshend, D.J., P.J. Dugan and M.W. Pienkowski 1984 The unsociable plover - use of intertidal areas by Grey Plovers. In Evans, P.R., J.D. Goss-Custard and W.G. Hale (Eds.) Coastal Waders and Wildfowl in Winter. pp. 140-159. Cambridge Univ. Press

Utter, J.M. and E.A. LeFebvre 1973 Daily energy expenditure of Purple Martins (*Progne subis*) during the breeding season: estimates using D_2O^{18} and time budget method. Ecology 54: 597-604

Wallgren, H. 1954 Energy metabolism of two species of the genus Emberiza as correlated with distribution and migration. Acta Zoologica Fennica 84: 1-110

Walsberg, G.E. 1983 Avian ecological energetics. In Farner, D.S., J.R. King and K.C. Parkes (Eds.) Avian Biology, Vol. 7, pp. 161-220. Academic Press, New York

Weathers, W.W. and K.A. Nagy 1980 Simultaneous doubly labeled water ($^3HH^{18}O$) and time budget estimates of daily energy expenditure in *Phainopepla nitens.* Auk 97: 861-867

Westerterp, K. 1973 The energy budget of the nestling Starling *Sturnus vulgaris*, a field study. Ardea 61: 137-158

Westerterp, K. 1976 How rats economize; Energy loss in starvation. Doctoral dissertation, University of Groningen

Whitlock, R.J. 1979 The ecological significance of energy conservation during roosting for wading birds. B.A. thesis, University of Stirling

Williams, B.K. 1983 Some observations on the use of discriminant analysis in ecology. Ecology 64: 1283-1291

Wishart, R.A. and S.G. Sealy 1980 Late summer time budget and feeding behaviour of Marbled Godwits (Limosa fedoa) in southern Manitoba. Can. J. Zool. 58: 1277-1282

Wolf L.L. and F.R. Hainsworth 1971 Time and energy budgets of territorial hummingbirds. Ecology 52: 980-988

APPENDIX 1: Computer analysis programs.

(a) Part common to all programs:

```
       DIMENSION X(3567),Y(3567),KIND(464),KBD(464),KZ(15)
       DIMENSION
       ID(464),ND(464),COX(464),COY(464),ALT(464),KD(464)
       CALL FTNCMD(´ASSIGN 2=GPDATA81´,17)
       CALL FTNCMD(´ASSIGN 7=TEESBAY´,16)
       DATA  KZ(1),  KZ(2),  KZ(3),  KZ(4),  KZ(5),  KZ(6), KZ(7),
       KZ(8), KZ(9), KZ
       -(10),  KZ(11),  KZ(12), KZ(13), KZ(14), KZ(15)/0140, 0210,
       0245, 0310,
       -0320,  0504,  0520,  0610,  0620,  0735, 0845, 0925, 0955,
       1120, 1140/
       READ(2,500,END=10)(ID(IA),KBD(IA),KD(IA),ND(IA),COX(IA),COY
       -(IA),ALT(IA),KIND(IA),IA=1,464)
10     READ(7,300,END=15)  (X(I),Y(I),I=1,3567)
15     WRITE(6,600)
       READ(5,650) IID
       KY=0
       DO 30 JM=1,15
       IF (IID.EQ.KZ(JM)) KY=1
30     CONTINUE
       IF (KY.NE.1) WRITE(6,800)
       IF (KY.NE.1) GO TO 15
       WRITE(6,700)
       READ(5,750) IZ
       WRITE(6,850)
       READ(5,860) JG
       WRITE(6,870)
       READ(5,880) JH
       WRITE(6,890)
       READ(5,900) IY
       WRITE(6,910)
       READ(5,920) IW
       WRITE(6,930)
       READ(5,940) IFIG
       CALL PAPER(1)
       CALL PSPACE(0.1,0.89,0.4,1.0)
       CALL MAP(-33.0,2500.0,0.0,1986.0)
       CALL BORDER
       ====== BASIC MAP ROUTINE ======
       CALL PTPLOT(X,Y,6,419,-2)
       CALL PTPLOT(X,Y,420,731,-2)
       CALL PTPLOT(X,Y,732,1100,-2)
       CALL PTPLOT(X,Y,1101,1264,-2)
       CALL PTPLOT(X,Y,1265,1354,-2)
       CALL PTPLOT(X,Y,1355,1427,-2)
       CALL PTPLOT(X,Y,1428,1452,-2)
       CALL PTPLOT(X,Y,1453,1627,-2)
       CALL BROKEN(2,6,2,6)
       CALL PTPLOT(X,Y,1628,1681,-2)
       CALL PTPLOT(X,Y,1682,1777,-2)
       CALL PTPLOT(X,Y,1778,1924,-2)
```

```
      CALL PTPLOT(X,Y,1925,1991,-2)
      CALL PTPLOT(X,Y,1992,2015,-2)
      CALL PTPLOT(X,Y,2016,2044,-2)
      CALL PTPLOT(X,Y,2045,2335,-2)
      CALL PTPLOT(X,Y,2336,2565,-2)
      CALL PTPLOT(X,Y,2566,2753,-2)
      CALL PTPLOT(X,Y,2754,2980,-2)
      CALL PTPLOT(X,Y,2981,3188,-2)
      CALL PTPLOT(X,Y,3189,3336,-2)
      CALL PTPLOT(X,Y,3337,3418,-2)
      CALL PTPLOT(X,Y,3419,3459,-2)
      CALL PTPLOT(X,Y,3460,3495,-2)
      CALL PTPLOT(X,Y,3496,3567,-2)
      CALL FULL
      CALL MAP(0.0,250.0,0.0,194.0)
      ====== DATA POINT PLOTTING ======
      CALL CTRMAG(15)
      CALL CTRORI(3.0)
      CALL PLOTCS(240.0,175.0,´GREY PLOVER´,11)
      CALL CTRSET(2)
      CALL PLOTCS(-20.0,175.0,´FIGURE:´,7)
      CALL PLOTNI(-20.0,136.0,IFIG)
      CALL CTRSET(1)
      IF (IW.EQ.1) CALL REDPEN
      IF (IW.NE.1) CALL BROKEN(2,5,2,5)
      IF (IW.NE.1) CALL THICK(2)
      CALL POSITN(20.0,70.0)
      CALL CIRCLE(3.0)
      CALL BLKPEN
      CALL FULL
      CALL THICK(1)
      CALL POSITN(10.0,70.0)
      CALL CIRCLE(3.0)
      CALL ITALIC(1)
      CALL PLOTNI(230.0,160.0,IID)
      CALL PLOTCS(20.0,65.0,´ : DAY´,6)
      CALL PLOTCS(10.0,65.0,´ : NIGHT´,8)
      CALL ITALIC(0)
300   FORMAT(1X,2F7.1)
500   FORMAT(I4,I2,I2,2X,I1,4X,2F4.1,18X,F3.1,1X,I1)
600   FORMAT(´WHICH BIRD DO YOU WANT?!!  (4 DIGIT I.D.)´)
650   FORMAT(I4)
700   FORMAT(´DO YOU REQUIRE LOWTIDE HEIGHTS ´/
      -´PRINTED AT EACH POINT ?´/
      -´TYPE 1 FOR YES´)
750   FORMAT(I1)
800   FORMAT(´INVALID BIRD I.D.´)
850   FORMAT(´DO YOU WISH TO EXCLUDE OBSERVATIONS ´/
      -´WHICH OCCURRED AT GREATER THAN +-2HRS.  OF LOW WATER?  ´/
      -´TYPE 3 FOR NO ........  AND 2 FOR YES´)
860   FORMAT(I1)
870   FORMAT(´DATA POTENTIALLY FOR : JAN,FEB,MAR,APR & MAY, ´/
      -´AFTER WHICH MONTH DO YOU REQUIRE ANALYSIS TO STOP?  ´/
      -´TYPE TWO FIGURE DIGIT FOR MONTH, E.G.  01 FOR JAN..´)
```

```
880   FORMAT(I2)
890   FORMAT(´DO YOU WISH A LINE DRAWN BETWEEN OBSERVATIONS ´/
      -´ON THE SAME DAY OR NIGHT ?´/
      -´TYPE 1 FOR YES´)
900   FORMAT(I1)
910   FORMAT(´DO YOU WANT A COLOURED MAP ?´/
      -´TYPE 1 FOR YES´)
920   FORMAT(I1)
930   FORMAT(´WHAT IS THE FIGURE NUMBER?  I2´/)
940   FORMAT(I2)
```

(b) Part specific to GPCIRC:

```
      CALL CTRMAG(6)
      DO 200 JC=1,464
      IF (ID(JC).NE.IID) GO TO 200
      IF (KD(JC).GT.JH) GO TO 200
      IF (KIND(JC).EQ.JG) GO TO 200
      CALL BLKPEN
      CALL THICK(1)
      CALL FULL
      IF (IZ.EQ.1) CALL PLOTNF(COX(JC),COY(JC),ALT(JC),1)
      IF (ND(JC).EQ.1.AND.IW.EQ.1) CALL REDPEN
      IF (ND(JC).EQ.1.AND.IW.NE.1) CALL BROKEN(2,5,2,5)
      IF (ND(JC).EQ.1.AND.IW.NE.1) CALL THICK(2)
      CALL POSITN(COX(JC),COY(JC))
      CALL CIRCLE(3.0)
      IF (IY.NE.1) GO TO 200
      DO 195 JD=JC,464
      IF (JD.EQ.JC) GO TO 195
      IF (ID(JD).NE.IID) GO TO 195
      IF (KD(JD).GT.JH) GO TO 195
      IF (KIND(JD).EQ.JG) GO TO 195
      IF (KD(JC).EQ.KD(JD).AND.KBD(JC).EQ.
      -KBD(JD).AND.ND(JC).EQ.ND(JD)) GO TO 193
      GO TO 195
193   CALL POSITN(COX(JC),COY(JC))
      CALL JOIN(COX(JD),COY(JD))
195   CONTINUE
200   CONTINUE
      CALL FULL
      CALL BLKPEN
      CALL GREND
```

(c) Part specific to GPDATES:

```
      CALL CTRMAG(6)
      DO 200 JC=1,464
      IF (ID(JC).NE.IID) GO TO 200
      IF (KD(JC).GT.JH) GO TO 200
      IF (KIND(JC).EQ.JG) GO TO 200
      CALL BLKPEN
      CALL FULL
      IF (ND(JC).EQ.1) CALL REDPEN
      CALL POSITN(COX(JC),COY(JC))
      CALL CIRCLE(6.0)
```

```
      CALL PLOTNI(COX(JC),COY(JC),KBD(JC))
      CALL TYPENI(KD(JC))
      IF (IY.NE.1) GO TO 200
      DO 195 JD=JC,464
      IF (JD.EQ.JC) GO TO 195
      IF (ID(JD).NE.IID) GO TO 195
      IF (KD(JD).GT.JH) GO TO 195
      IF (KIND(JD).EQ.JG) GO TO 195
      IF (KD(JC).EQ.KD(JD).AND.KBD(JC).EQ.
     -KBD(JD).AND.ND(JC).EQ.ND(JD)) GO TO 193
      GO TO 195
193   CALL POSITN(COX(JC),COY(JC))
      CALL JOIN(COX(JD),COY(JD))
195   CONTINUE
200   CONTINUE
      CALL FULL
      CALL BLKPEN
      CALL GREND
```

(d) Part specific to GPCHRON:

```
      AZ=1.0
      AY=1.0
      DO 100 JC=1,464
      IF (ID(JC).NE.IID) GO TO 100
      IF (KD(JC).GT.JH) GO TO 100
      IF (KIND(JC).EQ.JG) GO TO 100
      IF (ND(JC).EQ.1) GO TO 90
      JZ=IFIX(AZ)
      CNX(JZ)=COX(JC)
      CNY(JZ)=COY(JC)
      AZ=AZ+1.0
      GO TO 100
90    JY=IFIX(AY)
      CDX(JY)=COX(JC)
      CDY(JY)=COY(JC)
      AY=AY+1.0
100   CONTINUE
      CALL BLKPEN
      CALL FULL
      CALL PTPLOT(CNX,CNY,1,JZ,-2)
      IF (IW.EQ.1) CALL REDPEN
      IF (IW.NE.1) CALL BROKEN(2,5,2,5)
      IF (IW.NE.1) CALL THICK(2)
      CALL PTPLOT(CDX,CDY,1,JY,-2)
      CALL GREND
      STOP
      END
```

APPENDIX 2: Multivariate data analysis.

(1) Principal components analysis of meteorological and tidal data using:

V1 - height of daytime low water

V2 - minimum daily temperature

V3 - 7 day moving average minimum temperature

V4 - maximum daily temperature

V5 - 7 day moving average maximum temperature

V6 - mean daily windspeed

V7 - mean hourly maximum windspeed

V8 - duration of rainfall per 24 hours

V9 - number of hours sun per day

V10- mean daily saturation deficit

Four factors were produced with eigenvalues greater than 1.0.

In a discriminant analysis only two of these factors were needed to discriminate between the two observed types of behaviour.

(The factor score coefficient matrix is used to calculate factor scores from standardized variables (Zn) where Zn = (Vn - mean of Vn)/standard deviation of Vn.)

FACTOR SCORE FOR FACTOR 1 = 0.03466xZ1 + 0.2099xZ2 + 0.32699xZ3 + 0.25928xZ4 + 0.32393xZ5 - 0.03022xZ6 -0.03823xZ7 + 0.05922xZ8 + 0.03759xZ9 - 0.00555xZ10 1

FACTOR SCORE FOR FACTOR 3 = -0.01096xZ1 + 0.0835xZ2 - 0.06198xZ3 - 0.03623xZ4 - 0.04735xZ5 - 0.04472xZ6 - 0.04354xZ7 - 0.0561xZ8 + 0.36291xZ9 + 0.48922xZ10 2

From the standardized discriminant function coefficients:

Discriminant score = 0.97147 x FACT. SCORE FACTOR 1

$- 0.70258$ x FACT. SCORE FACTOR 3 3

Substituting 1 and 2 in 3, the standardized discriminant function coefficients for the original variables are:

Discriminant score = $0.0414xZ1 + 0.1453xZ2 + 0.3612xZ3 + 0.2773xZ4 + 0.348xZ5 + 0.0021xZ6 - 0.0066xZ7 + 0.097xZ8 - 0.2185xZ9 - 0.3491xZ10$ 4

These standardized discriminant function coefficients represent the relative contribution of its associated variable to the discriminant function. Therefore in the above case 4 the following variables contribute relatively little to the function and should be considered for removal: V1, V2, V6, V7, V8.

(2) Principal components analysis of meteorological data using:

V3 - 7 day moving average minimum temperature

V4 - maximum daily temperature

V5 - 7 day moving average maximum temperature

V9 - number of hours sun per day

V10- mean daily saturation deficit

Two factors were produced with eigenvalues greater than 1.0, and were both used in the subsequent discriminant analysis.

FACTOR SCORE FOR FACTOR 1 = $0.39232xZ3 + 0.31682xZ4 + 0.38053xZ5 - 0.09023xZ9 - 0.03327xZ10$ 5

FACTOR SCORE FOR FACTOR 2 = $-0.11613xZ3 + 0.05497xZ4 - 0.03502xZ5 + 0.67095xZ9 + 0.6208xZ10$ 6

From the standardized discriminant function coefficients:

Discriminant score = 1.01363 x FACT. SCORE FACTOR 1

- 0.66054 x FAC. SCORE FACTOR 2 7

Substituting 5 and 6 in 7.

Discriminant score = 0.4745xZ3 + 0.2848xZ4 + 0.4089xZ5 - 0.5347xZ9 - 0.4438xZ10 8

This disciminant function will classify 84 percent of dates into their correct class of either those on which normal or 'odd' foraging locations were observed. However, examination of the standardized coefficients reveals that the contribution of V4 to the function is much less than the rest, and consequently should be considered for removal.

(3) Principal components analysis of meteorological data using:

V3 - 7 day moving average minimum temperature

V5 - 7 day moving average maximum temperature

V9 - number of hours sun per day

V10- mean daily saturation deficit

Two factors were produced with eigenvalues greater than 1.0, and were both used in the subsequent discriminant analysis.

The standardized discriminant function coefficients for the original variables are:

Discriminant score = 0.5831xZ3 + 0.512xZ5 - 0.5395xZ9 - 0.4607xZ10 9

This disciminant function will classify 84 percent of dates into their correct classes, and so justifies the removal of V4. None of the variables now in the equation appear to be contributing less than any other, so the variable removal proceedure is finished.

The standardized variables in 9 can be transformed back into the original measurement variables by using the following:

$Z3 = (V3 - 4.1178)/1.949$　　$Z5 = (V5 - 7.1944)/2.3119$

$Z9 = (V9 - 2.2089)/2.3686$　　$Z10 = (V10 - 1.3425)/0.8387$

APPENDIX 3

Dry flesh weights and calorific values of worms taken by Grey Plovers after applying the correction of Dugan (1981b).

WORM SIZE (BILL LENGTHS)	DRY FLESH WEIGHT (mg.)	CALORIFIC VALUE (cal.)
1/4	1.91	9.12
1/2	3.66	17.55
1	10.60	50.88
1 1/2	22.24	106.73
2	28.85	138.46
2 1/2	36.50	175.21
3	51.72	248.26

1 calorie = 4.187 joules.

APPENDIX 4: Monthly estimates used in the energy budget calculations.

MONTH	MEAN MONTHLY TEMPERATURE (´C) (1)	ADDITIONAL FMR ABOVE basal FMR (Kcal/day)	NO. HOURS IN 10 HOURS OF LOW WATER, ENGAGED IN : ROOSTING	FLIGHT	NON-FLIGHT	NO. HOURS PER 24 HOURS ENGAGED IN: ROOSTING	FLIGHT	NON-FLIGHT
OCTOBER	9.1	10.59	0.06	0.09	9.85	7.5	1.4	15.1
NOVEMBER	7.7	12.46	0.20	0.09	9.71	7.64	1.4	14.96
DECEMBER	3.5	18.09	0.01	0.17	9.82	7.45	1.48	15.07
JANUARY	4.8	16.35	0.03	0.15	9.82	7.47	1.46	15.07
FEBRUARY	4.0	17.42	0.02	0.13	9.85	7.46	1.44	15.10
MARCH	6.7	13.80	0.02	0.13	9.85	7.46	1.44	15.10

(1) - Average for three years of 1980/81, 1981/82, 1982/83 from Hartlepool weather station.