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Kirby, Jeffrey.S.

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Aspects of the Breeding Biology of the Black-tailed Godwit
(*Limosa limosa*) with particular reference to Coloniality
and Anti-predator defence.

by Jeffrey S. Kirby.

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11 FEB 1985

Dissertation

1984 / 11.10.

ABSTRACT

Black-tailed Godwits (Limosa limosa), which nest solitarily as well as in colonies on the Ouse Washes, offer an opportunity to assess within one species the relative advantages and disadvantages of colonial nesting. Possible reasons were investigated, with particular reference to defence against predators. Colonies formed for social reasons rather than because suitable habitat was restricted. Neither the foraging requirements of adults nor of chicks could account for colonial nesting. Breeding success, although very low, was highest in the largest colony, that in a smaller colony being similar to that of single pairs. Flooding and predation were the main causes of nest failure. Colony birds benefitted from very effective group defence against avian predators and this was thought to be the main reason for colonial nesting in this species. It is not known why some individuals nested alone or how they fared in terms of nest defence and causes of breeding failure.

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INTRODUCTION

(i) The Study Species.

The Black-tailed Godwit formerly bred over much of East Anglia and north to Yorkshire, but became extinct in the early 19th century. The drainage of breeding habitats and persecution by shooting, netting and egg collecting were thought to be responsible (Cottier & Lea, 1969). In the early 20th century the numbers of passage and wintering Black-tailed Godwits in Britain increased markedly; this was attributed to high breeding success on the continent (Morley & Price, 1956). Birds bred irregularly from 1937 onwards at several localities in England and Scotland, and a regular breeding colony gradually established on the Ouse Washes (Cambridgeshire-Norfolk) from 1952. This area now supports between 40-60 pairs annually (C. Carson, pers. comm.) which is thought to represent 85% of the British breeding population (Sharrock, 1976).

The Black-tailed Godwit is still a rare breeding bird in Britain and is afforded strict protection under the Wildlife and Countryside Act of 1981. The degree of its rarity can be emphasised by comparing the British population with that of, for example, the Netherlands. The latter holds approximately 100,000 pairs, which represents 80% of the total population of western and central Europe. 1km^2 of good meadow-bird habitat in Holland may support 100 breeding pairs (Beintema, 1982).

The species has been the subject of relatively few studies. The majority of work was carried out by Lind (1961) in Denmark and Beintema (1982, 1983) in the Netherlands.



A comprehensive account of the species is given in Cramp & Simmons (1983). Detailed studies have been carried out in the non-breeding season on other members of the genus Limosa e.g on L. haemastica (Hagar, 1966), L. lapponica (Smith & Evans, 1973; Evans & Smith, 1975) and L. fedoa (Wishart & Sealy, 1980). However information on their breeding ecology is sadly lacking.

(ii) Solitary and Colonial Nesting.

The dispersion of breeding birds results in a proximal sense from the birds' response to both features of the environment and the presence or absence of other individuals of the species (Brown & Orians, 1970). The dispersion adopted should tend to maximise the inclusive fitness of individual birds and thus the numbers offspring they produce (Lack, 1968; Wiklund & Andersson, 1980).

The distribution of breeding birds can be random, regular or aggregated. Only species in which nesting groups result from the birds preference to nest near conspecifics, and not merely from non-random distribution of favourable nesting habitat, can be considered to be colonial or semi-colonial (Jehl, 1968). Some individuals of a species nest both in colonies and as single pairs. Fieldfares Turdus pilaris (Andersson & Wiklund, 1978; Wiklund & Andersson, 1980), Lapwings Vanellus vanellus (Rankin, 1979; Elliot, 1982) and Black-tailed Godwits (Cramp & Simmons, 1983) provide examples. On the Ouse Washes, the godwits nest in groups of different sizes as well as singly (R.E. Green, pers.comm.).

The various dispersion patterns are associated with a variety of different costs and benefits, many of which have been reviewed by Brown & Orians (1970), Wilson (1975), Morse

(1980) and Krebs and Davies (1981). Thus aggregations may occur for food, to reduce predation, avoid disturbance, for chick-rearing purposes or to be near conspecifics. Krebs & Davies (1981) suggest that food and predation are the main environmental factors in influencing grouping.

The advantage of nesting as a single, isolated pair is thought to be the avoidance of the higher predation rates associated with high nesting densities (Bertram, 1978). The risk of predation of individual nests within aggregations is not independent and once one of a group is found others will probably be taken as well. This has been demonstrated in several experimental studies (e.g. Tinbergen et al., 1967; Croze, 1970; Goransson et al., 1975; Andersson & Wiklund, 1978).

However, the widespread tendency for some species to nest in colonies implies that direct benefits must exist which lead to an overall decrease in predation. Such advantages may include predator swamping or dilution, more effective predator detection or group defence.

Predator swamping occurs when predators are unable to take more than a small proportion of a brief super-abundance of prey. This is most likely in large, synchronous breeding colonies, such as Black-headed Gulls Larus ridibundus (Patterson, 1965) and is perhaps less likely for the smaller groups in which waders nest. Dilution refers to the chance of any one individual being preyed upon. This decreases with increase in group size.

For many predators the success of an attack depends on surprise. However, more effective predator detection can be gained if prey live in groups (Hoogland & Sherman, 1976;

Bertram, 1980). The precise way in which prey vigilance changes with group size depends on how individuals in a group spend their time. Pulliam (1976) and Caraco (1979) produced a time-budget model to predict optimum individual time budgets in groups of different sizes. The model was tested with feeding flocks of the Yellow-eyed Junco (Caraco, 1979; Caraco et al., 1980) and highlighted how time budgets can be used to analyse the effects of different costs and benefits on group size.

Aggregations are more conspicuous but should be favoured when group defence is more effective than that by a single pair; this was demonstrated experimentally by Andersson & Wiklund (1978). Mobbing alerts potential prey to the presence of the predator and often drives the predator from the area (Morse, 1980). However mobbing involves a risk (e.g. Tinbergen, 1953) although the risk is spread amongst all the responding individuals. Together, the individuals which nest in aggregations form a protected zone around their nests; this was shown for Lapwings by Elliot (1982). The existence of such a zone is indicated by many references to the Lapwing as a "watch-dog species" for less aggressive waders which nest close to it (Lack, 1968; Campbell, 1975; Dyrce et al., 1981; Goransson et al., 1975). Protection by Lapwings is also claimed to be important for the Black-tailed Godwit (Cramp & Simmons, 1983). One cost of such aggregations, however, is the increased risk of predation when such active defence is not possible, for example at night or in the presence of particularly dangerous predators (Elliot, 1982).

Against this background I set out to:

a. Examine the breeding dispersion of the Black-tailed

Godwit.

- b. Compare the activity of individuals, foraging and anti-predator defence within breeding groups of different sizes.
- c. Assess the efficiency of nest defence by the Black-tailed Godwit.
- d. Obtain basic information on the breeding biology of the Black-tailed Godwit in Britain which maybe of use in terms of conservation and management.

STUDY AREA

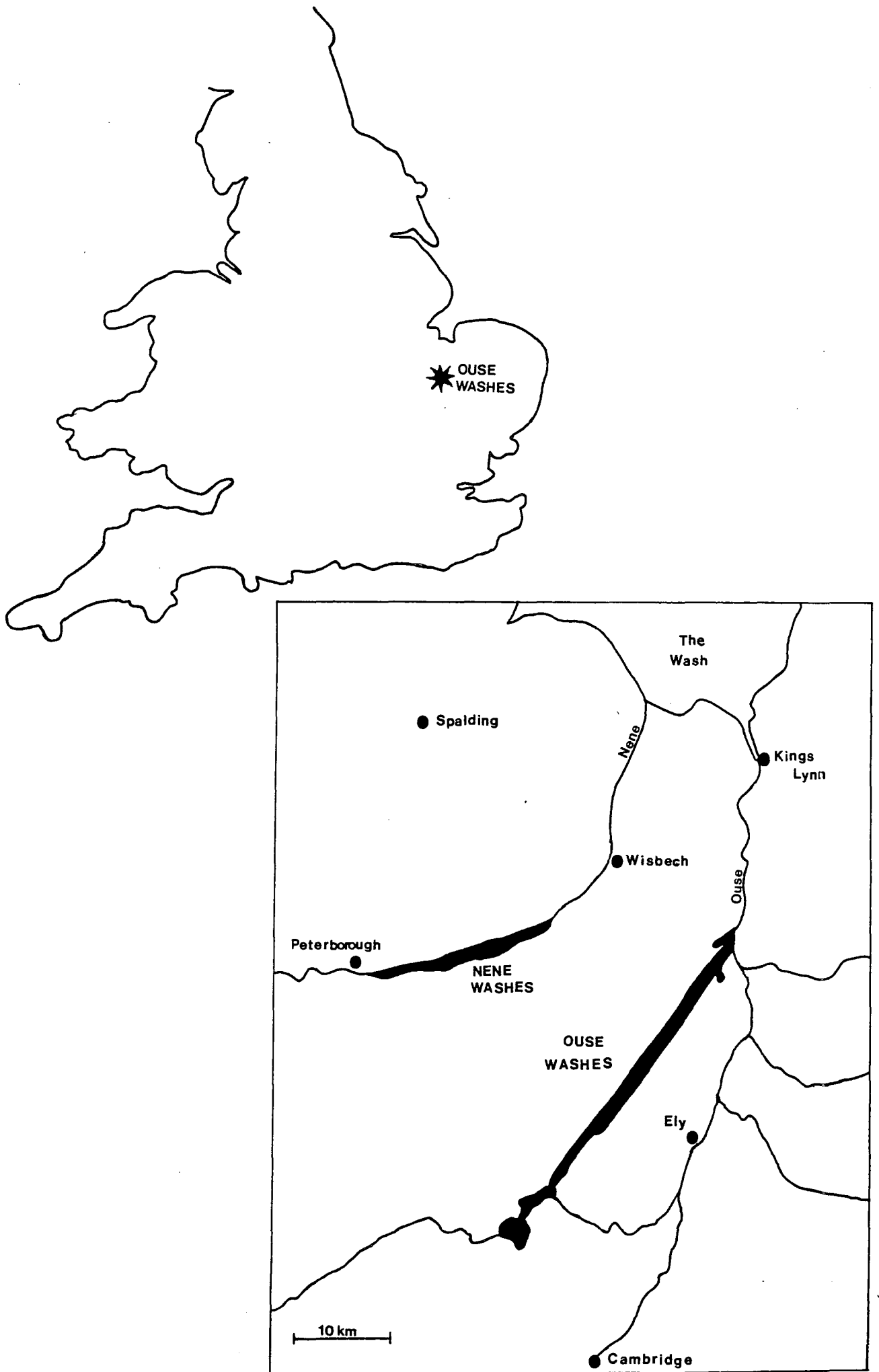
The Ouse Washes consist of the largest area of regularly flooded freshwater marshland left in Britain; it is situated within Cambridgeshire fenland (Fig.1a).

The area is contained by two parallel drainage rivers and is approximately 32km. long by 1km. at the widest point; the Ouse Washes complex covers about 2276ha. 75% of the washes lie 1 to 2km. above sea level and the majority is higher than the surrounding agricultural land which has sunken. The soils are predominantly peat with some smaller areas of silt; soil pH. is 6.5-7.5 (Thomas et al., 1981).

The drainage rivers were constructed in the 17th century to convey the water of the River Ouse more directly to its outfall in the Wash (Fig.1a). The land between was set aside to accommodate excess flood water in order to prevent the surrounding farmland from flooding. When the river levels dropped, water was released back into them.

Part of the Ouse Washes was declared as a Site of Special Scientific Interest in 1968 and the whole of it in 1971. The site is of national importance for its breeding birds and of international importance for its wintering wildfowl; the washes were listed by the Ramsar Convention in 1973. The Nature Conservation Review lists the Ouse Washes as a grade 1 open-water site and as a grade 1* (internationally important) neutral grassland site (Ratcliffe, 1977). The area forms the largest example of washland habitat in Britain and has been subject to less change than any other in the last 300 years.

The Washes still remain as a temporary storage area

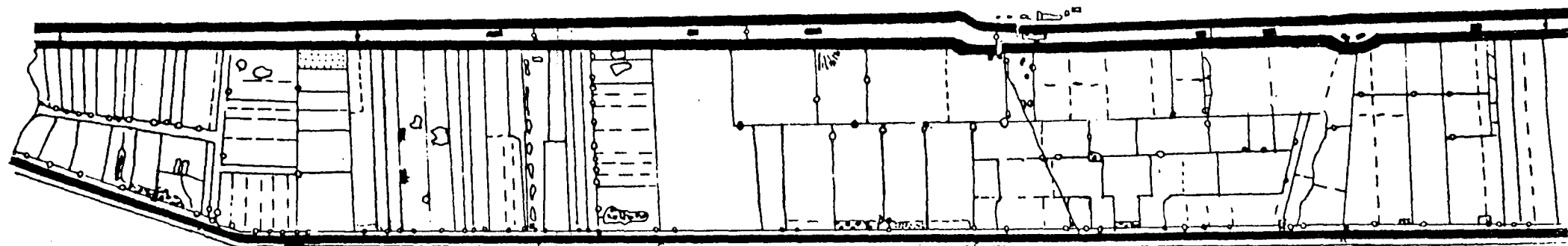


for flood water and are extensively flooded in most winters. Although, largely a single habitat area, three main sub-habitats can be distinguished; the washes or flood meadow fields, the ditch and river systems and the Osier beds and Willow holts. There are several permanent pools.

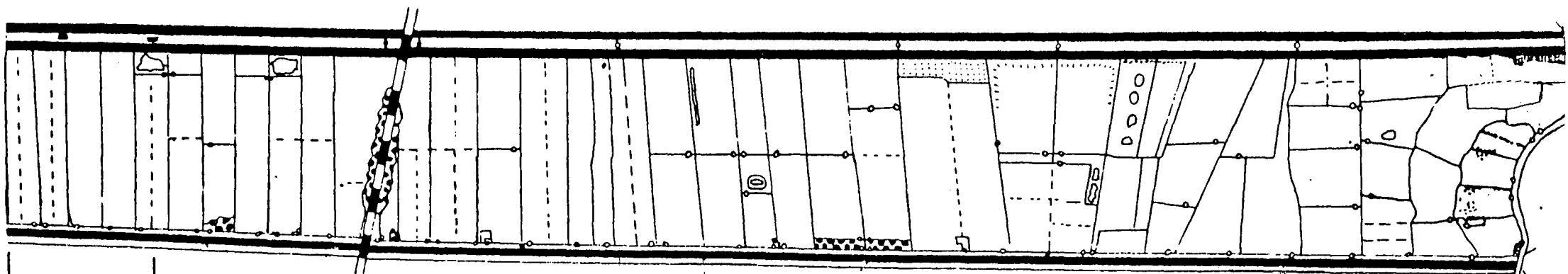
Two large segments (together representing 1,150 acres) of the Ouse Washes are managed by the Wildfowl Trust and the Royal Society for the Protection of Birds (R.S.P.B.) respectively. Due to the seasonal floods, agricultural land use is limited to mowing and grazing from Spring to Autumn. The aims of reserve management are to provide a variety of lengths of sward by controlling grazing by cattle, horses and sheep. On the R.S.P.B. section of the Ouse Washes, the reserve wardens sheperd about 2,000 head of stock daily in Summer.

Field work was confined to the R.S.P.B. section of the Ouse Washes and was concentrated mainly in two smaller areas (Fig.1b) known as the Singing Washes and the Tower Area, which were close to Godwit breeding colonies.

Fig. 1b. Diagram showing the R.S.P.B. section of the Ouse Washes; the two main study areas are indicated.



"Singing Washes"



"Tower Area"

MATERIAL AND METHODS

Field work was carried out between 17th. April and 15th. August 1984, during which time in excess of 250 hours of detailed observations were made. Observation periods varied between 1 and 8 hours and were made at all times of the day. No observations took place at night. 50% of all observations were made in the Tower area and 26% at the Singing Washes; the remaining observation time was divided between 6 other sites. All observations were confined to the R.S.P.B. section of the Ouse Washes.

In general, observations were made from the banks of the washes, either from the permanent hides situated there or out in the open. Thus, the majority of observations were made over long distances. Occasionally, where appropriate, it was necessary to reduce the distance of observation. At such times, a small portable hide was erected on the washes themselves; the hides were situated carefully so as to avoid disturbance. At the Singing Washes, observations were made from a small "trailer" hide situated on the bank and sometimes from a platform which was constructed at a height of approximately 18m. within a tree. In the Tower Area, scaffolding was erected close to the bank of the washes giving an elevation of approximately 6m. All observations were made using 10 X 50 binoculars and a 15-60 X 60 telescope mounted on a sturdy tripod.

BREEDING BIOLOGY

The distribution of breeding pairs was established by regular mapping of birds which were exhibiting pre-egg phase behaviour e.g displays. Nests were found by long

watches over an area and recording exactly where birds were seen to disappear. As soon as the approximate position of a nest was known, one person was guided to it either by using sign language or by using C.B. radios. Once in the vicinity of the nest, the person was told to stop and then to search for the nest. Some nests were found by watching birds flying into the area, such birds occasionally flew directly to the nest in order to take over incubation duties. Another, profitable way of finding nests was to follow birds back which had been involved in mobbing incidents. At all times, detailed notes were kept on the distribution and movements of Godwits. Once a nest had been found, its location was paced out precisely and mapped. A nest chronology was constructed by accurate mapping of breeding activity at all sites. Egg measurements (length and weight) were taken at all nests visited to calculate the approximate laying and hatching dates. At the same time, clutch size was recorded. Further visits to the nests were avoided so as not to cause too much disturbance or reveal nest positions to predators. Thus, the nests were visited again only on the day of hatching or if it was suspected that the nest was no longer in use. Hence, hatching success and the fate of nests which failed could be determined. Detailed records were made of pre-egg phase behaviour and the positions of such activities were mapped. The movements of pairs with chicks were obtained by regular mapping and long watches of known pairs or by regular mapping of all birds exhibiting young-phase behaviour within a colony. Regular checks on all other watches were carried out to search for breeding pairs which may have been missed; this task was made easier by

continuous liason with the reserve wardens. The rate of chick movements was estimated by making a number of assumptions; that no movements took place at night, that there was 15 hours of daylight each day and that the chicks were continuously on the move and at a constant rate. The validity of these assumptions is somewhat dubious.

ACTIVITY BUDGETS

Long watches of known individuals were made and the sequence and duration of events was timed. Such records were recorded directly into a dictophone and transferred to paper at a later time. Activity records were obtained for both members of a pair, for several pairs, in different colonies and as singles, at various times of day and at all stages of the breeding cycle. The latter was arbitrarily divided into the Pre-egg, Egg and Young phases. Continuous records of this kind varied in duration from just a few minutes to a maximum of 5 hours. In the final analysis only records of greater than 30 minutes were used and only those for individuals whose circumstances (e.g. Phase of breeding cycle) were known. The activity categories used were as follows: Feeding, Alert (bird vigilant), Courtship (including Copulation and Nest building), Preening, Flight (Free flight), Display Flight, Walking, Resting, Incubating, Mobbing, Interspecific interaction and Intra-specific interaction. Therefore, activity budget data was obtained and expressed as the percentage of the total duration of the observation period allocated to each activity. In addition, the duration of each bout of activity was known. The data obtained were initially tested for normality. According to such tests appropriate statistical techniques were used to

test for differences between the sexes, between situation and between phases of the breeding cycle.

FEEDING STUDIES

The location of feeding by known birds were mapped during all observation periods. These records were all transferred to one map so that the preferred feeding sites of each individual were determined. At a later date the topography of the feeding sites was investigated; surveying equipment was used. A coarse grid consisting of 56m. squares at the Singing Washes and 45m. squares at the Tower colony (producing a grid which divided up the area equally) was marked out using canes and a compass. Within each feeding area a finer grid was used, being 15 and 20 m. squares at Singing Washes and the Tower Area respectively. Equal numbers of points within and outside feeding areas were recorded. The relative height of each point to each other was recorded. The data obtained were used to produce a contour diagram for each field. The heights of feeding areas are compared with non-feeding areas statistically. Similarly the vegetation of both feeding and non-feeding areas was examined. 4 quadrats were taken at random within each feeding area and an equivalent number were taken at random points in non-feeding areas. Within each quadrat the percentage cover of each species present was recorded. The vegetative cover in the feeding areas were compared with that in the non-feeding areas by Discriminant Function Analysis. Data on feeding rates were collected where ever possible by recording the sequence of probes, steps and swallows that a feeding bird made during a timed period. This information was recorded into a dictophone. In addition, the exact sites at which

feeding rates were taken were recorded along with the sex of the bird involved and its identity where known.

SPECIES INTERACTION

All species interactions observed were recorded in detail. Maps were made of predator movements through the study areas during each observation period. To supplement this information, the height and tactics of each predator movement was recorded as was the response by breeding waders. If mobbing took place, the numbers of each species involved and the species mix involved was recorded. In addition, more specific information was recorded; such as which individual Godwits were involved, whether they came off the nest etc.. The relative effect of mobbing was judged subjectively. If the predator managed to obtain a prey item then this was also recorded. The responses of breeding waders to different predators at different periods through the season was examined statistically by using the proportion of birds that were mobbed when passing within a certain distance from defending Black-tailed Godwits; the Fisher exact test and the Mantel-Haenszel test were used. The movement of crows in and around Godwit colonies was examined in relation to mobbing by Lapwings and Godwits using the "Stepping down" technique of Stepwise Multiple Regression.

RESULTS

The Breeding Population.

A peak of 345 Black-tailed Godwits were recorded on the washes during the month of April (Appendix 1) although the majority of these were thought to be the race islandica (C.Carson, pers.comm.). By mid-April, at least 21 pairs were located on breeding territories.

Breeding pairs were distributed widely, some apparently choosing to nest close together whilst others were present as single pairs (Fig.2). Two colonies were established, a colony here being defined to include all birds that were nesting at a distance of less 150m. from its nearest neighbour. (This definition of a colony is based on an arbitrary decision, Elliot (1982) used 200m. whereas Cook in Elliot (1982) chose 182m. as the maximum distance for aggregated nests.). The first colony, at the Singing Washes, contained a maximum of 5 pairs; the second ("Tower colony") held up to 7 pairs. In addition, 3 pairs were present within another area ("Railway") and a minimum of 6 single pairs were recorded. Since the breeding pairs were both isolated and aggregated in their distribution the relative advantages and disadvantages of breeding in groups of different sizes could be explored.

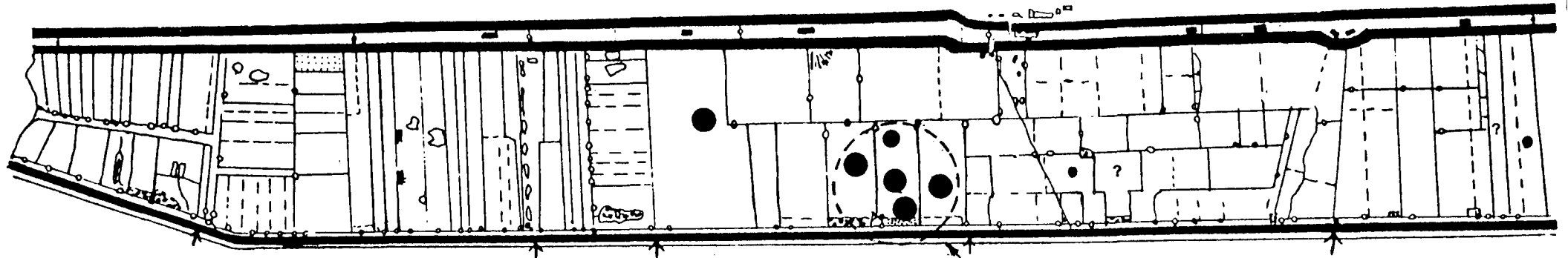
Nests proved to be extremely difficult to find. Only 9 were located accurately enough to allow them to be visited and only 2 of these belonged to single pairs. The locations of a further 6 nests were known approximately. In the Tower colony, 4 nests were visited; 3 were visited at the Singing Washes (Fig.3). The density of breeding birds could well be

Fig.2

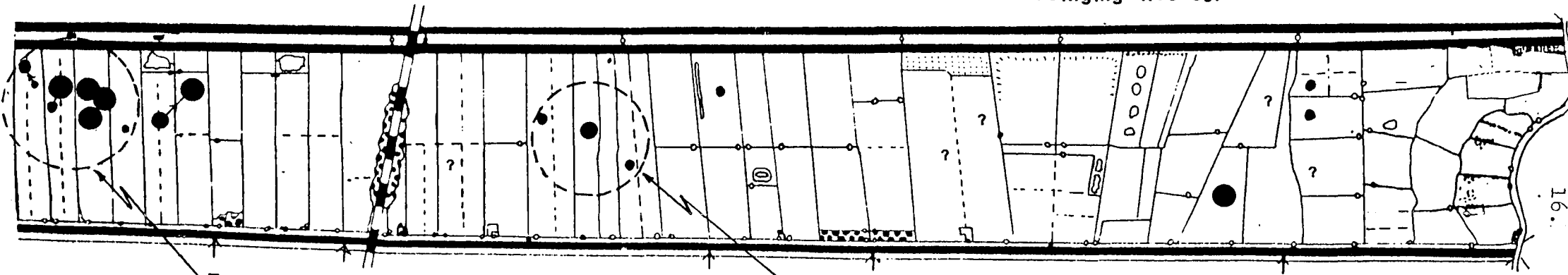
Positions of breeding Black-tailed Godwits (April 17th-1st May).

- KEY ? RECORDED ONLY ONCE
● RECORDED TWICE
● RECORDED THREE TIMES
● RECORDED MORE THAN THREE TIMES

Scale: 35mm = 1 km



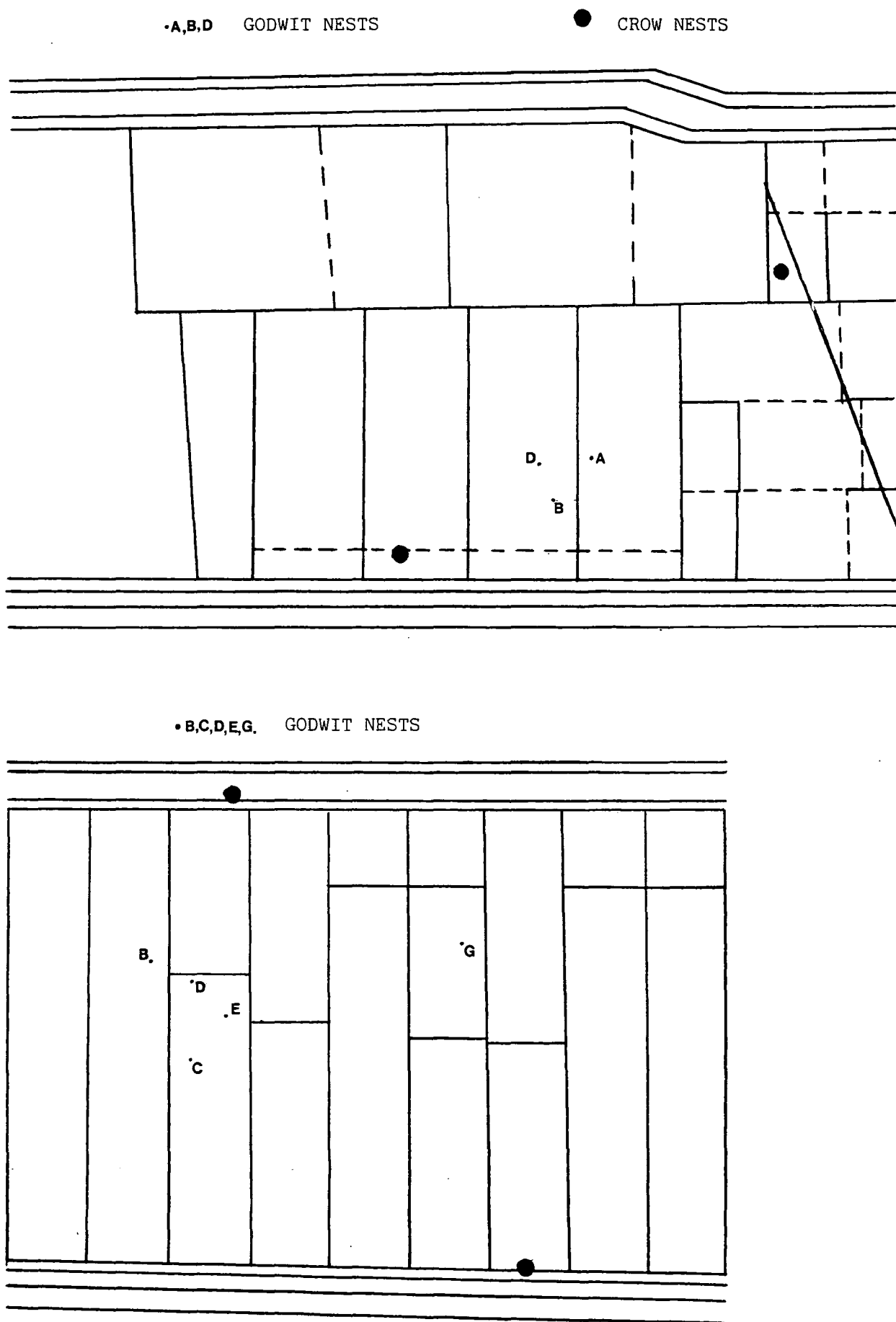
Singing Washes.



Tower.

Railway.

Fig. 3 Location of Godwit nests visited at the Singing Washes (upper) and Tower (lower) colonies.



important both in terms of the effectiveness of nest defence and in terms of individual activity budgets. At the Singing Washes, nests were separated by an average distance of 94.5m. (73.5-110.3m.); at the Tower colony by 152m. (94.5-220.5m.). Not only did the birds of the Singing Washes colony nest closer together, but they were also fewer in number and closer, on average (346m.) to the nearest Carrion crow nest. (The birds at the Tower colony nested on average 557m. from the nearest crow nest). This factor maybe important in terms of the level of predation encountered.

The timing of breeding activities are given in Tables 1 & 2. At the Singing Washes, incubation started as early as the 20th April; at the Tower, it generally started later. However, at the latter site, at least one nest (Nest B) was a replacement of a lost first clutch. The duration of incubation was between 23 and 25 days (n=7). Chicks were present at the Singing Washes colony from as early as 14th May. At the Tower colony, chicks were not seen until the 23rd May.

Pair Formation and Colony Establishment.

It is important to understand how the breeding dispersion observed might arise; this may indicate for what reasons some individuals aggregate and some not. Nesting groups may be due to selection for the same, favoured habitat variables (e.g for foraging or nest sites). Since aggregations occur, such areas could be in short supply. Males would then occupy them early, establish territories and advertise for a mate. In this way, single pairs could arise when all the favoured sites are occupied, the birds then having to nest elsewhere (perhaps in sites which are

Table 1. Symbols used in Table 2.

SYMBOL	MEANING
COP	Copulation recorded
Sc	Scraping
la	Intra-specific aggression
-P	Predator not mobbed
+P	Predator mobbed
①	Start of incubation*
i	Incubating bird present
x	Changeover at nest recorded
N	Nest found by visiting
Ⓜ	Eggs hatched
ⓓ	Nest deserted
Ⓟ	Nest predated
Ⓣ	Nest trampled
+Y	Adults with young
-Y	Adults without young

* Estimated from egg weights

Table 2. Timing of breeding activities.

Date	Singing Washes			First Lagoon Area (Tower)					Welney
	A	B	D	B	C	D	E	G	X
APRIL 19	COP; Sc	Ⓛ x							
21	Sc								
23	COP; -P	i +P		Ⓟ; +P +P	Sc COP; Sc				
25		i x							
27	la; +P	i x			Ⓛ i		COP		
29	Ⓛ	i; x la	COP; Sc; la COP	Sc	i la i +P	Sc Sc Sc Sc; la	Sc COP; Sc		
MAY 1		i							
3	i x	i	Ⓛ		x i	Sc Sc; +P			N; i Ⓟ
5		i; x i	i		i	+P			
7		i la	i		i				
9							Ⓛ		
11			x i	Ⓛ x	x i		i x		
13		Ⓜ							
15						Ⓛ	i		
17				+P x; i i x	i x i x		i x		
19									
21	Ⓛ							+P +P	
23			x i		+Y		i x i x		
25					+Y			i; N; +P	
27			x Ⓟ						
29								Ⓛ Ⓟ	
30							Ⓜ		
JUNE 2				Ⓜ +Y					
4									
6					-Y	Ⓜ			

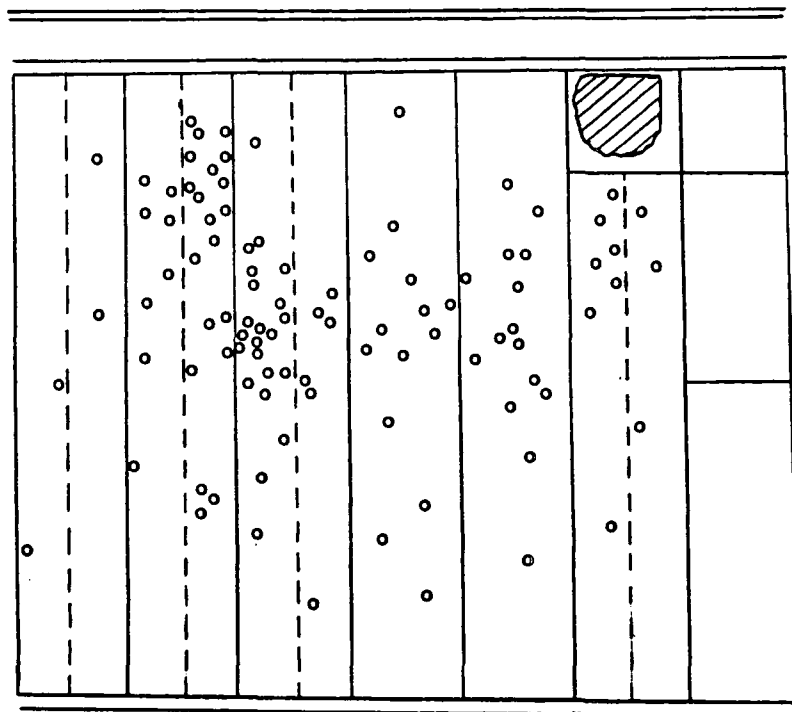
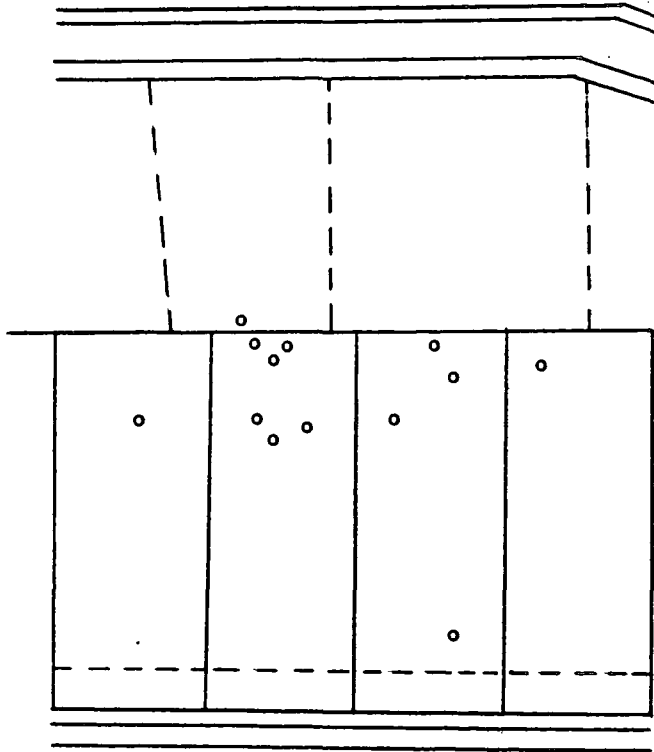
next best). However, if nesting near conspecifics is important then pair formation can occur at any location and before colony establishment. The pair may then choose to nest near established birds and thus aggregate. Conversely, they may either fail to locate other established pairs or choose not to.

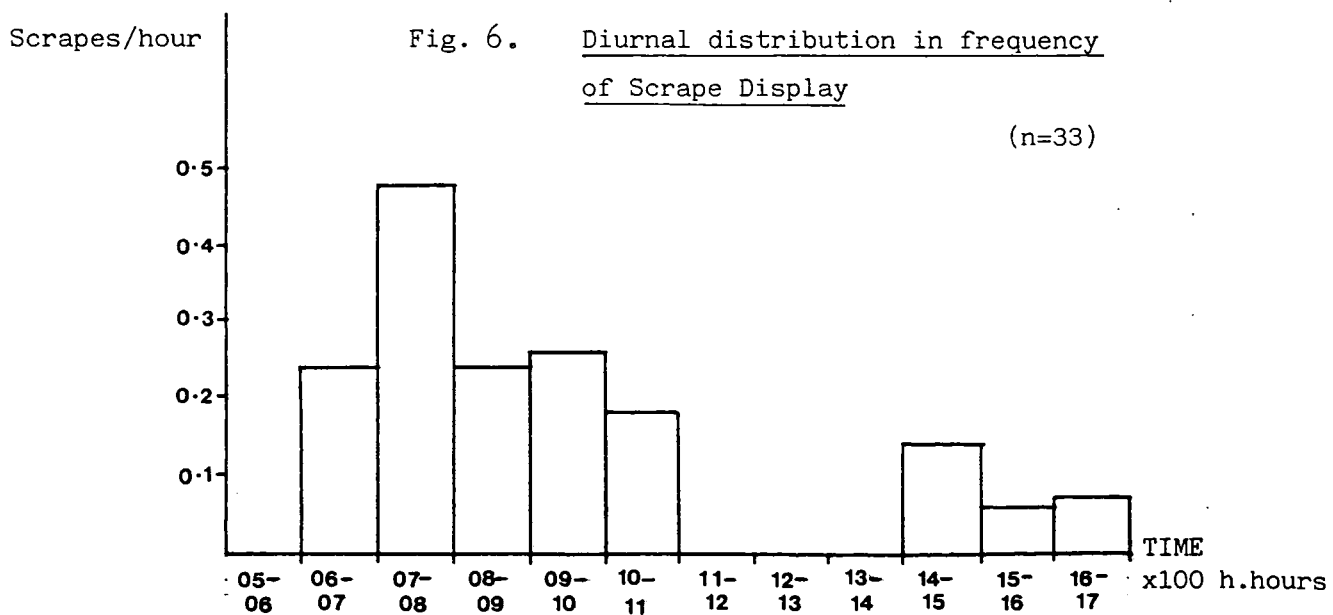
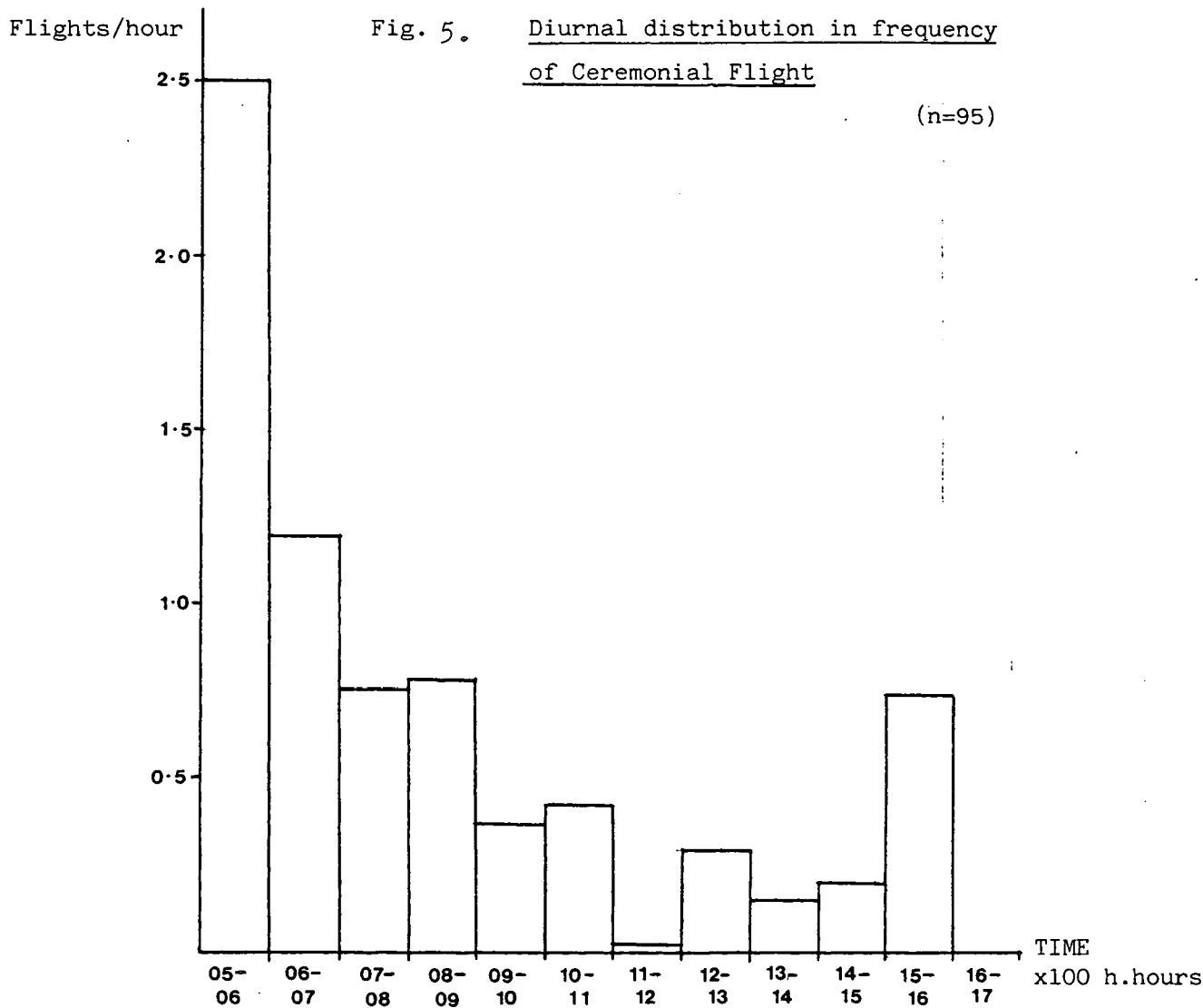
Pre-laying behaviour of the Black-tailed Godwit is described adequately in Cramp & Simmons (1983). Additional behavioural notes obtained during this study are presented in Appendix 2.

The most frequent display recorded was the Ceremonial flight which occurs only in the male; this accounted for 61% of all displays. The display is performed when attempting to establish a pair bond with a female; it is not confined to well defined areas (Cramp & Simmons, 1983). On the Ouse Washes, such displays were widely distributed (Fig.4) and individual birds often covered great distances during the course of a single flight. This suggests that the flight has little to do with the marking of territory boundaries. Thus, flights by stray males were often performed within the vicinity of established pairs and such intrusions were tolerated. The average duration of the Ceremonial flight was 2.7 minutes (n=25) and it was performed most frequently early in the morning (Fig.5). This behaviour is performed in order to attract a mate and occurred in a wide variety of locations and not only in the areas where colonies eventually established. In this way, pair formation took place extremely quickly, the majority of birds being present as pairs by April 17th.

Once pair formation had taken place, the birds wandered

Fig. 4. Spatial distribution of the ceremonial flight at both the Singing Washes (upper) and Tower (lower) colonies.





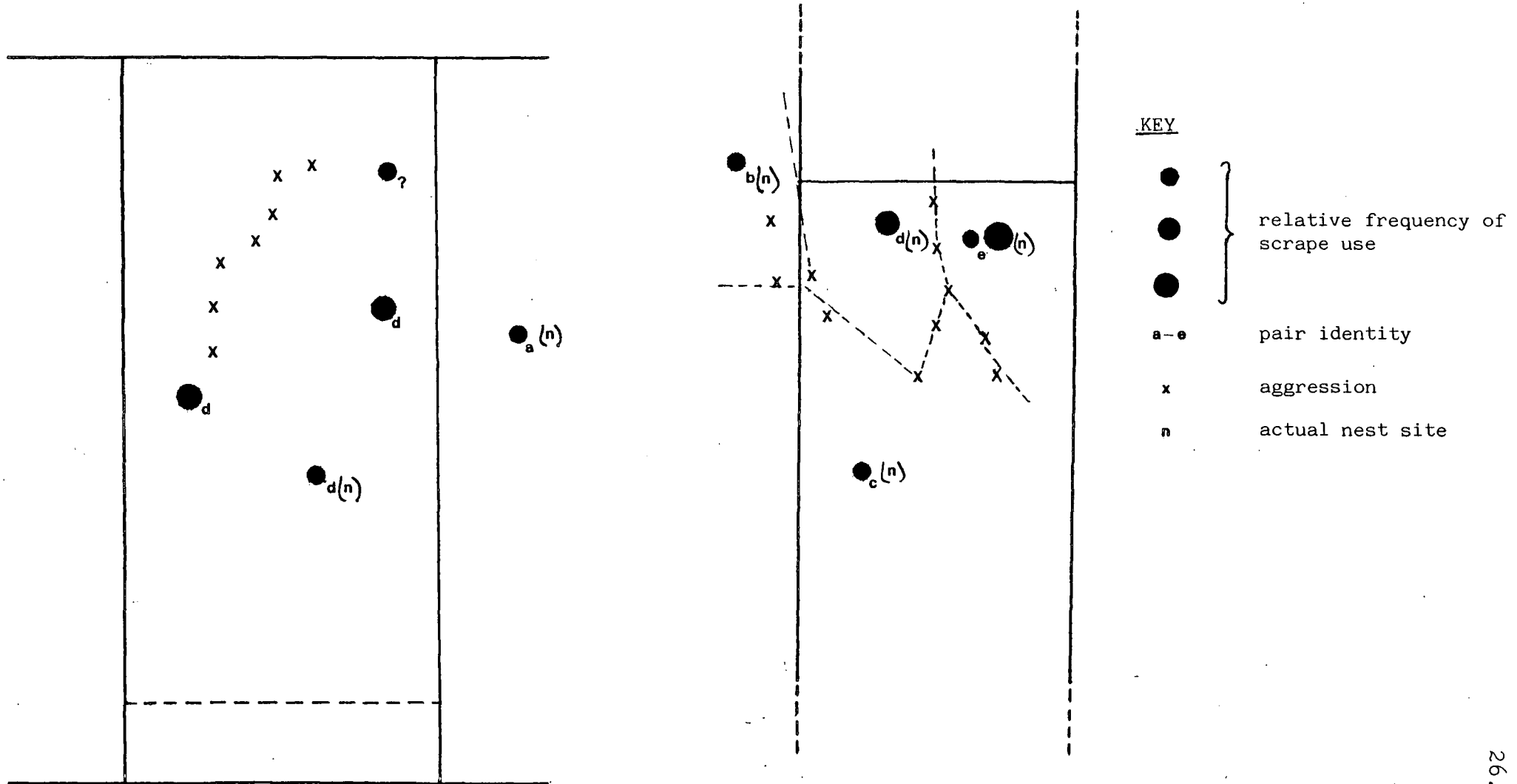
great distances within a large and irregular area. At this time encounters (often involving aggression) with other pairs and with unpaired birds (particularly males) were frequent; this may be important in choosing where to nest. Such encounters could give an indication of the likely density of pairs settling at that particular place, to be joined or avoided depending on the costs and benefits of nesting in groups. No communal displays were observed.

Each pair gradually concentrated its activities in a certain area by making and revisiting several scrapes and at the same time defending the area. At this time conspecifics would see where a neighbouring pair was going to nest. Inter-nest distances were established at this time, pairs attempting to nest too close to an already established pair being subject to much intra-specific aggression and disturbance. The Scrape Display (see Cramp & Simmons, 1983) represented 21% of all displays (n=33) recorded; 85% were initiated by the male. The duration of scraping varied between 0.5-28 minutes (Table 3). There was no significant differences in the time spent in scraping by the two sexes ($\bar{Q}=3.9$, $\bar{\sigma}=3.4$ mins.; $t=0.61$). The frequency of scraping varied during the day (Fig.6) but there was no significant relationship between the frequency of scraping and the number of days before the start of incubation. Each pair of birds made between 1 and 3 scrapes (Fig.7), each scrape being used many times. Therefore, it appears that several pairs of birds show interest in the activity of conspecifics and establish nests close together. In such a colony, the minimum distance between nests is determined by intra-specific interactions.

Table 3. Duration (mins.) of scraping in male and female
Black-tailed Godwit.

STATISTIC	MALE	FEMALE
n	38	38
\bar{x}	3.4	3.9
SD	5.87	5.1
min	0.5	0.5
max	28	22

Fig. 7. / Positions of scrapes and intra-specific interactions and frequency of scrape use (Singing Washes, left; Tower, right).



95% of all birds (n=49) involved in intra-specific aggressions were males. Most frequently only 2 individuals were involved (68% of cases) although 3 (20%) and sometimes 4 birds (12%) took part. Such interactions lasted 5.8 minutes on average (1-12 mins.; n=22). Aggression was often initiated in response to intruders and such disputes were more frequently recorded at the Tower colony (85%) than at the Singing Washes (15%). This maybe because more birds were present so that the chances of interactions were greater. It may have led to the greater inter-nest distances observed. The positions of male-male disputes may be used with caution to divide the Tower colony into 4 fairly distinct territories (Fig.7).

To conclude, pair formation took place prior to colony establishment, the breeding pairs then appearing to "home in" on nesting conspecifics. Inter-nest distances and perhaps colony size were established by male-male disputes. In this way breeding colonies were formed.

Breeding Season Activity.

If birds are nesting in groups not merely because suitable habitat is restricted, the activity budget of an individual nesting within a colony might be expected to differ from that of a single pair. Similarly the activity budget may vary according to the size of the group. For example, more effective predator detection maybe gained through increased overall vigilance of groups, despite less time spent alert by individuals in aggregations than when alone. Similarly, one might also expect each individual within a large colony to spend less time mobbing a predator than an individual within a smaller colony, all other things

being equal.

In total, I obtained approximately 150 hours of activity budget data (Table 4). During the pre-egg phase, 27 and 33 hours of data were recorded at the Singing Washes and Tower colonies respectively. During the egg phase, 35 and 20 hours of data were obtained from the same locations. Unfortunately, only 12 hours of activity budgets were recorded for single pairs, these being both more difficult to find, and to observe. After the chicks had hatched, 9 hours of data was obtained for pairs effectively operating as single pairs (because they had moved away from breeding colonies) and 20 hours for pairs within the Tower colony. The data obtained allow a comparison between the Singing Washes (1-3 pairs) and the Tower colonies (4-6), but insufficient was obtained on single pairs to establish statistically significant results. The percentages of total time spent in each activity and their durations provided severely skewed data, on which transformations were ineffective. Thus, Non-Parametric tests were used. Because daylength did not change appreciably between late April and mid-June percentages are assumed to be equivalent to total time spent in each activity.

The types of activity recorded (Tables 5-7) were Feeding, Alertness, Preening, Flight, Walking, Inter-specific interaction, Intra-specific interaction, Mobbing, Courtship, Display flight, Incubation and Resting.

The activity budget maybe expected to vary not only between the size of the group in which a bird is nesting but also according to a number of other variables. Thus, activity budgets were obtained for individuals at different times of the day, both sexes, for many different individuals,

11-11-11

Table.4. Duration of Observation periods (mins.) when recording the activity of individual Black-tailed Godwits.

PHASE	PAIR	SEX	No.of Observation periods.	\bar{X} Duration	Total
Pre-egg	SW/A	M	6	62.5	375
		F	6	61.5	369
	SW/D	M	9	50.6	455
		F	9	48.3	435
	T/B	M	1	(55)	55
		F	1	(55)	55
	T/C	M	3	72.0	216
	T/D	F	4	57.8	231
		M	10	21.8	218
	T/E	F	12	21.1	253
M		5	36.8	184	
		F	6	27.8	167
Egg	SW/B	M	10	69.1	691
		F	8	96.4	771
	SW/D	M	5	98.4	492
		F	2	75.0	150
	T/A	M	1	(60)	60
		F	1	(60)	60
	T/Bl	M	1	(62)	62
		F	0	-	-
	T/Bl1	M	3	24.0	72
		F	2	8.0	16
	T/C	M	7	44.7	313
		F	9	53.8	484
	T/E	M	4	26.5	106
F		1	(11)	11	
Y	M	3	105.7	317	
	F	4	102.3	409	
Young	SW/B	M	6	48.5	291
		F	6	56.3	338
	J	M	6	44.0	264
		F	5	50.6	253
	T/1-1V	M	7	43.9	307
		F	8	34.4	275

Table 5. Pre-egg phase activity expressed as mean percentage of total time observed.

(1-5 = time of day)*

ACTIVITY	PAIR	MALE					FEMALE				
		1	2	3	4	5	1	2	3	4	5
FEEDING	SW/A	81	65	59	66	-	76	42	69	-	-
	SW/D	80	86	93	74	79	84	97	65	73	100
	T/B	-	88	-	-	-	-	81	-	-	-
	T/C	-	58	-	-	-	-	39	-	-	-
	T/D	35	62	-	-	-	85	80	-	-	-
	T/E	-	83	-	-	-	80	-	-	-	-
ALERT	SW/A	4	5	0	0	-	6	4	6	-	-
	SW/D	0	0	0	0	0	0	0	0	0	0
	T/B	-	3	-	-	-	-	2	-	-	-
	T/C	-	0	-	-	-	-	0	-	-	-
	T/D	12	0	-	-	-	0	0	-	-	-
	T/E	3	0	-	-	-	0	-	-	-	-
COURTSHIP	SW/A	3	6	6	0	-	11	37	0	-	-
	SW/D	4	4	0	6	0	4	3	0	4	0
	T/B	-	6	-	-	-	-	15	-	-	-
	T/C	-	60	-	-	-	-	49	-	-	-
	T/D	33	6	-	-	-	6	4	-	-	-
	T/E	12	0	-	-	-	20	-	-	-	-
INTRA-SPECIFIC INTERACTION	SW/A	-	0	11	0	-	0	0	0	-	-
	SW/D	-	0	0	0	20	0	0	0	0	0
	T/B	-	0	-	-	-	-	0	-	-	-
	T/C	-	10	-	-	-	-	0	-	-	-
	T/D	22	29	-	-	-	3	0	-	-	-
	T/E	4	0	-	-	-	0	-	-	-	-

* Time of day categories:

1=>0900; 2=0900-1200; 3=1200-1500; 4=1500-1800; 5=>1800.

and for each phase of the breeding cycle. Unfortunately, little information was obtained for "off-duty" females, for these tended to fly elsewhere when relieved from incubation duty by the male. Statistical analysis of activity budget data is confined to activities in which the volume of data is sufficient to examine these variables.

Diurnal activity changes have been reported for many bird species. In species that can not forage at night, feeding might be expected to be most intense early in the morning in order to replace the food reserves used during the night. However, this may not be appropriate to Godwits, since they feed by touch and not by sight. Similarly, the activity of predators might also be high at this time of day especially if they have hungry chicks to feed. It follows that the proportion of time spent in vigilance or mobbing might have to be highest early in the day. Only Courtship seemed to change according to the time of day; more time was allocated to this activity in the morning (Table 8). The proportion of time spent feeding was not especially high in early morning except perhaps for males during the incubation period; at this time, males may incubate at night which would account for intense feeding during early morning. A higher level of vigilance or mobbing during the morning was not observed.

Differences between the activity budgets of birds within small groups of different sizes maybe masked by individual variation, within each group of birds, in time allocated to each behaviour. Some of this variability maybe removed if data from different parts of the breeding cycle are treated seperately. During the pre-egg phase, feeding and courtship declined and increased respectively, towards

Table 8. Mean diurnal activity changes according to phase of breeding cycle.
 (values are expressed as % of total observation time &
 are based on repeated observations of 6 individual pairs).

ACTIVITY ¹	PHASE	MALE					FEMALE				
		* 1	2	3	4	5	1	2	3	4	5
FEEDING	P	65	74	76	70	79	81	68	67	73	100
	E	88	70	47	83	61	1	1	0	0	31
	Y	-	18	41	36	-	-	25	80	35	-
INCUBATION	P	-	-	-	-	-	-	-	-	-	-
	E	0	0	33	0	21	99	99	96	100	68
	Y	-	-	-	-	-	-	-	-	-	-
ALERT	P	5	1	0	0	0	2	1	3	0	0
	E	6	11	6	4	4	0.4	0	1	0	0
	Y	-	54	43	61	-	-	45	13	38	-
COURTSHIP	P	13	14	3	3	0	10	22	0	4	0
	E	-	-	-	-	-	-	-	-	-	-
	Y	-	-	-	-	-	-	-	-	-	-
INTRA-SPECIFIC INTERACTION	P	13	7	6	0	20	1	0	0	0	0
	E	-	-	-	-	-	-	-	-	-	-
	Y	-	-	-	-	-	-	-	-	-	-
MOBBING	P	-	-	-	-	-	-	-	-	-	-
	E	3	3	2	4	0	2	0	0	0.3	0
	Y	-	4	1	4	-	-	0	1	4	-
RESTING	P	-	-	-	-	-	-	-	-	-	-
	E	4	9	0	1	5	0	0	0	0	0
	Y	-	18	9	4	-	-	12	2	18	-

1. Only the main activities are included.

* Time of day categories.

the start of incubation (Figs.8&9).

Sexual differences in the time allocated to various activities were apparent. Differences between male and female activity are considered separately for each phase of the breeding cycle. During the Pre-egg phase (Table 9) both sexes fed for similar amounts of time (c.70%) and the duration of each feeding bout was similar (Table 10). Males were slightly more vigilant (1.9%) than females (1.4%). A similar amount of time was allocated by males and females to Courtship (pair displays and nest building) although females spent significantly longer in each courtship bout than did males ($z=-2.76$; $P=0.005$), because they remained for longer in the scrape than males (see Appendix 2). The time allocated to intra-specific interactions, although not significantly different, was somewhat higher in males. Similar amounts of time are allocated to other activities. Thus, during the pre-egg phase the activity budgets were very similar although males may have been more vigilant and more aggressive towards conspecifics.

Statistically rigorous comparisons between the behaviour of the sexes during the Egg-phase were not possible because little information was obtained for off-duty females. From the small quantity of data obtained, it appears that females incubated for 98% of the time, males incubating for much less (23%). During most observation periods the female was incubating and often for all of that period; "spot checks" on nests often confirmed the females presence. Therefore it appears as though females do most of the incubation, at least during the day. Feeding in males accounted for 80% of total time, mobbing for 7% in males and

Figs. 8&9. Changes in time spent feeding (upper) and courting (lower) according to exact stage of breeding cycle.

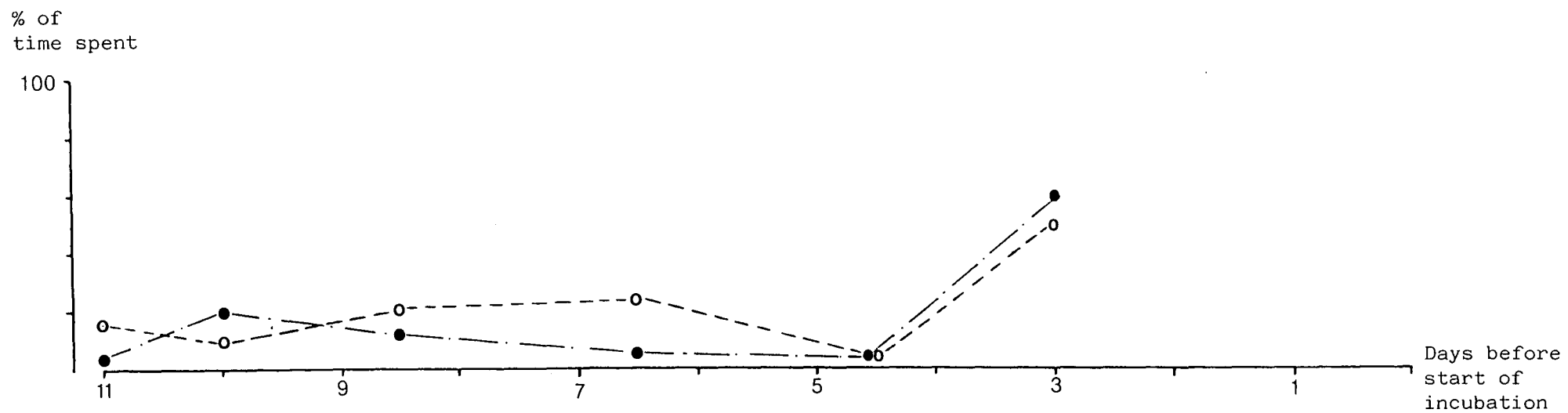
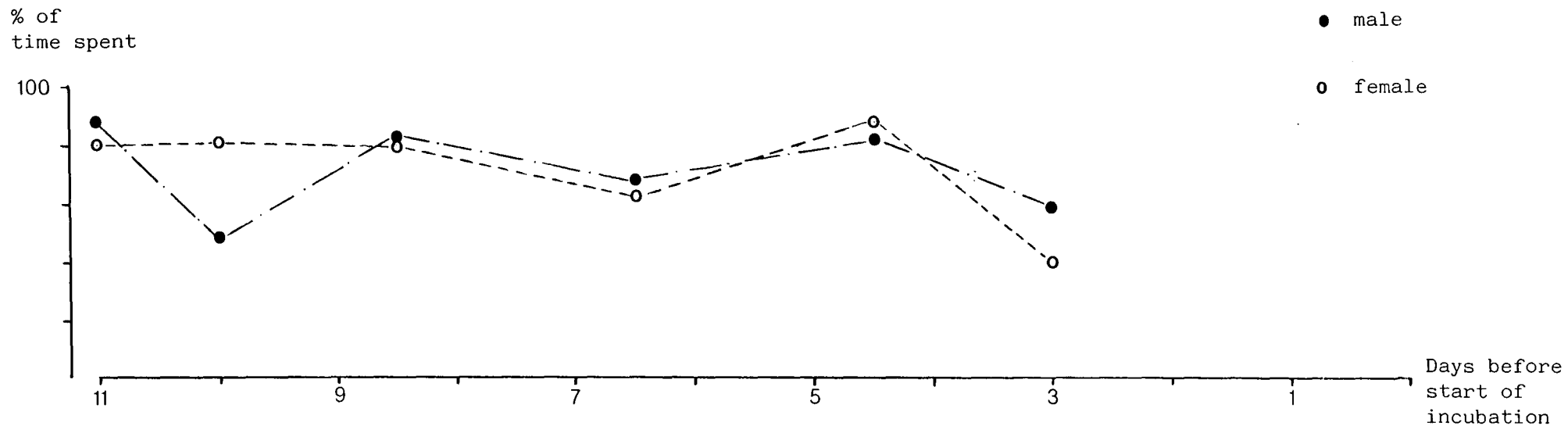


Table 9. Sex differences in activity expressed as a percentage of total time observed.

PHASE	ACTIVITY	SEX	\bar{X}	SD	SAMPLE SIZE	MANN-WHITNEY U TEST*			SIGNIFICANCE
						MEAN RANK	Z	2-TAILED P	
PRE-EGG	FEED	M	72.1	15.5	14	13.2	-0.53	0.59	N.S.
		F	74.7	18.0	13	14.9			
	ALERT	M	1.9	3.4	14	14.3	-0.23	0.82	
		F	1.4	2.4	13	13.7			
COURT	M	10.4	16.5	14	13.9	-0.07	0.94		
	F	11.8	15.3	13	14.1				
INTRA-	M	6.1	10.1	14	16.0	-1.87	0.06		
	F	0.2	0.8	13	11.9				
YOUNG	FEED	M	30.5	23.9	11	10.7	-0.25	0.81	N.S.
		F	39.7	37.4	10	11.4			
	ALERT	M	53.3	26.2	11	13.0	-1.56	0.12	
		F	31.1	30.5	10	8.8			
MOBB	M	2.9	3.9	11	12.2	-1.05	0.29		
	F	1.6	3.2	10	9.7				
REST	M	10.5	20.2	11	11.4	-0.30	0.76		
	F	11.0	17.7	10	10.6				

* Z and P corrected for Ties

Table 10. Sex differences in the average duration (minutes) of Godwit activities.

PHASE	ACTIVITY	SEX	\bar{X}	SD	SAMPLE SIZE	MANN-WHITNEY U TEST*			SIGNIFICANCE
						RANK MEAN	Z	2-TAILED P	
PRE-EGG	FEED	M	9.2	9.5	108	96.9	-1.07	0.29	N.S.
		F	10.4	11.1	93	105.7			
	COURT	M	3.7	6.5	41	34.4	-2.76	0.005	
		F	5.3	6.6	41	48.6			
YOUNG	FEED	M	3.7	5.0	40	56.0	-0.92	0.36	N.S.
		F	5.9	12.1	79	62.0			
	ALERT	M	4.4	5.8	100	136.4	-3.26	0.001	
		F	2.5	3.2	138	107.3			

* Corrected for ties

5% in females. Males were apparently more alert (11%) than females (2%). Therefore, during incubation, the activity budgets were quite different between the sexes.

During the Young phase (Table.9.) both sexes fed for similar amounts of time (c.35%) ; feeding bouts were of similar duration (Table.10.). Males spent more time alert than females and the average duration of vigilance was significantly longer in males ($z = -3.26; P=0.01$). At this time, the amount of time spent mobbing was similar by the two sexes (c.2%).

The activity budgets of individuals within the larger (Tower) colony were compared with those of individuals within the smaller (Singing Washes) colony during the Pre-egg phase and for males only in the Egg-phase. For the Chick phase, comparison has been made between behaviours of single pairs and those within a colony.

During the Pre-egg phase (Table.11.) males allocated less time to feeding in the Tower colony than at the Singing Washes although the difference was not significantly different. The average duration of feeding was similar (Table.12.). Similar amounts of time were spent being vigilant (c.2%) by males within the two colonies. However, significantly more courtship occurred in the larger colony (21%) than in the smaller one (3%; $z = -2.28; P=0.02$). Similarly a significantly greater amount of time was devoted to aggression by males at the larger colony ($z = -2.1; P=0.04$). For females, similar amounts of time (Table.13.) and similar durations (Table.14.) of most activities are recorded although, as with males, the amount of time allocated to courtship is significantly higher ($z = -2.70; P=0.007$). Therefore, in the larger colony

Table 11.

Differences in the time spent on various activities by male Black-tailed Godwits
in two colonies.

PHASE	ACTIVITY	SEX	\bar{X}	SD	SAMPLE SIZE	MANN-WHITNEY U TEST*			SIGNIFICANCE
						RANK MEAN	Z	2-TAILED P	
PRE-EGG	FEED	SW ¹	74.3	14.4	13	13.9	-1.01	0.31	N.S.
		T	58.0	30.8	11	10.9			
	ALERT	SW	1.1	2.5	13	11.1	-1.21	0.23	N.S.
		T	2.8	4.4	11	14.1			
COURT	SW	2.8	2.6	13	9.5	-2.28	0.02	S	
	T	20.9	27.6	11	16.1				
INTRA	SW	2.4	6.1	13	10.1	-2.10	0.04	S	
	T	8.9	14.4	11	15.4				
EGG	FEED	SW	78.4	19.2	15	14.0	0	1.0	N.S.
		T	75.8	22.2	12	14.0			
	ALERT	SW	5.0	6.8	15	14.0	0	1.0	N.S.
		T	7.4	12.1	12	14.0			
INTRA	SW	0.28	0.6	15	14.0	0	1.0	N.S.	
	T	4.5	10.6	12	14.0				
MOBB	SW	2.6	4.4	15	14.5	-0.38	0.7	N.S.	
	T	3.7	7.4	12	13.4				

* Corrected for ties

1. SW= Singing Washes; T- Tower colony.

Table 12. Differences in the mean duration (minutes) of male Black-tailed Godwit activities in two colonies.

PHASE	ACTIVITY	LOCATION	\bar{X}	SD	SAMPLE SIZE	MANN-WHITNEY U TEST*			SIGNIFICANCE
						MEAN RANK	Z	2-TAILED P	
PRE-EGG	FEED	SW	10.6	10.7	61	59.0	-1.69	0.09	N.S.
		T	7.5	7.4	47	48.7			
	COURT	SW	1.7	0.9	13	17.5	-1.15	0.24	
		T	4.7	7.8	27	21.9			
EGG	FEED	SW	18.1	20.2	53	50.0	-1.45	0.15	N.S.
		T	11.7	11.0	39	41.8			
	ALERT	SW	1.8	1.6	29	49.9	-1.44	0.15	
		T	1.8	2.6	22	41.9			
YOUNG	ALERT	Singles	4.9	6.0	65	54.6	-1.95	0.051	(S)
		T	3.5	5.4	35	42.8			

* Corrected for ties

Table 13. Differences in the time spent on various activities by female Black-tailed Godwits at two colonies.

PHASE	ACTIVITY	LOCATION	\bar{X}	SD	SAMPLE SIZE	MANN-WHITNEY U TEST*			SIGNIFICANCE
						MEAN RANK	Z	2-TAILED P	
PRE-EGG	FEED	SW	71.2	20.1	12	13.3	-0.52	0.60	N.S.
		T	62.2	30.8	12	11.8			
	ALERT	SW	1.8	3.0	12	12.8	-0.28	0.78	N.S.
		T	0.9	1.5	12	12.1			
	COURT	SW	5.6	10.4	12	8.7	-2.70	0.007	S
		T	24.8	26.4	12	16.3			
	INTRA	SW	0.0	0.0	12	11.0	-1.81	0.07	N.S.
		T	0.6	1.4	12	14.0			

* Corrected for ties

Table 14. Differences in the mean duration (minutes) of female Godwit activities according to social situation.

PHASE	ACTIVITY	LOCATION	\bar{X}	SD	SAMPLE SIZE	MANN-WHITNEY U TEST			SIGNIFICANCE
						MEAN RANK	Z	2-TAILED P	
PRE-EGG	FEED	SW	11.7	13.2	45	48.4	-0.50	0.62	N.S.
		T	9.1	8.7	48	45.7			
	COURT	SW	4.4	6.3	11	18.6	-0.78	0.43	N.S.
		T	5.7	6.8	30	21.9			
YOUNG	FEED	SINGLE	7.3	14.4	51	42.1	-1.15	0.25	N.S.
		T	2.9	3.9	62	36.0			
	ALERT	SINGLE	2.1	2.9	71	62.0	-2.32	0.02	S
		T	2.9	3.6	67	77.5			

* Corrected for ties

(Tower) males seem to spend less time feeding and more time in aggression with conspecifics and courtship.

During the Egg phase the differences between the two colonies might be expected to be greater. However, males spend similar amounts of time (Table.12.) feeding (c.76%), alert (c.6%), mobbing (c.3%) and on intra-specific interactions (less than 5%). Similarly the duration of activity bouts (Table.12.) are alike.

During the Young phase the comparison is between single pairs and colonial pairs and it is perhaps for this situation that one would expect the greatest differences. Males may spend more time feeding (Table.15.) in the colony than as single pairs; for females the converse was true. The duration of feeding bouts (Table.14.) was not significantly different although apparently higher in females of single pairs. The males of single pairs were more vigilant than those within colonies (Table.15.); the duration of alertness (Table.12.) was significantly longer in single males ($z = -1.95; P = 0.05$). Females in the colony were more alert than single females (Table.15.); the duration of alertness (Table.14.) was significantly longer ($z = -2.32; P = 0.02$). In both sexes, more mobbing was seen in single pairs (Table.15.). The proportion of time spent resting by males was higher in single pairs but the converse was true for females.

The phase of the breeding cycle clearly influenced both the time allocated to, and the mean duration of, various activities. Some were recorded only during certain phases of the breeding cycle. Obviously, incubation occurred only during the Egg-phase, courtship in the Pre-egg phase etc. In males (Tables.16&17.) the time spent feeding varied significantly

Table 15. Activity differences in the chick phase
according to social situation.

Mean values.

ACTIVITY	SEX	SINGLE PAIRS	TOWER COLONY
FEEDING	M	22.4	37.3
	F	55.6	24.0
ALERT	M	65.0	43.5
	F	28.8	41.8
MOBBING	M	3.6	2.3
	F	3.2	0
RESTING	M	8.8	2.3
	F	5.6	20.5

Table 16. Activity differences according to phase of breeding cycle in male Black-tailed Godwits.

ACTIVITY	PHASE	\bar{X}	SD	SAMPLE SIZE	KRUSKAL WALLIS 1ANOV.*			SIG.
					MEAN RANK	CHI-SQUARE	P	
FEED	P	72.8	18.3	23	30.7	10.08	0.0065	S
	E	63.7	30.0	25	27.7			
	Y	13.3	19.1	5	6.6			
ALERT	P	1.5	3.1	23	19.8	19.79	0.0001	S
	E	6.5	9.7	25	28.8			
	Y	69.4	17.2	5	51.0			
MOBBING	P	0.0	0.0	23	21.5	10.31	0.0058	S
	E	2.5	5.6	25	31.0			
	Y	2.0	2.8	5	32.2			
INTRA	P	4.0	10.8	23	27.6	1.72	0.42	N.S.
	E	2.6	7.4	25	27.8			
	Y	0.0	0.0	5	20.5			
RESTING	P	0.1	0.6	23	22.4	7.19	0.027	S
	E	4.4	8.5	25	30.1			
	Y	3.6	5.4	5	32.1			

* Corrected for ties

Table 17. A more detailed analysis of activity differences according to phase of breeding cycle in male Black-tailed Godwits.

ACTIVITY	PHASE(S)	\bar{X}	SD	SAMPLE SIZE	MANN-WHITNEY U TEST*			SIG.
					MEAN RANK	Z	2-TAILED P	
FEED	P	72.8	18.3	23	25.8	-0.62	0.54	N.S.
	E	63.7	30.0	25	23.3			
	P+E	74.3	19.2	48	29.1	-3.11	0.002	
	Y	13.3	19.1	5	6.6			
ALERT	P	1.5	3.1	23	19.8	-2.44	0.015	S
	E	6.5	9.7	25	28.8			
	E	6.5	9.7	25	13.0	-3.54	0.0004	
	Y	69.4	17.2	5	28.0			
MOB	E	2.5	5.6	25	15.4	-0.19	0.85	N.S.
	Y	2.0	2.8	5	16.1			
	P	0.0	0.0	23	21.5	-3.20	0.0014	
	E+Y	2.6	5.2	30	31.2			
REST	E	4.4	8.5	25	15.3	-0.27	0.79	N.S.
	Y	3.6	5.4	5	16.3			
	P	0.1	0.6	23	22.4	-2.66	0.0079	
	E+Y	4.2	8.0	30	30.5			

* Corrected for ties

according to phase of the breeding cycle ($\chi^2=10.1;P=0.007$). Similar amounts of time were spent feeding in the Pre-egg and Egg phase although much less time was spent feeding in the Young phase ($z= -3.1;P=0.002$). The duration of the feeding bout (Table.18.) was longest during the Egg phase and significantly shorter during the Pre-egg ($z= -3.04;P=0.002$) and Chick phases ($z= -5.9;P=0.001$). Similarly in females (Table. 19.), the amount of time allocated to feeding was significantly less during the Young phase than the Pre-egg phase ($z= -2.27;P=0.02$); the duration of feeding bouts was also significantly shorter ($z= -5.4;P=0.0001$).

In males (Tables.16&17), the amount of vigilance also differed significantly with phase of the breeding cycle ($\chi^2= 19.8;P=0.0001$) such that significantly more time was spent vigilant during each successive phase. In females the time spent alert was longer during the Young phase ($z= -3.7; P=0.0003$) than during the Pre-egg phase. The duration of vigilance (Table.18.) did not differ significantly between phases.

For males (Table.16&17.) time spent mobbing varied significantly with phase ($\chi^2=10.3;P=0.006$); it was similar during the Egg and Young phases but significantly higher at these times than during the Pre-egg phase ($z= -3.2;P=0.001$). For females (Table.19), mobbing was also significantly greater during the young phase ($z=-2.5; P=0.01$).

The amount of time allocated to Resting varied significantly with phase ($\chi^2=7.2;P=0.03$) in male Godwits (Table 16). There was no difference between the egg- and chick phases (Table 17) although at such times the amount of Resting was higher than during the Pre-egg phase ($z=2.7;$

Table 18. Differences in the mean duration (minutes) of Godwit activities according to phase of breeding cycle.

ACTIVITY	SEX	PHASE	MEAN	SD	SAMPLE SIZE	MANN-WHITNEY U TEST*			SIGNIFICANCE
						MEAN RANK	Z	2-TAILED P	
FEEDING	M	P	9.2	9.5	108	89.0	-3.04	0.002	S
		E	15.4	17.2	92	114.0			
		E	15.4	17.2	92	79.5	-5.9	0.0001	S
		Y	3.7	5.0	40	36.5			
	F	P	10.6	11.2	90	104.1	-5.4	0.0001	S
		Y	5.9	12.0	79	63.2			
ALERT	M	E	1.8	2.1	51	58.0	-3.67	0.0002	S
		Y	4.4	5.8	100	85.2			
	F	P	1.8	1.3	12	78.0	-0.26	0.79	N.S.
		Y	2.5	3.2	137	74.7			

* Corrected for ties

Table 19. Activity differences according to phase of breeding cycle in female Black-tailed Godwits.

ACTIVITY	PHASE	\bar{X}	SD	SAMPLE SIZE	MANN-WHITNEY U TEST*			SIG.
					MEAN RANK	Z	2-TAILED P	
FEED	P	74.8	19.2	19	22.3	-2.27	0.023	S
	Y	47.5	33.7	17	14.3			
ALERT	P	1.3	2.5	19	12.8	-3.63	0.0003	S
	Y	34.5	28.0	17	24.9			
MOB.	P	0.0	0.0	19	16.0	-2.50	0.012	S
	Y	1.5	3.1	17	21.3			
REST	P	0.0	0.0	19	16.5	-2.21	0.027	S
	Y	5.0	12.1	17	20.7			

* Corrected for ties

$P=0.008$). In females (Table 19), a significantly higher proportion of total time was spent Resting during the young phase than in the Pre-egg phase ($z=-2.21$; $P=0.027$).

Foraging Behaviour.

Factors such as foraging requirements may influence dispersion patterns (Lack, 1968). It is thus necessary to isolate the effects of this factor when considering the influence of other factors, such as predation, on the breeding dispersion of birds. Some workers consider that food availability is of little importance to the siting of territories (e.g Klomp, 1954; Elliot, 1982). Others, however, have considered food availability to be important; e.g cowpat density was involved in the selection of nest-sites by Lapwings and Redshank (Rankin, 1979).

For the godwits, I determined their preferred feeding sites to examine whether birds fed within their territories, close by or at greater distances. Feeding sites varied according to the phase of the breeding cycle and the sex of the bird involved. Table 20 gives the average distances from the nest sites at which birds fed; feeding sites are shown in Figs. 10-16.

During the Pre-laying period both birds of a pair fed together. At the Singing Washes, pair D fed at distances up to 132m. from their nest. However, during the egg-phase both the male ($t=2.41$; $P<0.05$) and the female ($t=2.34$; $P<0.05$) fed at significantly shorter distances. Similarly, pair A individuals tended to feed closer to the nest during the incubation (egg) phase. At the Tower colony, male B fed significantly closer to the nest during the egg-phase ($t=2.70$; $P<0.05$). However, the male of pairs D and E fed at similar

Table 20. Average distance (m) of feeding sites from the nest site in male and female Black-tailed Godwits.

PAIR	SEX	PHASE OF CYCLE	
		PRE-EGG	EGG
SW/B	M	No data	50 ± 23 (n=19)
	F	No data	155 ± 175 (n=12)
SW/D	M	132 ± 22 (n= 5)	84 ± 42 (n=13)
	F	132 ± 21 (n= 5)	89 ± 36 (n= 5)
SW/A	M	104 ± 56 (n= 8)	53 (n= 2)
	F	115 ± 50 (n= 7)	123 (n= 3)
T/B	M	91 ± 30 (n= 6)	48 ± 23 (n= 6)
	F	87 ± 32 (n= 5)	214 ± (n= 1)
T/C	M	46 ± 24 (n= 4)	39 ± 16 (n= 7)
	F	46 ± 24 (n= 4)	298 ± 94 (n= 5)
T/D	M	60 ± 65 (n=11)	35 ± 15 (n= 4)
	F	59 ± 65 (n=11)	No data
T/E	M	113 ± 88 (n= 6)	69 ± 24 (n= 6)
	F	147 ± 114 (n= 6)	102 ± (n= 3)

Fig.10. Pre-egg and Egg phase feeding locations of pair A individuals, Singing Washes.

⊗ Nest site

• Male

○ Female

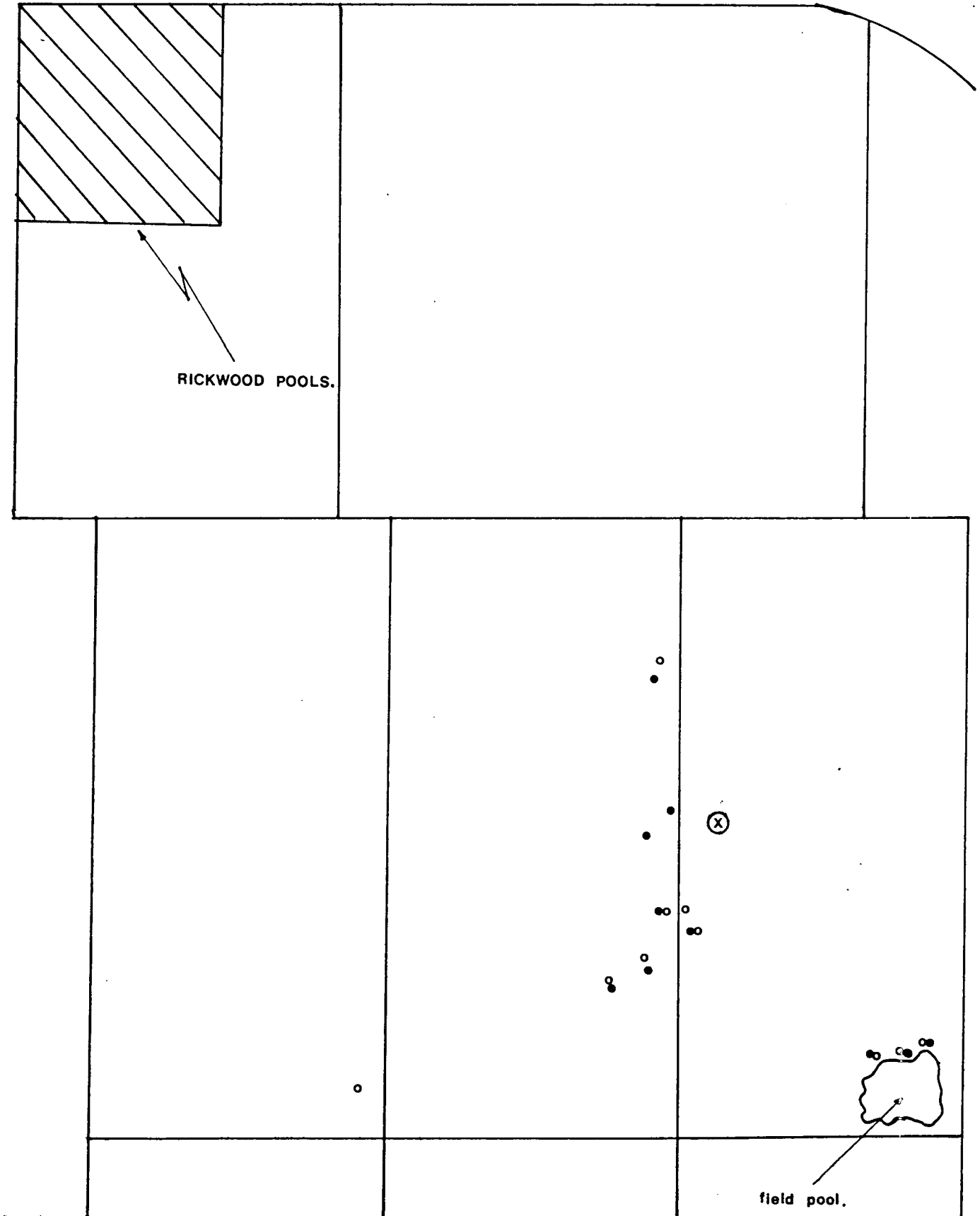


Fig. 11. Pre-egg phase and Egg-phase feeding locations of pair B individuals, Singing Washes.

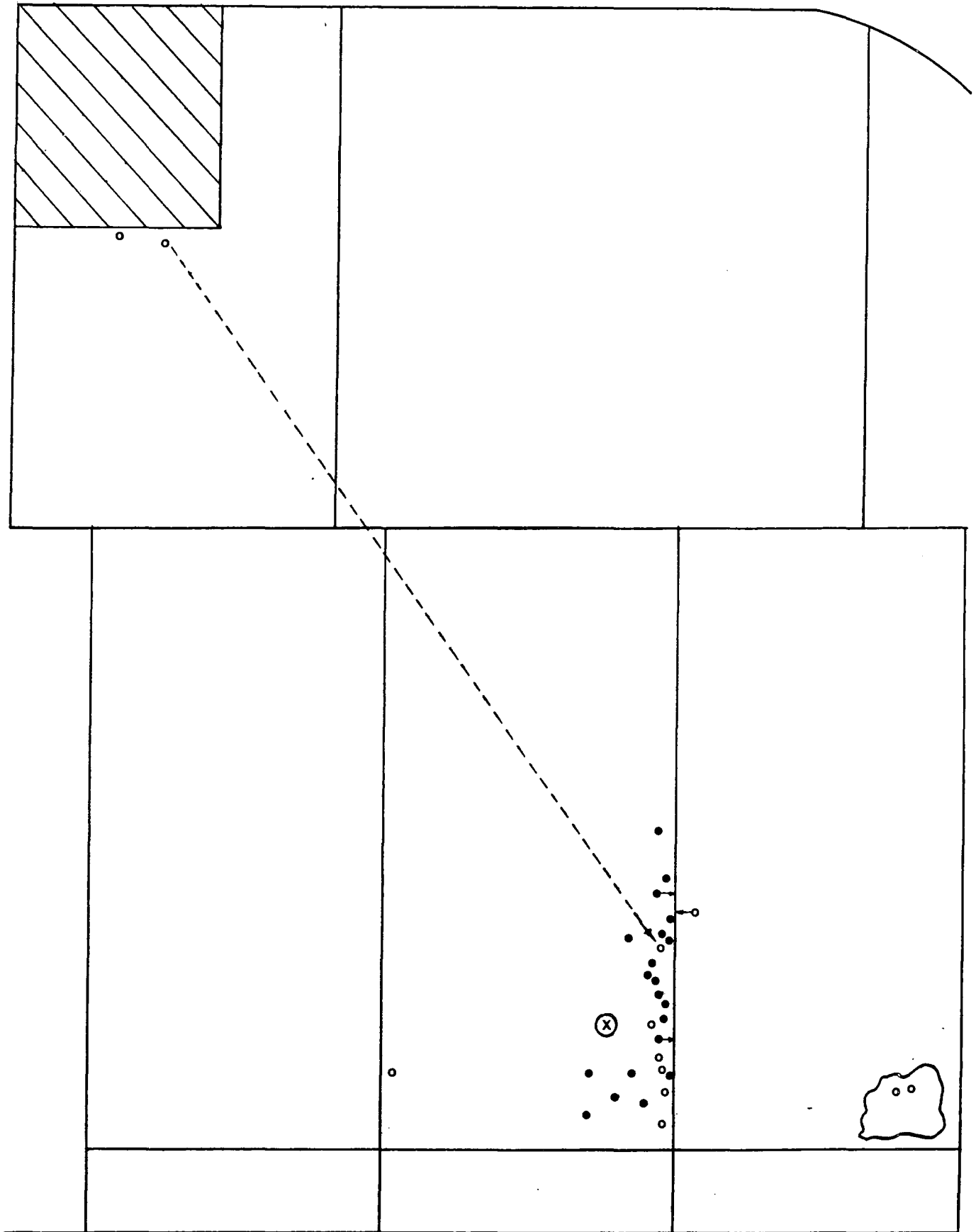


Fig. 12. Pre-egg phase and Egg-phase feeding locations of Pair D individuals, Singing Washes.

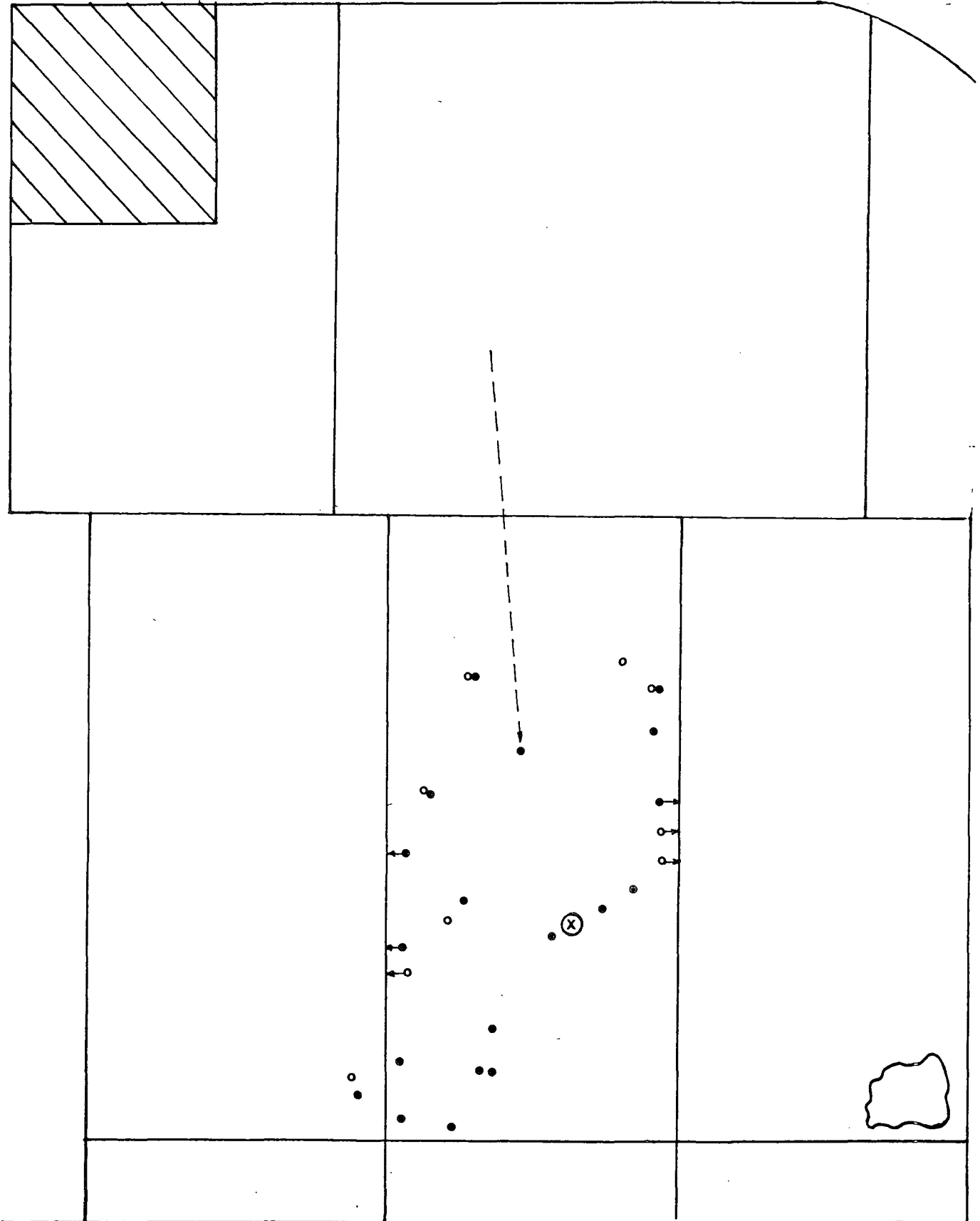


Fig. 13. Pre-egg and Egg-phase feeding locations of Pair B individuals,
Tower colony.

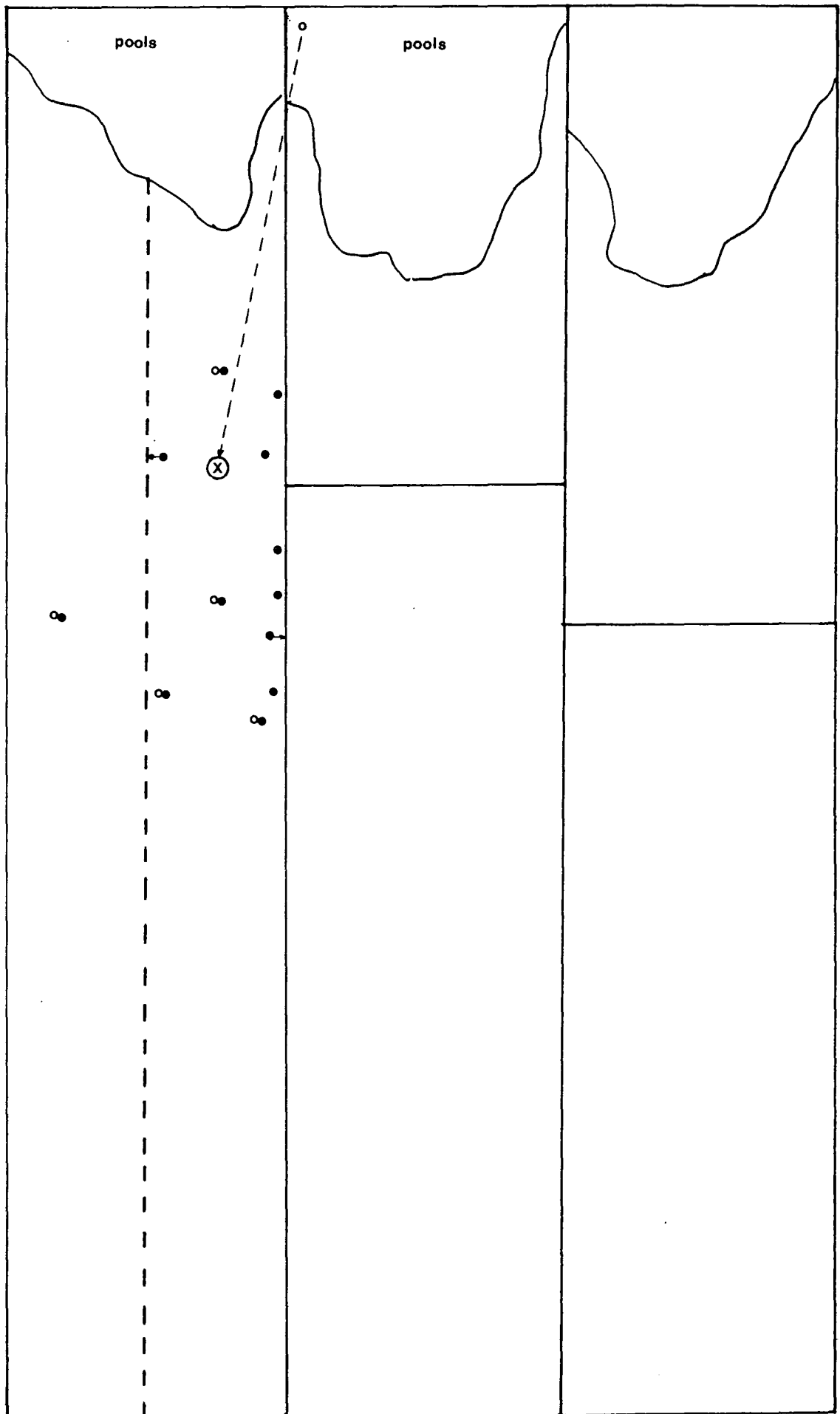


Fig.14. Pre-egg phase and Egg-phase feeding locations of Pair C individuals, Tower colony.

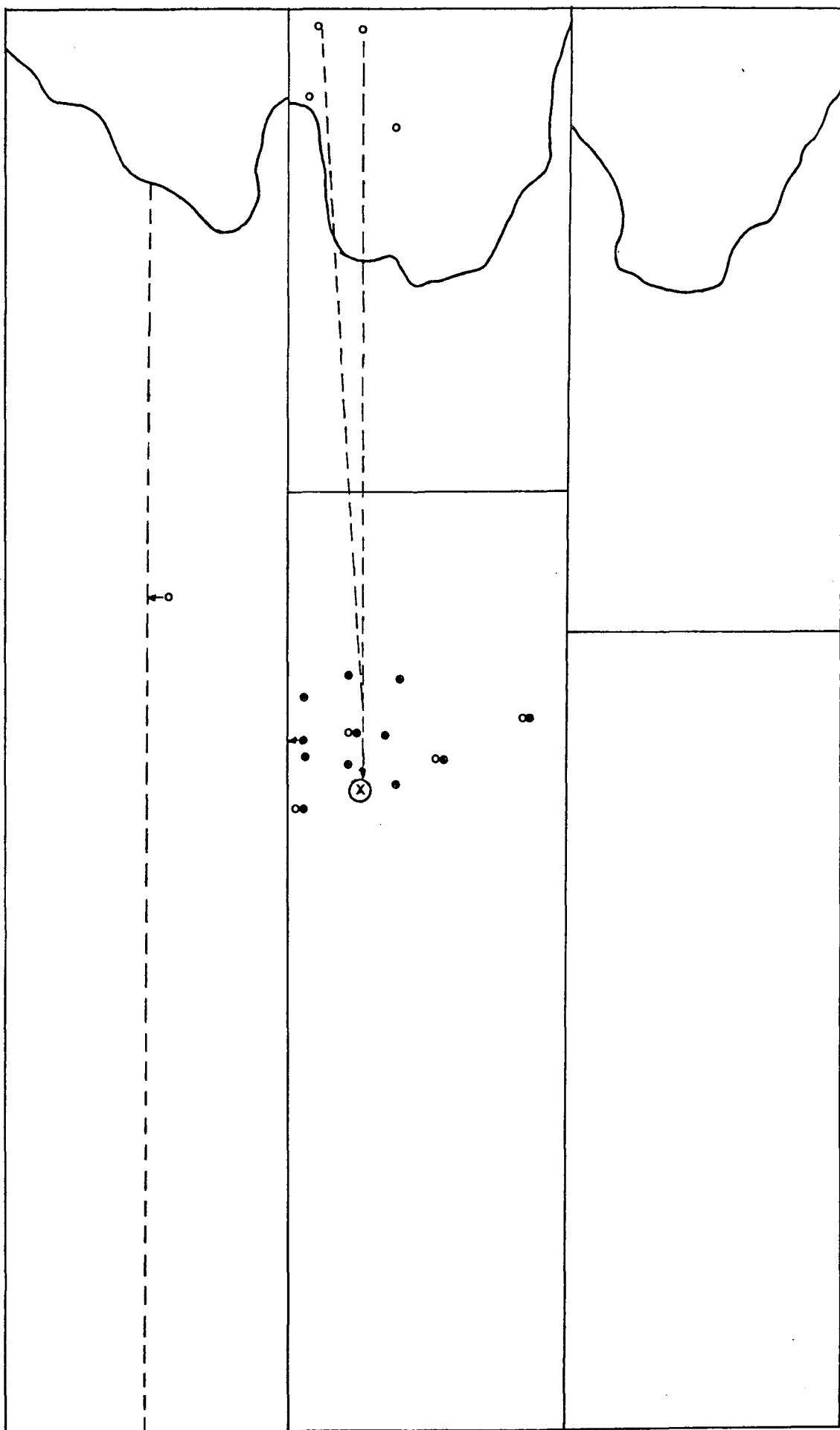


Fig.15. Pre-egg phase and Egg-phase feeding locations of Pair D individuals, Tower colony.

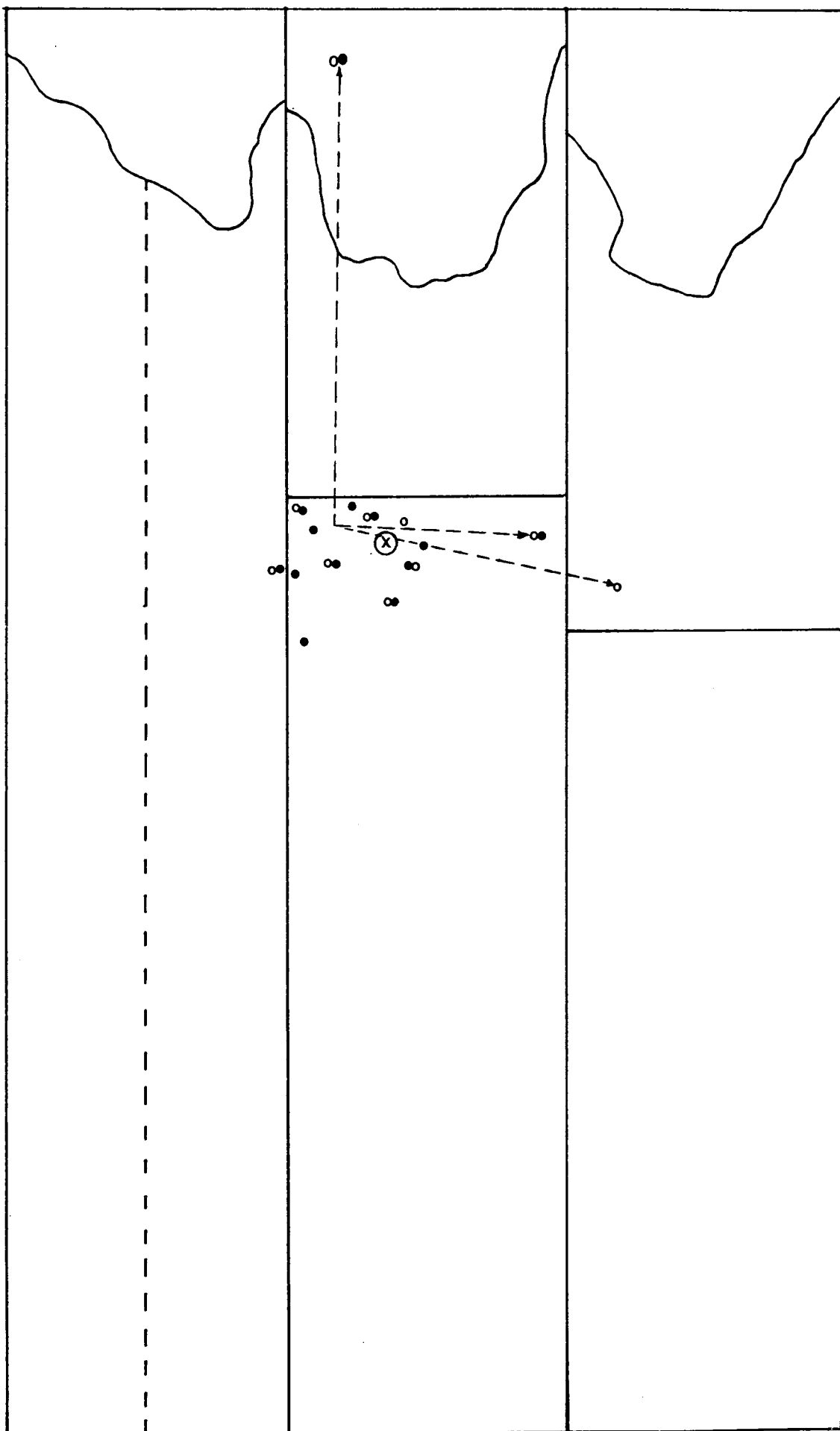
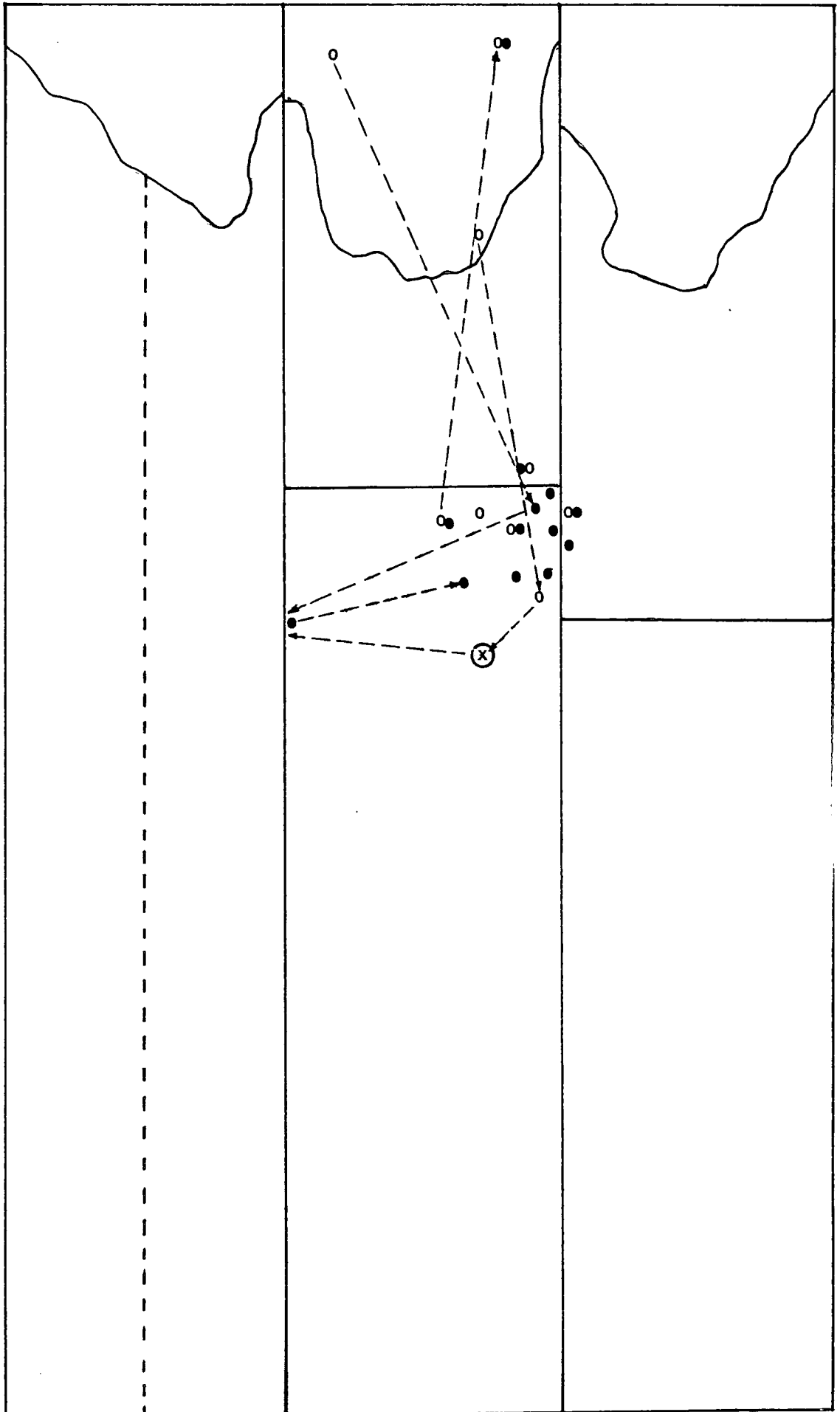


Fig.16. Pre-egg phase and Egg-phase feeding locations of Pair E individuals, Tower colony.



distances from the nest site at both stages of the breeding cycle; but female C fed significantly closer to the nest during the pre-egg phase ($t=5.18$; $P<0.01$). Overall, there was a tendency for both birds of a pair to feed at greater distances from the nest during the pre-egg phase than during the egg-phase. At this time the pair wandered around a large "courtship" area, presumably in search of suitable nesting sites. However, males in particular remained close to the nesting site during incubation. Thus, wandering during the pre-egg phase could also have provided the chance of sampling the feeding environment within the general vicinity of the colony. Presumably it would be advantageous, in terms of nest defence, to have good feeding grounds close to the nest. This would ensure that the off-duty bird was close by and able to respond to predators; the incubating bird may then remain on the nest.

The position of favoured feeding sites often varied between members of the pair. For pair A, at the Singing Washes (Fig.10), sightings of feeding birds were few but they suggest that the female fed at greater distances from the nest than the male. For pair B (Fig.11) the difference was obvious, the female feeding significantly further away ($t=2.83$; $P<0.01$), but in pair D (Fig.12) the feeding ranges of the sexes overlapped. At the Tower colony (Table 20), the female of pair B probably fed at greater distances than the male (Fig. 13) and of pair C, definitely so ($t=3.21$; $P<0.01$). Females D and E also tended to feed at greater distances from the nest than did males. Females often utilised pools of standing water and the damper regions of fields as feeding areas. Hence, the territory seems to supply adequate feeding

for the male but fails to do so for the female who perhaps requires a better food supply in order to gain food at a faster rate during the short periods spent off the nest during incubation.

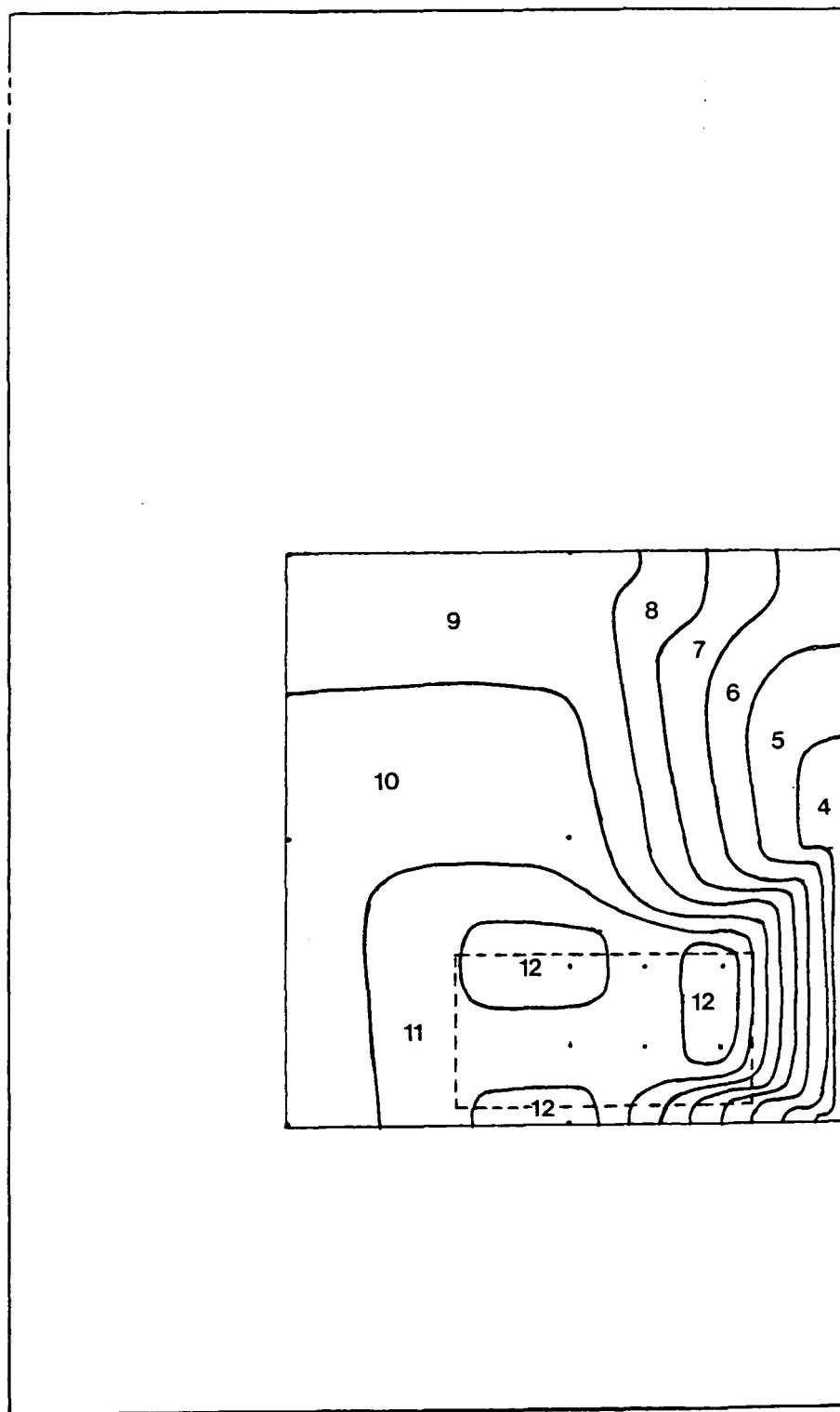
During the breeding season, the Black-tailed Godwit obtains the majority of its food by probing into soft soil (Witherby et al., 1940). A wide range of soil invertebrates are taken (see Cramp & Simmons, 1983). The presence of favourable feeding sites may be important in both nest site and nesting area selection and may also play a role in determining colony size. In order to investigate the characteristics of the preferred feeding sites I examined their topography. One might expect godwits to feed in hollows where the ground may be damper and more penetrable. The topography of the preferred feeding area of each bird was compared with that of other areas of the nesting field at similar distances from the nest (Table 21; Figs.17-21). None of the feeding areas used by birds of the Tower colony were significantly different from other areas of the fields, and of birds from the Singing Washes, only pair A fed at a "field pool" located at a significantly lower level than other available areas ($t=2.86$; $P<0.05$).

The vegetation of a site may often reflect a particular set of physical and chemical environmental conditions. If preferred feeding sites can be distinguished from other nearby sites in terms of their plant composition, then this may suggest which properties of the site make it favourable. For example, the vegetation of grazed sites is often characteristic of soils rich in nutrients with plants tending to be of low and creeping form. Birds feeding in such

Table 21. Average heights of feeding areas and non-feeding areas.
 Heights were measured relative to each other.

PAIR	FEEDING AREAS	NON-FEEDING AREAS
Singing Washes B	1.48 ± 0.08 (n=6)	1.56 ± 0.05 (n=9)
Singing Washes A	1.75 ± 0.03 (n=6)	1.61 ± 0.12 (n=8)
Singing Washes D	1.54 ± 0.09 (n=24)	1.55 ± 0.13 (n=48)
Wortleys (Tower) C	1.55 ± 0.04 (n=6)	1.49 ± 0.12 (n=8)
Wortleys (Tower) D	1.59 ± 0.012 (n=6)	No data
Wortleys (Tower) E	1.5 ± 0.05 (n=6)	1.53 ± 0.1 (n=15)
Sand & Gravel (Tower) B	1.54 ± 0.05 (n=6)	1.29 ± 0.04 (n=11)

Fig. 17. Topography of the feeding area on 1st Singing Wash.
High numbers represent low sites.
Feeding area is enclosed by dotted lines.



Scale: 1cm = 13.9m

Fig. 18. Topography of feeding areas on 2nd Singing Wash.

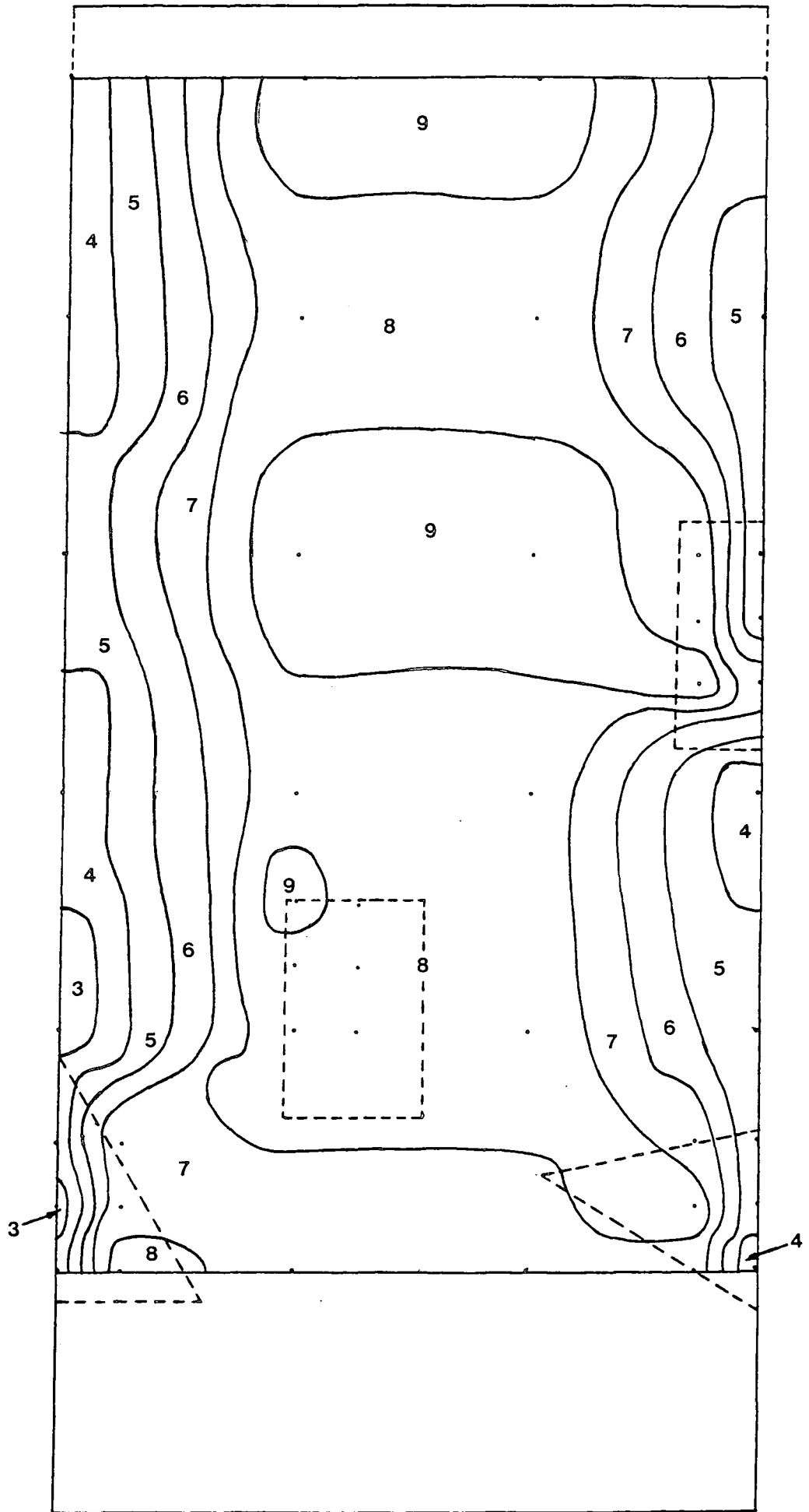


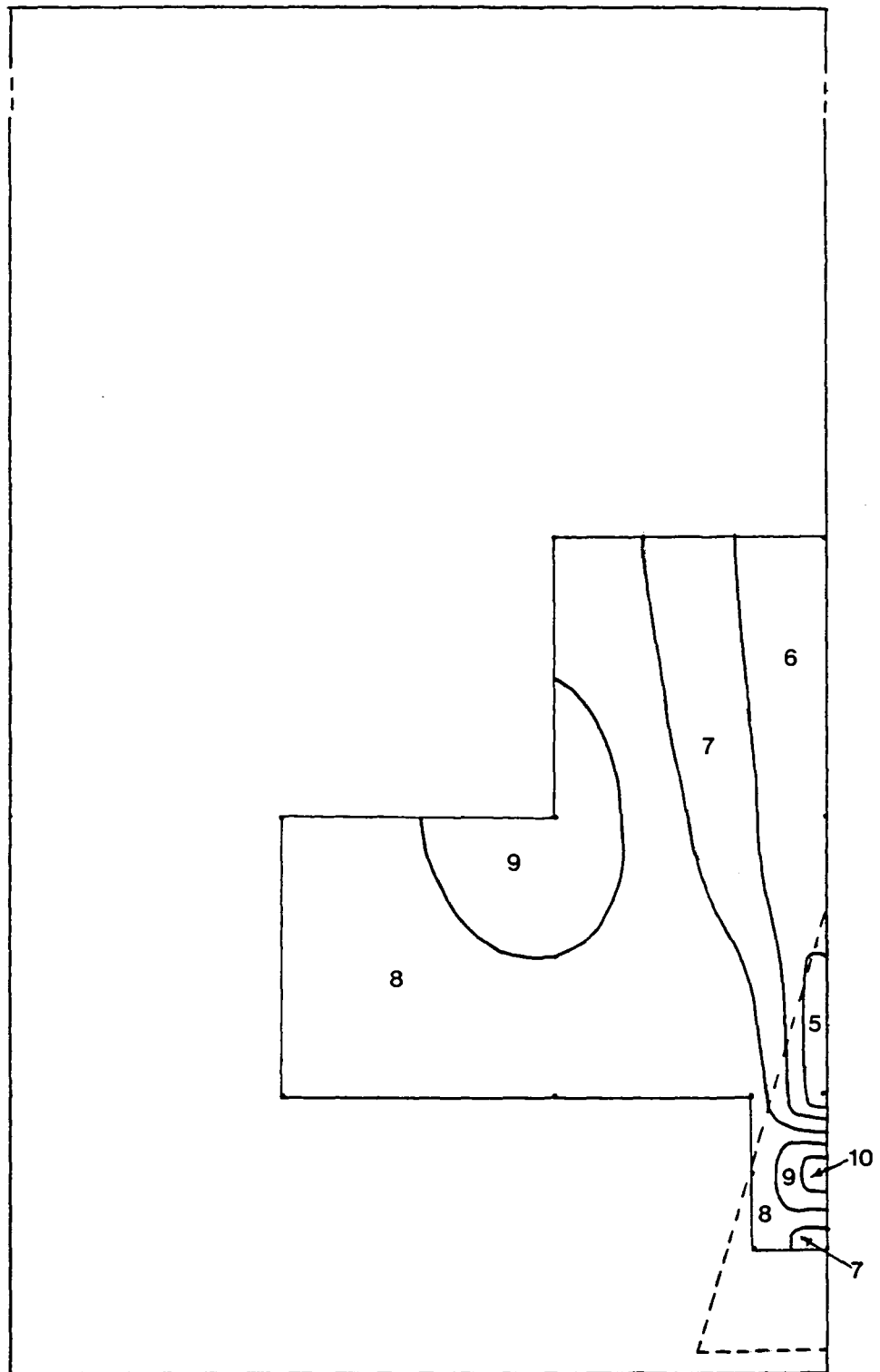
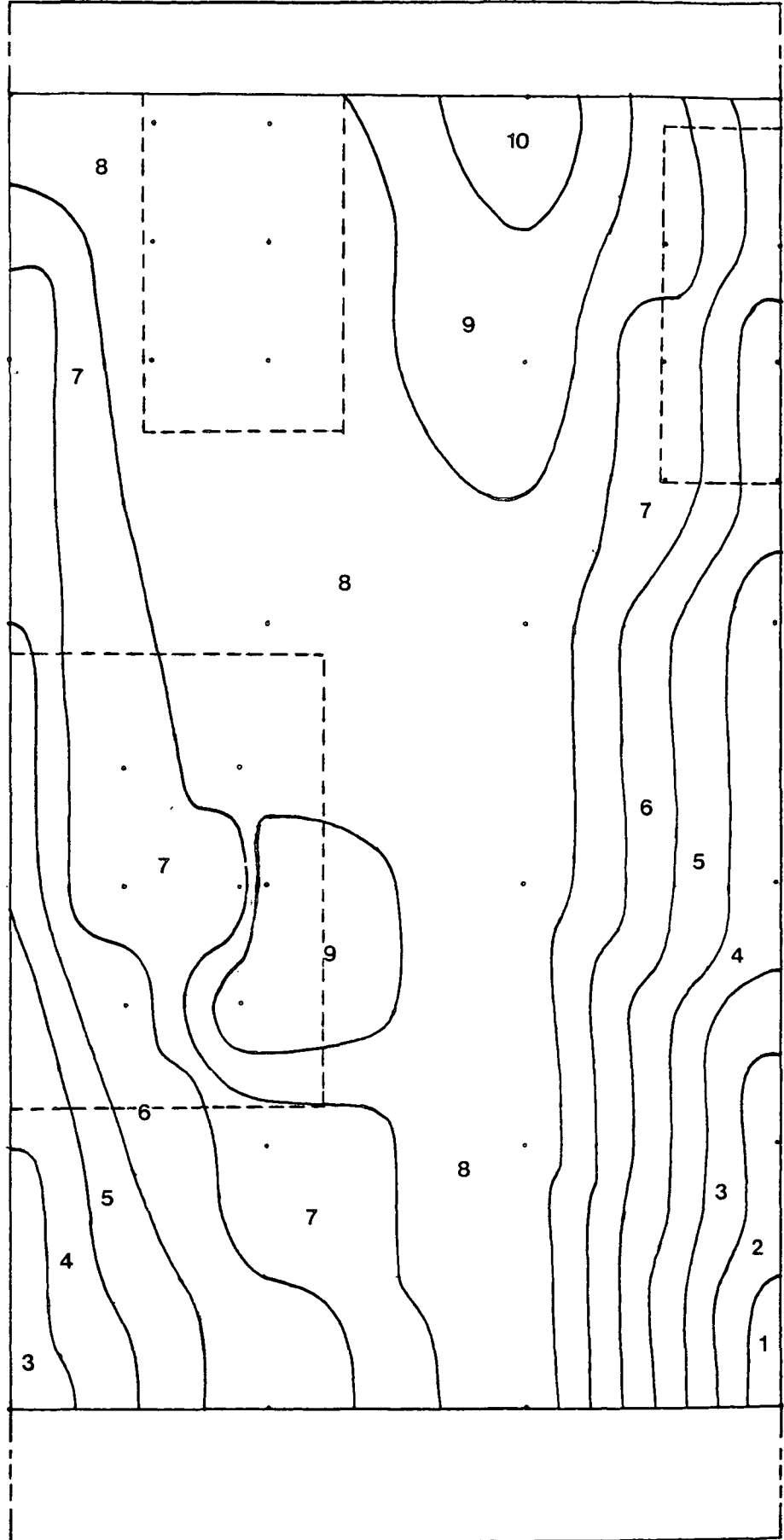
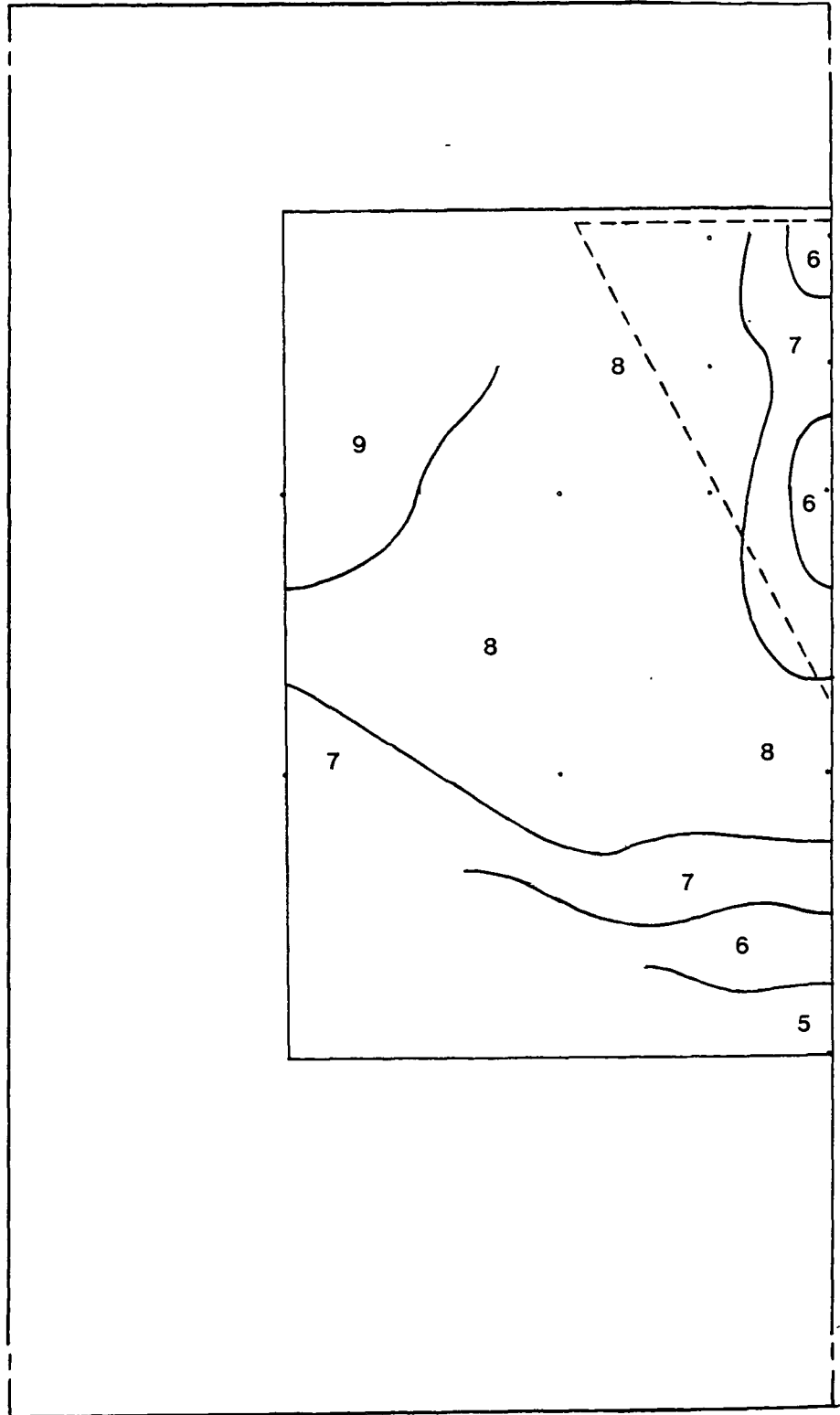
Fig.19. Topography of the feeding areas on 3rd Singing Wash.

Fig.20. Topography of feeding areas on 'Wortley's Wash' (Tower).



Scale: 1cm = 11m

Fig. 21. Topography of the feeding area on 'Sand & Gravel' (Tower).



sites could find it easier to detect predators than in a taller stand of vegetation. For such reasons, I examined the vegetation of feeding areas and non-feeding areas chosen at random (Appendix 3).

At the Singing Washes, feeding areas could be distinguished from the non-feeding areas by the composition of the vegetation (Table 22). Polygonum amphibium and Cirsium spp. together accounted for 53.6% of the discrimination between feeding and non-feeding areas. Ranunculus repens accounted for 15.4% and Caltha palustris, 9.1%. Phalaris arundinacea, Achillea millefolium, Myosotis scorpioides, Eleocharis palustris and various Graminae were more characteristic of feeding than non-feeding sites. Potentilla anserina, Plantago spp., Mentha aquatica, Carex spp. and Filipendula ulmaria occurred only in non-feeding areas. For reasons that are not clear, at the Tower colony, discrimination between sites on the basis of vegetation was not possible (Table 23).

Measurement of feeding rates of godwits was undertaken to examine whether females acquired food more rapidly than males when flying off to supposedly better feeding sites, and to give a first indication of the spatial distribution of invertebrate foods. There was little difference in feeding activities (probing, stepping and swallowing) of male and female birds (Table 24-26) although females acquired food at a slightly faster rate, on average than males.

The rate at which such feeding activities are executed may be expected to be inter-correlated. For example, at a poor feeding site, the intensity of probing may be low and the rate of stepping high; this would move the bird, with continued sampling, out of the poor feeding site. Similarly,

Table 22. Summary of Discriminate function analysis of the vegetation of feeding and non-feeding sites at Singing Washes.

Coefficients of Discriminant function			
<u>Variable</u>	<u>Lambda</u>	<u>Standardised Lambda</u>	<u>Percentage added</u>
1	-0.05	-0.98	-4.00
2	-0.05	-0.67	7.95
3	-0.12	-0.97	26.81
4	-0.04	-0.42	1.00
5	-0.05	-0.19	2.50
6	-0.08	-0.55	-2.13
7	0.07	0.20	2.27
8	-0.22	-0.62	7.91
9	-0.16	-0.88	26.72
10	0.20	1.01	15.41
11	-0.26	-0.93	9.13
12	-0.04	-0.63	6.02

Probability that samples originate from the same normal distribution = 0.12

Estimated probability of misclassification

on feeding sites = 0.23

on non-feeding sites = 0.36

Percentage of samples correctly assigned by the linear function

feeding sites = 87.5%

non-feeding sites = 62.5%

Percentage of samples correctly assigned by the quadratic function

feeding sites = 100%

non-feeding sites = 75%

Table 23. Summary of Discriminate function analysis of the vegetation of feeding and non-feeding sites at the Tower colony.

Coefficients of Discriminant function

Variable	Lambda	Standardised Lambda	Percentage added
1	-0.002	-0.03	0.59
2	0.08	1.09	1.07
3	-0.06	-0.95	8.05
4	0.19	0.77	-3.20
5	-0.02	-0.19	-1.37
6	-0.02	-0.02	-0.09
7	0.64	1.48	16.00
8	0.48	1.10	2.67
9	0.15	0.62	-6.38
10	-0.53	-0.10	-2.23
11	-0.20	-0.56	0.27
12	-0.39	-0.42	22.07
13	0.18	0.50	-1.98
14	0.72	1.63	24.19
15	1.39	0.90	1.95
16	0.42	2.25	38.39

Probability that samples arise from the same normal distribution = 0.42

Estimated probability of misclassification

on feeding sites = 0.15

on non-feeding sites = 0.45

Table 24. Feeding rates of pre-egg phase males.

(FP = field pool; F = field)

DATE	LOC.	PAIR	DURATION (mins)	ACTIVITY MIN ⁻¹		
				PROBE	STEP	SWALLOW
20/4	FP	SW/A	1-10	4.29	11.1	0
			2-30	7.6	25.6	0
			1-54	3.16	4.7	0
			1-59	11.1	22.2	1.51
			2-33	15.3	62.0	0
			1-00	9.0	9.0	4.0
			1-57	5.13	26.2	2.05
			1-08	4.41	22.9	1.77
			2-12	9.09	10.0	2.29
			0-39	21.54	21.5	1.54
			1-20	12.75	17.3	1.50
			1-30	10.00	20.0	2.00
			1-27	8.97	37.9	1.38
			1-28	8.18	22.5	4.09
			1-15	8.00	14.4	5.60
			0-20	24.00	54.0	0
			1-20	11.25	24.8	2.25
			1-28	8.18	12.3	2.27
			1-28	13.64	28.6	0.68
			2-19	10.79	20.7	2.16
2-38	5.32	49.0	0.38			
21/4	FP	SW/A	2-20	6.43	42.4	0
			0-45	6.67	61.3	0
			1-14	11.35	21.1	4.05
			1-40	13.20	24.6	0.6
			1-40	11.4	16.2	5.4
			0-30	10.0	18.0	4.0
22/4	F	SW/A	3-07	13.16	12.2	1.93
29/4	F	SW/D	2-20	13.33	6.5	1.33

Table 25. Feeding rates of pre-egg phase females.

DATE	LOC.	PAIR	DURATION (mins)	ACTIVITY MIN ⁻¹		
				PROBES	STEPS	SWALLOWS
20/4	FP	SW/A	1-22	9.51	22.0	0
			0-45	12.0	30.7	5.33
			1-02	10.65	9.7	4.84
			0-26	9.23	6.9	0
			0-59	12.20	14.2	5.09
			1-08	8.82	29.1	1.77
			1-21	7.41	23.0	3.70
			0-53	11.32	43.0	2.26
			1-05	11.08	28.6	2.77
			1-28	8.86	17.0	4.09
			1-32	9.78	9.8	4.57
			0-41	10.24	29.3	0
21/4	FP	SW/A	1-20	10.50	24.0	3.0
			2-04	9.68	14.5	3.87
			1-05	12.92	32.3	0
			2-15	9.33	15.1	4
			2-25	10.22	9.1	1.78
			2-05	9.6	6.2	4.32
			2-05	9.6	11.5	3.36
			1-02	11.61	10.6	2.90
			2-36	10.0	16.2	3.46
			1-00	11.0	10.0	6.0
24/4	F	T/C	1-55	9.39	42.8	0.52
			0-50	16.80	40.8	-
28/4	F	SW/D	1-05	14.77	11.1	4.62
			1-20	18.0	14.3	0.75
			1-20	15.75	12.8	0.75
			2-45	14.91	9.5	1.45

Table 26. Feeding rates of off-duty birds.

DATE	LOC.	PAIR	SEX	DURATION (mins)	ACTIVITY MIN ⁻¹		
					PROBE	STEP	SWALLOW
22/4	F	SW/B	♂	2-30	12.0	12.2	3.20
			♂	0-45	14.67	15.6	1.33
24/4	F	T/A	♂	1-30	17.33	15.3	-
28/4	F	SW/B	♂	3-20	16.50	6.3	0.30
			♂	2-02	16.72	18.2	0.98
			♂	2-15	17.33	20.4	2.67
			♂	2-05	15.36	12.0	2.40
			♂	2-47	13.29	12.9	3.59
			♂	1-30	14.0	15.3	2.0
29/4	F	SW/B	♂	2-20	13.71	8.1	2.14
1/5	F	Y	♂	3-20	14.70	14.7	2.10
			♂	3-40	12.82	28.6	3.27
			♂	3-37	12.17	19.9	-
			♂	1-03	8.57	39.7	-
2/5	F	Y	♂	2-30	12.80	23.6	0.4
5/5	F	SW/B	♂	1-48	13.33	11.1	-
			♂	2-12	12.73	27.3	-
15/5	F	SW/D	♂	1-18	17.69	18.5	0.77
			♂	2-21	20.85	19.1	2.55

the degree of probing and swallowing may be related; where feeding is good (high swallowing rate) then a fast probing rate may be expected. However, there was no significant relationship between either stepping and probing or probing and swallowing, although the number of steps taken declined as the number of swallows made increased (Fig. 22). Thus, if feeding was profitable then the bird remained relatively still; this implies the food to be abundant at that point or aggregated.

Observations on pair A (Singing Washes) feeding at a field pool suggest that the female made a similar number of probes per minute, but moved less and swallowed more often. This implies that the female was gaining food faster. Female Black-tailed Godwits have a longer bill than males (Prater et al., 1977; Cramp & Simmons, 1983) and this may be responsible for the differences in the rate of food acquisition. Although observations were few, a male of another pair feeding on one of the permanent pools to which off-duty females flew, probed fast, moved little and swallowed prey at a fast rate. This suggests that feeding at such pools was extremely profitable.

Breeding Biology.

Information on the breeding biology of the Black-tailed Godwit in Britain is sparse, apart from a paper by Richardson (1971). In the context of the present project, I sought information on breeding success within colonies of different sizes, and on nest predation and other causes of nest failure.

A minimum of 21 pairs of birds attempted to breed, 15 of these being located within 3 colonies (Table 27). Most

Fig. 22. The relationship between the number of steps and swallows taken whilst feeding.

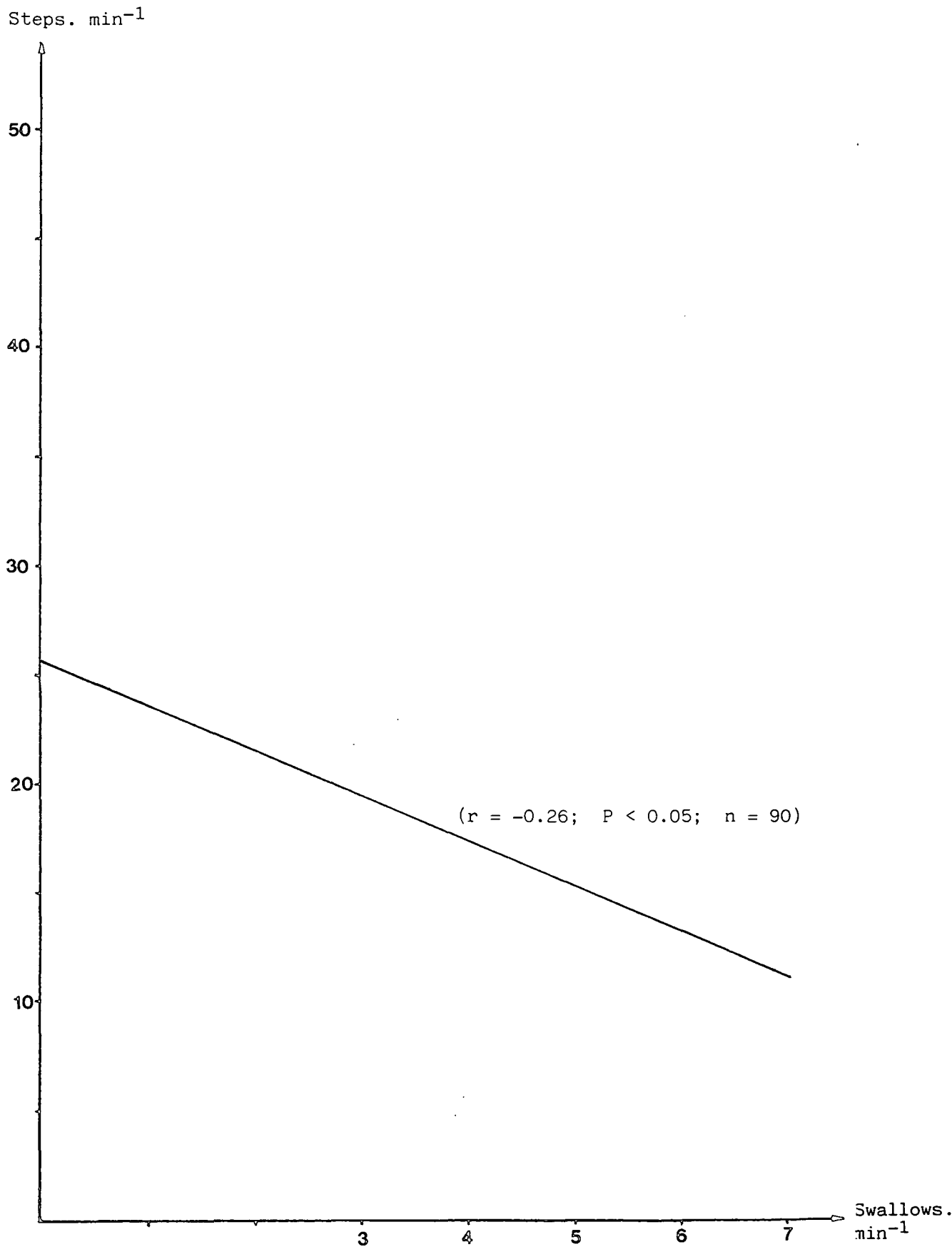


Table 27. Breeding data for Black-tailed Godwits nesting in colonies and as single pairs.

	Singing Washes	Tower Colony	Other Small Colony	Single Pairs	Total
No. of breeding pairs	5	7	3	6	21
No. of nests (inc. repeats)	5	9	3	7	24
No. of eggs laid	12 + 8* = 20	24 + 12* = 36	12*	8 + 20* = 28	96*
No. of successful nests	1	4	1	1	7
No. of eggs hatched	4	16	?	?	20+
No. of chicks fledged (min)	(1)	(3-6)	(1)	(1)	(6-9)
% of eggs laid producing flying young	(5)	(8.3-16.7)	(8.3)	(5)	(6.3-9.4)

* Estimated

? Not known

Figures in brackets are speculative

first clutches consisted of 4 eggs, although 3 eggs is the commoner size of repeat clutches (R.E.Green, pers.comm.). 29% of all nests were successful, the majority of these were situated within the Tower colony. A minimum proportion of only 20.8% of the eggs laid hatched; at the Singing Washes, 20% hatched whereas at the Tower colony the figure was twice as high (44%).

The causes of nest failure (Table 28) were varied. An estimated 25% of all nests were lost through flooding, 12.5% to predation, 8.3% were deserted and 4.2% trampled. The causes of nest failure of a further 20.8% of cases were not known. At the Singing Washes, desertion and predation accounted for 20% each of nest failures; at the Tower, predation and flooding were the main reasons for failure. The causes of failure of nests of single pairs were largely unknown (42.8%). Pairs with chicks at the time of flooding (late May) seemed able to survive.

Sightings of chicks were infrequent and often involved only one individual. 3 pairs were known to have reared one chick each to fledging; 2 of these originated from the Tower colony, the other was a single pair. In total an estimated 6-9 chicks reached flying age. This represents 6.3 - 9.4% of the maximum production possible. A maximum of 7 juveniles were counted together on any one occasion in the post-breeding flock.

In summary, predation accounted for a significant proportion of nest failures although overall, flooding was the major cause of losses. Breeding success was highest in the largest of the 2 main colonies; that of single pairs was apparently as high as that of the smaller colony in

Table 28. Outcome of Godwit nests.

	Singing Washes	Tower Colony	Other Small Colony (Railway)	Single Pairs	Total
% trampled	0	0	?	14.3	4.2
% predated	20	22.3	?	?	12.5
% flooded	0	33.3	66.7	14.3	25.0
% deserted	20	?	?	14.3	8.3
% hatched	20	44.4	33.3	14.3	29.2
% unknown	40	-	-	42.8	20.8

this one year.

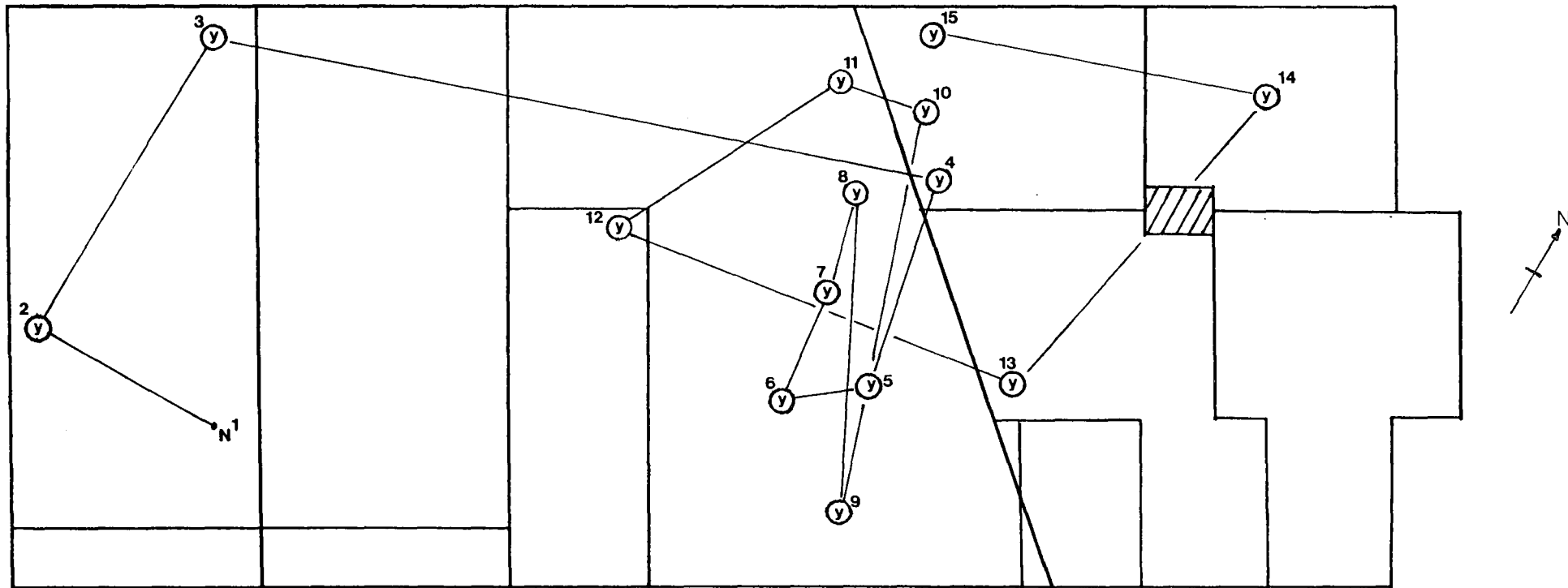
Chick Movements.

It is possible that nest sites and colonies are situated in areas which provide good food supplies for the chicks. For Lapwings, Rankin (1979) considered this to be the case. However, Redfern (1982) thought that the habitat requirements for nesting and chick rearing may be different and hence Lapwing chicks may be moved away from a nesting area. Godwit chicks are highly mobile (Cramp & Simmons, 1983) and are capable of travelling distances of several kms.

The day to day movements of pairs with chicks were followed for 2 single pairs and for 4 pairs from the Tower colony. The chicks of Pair B (Singing Washes) were moved very rapidly away from the nesting colony (Fig 23) and adults were soon effectively operating as a single pair. The distance moved between fixes was extremely variable (Table 29) and ranged from 74-363m. The highest rate of movement was recorded when the chicks were very young. The chicks of the second pair (pair J) were also very young when discovered (Fig.24). Rates of movement (Table 30) varied between 1.4 and 70 m/hr. The average rate of movement (26.4 m/hr) was similar to that of the previous pair (28.2 m/hr). However, pair B roamed over a much larger area.

During the first 10-20 days after hatching, pairs with chicks remained within the vicinity of the Tower colony (Fig. 25; Table 31). One pair then moved to the west of the main colony area where it then remained. Another moved to the north and stayed there. The two remaining pairs then moved together for approximately 1km. to the north-east and away

Fig. 23. Diagram showing the movement of pair SW/B and chicks from the nest site.
(Numbers represent order of movement; N = nest site)

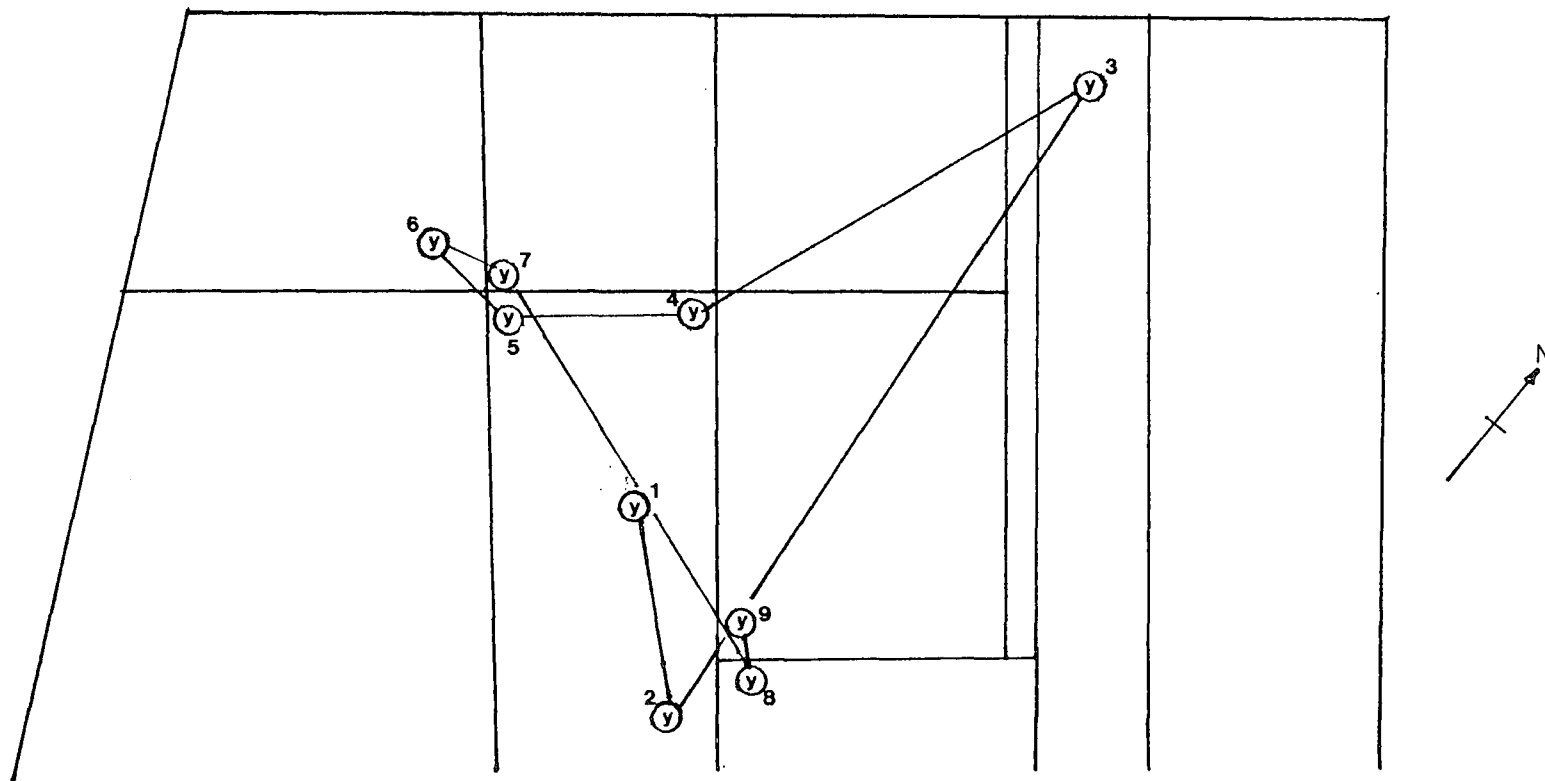


Scale: 1mm = 5.26m

Table 29. Key to the positions and movement of the chicks of pair SW/E.

<u>Position Number</u>	<u>Distance of movement (m)</u>	<u>Duration of movement (hrs)</u>	<u>Rate of movement (m/hr)</u>
1			
2	168.3	34	4.95
3	289.3	2.5	115.72
4	631.2	20.5	30.79
5	189.4	21.5	8.81
6	78.9	14.0	5.64
7	105.2	29.5	3.57
8	94.7	10.8	8.81
9	278.8	131.0	2.13
10	352.4	7.5	46.99
11	73.6	3.5	21.03
12	226.2	2.0	113.10
13	362.9	85.0	4.27
14	331.4	60.0	5.52
15	284.0	12.0	23.67

Fig. 24. Diagram showing the movements of pair J with chicks.



Scale: 1mm = 5.26m

Table 30. Key to the positions and movement of the chicks of Pair J.

<u>Position Number</u>	<u>Distance of movement (m)</u>	<u>Duration of movement (hrs)</u>	<u>Rate of movement (m/hr)</u>
1			
2	147.3	105.00	1.40
3	526.0	117.00	4.50
4	315.6	4.50	70.10
5	126.2	3.50	36.10
6	68.4	24.00	2.85
7	52.6	2.75	19.13
8	331.4	4.50	73.60
9	42.1	12.80	3.30

Fig. 25. Diagram showing the movements of birds with chicks from the Tower colony.

(Large arrows represent main movements; N = nest sites)

Scale: 1mm = 5.25m

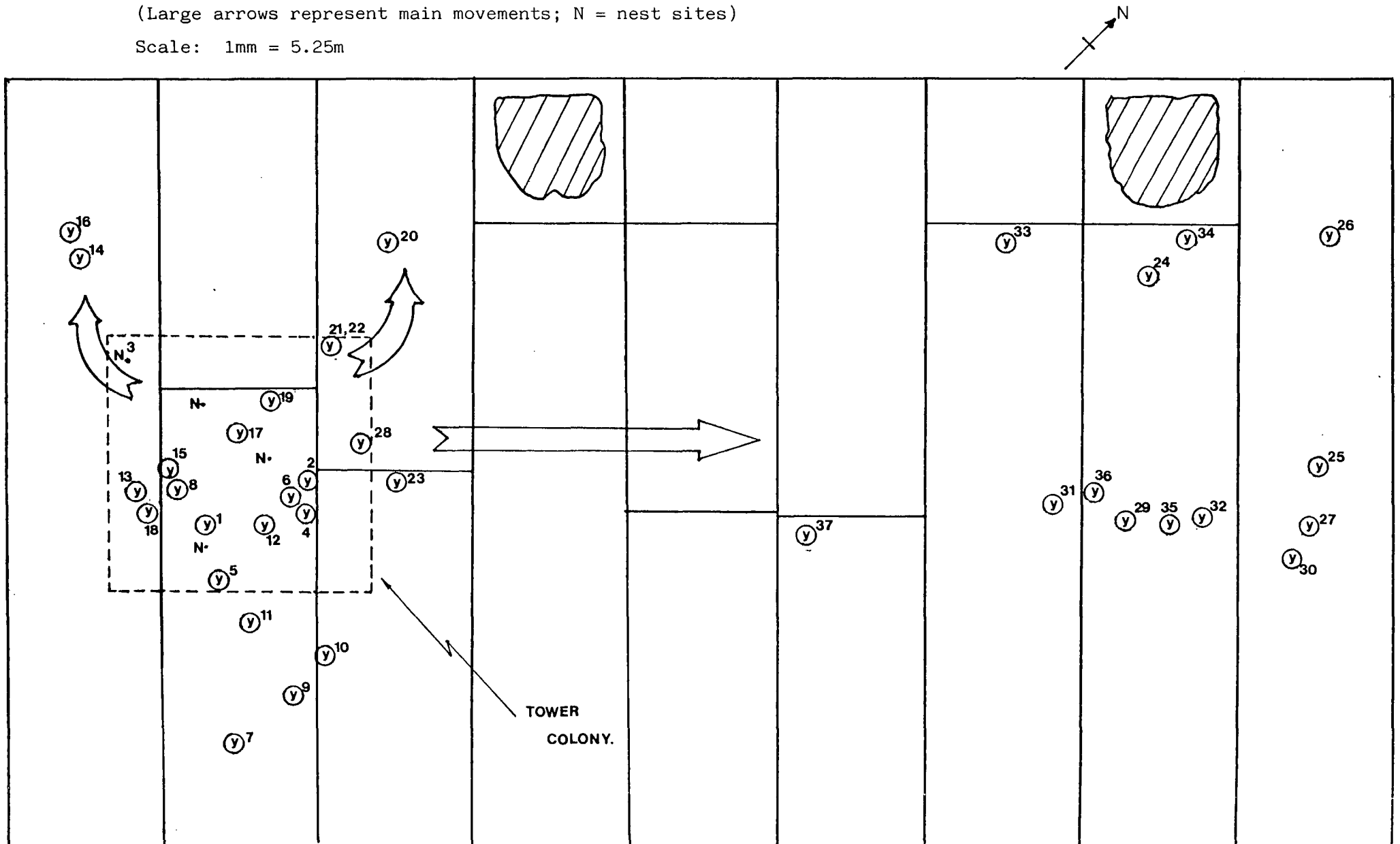


Table 31. Key to positions of birds with chicks originating from the Tower colony.

<u>Position</u>	<u>Date</u>	<u>Time</u>	<u>Position</u>	<u>Date</u>	<u>Time</u>
1	20/5	0900	20	14/6	0900-1030
2	23/5	0900	21	16/6	1400
3	2/6	0800-1100	22	19/6	1000
4	"	"	23	20/6	1200
5	3/6	1030-1430	24	"	1130
6	6/6	0700-1100	25	"	"
7	"	0700	26	21/6	0930-1030
8	"	1100	27	"	"
9	7/6	1500-1700	28	"	1045
10	"	"	29	23/6	0630
11	10/6	0900-1100	30	"	"
12	"	"	31	24/6	1430
13	"	"	32	"	"
14	12/6	1400-1700	33	25/6	1100
15	"	"	34	27/6	"
16	13/6	1000-1200	35	"	1400
17	"	"	36	10/7	0800
18	14/6	0900-1030	37	11/7	0900
19	"	"			

from the colony.

Thus, godwit chicks are extremely mobile and may move distances in excess of 1km. and survive. In general, they are moved away from the immediate vicinity of the colony but the time at which this takes place varied.

Anti-predator Behaviour.

Aggregation may serve an anti-predator function. The responses to predators are particularly well developed among waders, varying from avoidance to physical attack, and any one species may exhibit a variety of responses (Simmons, 1952). I investigated not only whether aggregation increased the efficiency of anti-predator defence but also whether the defending godwits altered the behaviour of the predators in such a way as to decrease the probability of successful predation at the godwit nests. To do this, I examined whether anti-predator activity resulted in partial or complete exclusion of predators from a zone around the nest or a group of nests.

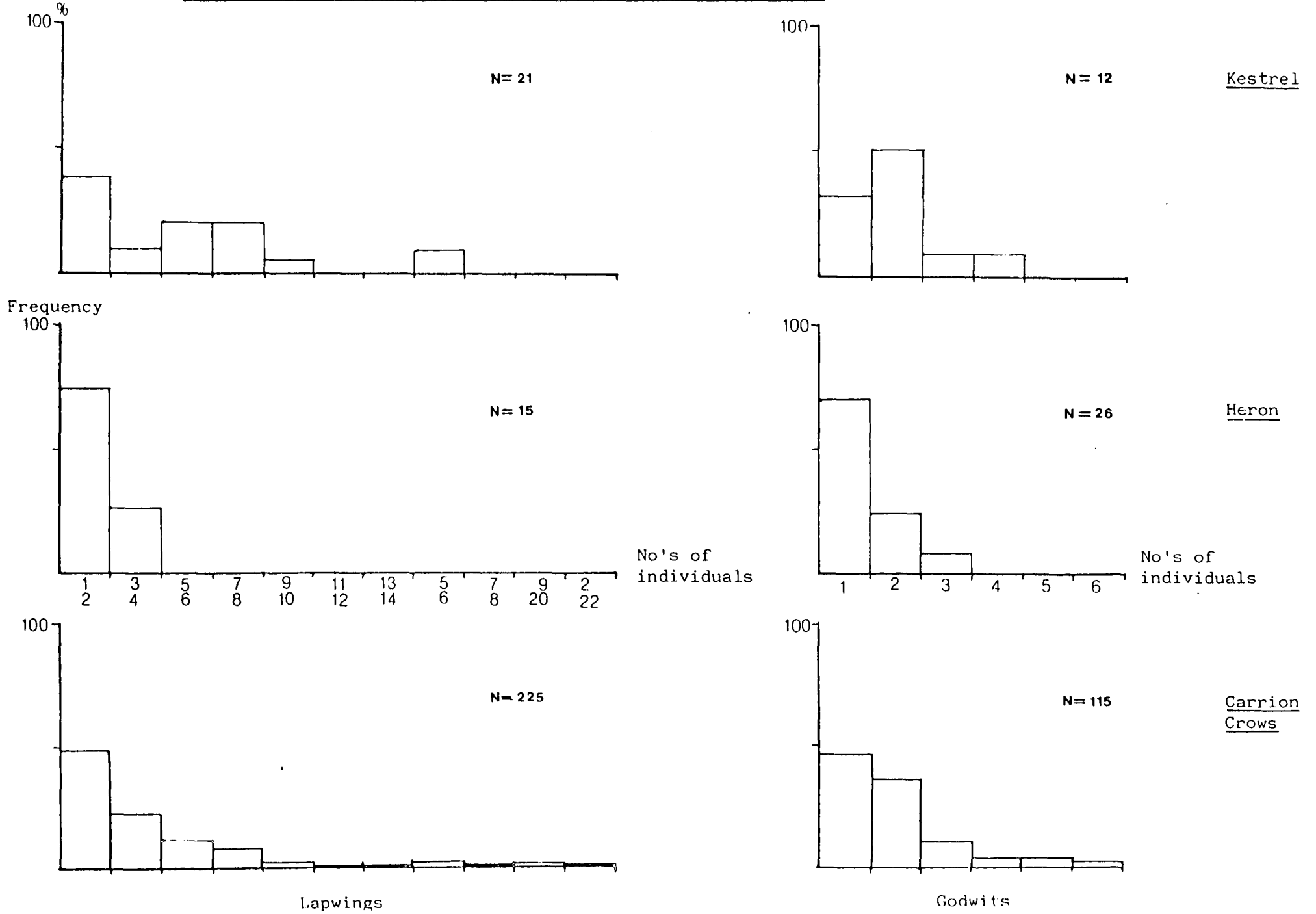
During this study a wide variety of "mobbable" species were recorded within the two main colonies; however, 3 species made up the majority of sightings. 354 overflyings by Carrion crows (Corvus corone corone) were observed, of which 71% were mobbed by either Lapwings or Black-tailed Godwits. 60 sightings of Grey herons (Ardea cinerea) and 36 of Kestrels (Falco tinnunculus) were also made; 62% and 81% of these, respectively, were mobbed. Other species recorded included Marsh Harrier (Circus aeruginosus), Cuckoo (Cuculus canorus) various Gulls (Laridae). Mammalian predators recorded were Fox (Vulpes vulpes), Stoat (Mustela erminea) and Weasel (M. nivalis).

The majority of crows were mobbed by Lapwings only (63%) although many were mobbed by both Lapwings and Godwits (32%). Conversely, 56% of all Herons were mobbed by Godwits alone, 28% by Lapwings and only 17% by both species. 60% and 30% of Kestrels were mobbed by Lapwings alone and Godwits alone, respectively. Bearing in mind that there are probably far more Lapwings available to mob than Godwits; the former may be more responsive to crows and Kestrels and the latter to Herons (the data on the numbers of Lapwings was not available to test this).

Groups of birds are often more effective at mobbing a predator than are just a few individuals (Lemmetynen, 1971; Fuchs, 1977; Elliot, 1982 etc.). Therefore the number of birds involved in mobbing events is important; this varies considerably, especially for Lapwings (Fig.26). If the predator involved was a crow then a single Godwit was most likely to respond. Also, frequently only a single Lapwing was involved although up to 4 was common. A maximum number of 6 Godwits and 22 Lapwings were involved in mobbing events. In general, fewer birds of either species mob Herons presumably because they are much less of a threat. In response to Kestrels, 2 Godwits were most frequently involved and between 1 and 8 Lapwings. Thus, to judge by the numbers of mobbing individuals, both Kestrels and crows represent a significant threat.

The responses of Lapwing and Godwits varied according to the type of predator involved; the response of predators also varied. Godwit attacks are generally very vicious (e.g Richardson, 1971; Cramp & Simmons, 1983). Mobbing by Godwits caused both Kestrels and crows to

Fig. 26. The numbers of Lapwings and Godwits mobbing various predators.



retreat from the area as quickly as possible; conversely, Herons continued on their way regardlessly. Frequently, the alarm calls of Godwits were enough to deter intruders and contact was not necessary. Lapwing mobbing was more prolonged and appeared to be much less effective. Crows passing high over an area were less likely to be mobbed than those passing through at low levels. Crows often climbed higher to escape from mobbing and then retreated. Large groups of Lapwings were generally more effective at deterring predators than smaller groups or singles; their effect was similar to that of Godwit mobbing. Sometimes crows were seen to persist despite being mobbed, apparently quite effectively; this was often when they had discovered a nest and were making repeated journeys to empty it. Additional behavioural observations are given in Appendix 2.

The response of an individual to a predator may vary according to the parental role of the bird at the time. As discussed previously, female Godwits incubated for most of the day and the males were generally more vigilant and aggressive.

I examined the frequency of mobbing behaviour by Godwits to find out whether males were primarily responsible for nest defence. During the pre-laying period, in general, an intruder was ignored by the female but mobbed by the male. During the incubation phase, in most cases (60%; n=25) only the male mobbed an intruding predator; the female remained on the nest. In a further 27% of cases, in which the male was apparently absent, the female left the nest to mob. In only 13% of cases did both birds mob a predator. Whilst with chicks, one of the parents remained vigilant whilst the other

fed; in 61% of cases (n=20) predators were mobbed by the vigilant bird. Both birds were involved in mobbing at all other times. Therefore when the birds have eggs the male was generally responsible for nest defence; whilst with chicks, both sexes were equally involved.

Any differences in terms of activity budgets, the apparent effectiveness of colony defence or the degree of nest predation between two colonies may be related not only to colony size but also to differences in the use of each area by predators. The frequency of crow flights over the two study areas was found to vary with season (Fig.27); flights were few in early May but increased to a plateau level in late May and there after. This increase coincides with the estimated hatching period of most of the crow nests. The frequency of crow intrusions was generally higher at the Tower colony than at the Singing Washes; the converse was true for Kestrels (Fig.28) although both godwit colonies were subject to a similar rate of intrusion by Herons.

The responses of many waders are related to the type of predator and the degree of danger it may represent (Simmons, 1952; 1955). Also, the distance at which predators are detected may be important to the type of response observed; this distance may be related to prey group size, e.g. in Bank Swallows Riparia riparia (Hoogland & Sherman, 1976). Anti-predator responses have been shown to vary in relation to the stage of incubation and breeding season (e.g. Lemmetyinen, 1971).

I found that the responses of breeding Black-tailed Godwits varied with predator type, distance of approach

Fig. 27. Frequency of Crow passes during the breeding season.

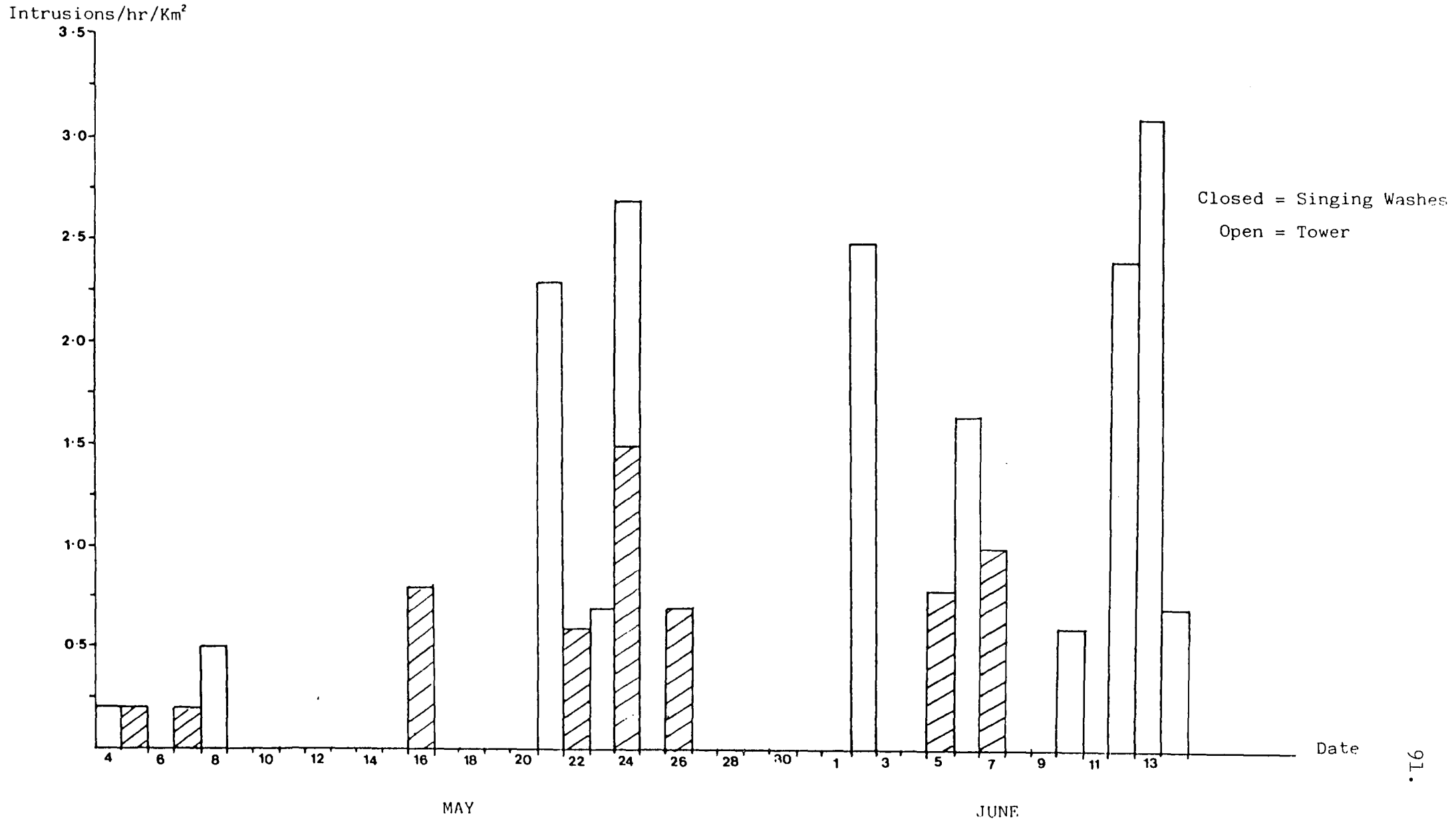
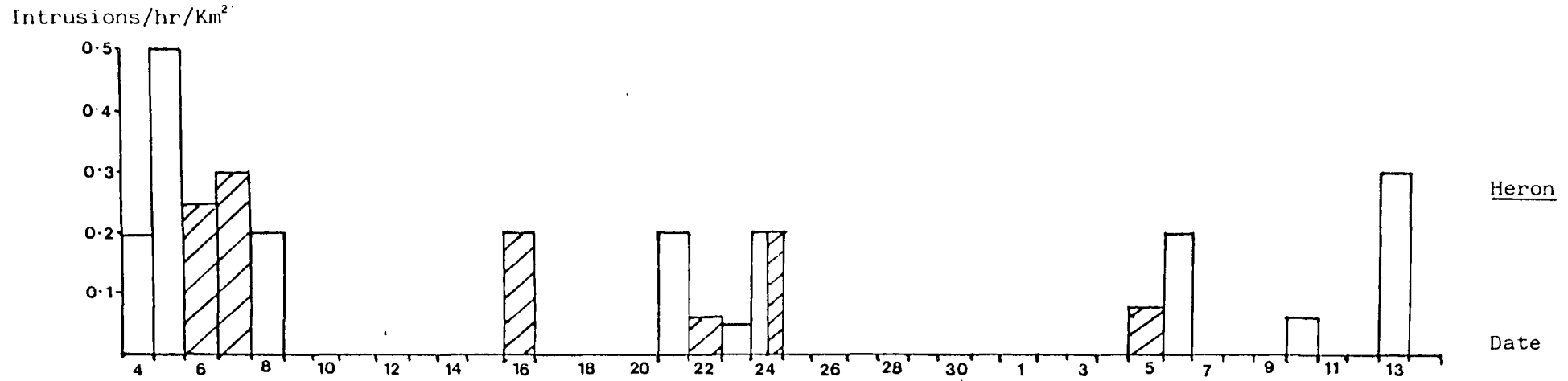
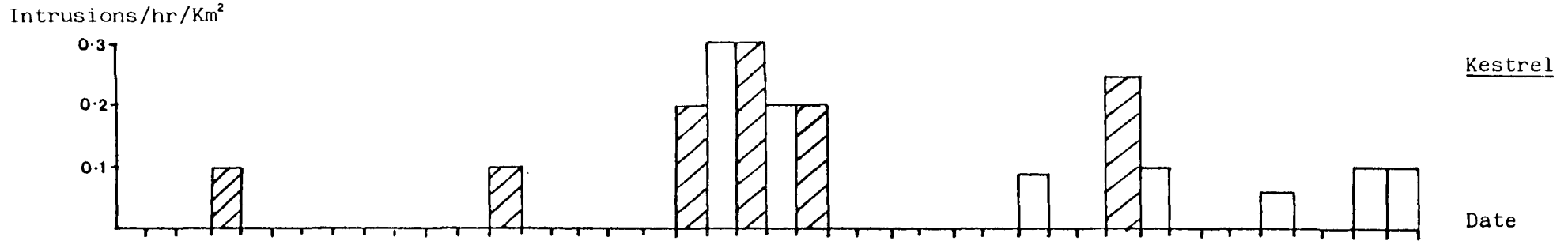


Fig. 28. Frequency of passes by Kestrels (upper) and Herons (lower) during the breeding season.



and the stage of the breeding cycle. With crows (Table 32), the closer the approach, the higher the likelihood of mobbing; there was no significant difference according to the stage of the breeding cycle (Tables 35 & 36). With Herons (Table 34), no relationship with distance was apparent; similarly there was no seasonal difference in the likelihood of mobbing (Table 35). However Kestrels provoked the most interesting response (Table 33). At all distances (Table 35), Kestrels were significantly more frequently mobbed during the chick stage ($P=0.004$; Fisher's exact test). Treating the sites and distances separately (Table 36) a significant difference, in the likelihood of Kestrels being mobbed by godwits, still existed between the egg and chick phases ($z=2.84$; $P=0.005$). Therefore the mobbing response varied according to the type of predator encountered. In addition, seasonal variation occurred in the response to Kestrels only.

As already described, Black-tailed Godwits were extremely effective at deterring predators from the nesting area. Therefore one might expect predators to avoid those areas within possible foraging grounds around their nests which are occupied by breeding Godwits. The size of such a defended area and the efficiency with which it is defended might be expected to be related to the size of the nesting group. This I examined below, bearing in mind that even if the defending species does exclude predators from a zone around the nests, this alone is not proof that colonial nesting has evolved for this purpose. Such observations need to be supplemented by information to show that the exclusion of predators led to a decrease in nest predation.

Table 32. Seasonal trends in the mobbing of Crows and distance of approach.

LOCATION	PHASE	MOBBED?	DISTANCE OF APPROACH (m)		
			0-100	100-200	200-300
SINGING WASHES	EGG	YES	19	5	5
		NO	0	13	17
	YOUNG	YES	0	3	0
		NO	0	1	1
TOWER	EGG	YES	12	5	3
		NO	5	20	55
	YOUNG	YES	11	8	2
		NO	10	12	25

Table 33. Seasonal trends in the mobbing of Kestrels.

LOCATION	PHASE	MOBBED?	DISTANCE OF APPROACH (m)		
			0-100	100-200	200-300
SINGING WASHES	EGG	Y	1	0	0
		N	8	7	1
	YOUNG	Y	2	1	1
		N	0	1	0
TOWER	EGG	Y	0	0	0
		N	2	1	0
	YOUNG	Y	2	0	0
		N	1	1	2

Table 34. Seasonal trends in the mobbing of Herons and distance of approach.

LOCATION	PHASE	MOBBED?	DISTANCE OF APPROACH (m)		
			0-100	100-200	200-300
SINGING WASHES	EGG	Y	12	0	0
		N	11	5	3
	YOUNG	Y	1	0	0
		N	0	0	0
TOWER	EGG	Y	4	3	0
		N	5	4	1
	YOUNG	Y	4	0	0
		N	0	0	3

Table 35. Analysis of seasonal trends in the response to predators at all distances less than 300m.

'PREDATOR'	PHASE	MOBB?	STATISTIC	SIG.
CARRION CROW	EGG	Y = 49	$\chi^2 = 0.09$ P ~ 0.75	N.S.
		N = 110		
	YOUNG	Y = 25		
		N = 49		
KESTREL	EGG	Y = 1	Fisher exact P = 0.004	S
		N = 19		
	YOUNG	Y = 6		
		N = 5		
HERON	EGG	Y = 19	Fisher exact P = 0.268	N.S.
		N = 29		
	YOUNG	Y = 5		
		N = 3		

Table 36. Analysis of seasonal trends in the response to predators using distance catagories; 0-100m (1), 100-200m (2) and 200-300m (3).

PREDATOR	PHASE	MOBB	DISTANCE			MANTEL-HAENSZEL TEST		SIG
			1	2	3	Z	P	
CARRION CROW	EGG	Y	31	10	8	0.68	0.50	N.S.
		N	5	33	72			
	YOUNG	Y	11	11	2			
		N	10	13	26			
KESTREL	EGG	Y	1	0	0	2.84	0.005	S
		N	10	8	1			
	YOUNG	Y	4	1	1			
		N	1	2	2			
HERON	EGG	Y	16	3	0	1.52	0.13	N.S.
		N	16	9	4			
	YOUNG	Y	5	0	0			
		N	0	0	3			

Attempts at Predation by Crows.

Crow movements in the area of the Singing Washes colony are shown in Figs. 29-31. During the time when there were 3 active godwit nests (Fig. 29), crow movements were few. However, even at this time the crows passed most frequently along the edges of the nesting fields, but flew over the field to the south-west. Later in the season (Fig. 30), when a single godwit nest remained on the centre field, crow flights were more frequent. They continued to use most of the surrounding area but now flew closer to the nesting area. The central area was still defended but the crows persisted in trying to penetrate into the area that they had not previously used. Much of the field to the north-east remained un-used. When all the godwits had gone (Fig. 31) a short period of observation showed that the crows had begun to utilise the former (now undefended) nesting area, although apparently not to its full extent.

In the area of the Tower colony, crow movements through the season were equally dynamic (Figs. 32-36). In April (Fig. 32), when only one godwit nest was established, crow movements were few. They frequently flew along the river bank edges of the washes. Later, in mid-May (Fig. 33), crow flights were more frequent. 3 Godwit's nests were now being incubated and one pair had chicks. Crow traffic was still heavy along the far edge of the nesting fields and movements onto fields from this area extended only a short way. A central area of the nesting fields was defended by godwits and was not used by crows. Later, when two pairs had young (Fig. 34) the crows were still unable to penetrate into the breeding colony. The pair with young on the south-western

Fig. 29. Map showing Crow movements at the Singing Washes (5th-16th May)
when 3 pairs of Godwits had eggs.

● Positions of nests

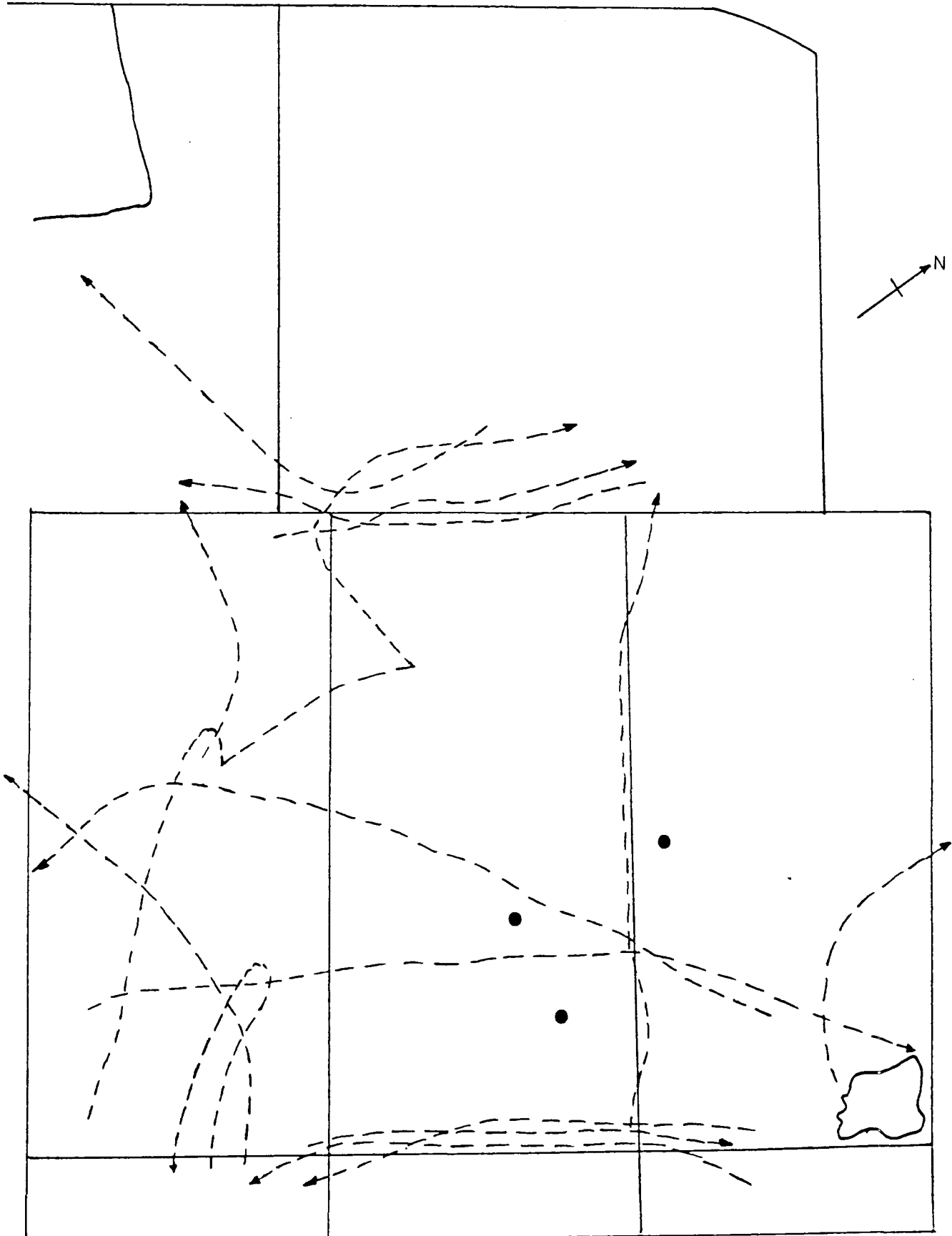


Fig. 30. Map showing Crow movements at the Singing Washes (22nd-26th May)
when only one Godwit nest remained.

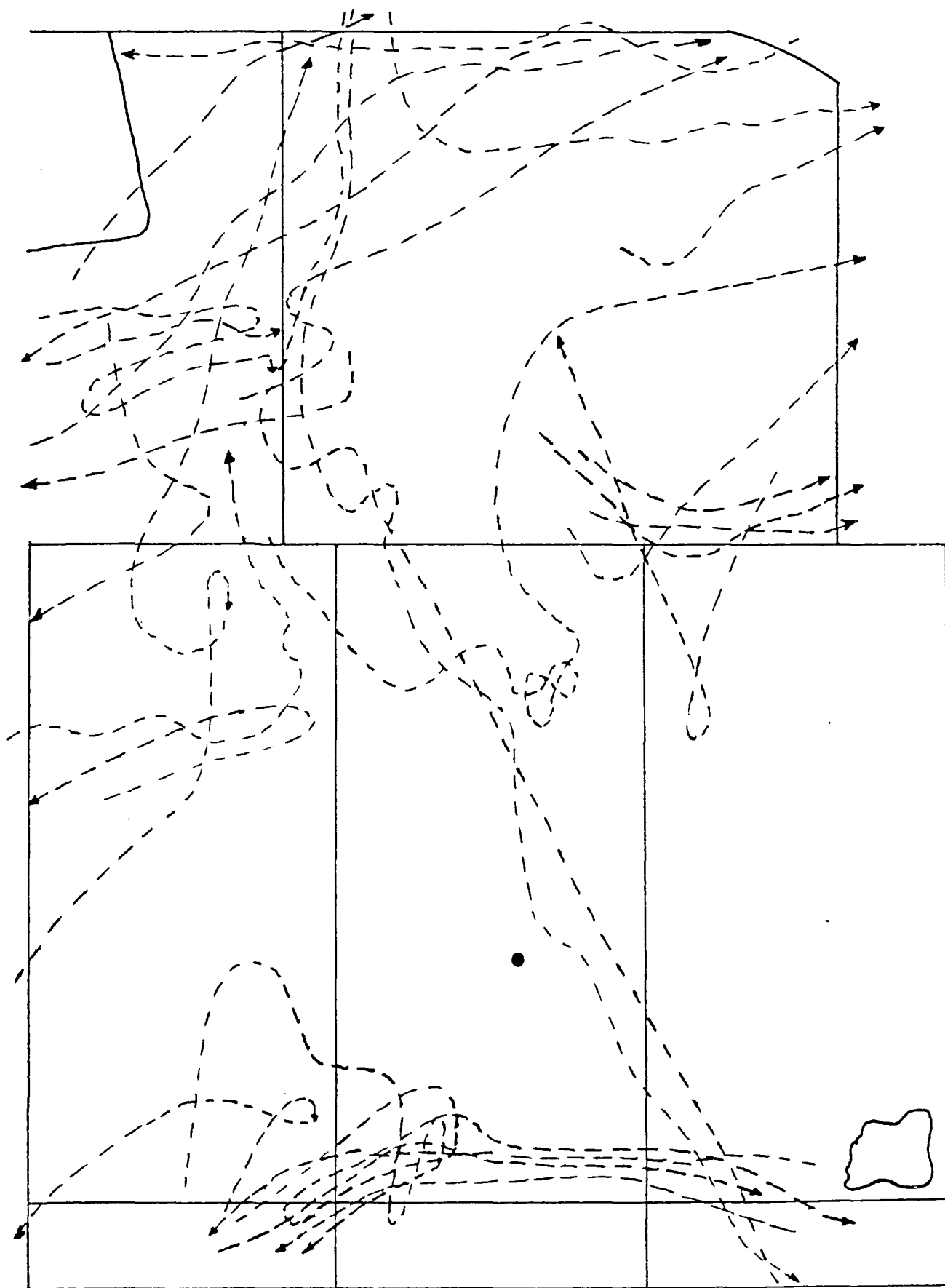


Fig.31. Map showing Crow movements at the Singing Washes (5th-7th June)
when all Godwits had left.

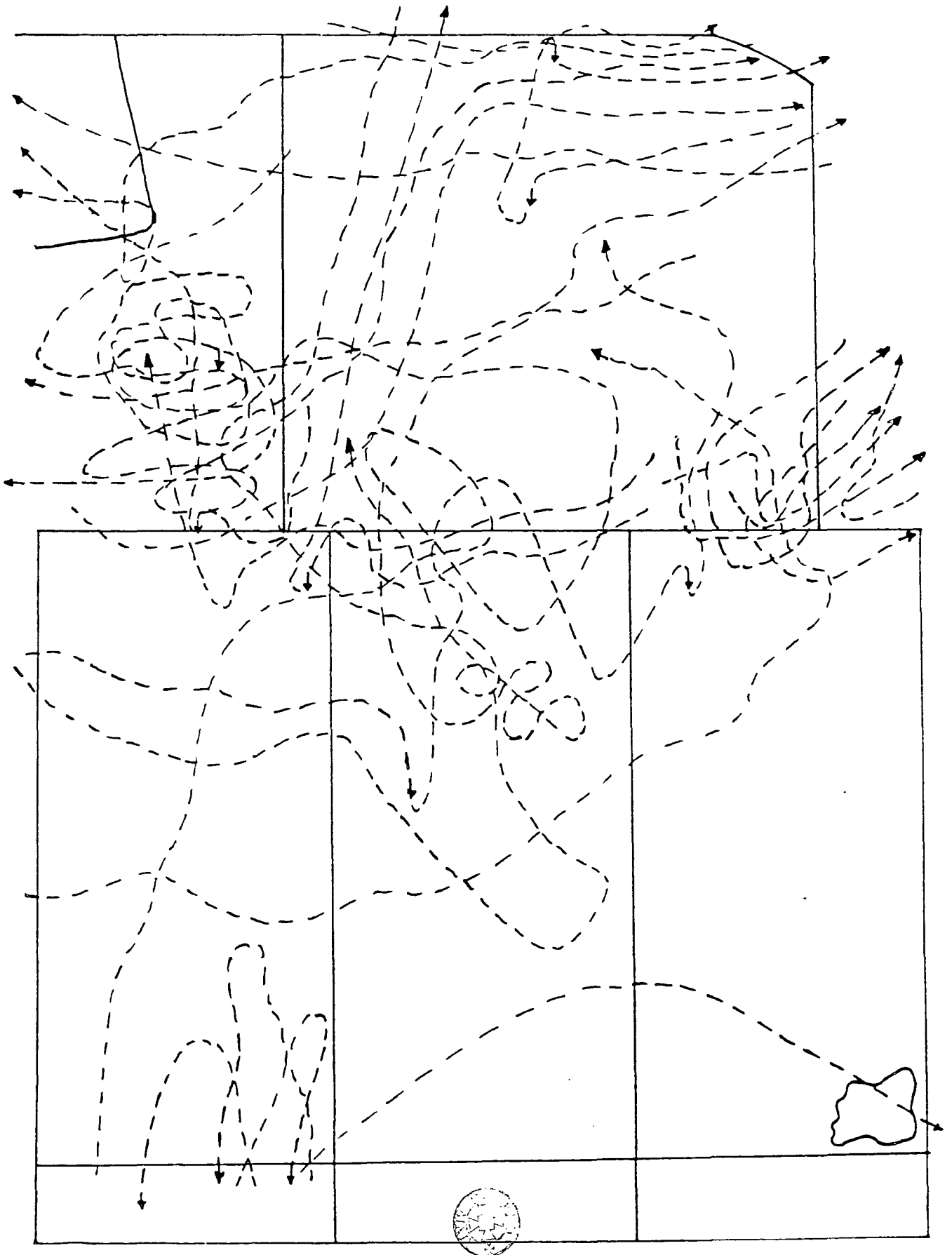


Fig. 32. Map showing Crow movements in the Tower area (26th April-4th May)
during the period when 1 Godwit nest was established and a minimum
of 4 pairs were present.

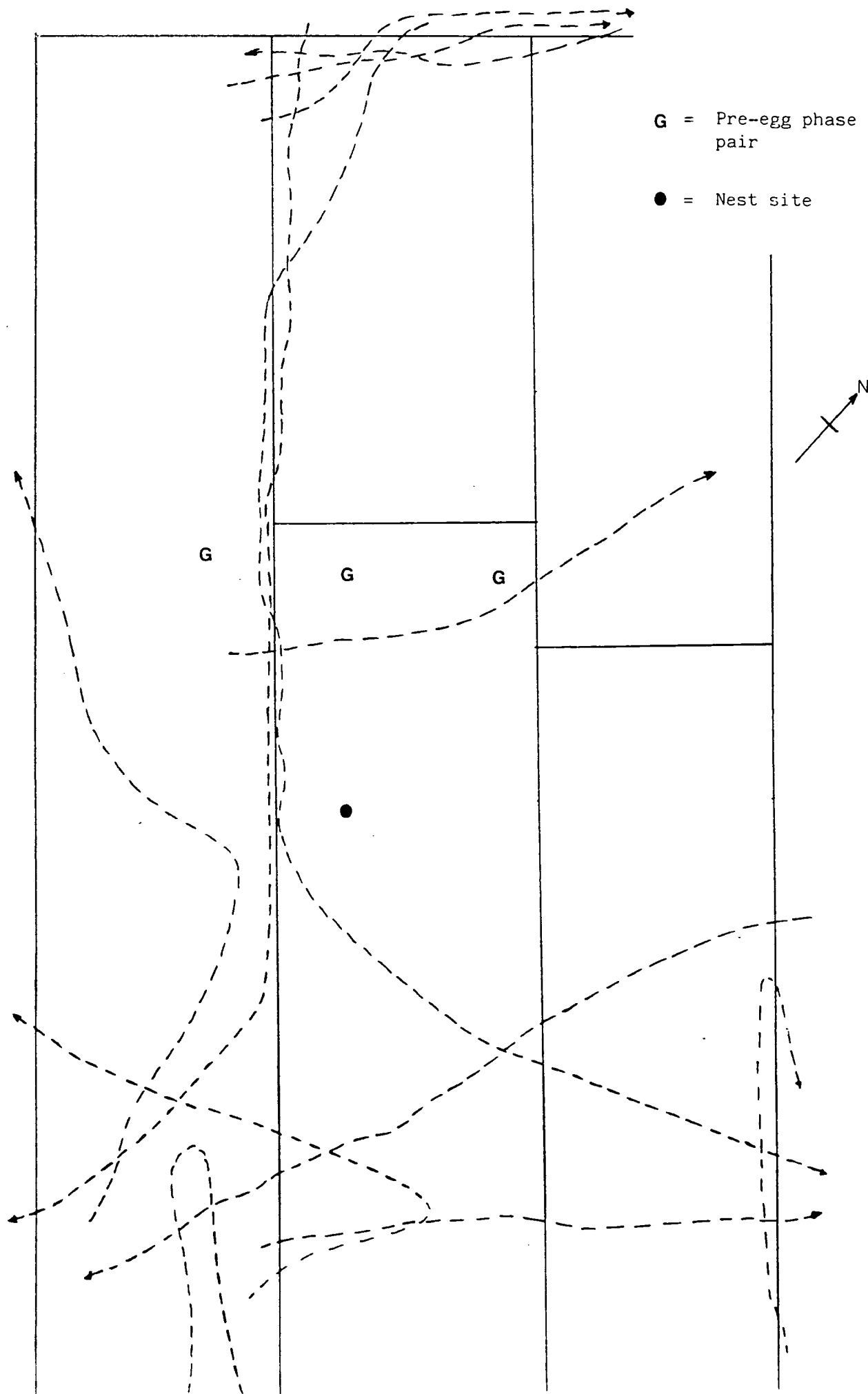


Fig. 33. Map showing movements of Crows in the Tower area (8th-24th May) 103.
when 3 nests and one brood of chicks were present.

Y = Godwit with chick

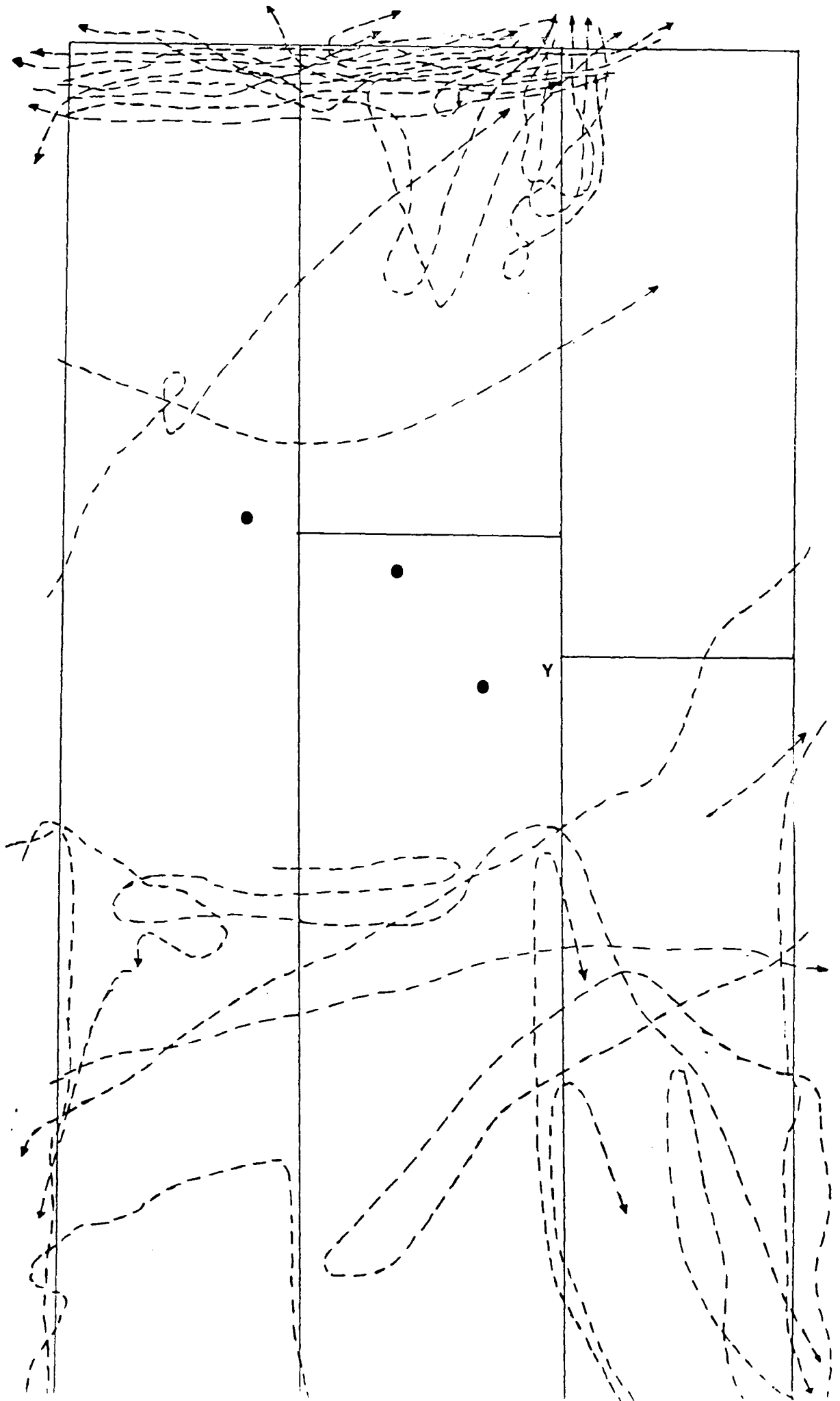
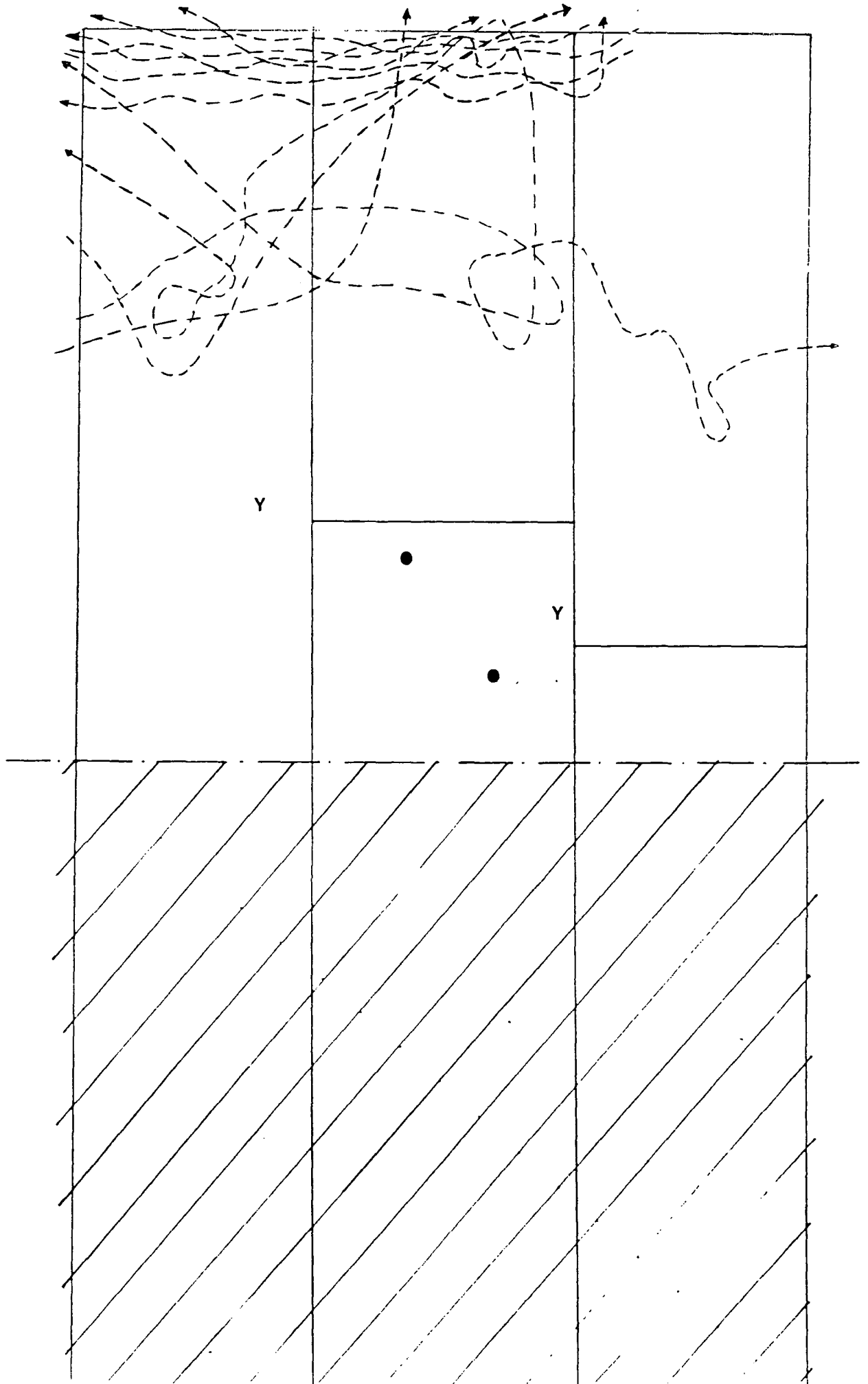


Fig. 34. Map showing movements of Crows over half of the Tower area (2nd June)
when 2 nests and 2 pairs with young were present.



field prevented the crows from utilising that field. In June (Fig.35), 4 pairs had young within a relatively small area on the central field. Note, that since the field to the south-west was now undefended, it was used immediately by foraging crows. The area defended by the godwits was now much smaller and the crows ranged widely over the surrounding area. However, the central colony remained intact. When only 3 pairs of Godwits with young remained (Fig. 36) the situation changed again. One pair moved back to the southwestern field and prevented crows from using the top section of that field. Again a central defended area remained, through which crows did not fly. Thus we can conclude that defence by the Godwit colony was effective. When the birds had chicks the defended area was mobile and the size of the area defended was determined by the spread of Godwit individuals. A larger area may have been defended during the egg-phase than during the chick rearing period (compare figs. 33&35). Crow foraging patterns are dynamic and changed rapidly to utilise foraging space as and when it became available to them.

For single pairs (Figs. 37&38) the situation was similar. During the egg-phase (Fig.37) the single pair effectively defended a certain limited area; crow movements generally did not take place within this area although crows foraged around it. The area defended by a single pair was smaller than that defended by a colony (compare figs.33 & 37). During the chick phase (Fig. 38), the area defended was smaller than that during both the egg-phase and of that defended by colonial birds with young.

The numbers of crow movements and the numbers and distribution of mobbing attempts by Lapwings and Godwits are

Fig. 35. Map showing Crow movements in Tower area (6th-10th June) when there were 4 pairs with chicks all on the same field.

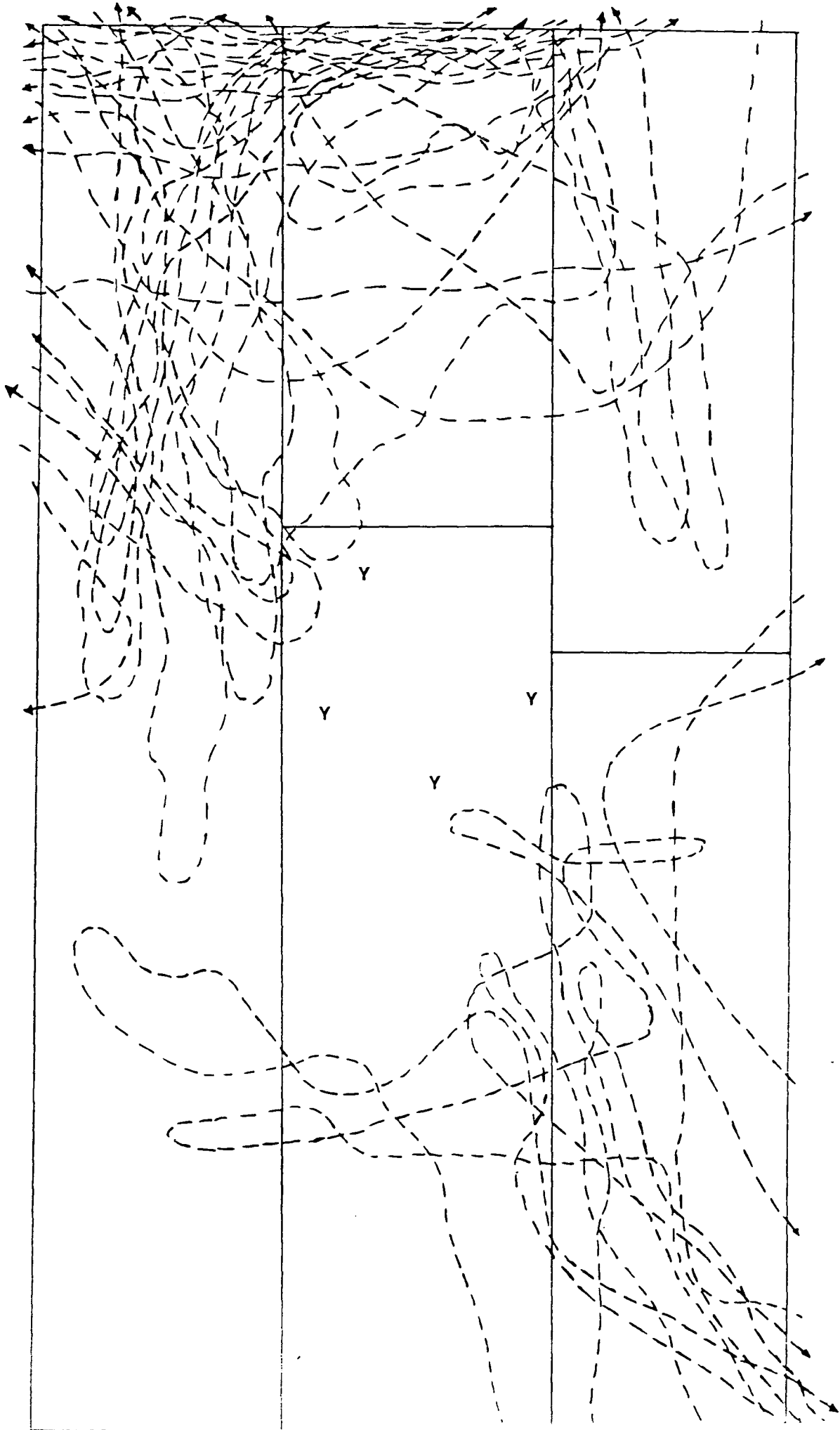


Fig. 36. Map showing Crow movements in Tower area (12th-14th June) when 3 pairs with chicks were present.

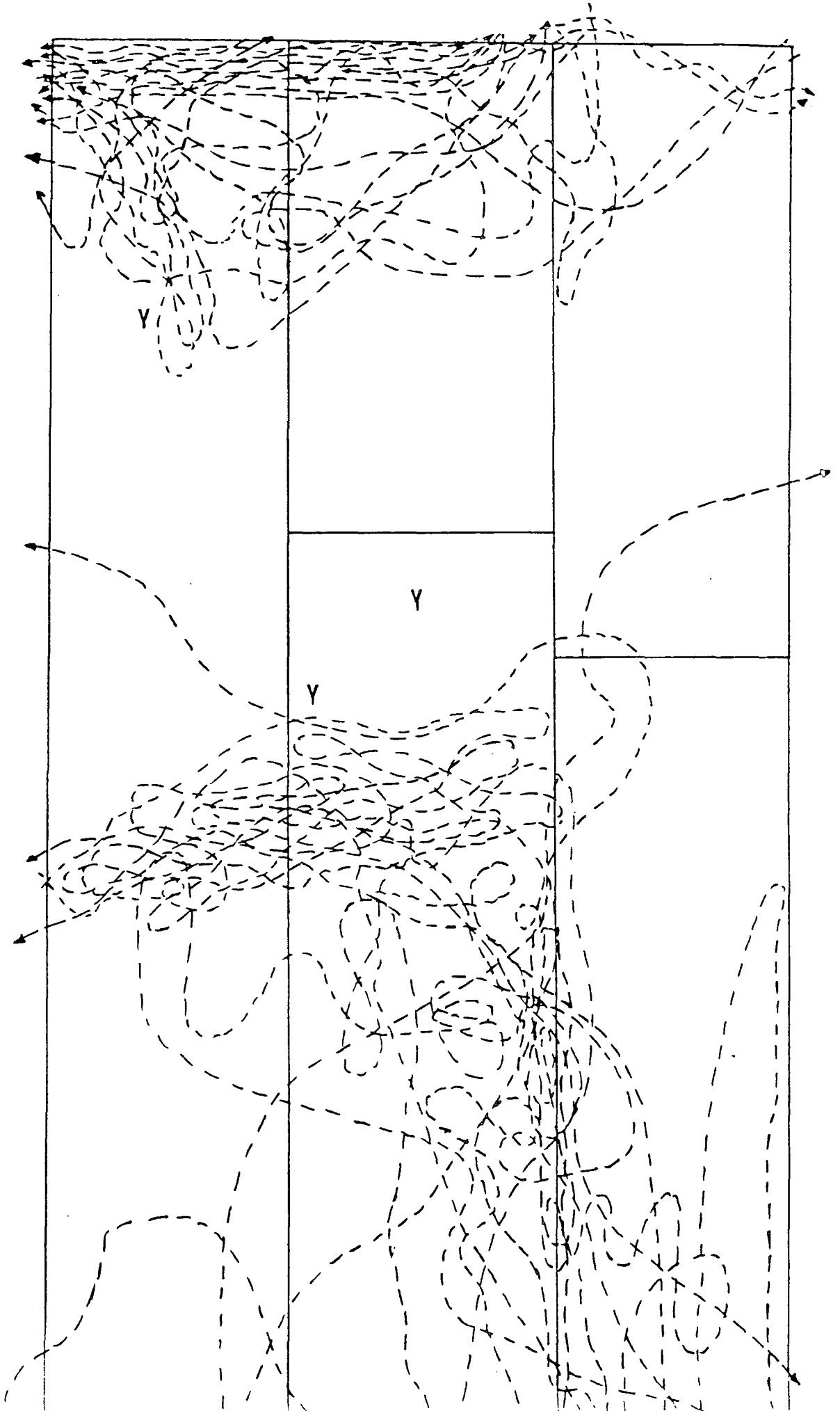


Fig. 37. Map showing Crow movements around the nest of a single pair
(25th May).

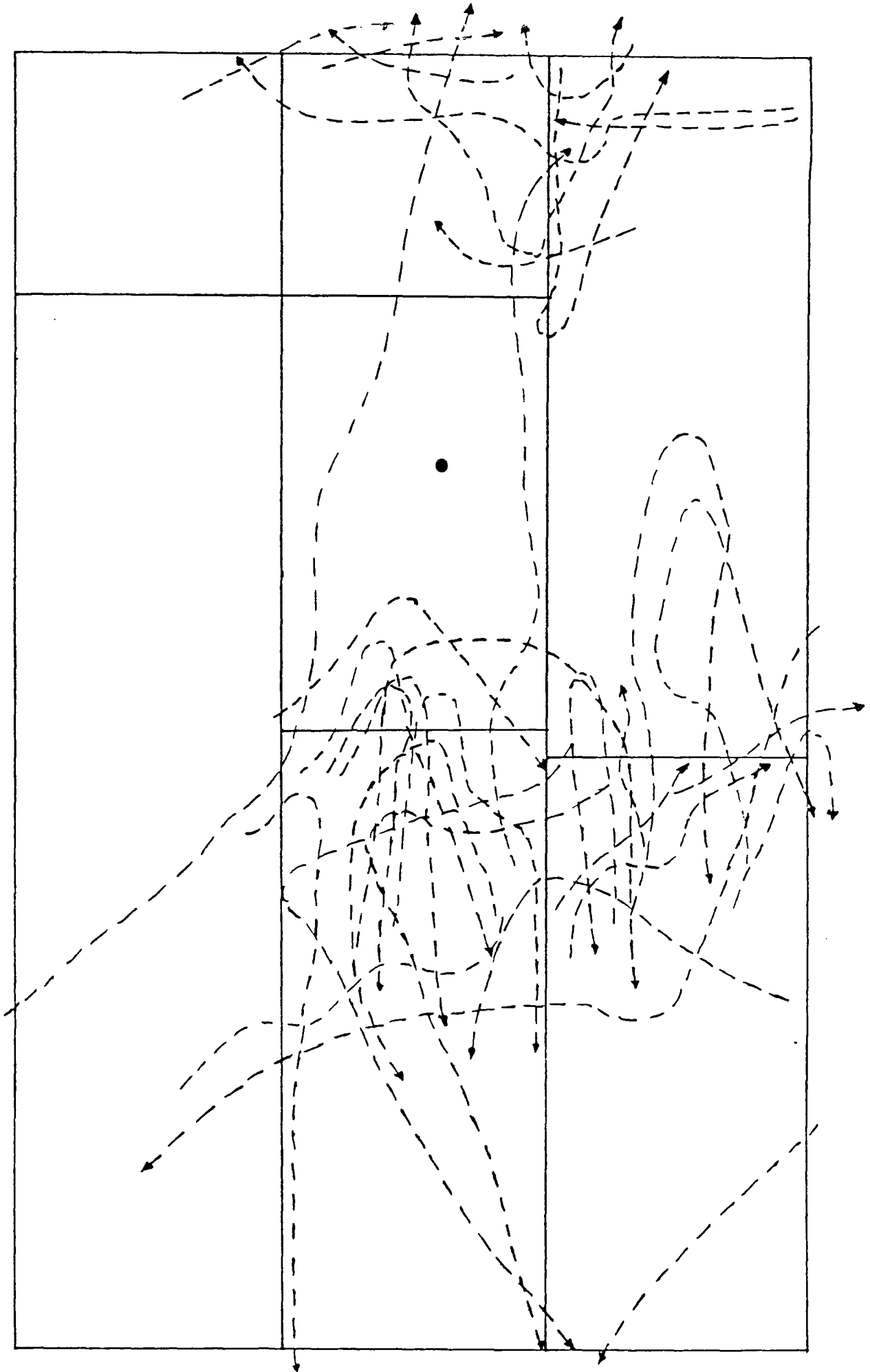
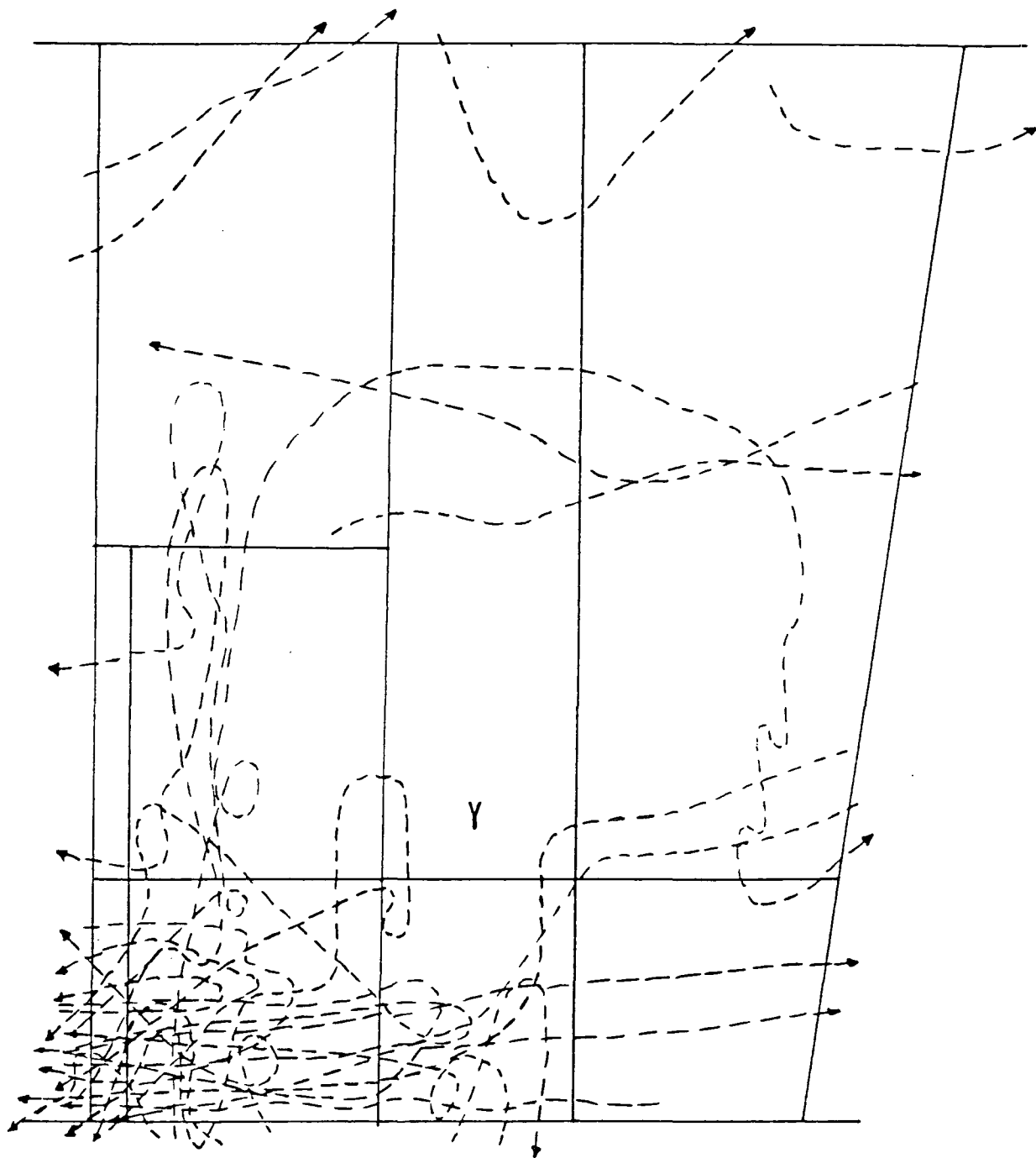


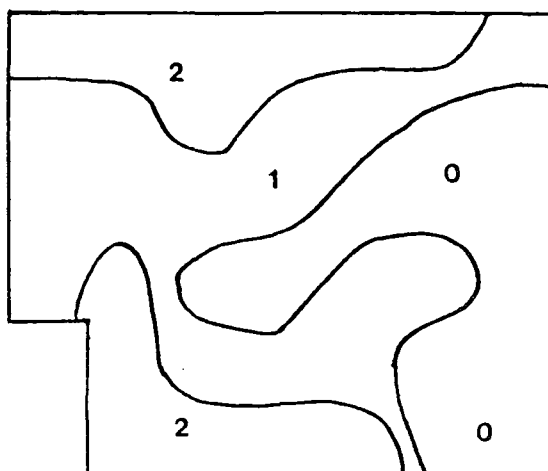
Fig. 38. Map showing movements around a single pair with young
(19th-22nd June).



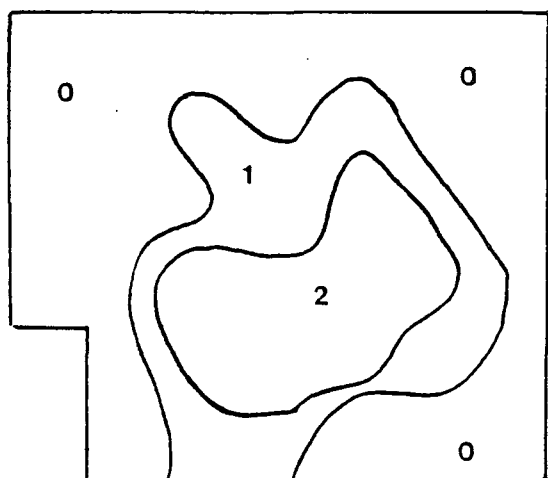
presented in Appendices 5&6. I analysed the frequency of crow movements through each colony by Stepwise Multiple Regression in relation to mobbing by Godwits and Lapwings. In the Singing Washes colony (Fig. 39) crow movements were correlated with the frequency of mobbing by Godwits. The crows tended to avoid areas in which they were frequently mobbed by Godwits (Table 37); the relationship is significant ($t=-2.75$; $P<0.01$). However there was no significant relationship (Fig.39 ; Table 37) between crow movements and either mobbing by Lapwings ($t=0.45$; $P>0.50$) or distance from crow nest ($t=-1.35$; $0.1<P<0.2$). At the Tower colony the results are similar (Fig.40 ; Table 37). Again there was no relationship between crow movements and Lapwing mobbing ($t=-1.57$; $0.1<P<0.2$). However, crow movements were significantly related to both Godwit mobbing ($t=-3.79$; $P<0.001$) and distance from the crow's nest ($t=-4.63$; $P<0.001$). Therefore, mobbing by Godwits was a key determinant of crow movement in and around both the colonies studied whereas Lapwing mobbing was not.

Fig. 39. Diagrams showing Crow movements and mobbing by Godwits and Lapwings at the Singing Washes colony.

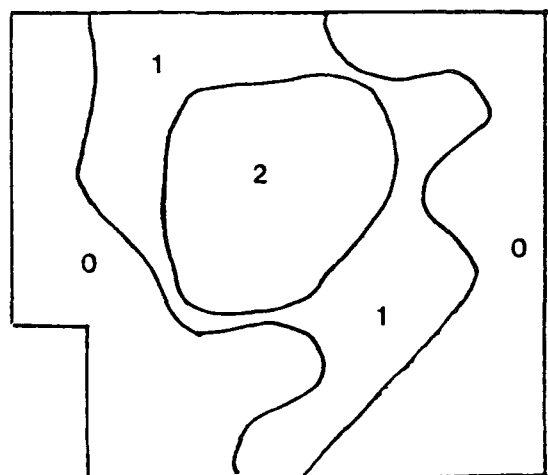
(0 = 0-33%; 1 = 33-67%; 2 = 67-100%)



Crow movements

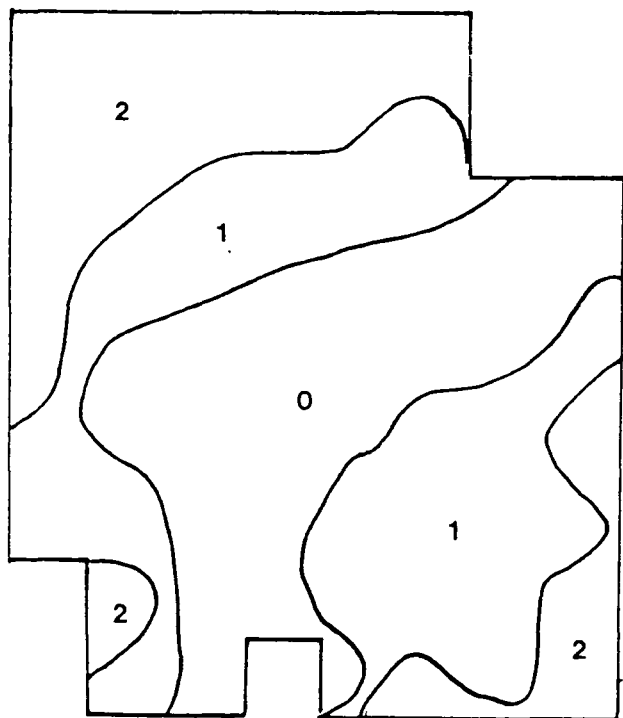


Mobbing by Godwits



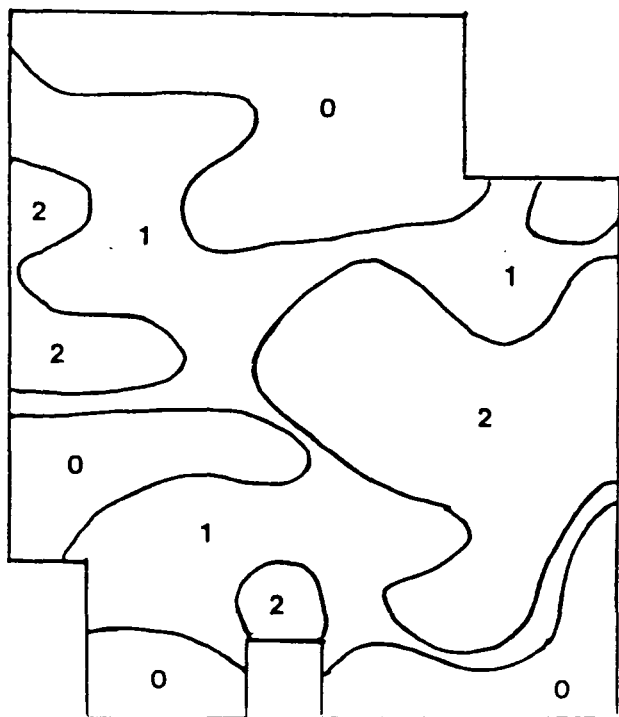
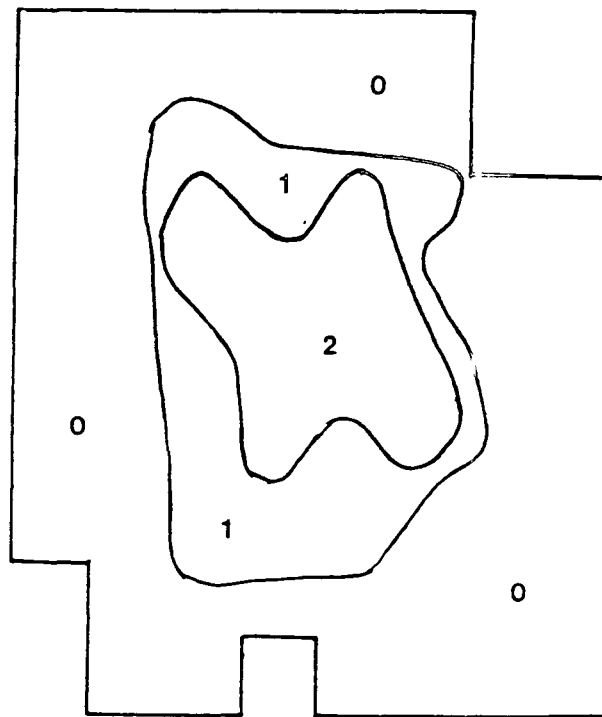
Mobbing by Lapwings

Fig. 40. Diagrams showing Crow movements and mobbing by Godwits and Lapwings at the Tower colony.



Crow movements

Mobbing by Godwits



Mobbing by Lapwings

Table 37. Stepwise Multiple Regression of Crow use of 100 x 100m squares (passes hr⁻¹) on the intensity of mobbing by Godwits and Lapwings and distance from Crow nest.

<u>Singing Washes</u> (N = 35)	<u>t</u>	<u>P</u>	<u>SIG.</u>
Godwit Mobbing ¹	-2.75	< 0.01	✓
Lapwing Mobbing ¹	0.45	> 0.50	X
Distance from Crow Nest	-1.35	0.1 < P < 0.2	X
<u>Tower area</u> (N = 65)	<u>t</u>	<u>P</u>	<u>SIG.</u>
Godwit Mobbing ¹	-3.79	< 0.001	✓
Lapwing Mobbing ¹	-1.57	0.1 < P < 0.2	X
Distance from Crow Nest	-4.63	< 0.001	✓

¹ % of Crow passes mobbed

DISCUSSION

(i) Reasons for Colonial Nesting.

During the summer of 1984, only 21 pairs of Black-tailed Godwits attempted to breed on the Ouse Washes, approximately half of the breeding population in previous summers. The low numbers were thought to reflect the poor breeding of previous years (C.Carson, pers.comm.).

Pair formation was rapid; elsewhere, some have been observed to be already paired on arrival at the breeding grounds (Cramp & Simmons, 1983). After pairs had formed, social attraction to conspecifics led 71% of all pairs to breed within colonies; others bred singly for unknown reasons. Colonies were established for social reasons rather than as a result of shortage of suitable breeding or feeding habitat; this agrees with the conclusion of Hoogland & Sherman (1976) for Bank Swallows, Krebs & Davies (1981) and Elliot (1982) for Lapwings.

Inter-nest distances within colonies were established by interactions between males, which were more frequent at the larger of the two main breeding colonies and probably caused the nests to be further apart than at the smaller colony. Alternatively or additionally, the smaller colony was closer to an occupied Carrion crow's nest, and the shorter inter-nest distance may have facilitated nest defence by the godwits. However, Elliot (1982) found that lapwings nesting closer to crow nests did not have smaller inter-nest distances. Intra-specific aggression could possibly determine group size, and in this way some pairs may be forced to nest singly; though I have no proof of this for

godwits.

29% of all nests were successful; hatching success was twice as high (44%) in the larger of the two colonies, and similar to the level of 48.6% recorded in the Netherlands (Cramp & Simmons, 1983). However, this is much lower than hatching success in the majority of waders (see e.g. Holland et al., 1982). Overall breeding success was very low (6-9% of maximum possible); flooding and predation were the main causes of nest failure. Although I did not specifically examine the point in this study, nests were not obviously positioned so as to reduce the risk of flooding. Losses by cattle trampling were reduced by active management, namely delaying grazing on nesting fields until the birds had gone. Breeding success was lower in the smaller of the two colonies this site also being closer to the nearest crow nest. Elliot (1982) showed that lapwings nested significantly further than expected from all trees and further still from trees containing crow's nests (see also Rankin, (1979) & Lemmetyinen (1971)). However, it is not certain whether predation was higher in the smaller godwit colony. The breeding success of single pairs was similar to that of the smaller colony.

Klomp (1954) and Elliot (1982) did not consider foraging requirements of either adults or chicks to be an important reason for colonial breeding. However, Rankin (1979) and Krebs & Davies (1981) felt that it may be important. I found that pre-laying pairs of godwits roamed around the nesting area and in this way may have been sampling the feeding sites available to them. They could then have chosen a nest site close to a suitable feeding area. Males, in

particular, fed close to the nest, which enabled them to defend it against predators. Females fed at greater distances, at pools and in the damper regions of fields. Pools seemed to provide particularly good feeding which may have allowed off-duty females to obtain food quickly. Therefore, the immediate area of the colony provided adequate feeding for the male, but not for the female. It seems likely that colonial nesting in Black-tailed Godwits has little to do with foraging.

There was some evidence that in a given site females foraged more successfully than the males. Like most British waders, the female godwit's bill is longer than the male's (Prater et al., 1977), and this may be responsible for the observed difference in foraging success. Sexual dimorphism in the bill size may reduce competition for food (e.g Selander, 1966); here the two sexes were not in direct competition whilst feeding, and this may be more important on the wintering grounds.

Male Black-tailed Godwits may feed in sites which were relatively low lying and grazed. For example, on the Ouse Washes a luxuriant growth of Eleocharis palustris and Polygonum amphibium characterised temporary pools; Deschampsia caespitosa predominated in grazed areas, where P.amphibium, E.palustris and Ranunculus repens were more frequent (Thomas et al., 1981). These species were associated with the feeding areas on the Singing Washes. Such sites may provide an easily penetrable substrate which is nutrient rich, and possibly rich also in invertebrate foods.

Rankin (1979) showed that lapwing chicks on a Cumbrian saltmarsh remained in the nesting area, the area itself being

selected to provide adequate food for the chicks. However, Redfern (1982) considered that nesting and foraging by lapwing chicks may occur in different habitats inland. Godwit chicks were highly mobile and were moved by the parents away from the breeding colony. This agrees with Cramp & Simmons (1983) who report that chicks may cover 150-200m. in a few hours after hatching and on one occasion, 700m. in 2 days. The reasons for chicks movements were not investigated during this study. My observations suggest that it is unlikely that colonies arose only in areas which were most suitable for chick-rearing.

The activity budget of adult Black-tailed Godwits varied according to a number of factors, including time of day, sex, phase of breeding cycle and group size. Males fed more early in the day, possibly because they incubate at night as suggested by Cramp & Simmons (1983). I had hoped to check this using radio-telemetry, but as this technique might have caused too much disturbance to such a rare breeding bird, the R.S.P.B. were not prepared for me to use it at the Ouse Washes.

During the pre-laying phase, male and female activity budgets were similar, although males were more vigilant and aggressive. During the egg phase they differed, with incubation by day predominantly by the female. This was true also for lapwings (Elliot, 1982). Males spent a high proportion of their time feeding and vigilant, as also in lapwings (Elliot, 1982). Similarly, whilst with chicks, males were more vigilant.

As the breeding cycle progressed the amount of time spent feeding by the adults decreased and vigilance increased.

Presumably this was necessary in order for adults to stay in contact with the actively moving chicks.

Differences in individual activity budgets may occur amongst groups of different sizes. Bertram (1980) found that each individual in a group spends a smaller proportion of its time scanning for predators than if alone, but that the overall vigilance of the group increased slightly with group size. I found that the amount of vigilance was similar for individual godwits within the two main breeding colonies; this may mean that the difference in group size between these colonies was not sufficient to reveal differences in the degree of individual vigilance. During the pre-laying phase, males were more aggressive and did more courtship in the larger colony. Since more birds were present, it may have been necessary to court more frequently to maintain the pair bond.

In the chick phase, single pairs were compared with colonial ones. Males attended to the chicks in single pairs and females in colonies. It is uncertain why this should be. Since mobbing was more frequent by single pairs, it is perhaps necessary for the more aggressive male, who may be more effective, to remain on guard.

(2) Predation and Anti-predator Behaviour.

During this study the predators most frequently recorded were birds- crows, Kestrels and Herons. It is worth remembering that intrusions by mammalian predators may be under-estimated due to both their nocturnal habits (e.g Fox) and/or ability to conceal themselves (e.g Weasel).

Up to 6 Black-tailed Godwits and 22 Lapwings were involved in mobbing events; Elliot (1982) recorded a maximum

of 21 lapwings, although the mean number was 2.8 ± 1.1 . The number of defending birds seemed to reflect the degree of danger represented by the predator. Kestrels were mobbed by relatively more birds of each species, than crows. Kestrels may be more dangerous because they are a threat towards both adults and chicks, which represent a greater parental investment than a clutch of eggs.

Attacks by lapwings on predators were rarely as effective as those by godwits, although their effectiveness increased with group size. Rankin (1979) and Elliot (1982) agreed that lapwing defence was more effective en masse.

During incubation, the male most frequently responded to intrusion by a predator, whilst the female remained on the nest; Elliot (1982) obtained the same result for lapwings. When the male was absent, the female was forced to leave the nest to mob an intruder. Both birds were more frequently involved in mobbing events whilst they had chicks. Again this may represent the result of a greater level of parental investment in the brood, or may be because widely spaced chicks are more difficult to defend.

Andersson et al. (1980) produced a model predicting that the optimal level of parental defence increases with offspring age. As predicted, parent Fieldfares increased their level of defence throughout the nest period. Other workers came to the same conclusion for different species e.g Lemmetyinen (1971) for Terns; Curio (1975) for Pied Flycatchers & Elliot (1982) for Lapwings. In my study, Kestrels were mobbed significantly more when the godwits had chicks than eggs. At this time, Kestrels may simply be more of a threat. However, the situation may be more

complex, and may involve both the degree of parental investment and a reduction in the probability that re-nesting (due to loss of brood) can take place.

Breeding godwits defended a zone around their nests from which crows were excluded. The defended zone was mobile whilst the birds had chicks; these results agree with Cramp & Simmons (1983).

Crow movements in the vicinity of godwit colonies were determined by the frequency of mobbing by the godwits, the crows avoiding the area in which they were frequently mobbed. Lapwings did not influence crow movements. In contrast, Elliot (1982) recorded that the presence of breeding lapwings excluded crows from areas adjacent to lapwing nests, even when these areas had been used significantly more by foraging crows prior to the lapwings' return.

As mentioned earlier, it is necessary to provide information to show that this exclusion of predators leads to a decrease in nest predation. Rankin (1979) found a lower predation rate on lapwing nests which were aggregated. In order to test this, and the relative efficiency of godwit and lapwing nest defence, an experiment involving the use of artificial nests was carried out by R.E.Green & G.J.M.Hirons. Three study areas were chosen, one defended by the godwit colony, the others being defended by lapwings alone; the former was 550m. from the nearest crow nest, the others being 480 and 700m. from the crow nest. By day 5 of the experiment, 50% of the nests placed within the godwit colony were intact, but only 10% and 20% of nests remained in lapwing defended areas. Of the predated nests, all took longer than 1 day to be emptied completely in the godwit colony, whereas 83% of

those in areas defended by lapwings were emptied within the same day (R.E.Green, pers.comm.). Thus, nests placed within the godwit colony survived longer and even when discovered were predated more slowly. I believe, therefore, that the exclusion of predators from godwit colonies must reduce the rate of predation by avian predators.

Cramp & Simmons (1983) state that pairs of Black-tailed Godwits show a tendency to nest in close proximity to lapwings from which they may obtain a high degree of protection. From my observations, on the contrary, it is more probable that lapwings and other waders gain protection from nesting near Black-tailed Godwits.

To conclude, Black-tailed Godwits appear to nest colonially in order to benefit from group defence of the nesting area. In such a way, predation rates are likely to be reduced. It is not known why some godwits nest in isolation and what the consequences are.

SUMMARY

1. Aspects of the breeding biology of the Black-tailed Godwit were studied during the summer of 1984 at the Ouse Washes (Cambridgeshire and Norfolk). In particular, the causes and consequences of coloniality was examined with special reference to the role of predation.

2. Only 21 breeding pairs were present; 57% of these nested in colonies, the remaining nesting sub-colonially or as single pairs.

3. Comparisons between 2 nesting colonies were made; one contained up to 3 pairs, the other a maximum of six. The nests were closer together on average at the smaller colony (95m.) than at the large colony (152m.); the former was closer to the nearest crow nest.

4. 29% of nests were successful, the majority of these being within the larger breeding colony. The most important causes of nest failure were flooding (25%) and predation (13%); the cause was not known in 21% of cases.

5. Between 6-9 chicks were thought to have reached fledging; this represents between 6.3-9.5% of the maximum production possible. The largest colony contributed most to this; the smaller colony and single pairs contributed equally.

6. Foraging behaviour was examined to see if colony areas were utilised for, and perhaps selected for this purpose. Females fed at significantly greater distances from the nest than males did and tended to utilise permanent pools and the damper regions of fields. They often fed away

from the breeding colony. Also, females may have been more successful at obtaining food than males. Permanent pools seemed to represent good feeding sites.

7. Males rarely left the breeding colony to feed and used preferred feeding sites close to the nest. Such feeding sites were indistinguishable in terms of their topography although discrimination in terms of their plant composition maybe possible.

8. Colony areas maybe selected to provide the necessary habitat for chick-rearing. However, Godwit chicks were extremely mobile and travelled great distances. In all cases, the chicks were moved out of the nesting area although the timing of this movement varied.

9. Colony establishment was studied and male-male aggression was thought to be important in the establishment of nearest neighbour distances. Such disputes were more frequently observed at the larger of the two colonies and may have been responsible for the greater inter-nest distances recorded there.

10. Individual activity budgets were constructed to allow comparisons between the two main breeding colonies. However, the time-budget varied also with sex, individual and the phase of the breeding cycle.

11. During the pre-laying phase, the activity budget was very similar between the sexes with both allocating some 70% of their time to feeding. However, males were generally more viligant and more aggressive towards conspecifics. During incubation, comparisons between the sexes were not possible. However, females apparently incubate far more than the males who spent 80% of their time feeding. During

the young phase, males were more vigilant and vigilant for significantly longer.

12. The phase of the breeding cycle was important. In both sexes, less time (35%) is spent feeding during the chick-period than at any other time and the length of the feeding bout is also shorter. Males become progressively more vigilant through the breeding season, females, are also more vigilant in the chick phase than during the pre-lay period.

13. During the pre-egg and egg- phases it was possible to compare between the 2 colonies for Godwit males only. During the former, similar amounts of time are spent feeding and in vigilance, although males in the larger colony indulge in significantly more courtship and aggression. During the egg phase, the activity budgets are very similar.

14. In the chick-rearing period, single pairs and colonial pairs could be compared. In all cases, one individual of the pair was primarily attending to the chicks whilst the other was feeding. In single pairs, males spent less time feeding, were more vigilant and vigilant for significantly longer than males in colonies. However, in colonies this is true for female. Hence, the male attends to the chicks in single pairs whereas the female does in colonies. In both sexes, there appears to be more time allocated to mobbing in pairs; thus, mobbing is shared out more between the individuals within the colony situation.

15. The Carrion crow, Heron and Kestrel were the most numerous predator species recorded within the study areas. The Lapwing and the Black-tailed Godwit were the main defending species.

16. The number of mobbing individuals varied with the degree of danger that a predator represents. Thus, crows were most frequently mobbed by 1-2 Godwits and 1-4 Lapwings and Kestrels by 2 Godwits and 1-8 Lapwings. Herons, being less of a threat, were mobbed by fewer individuals of either species.

17. Black-tailed Godwits were extremely effective at mobbing predators, causing them to retreat from the area very rapidly. Lapwings were less effective, although their relative effectiveness was increased by increasing the number of individuals in the attack.

18. Specific information on known individuals showed that during incubation the male would most frequently attack an intruder; the female remained on the nest. In the males absence, the female would leave the nest to mob. When with chicks, the bird in attendance most frequently responded although mobbing by both individuals was more common at this time.

19. The frequency of crow intrusions was higher at the larger of the two main breeding colonies.

20. The response of breeding Black-tailed Godwits to an intruder varied according to predator species, the distance of approach and the phase of the breeding cycle. Kestrels were mobbed significantly more frequently during the chick phase than during the egg phase. At this time, Kestrels presented more of a threat, parental investment was high and the chance of breeding again that season was low.

21. Godwits established a protected zone around their nests, from which crows were excluded. The size of the protected zone increased with the size of the nesting group

and was related to the spread of defending birds. The protected zone of single pairs is smaller than that of a colony.

22. During the chick-rearing phase the defended zone is mobile and is generally smaller than that defended during the incubation phase.

23. Crow hunting patterns were significantly correlated with the probability of mobbing by Godwits such that they avoided the area in which they were most likely to be mobbed by this species. Lapwings had no significant effect on crow movements. The defence of a colony by Black-tailed Godwits was sufficiently efficient so as to be likely to produce reduced predation rates. Lapwings were considered to be relatively inefficient.

24. Crow hunting patterns were dynamic enough to allow them to utilise new ground as soon as it became available to them.

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Appendix 1. Minimum numbers of Black-tailed Godwits on the Ouse Washes
(RSPB section) April-July 1984.

DAY	April	May	June	July
1st		20	6	13
2nd		25	4	10
3rd		10	4	24
4th		8	8	4
5th	12	10	3	2
6th		5	5	1
7th	2	5	2	1
8th		3	1	5
9th	18	12	1	13
10th	50	5	25	10
11th	100	6	1	15
12th	290*	2	14	8
13th	200	4	16	1
14th	80	10	9	
15th	5	10	9	
16th	80	34		8
17th	345	17		
18th	260	11	18	
19th	270	11	4	2
20th	2	10	15	
21st	80	7		5
22nd	6	7	12	
23rd	70	4	24	1
24th	25	6	4	4
25th	25	6	4	5
26th	10	4	6	
27th	10	4	4	8
28th	6	20	16	4
29th	50	10	10	5
30th	40	8		2
31st	-	6	-	4

* Including 180 I. islandica

Appendix.2. Behavioural Observations.

1. Only 1 out of 95 Ceremonial flights recorded consisted of all 5 phases (see Cramp & Simmons, 1983), the majority consisting of stages 1,3,4 and 5 only. In the one complete flight, "tumbling" included only 2 dives and ascents.
2. The "Extended Wings High" display always concluded the Ceremonial flight.
3. In the "Scrape Display" either bird would run excitedly to the nest and begin scraping. The other would then approach and when close the first bird would slowly back out from the scrape but remain motionless, with body tilted forward, at the side of the scrape. The second bird would then enter the scrape and begin scraping. Occasionally both birds would occupy the scrape at the same time, sitting side by side.
4. The Scrape Display often led to Nest building. On one occasion a male spent c.46 mins. picking up small fragments of grass and placing them in and around the edge of the scrape. Then the female spent c.16 mins. apparently removing grass pieces from the scrape.
5. Male "Sparing" bouts were frequent. The birds involved would chase each other around mainly on the ground. They would face each other and stand alert, and then each would try to rise above the other and strike down with feet. Fighting, alternate bowing, jumping and pecking were commonly involved.
6. The Anti-Predator response of Lapwings to Kestrels was very distinctive. On sighting the predator many lapwings would rise into the air and circle uttering a distinctive call ;

this was different to that heard for other predators. Some of the lapwings would make contact and chase the Kestrel, whilst others remained high in the air, still calling for several minutes.

7. Ground Predators invoked a "hovering response" rather than active mobbing.

Appendix .3. The vegetation of feeding areas and non-feeding areas on the Singing Washes.

(1) Feeding Areas

Plant Species	% Cover within 24 quadrats											
Glyceria maxima (1)	20, 30, 30, 60	40, 20, 40, 30	30, 40, 35, 80	60, 60, 40, 80	30, 3, 50, 50	30, 10, 40, 50						
Phalaris arundinacea (2)	30, 30, 20, 30	40, 15, 10, 40	5, 20, 25, 5	40, 20, 40, 5	40, 5, 10, 20	10, 10, 40, 45						
Polygonum amphibium (3)	10, 0, 0, 0	0, 0, 0, 0	15, 0, 0, 0	0, 0, 5, 0	10, 5, 10, 15	5, 0, 2, 0						
Potentilla anserina (4)	0, 0, 0, 0	3, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0						
Plantago spp. (5)	5, 10, 15, 0	0, 0, 10, 0	15, 5, 10, 10	5, 2, 5, 0	0, 0, 0, 0	1, 20, 0, 2						
Eleocharis palustris (6)	10, 20, 5, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	50, 20, 0, 0						
Mentha aquatica (7)	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 80, 0, 0	0, 0, 0, 1						
Senecio jacobaea (8)	0, 0, 5, 0	0, 2, 2, 0	0, 0, 0, 0	3, 0, 0, 0	0, 0, 0, 5	0, 0, 0, 0						
Rumex spp. (9)	0, 0, 5, 10	20, 30, 15, 0	5, 0, 20, 0	1, 5, 3, 2	0, 0, 0, 5	0, 0, 5, 0						
Carex spp. (10)	5, 5, 0, 0	0, 40, 20, 15	0, 5, 10, 0	15, 0, 0, 0	0, 0, 40, 2	0, 0, 0, 0						
Myosotis scorpioides (11)	0, 0, 0, 0	0, 0, 2, 0	5, 0, 0, 15	5, 0, 0, 0	1, 0, 0, 0	0, 0, 1, 0						
Achillea millefolium (12)	0, 2, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0						
Cirsium spp. (13)	0, 0, 3, 0	0, 1, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 10, 0, 0	0, 0, 0, 0						
Ranunculus repens (14)	0, 0, 5, 5	0, 5, 5, 0	15, 5, 5, 5	10, 20, 5, 0	0, 5, 0, 10	0, 0, 0, 0						
Caltha palustris (15)	0, 0, 5, 0	0, 0, 0, 0	10, 5, 0, 0	5, 10, 0, 2	0, 0, 0, 5	0, 5, 0, 0						
Filipendula ulmaria (16)	0, 0, 0, 0	0, 0, 0, 0	2, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0						
Gramineae (17)	50, 60, 40, 0	20, 20, 15, 20	50, 50, 30, 5	40, 15, 10, 5	30, 40, 20, 30	20, 75, 20, 0						

(2) Non-feeding Areas

Plant Species	% Cover within 24 quadrats											
1	50, 60, 20, 30	10, 30, 20, 30	30, 70, 75, 60	40, 30, 60, 40	30, 40, 40, 30	35, 20, 30, 40						
2	40, 45, 30, 40	50, 20, 30, 30	30, 20, 10, 10	30, 50, 20, 50	10, 10, 20, 10	30, 15, 15, 25						
3	0, 0, 50, 0	15, 10, 10, 0	10, 5, 5, 5	15, 0, 5, 0	10, 0, 0, 10	15, 15, 10, 5						
4	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0						
5	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0						
6	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 50, 0, 10	30, 0, 10, 20						
7	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0						
8	0, 0, 0, 0	0, 0, 0, 0	20, 0, 0, 20	0, 0, 0, 5	0, 0, 0, 0	0, 0, 0, 0						
9	10, 5, 2, 0	0, 0, 0, 15	0, 0, 5, 5	5, 5, 10, 1	0, 5, 10, 10	5, 5, 10, 5						
10	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0						
11	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 10	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0						
12	1, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0						
13	0, 0, 0, 0	0, 0, 0, 0	10, 10, 5, 5	0, 0, 25, 0	0, 0, 10, 0	0, 20, 0, 10						
14	0, 0, 0, 5	0, 0, 20, 10	5, 5, 20, 0	10, 10, 0, 5	0, 0, 0, 0	0, 0, 0, 0						
15	0, 0, 0, 5	0, 0, 0, 0	10, 0, 10, 0	10, 5, 0, 5	0, 0, 0, 0	0, 0, 5, 5						
16	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0						
17	0, 0, 45, 40	30, 40, 40, 50	50, 20, 20, 20	40, 20, 30, 25	80, 30, 30, 30	40, 15, 30, 20						

Appendix .4. The vegetation of feeding areas and non-feeding areas at the Tower colony.

(1) Feeding Areas

Plant Species	% Cover within 16 quadrats											
G. maxima (1)	50, 40, 35, 40	20, 40, 30, 20	15, 20, 40, 25	25, 40, 30, 20								
Phalaris arundinacea (2)	60, 40, 50, 45	45, 50, 30, 30	40, 40, 30, 20	40, 30, 30, 40								
P. amphibium (3)	20, 0, 20, 0	20, 15, 0, 0	0, 0, 5, 10	15, 20, 20, 0								
Plantago spp. (4)	0, 5, 10, 0	0, 0, 0, 5	5, 0, 5, 0	0, 5, 10, 10								
E. paulstris (5)	20, 30, 0, 10	10, 15, 10, 30	0, 0, 5, 0	20, 5, 15, 20								
Mentha aquatica (6)	0, 0, 0, 0	0, 2, 0, 0	0, 0, 2, 0	2, 0, 0, 5								
S. jacobaea (7)	10, 0, 0, 0	0, 0, 0, 0	0, 5, 5, 5	0, 0, 0, 0								
Rumex spp. (8)	0, 5, 0, 2	0, 5, 5, 0	0, 0, 5, 0	0, 1, 1, 0								
Carex spp. (9)	0, 0, 0, 0	5, 0, 0, 0	0, 0, 0, 0	5, 0, 0, 0								
M. scorpioides (10)	0, 5, 0, 0	0, 0, 0, 0	5, 0, 0, 5	0, 0, 0, 0								
Cirsium spp. (11)	0, 2, 0, 2	0, 0, 2, 0	10, 5, 0, 0	5, 0, 0, 2								
R. repens (12)	5, 0, 0, 0	5, 5, 0, 0	0, 0, 0, 0	5, 5, 5, 0								
C. palustris (13)	2, 0, 0, 0	0, 5, 0, 0	0, 5, 0, 0	5, 5, 5, 5								
F. ulmaria (14)	0, 5, 5, 0	0, 0, 0, 0	10, 5, 0, 2	0, 0, 2, 0								
Lythrum salicaria (15)	0, 1, 0, 1	0, 0, 0, 0	0, 1, 0, 2	0, 0, 0, 0								
Gramineae (16)	10, 15, 10, 10	25, 20, 20, 30	20, 15, 15, 20	30, 20, 15, 25								

(2) Non-feeding Areas

Plant Species	% Cover within 16 quadrats											
1	30, 30, 20, 40	60, 75, 60, 50	60, 70, 40, 50	30, 30, 40, 20								
2	60, 65, 50, 45	10, 20, 30, 20	35, 20, 20, 40	45, 60, 60, 30								
3	60, 50, 40, 50	10, 5, 10, 0	0, 0, 0, 0	0, 5, 10, 5								
4	0, 2, 5, 10	10, 10, 5, 0	0, 0, 0, 5	5, 5, 10, 0								
5	20, 25, 30, 5	5, 0, 0, 10	10, 10, 5, 0	0, 5, 5, 10								
6	0, 0, 0, 0	0, 2, 0, 0	0, 0, 5, 0	0, 0, 0, 0								
7	0, 0, 0, 0	0, 0, 0, 5	0, 0, 0, 0	2, 0, 0, 0								
8	5, 0, 5, 0	0, 0, 5, 0	0, 5, 0, 0	0, 5, 0, 0								
9	0, 5, 0, 0	0, 5, 0, 0	0, 10, 0, 10	0, 5, 0, 20								
10	0, 2, 0, 0	0, 0, 0, 0	0, 5, 0, 0	0, 1, 0, 5								
11	0, 2, 0, 2	0, 5, 0, 0	0, 10, 0, 0	0, 0, 5, 0								
12	10, 5, 0, 0	0, 5, 15, 0	0, 5, 5, 0	5, 5, 10, 5								
13	0, 5, 0, 0	5, 0, 5, 0	0, 5, 5, 0	0, 0, 10, 0								
14	5, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 5	0, 5, 0, 0								
15	2, 0, 0, 0	0, 0, 0, 0	0, 2, 0, 0	0, 0, 0, 0								
16	10, 15, 20, 10	15, 10, 20, 15	15, 10, 20, 15	10, 5, 15, 20								

Appendix .5. Number of passes of Carrion Crows through 100m² segments of Singing washes and distances to Crow nest.

22	20	17	18	21	13	9
7	11	17	10	10	2	1
10	11	11	7	4		
8	9	3	4	7	5	4
	15	6	6	8	3	3
	22	16	11	10	5	1

Crow passes
(April 20th-June 7th)

14	14	11	14	15	10	3
6	8	10	5	8		
6	8	7	5	3		
7	9	2	3	7	5	4
	12	5	5	7	2	3
	16	15	11	10	4	

Crow passes during period
when Godwit nests active
(April 20th-May 26th)

5	5	5	5	6	7	2
4	4	4	4	5	6	6
3	3	3	4	5	5	6
2	2	2	3	4	5	6
	1	2	3	4	5	6
	0	1	2	3	4	5

Distance to Crow nest from
centre of each 100m² segment

Appendix.5. (cont.) Numbers of anti-Crow mobs within 100m² segments of the Singing Washes.

	1			3		
		4	1	4		
	1	1	2	3		
	1	2	3	6	4	
	2	4	5	5	1	
	2	7	6	2		

Mobs by Godwits
and Lapwings together
(April 20th-June 7th)

7	9	6	7	6		
	4	15	8	9	1	
	4	8	6	4		
1		2	3	4	2	
	1	1	1	4	1	
		1	4	3	1	

Mobs by Godwits and Lapwings
together or Lapwings alone
(April 20th-June 7th)

7	9	6	7	6		
	4	16	9	9	1	
	4	8	6	4		
1	1	3	4	6	4	
	2	4	5	6	2	
	2	8	7	4	1	

All mobbing
(April 20th-June 7th)

Appendix .6. Number of passes of Cattle Crows through 100m² segments of the Tower colony.

7	19	21	22	28	4		
2	5	3	4	6	1		
3	5	3	3	2	2	1	1
2	5	4	2	2	2	1	1
2	2	2	2	1	1		3
1	2	1		2	3	4	5
	5	2	2	5	3	5	3
	4	2	2	4	4	3	4
	3	2		2	5	3	5

Crow passes

117	275	303	318	405	58		
33	72	43	58	87	14		
50	46	19	19	13	13	9	9
33	29	18	9	9	9	6	9
33	12	9	9	5	5		27
17	12	5		9	14	23	46
	29	9	9	23	14	29	27
	36	12	12	25	25	27	81
	27	12		12	31	27	102

Crow passes per 100 hours

Appendix .6. (cont.) Number of anti-Crow mobs within 100m² segments of the Tower colony.

			2	4			
1	2	1	1	1			
2	3						
2	2	1	1	2	1	1	1
2	2	1	2	1	1		2
				2	3	3	4
	1	1	1	3	3	5	1
	1	2	1	1	2	1	1
					1	1	1

Mobs by Lapwings only

				1			
		1					
		2	1	1			
		3	2	2			
			2	1	1		
				1	2		
				2			
		1	1				

Mobs by Lapwings and Godwits

			2	4			
1	2	2	1	1			
2	3	2	1	1			
2	2	3	2	2	1	1	1
2	2	1	2	1	1		2
				2	3	3	4
	1	1	1	3	3	5	1
	1	2	1	1	2	1	1
					1	1	1

All mobbing

