Studies on the breeding biology of the kittiwake (rissa tridactyla) using marked individuals

Wooller, R. D.

Wooller, R. D. (1973) *Studies on the breeding biology of the kittiwake (rissa tridactyla) using marked individuals*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/8805/

STUDIES ON THE BREEDING BIOLOGY OF THE KITTIWAKE (*RISSA TRIDACTYLA*) USING MARKED INDIVIDUALS

R. D. Wooller, B.A. (York)

being a thesis presented in candidature for
the degree of Doctor of Philosophy in the
University of Durham, 1973

ABSTRACT

The attendance and activity of the members of Kittiwake pairs at their breeding sites was monitored throughout 5 successive breeding seasons using a radioisotope-marker technique.

The seasonal occupation of the colony from January to November is described, together with the patterns of site occupation, nest-building, egg laying, incubation and brooding behaviour. Pair members share almost equally the duties of incubation and the brooding and feeding of the young. Although one partner can compensate considerably for the absence of its mate, both sexes must normally contribute for breeding to be successful.

A high peak of activity prior to laying probably brings the female into ovulatory condition, and strengthens the pair bond just before shared incubation places the greatest strain upon it. These effects are probably mediated through arrival displays on the site.

Comparisons revealed that established pairs and older, more experienced breeding individuals showed higher levels of activity and attendance than less experienced birds. The former also integrated their patterns of behaviour more effectively, and this probably contributes to their greater reproductive success.

Naive individuals showed a marked improvement in their breeding activity during their second year together. However some inexperienced breeding individuals integrate their activities very successfully at their first attempt,

whereas some experienced individuals do not. It is suggested that some measure of compatibility may be necessary for successful co-ordination of breeding activities between pair members.

This idea of compatibility is consistent with the very considerable degree of heterogeneity in the patterns of pair behaviour recorded within the population, although established pairs showed very similar patterns in successive years.

ACKNOWLEDGEMENTS

This research was performed while at the University of Durham, and my thanks go to Professor D. Barker for the facilities provided in the Department of Zoology.

I am especially grateful to Dr. J. C. Coulson for his guidance and encouragement throughout this work, and it is largely due to his efforts that a colony of marked individuals was available for study. I am also indebted to all the other people who have collected information and ringed adults and young at North Shields over the years. Mr. A. F. Hodges pioneered the use of time-lapse photography at the colony and I am most grateful to him and to Mrs. Fiona Dixon for much stimulating discussion during this work.

Swan Hunter (Shiprepairers) Ltd. (formerly Smith's Dock Co. Ltd.) and their employees have continued to afford considerable help and facilities at North Shields and I am very grateful to them for their continuing protection of the colony. My thanks also go to the Farne Islands Committee of the National Trust for permission to work on these islands.

Dr. S. M. Evans of the University of Newcastle upon Tyne provided much helpful assistance regarding the use of the Sonagraph. I am also greatly obliged to Messrs. I. Dennison and E. Henderson for technical and photographic assistance, and to Mrs. Ruth Reed who typed the manuscript.

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INTRODUCTION

Background and aims

The Kittiwake is an obligatorily colonial, cliff-nesting gull. Like many seabirds the species has a low annual mortality rate and some Kittiwakes breed for 15 years or more. Since many individuals retain the same mate for several breeding seasons, the pair relationship may become elaborated into a complex bonding system.

Prolonged experience with one mate results in a more successful breeding performance (Coulson 1966a) although the complexity involved may increase the possibility of disjunction during the orderly progression through the events of the breeding cycle. The enhanced efficiency of long-established pairs has been attributed to their greater mutual stimulation and better integration of breeding behaviour (Coulson 1972). This co-ordination of events between two members of a breeding pair is a different matter from the synchronisation of breeding events in a population and may be more essential to reproductive success.

Any previous experience of breeding may greatly facilitate the development of laying, incubation and parental behaviour as has been shown in the laboratory with Ring Doves (Lehrman & Wortis 1960, 1967; Lott & Comerford 1968). In this species birds recognize their former mates after many months of isolation, and return to mate with them (Erickson & Morris 1972), such pairs having greater reproductive success than unfamiliar pairs. This pair-bond they attributed to recurrent episodes of display between the members of the pair (Morris & Erickson 1971) strengthened by such activities as allopreening, billing, courtship feeding and the exchange of nest material.

Erickson & Morris also found that unfamiliar pairs of Ring Doves failed to hatch their eggs more often than familiar ones, but that there were no apparent differences in the success of raising young. An identical situation exists in the Kittiwake (Coulson 1966a). In the Gannet, Nelson (1964) has also found that young parents are less efficient than older ones in the incubation of their eggs and the care of their young just after hatching. However, they fed their young just as frequently and the young fledged at the same age.

Incubation is probably the period when most strain is placed on the pair-bond, since the partners only meet to hand over incubation duties. Without reinforcement from frequent pair interactions, they must integrate their activities such that the eggs or young chicks are not left unattended. It seems likely that this integration would be more efficient among pairs which had bred together previously.

However, previous breeding experience does not necessarily lead to successful integration. Slater (1970) found wide variation between pairs of Bengalese Finches in their laying dates, although all were experienced breeders and had been kept under control conditions for at least a month. He attributed this to differences in the extent to which the new partner was morphologically and behaviourly compatible with an expected image (akin to the Sollwert of Hinde 1966) built up as the result of previous sexual and social experience. The pair-bond he conceived as a model of the partner built up as a result of proximity.

The Kittiwake defends only its nest and a very small territory around the nest. All pair activities take place at the nest site, and the young are necessarily confined to the cliff site until they can fly. Thus it is possible to monitor reasonably easily all breeding activities of selected individuals while they are at their breeding colony.

This was done during this study to investigate some of the ways in which long-established pairs differed from newly-formed ones, and experienced partners from naive ones. In this way it was hoped to elucidate some of the factors contributing to the greater success of experienced birds, especially during the incubation phase.

The Species

Kittiwakes and their colonies in north-eastern England have been the subject of a series of studies by Coulson & White (1956, 1958a, 1958b, 1959, 1960, 1961) and Coulson (1963, 1966a, 1972). Other studies on the species include those of Paludan (1955) in Denmark, Cullen (1957) on the Farne Islands, Northumberland, and Maunder & Threlfall (1972) in Newfoundland. Investigations on more northerly colonies have been made in Alaska (Swartz 1966) and the U.S.S.R. (Belopol'skii 1961).

Breeding birds have been shown to have almost complete colony tenacity (Coulson & White 1958b, Coulson 1972). At lower latitudes such as north-eastern England, some individuals may remain at their colony for over 9 months in every year.

However, as with many other seabirds, our knowledge of what happens to the species away from its breeding colonies is extremely limited. Ringing recoveries suggest extensive dispersal of young Kittiwakes over the two years following their departure from their natal colony. Adult birds have little time left when away from their colony for extensive movements (Coulson 1966b).

During the breeding season the feeding range of the Kittiwake is probably well under a 100 mile radius from the colony (Coulson 1966b) and may be nearer the maximum of 35 miles suggested by Pearson (1968) for birds from the Farne Islands.

The Study Population

In recent years the Kittiwake, like some other gulls (Cramp 1971), has taken to nesting on buildings. One such colony, on the window ledges of a warehouse at North Shields, Northumberland ($55^{o}01'N$; $1^{o}26'W$), has been studied since its foundation in 1949. Since 1955/1956 almost all the breeding birds have been individually colour-ringed.

The nearest large colony of Kittiwakes is at Marsden Rock (3,500 pairs) and there are smaller colonies further up the River Tyne, near Newcastle (Fig. 1). Birds from the North Shields colony roost with others in several places at the mouth of the Tyne. They may be seen there in autumn and early winter when the colony has been deserted after the breeding season, and also during the re-occupation of the colony in early January.

The relatively small size of the colony and the need for continuation of long-term studies precluded much experimental disturbance. Some additional information was collected while on the Farne Islands, Northumberland ($55^{\circ}37$'N; $1^{\circ}37$'W) during 1970 and 1971.

The colony at North Shields grew in size from 1949 until about 1965 when it stabilised at just under 100 breeding pairs (Fig. 2). Only in one year has the mean clutch size fallen below 2.0 or the mean number of young fledged per pair below 1.0. The proportion of window ledges containing two breeding pairs has increased with the size of the breeding population (Fig. 3). In such an intensely colonial species as the Kittiwake interactions between individuals are frequent, resulting in severe competition for sites within the established breeding areas (Coulson 1971).

Centre and Edge Effects

Although the physical qualities of the window sites available are all equal, Coulson (1968) has shown that there is marked segregation between the birds at the centre of the colony and those at the edge. Birds breeding in the centre of the colony have a lower mortality rate, larger clutch size, greater breeding success, fledge more young per pair, change mate less often, and

Figure 1. The Kittiwake colonies on and near the River Tyne in north-eastern England, showing the position of the North Shields study population

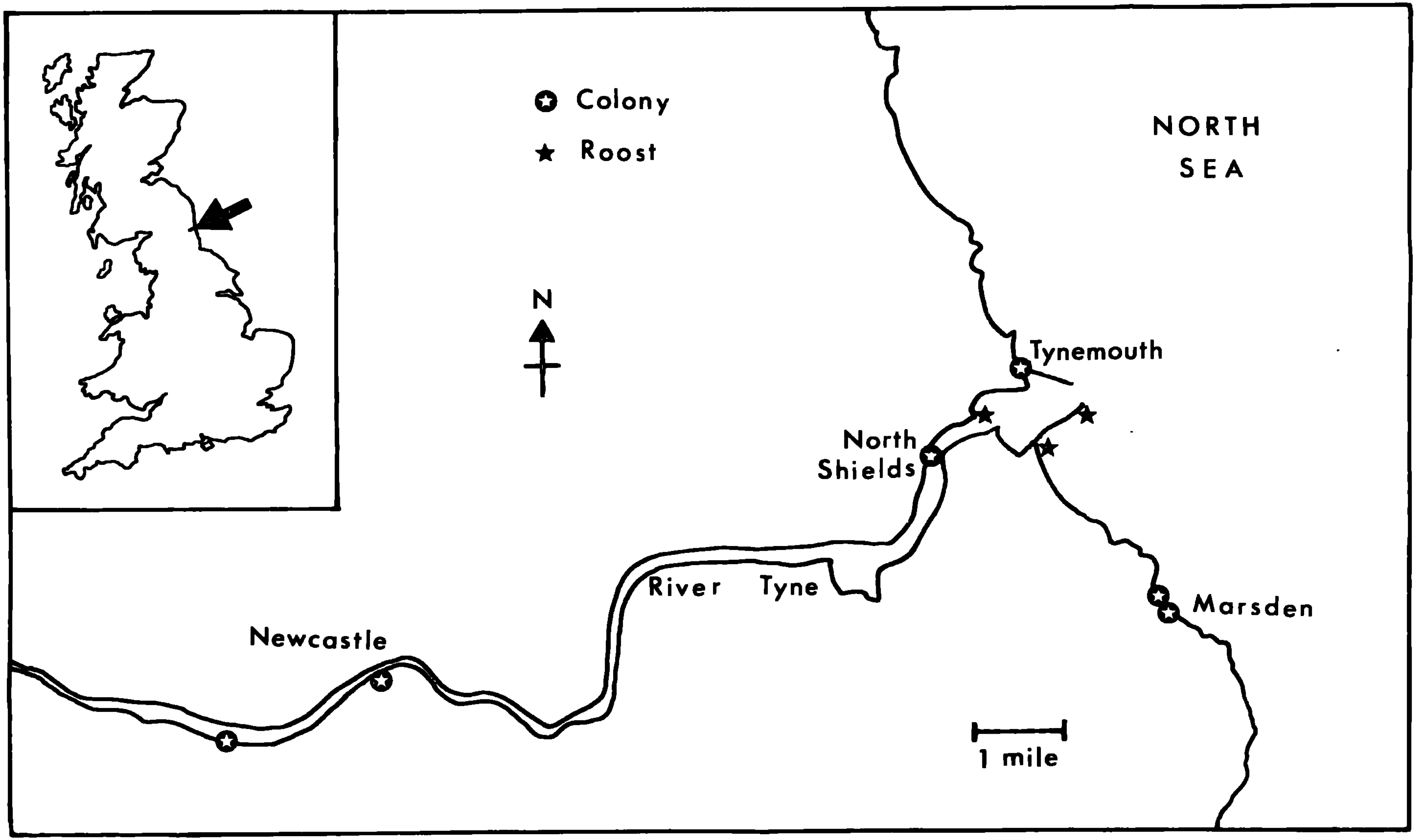
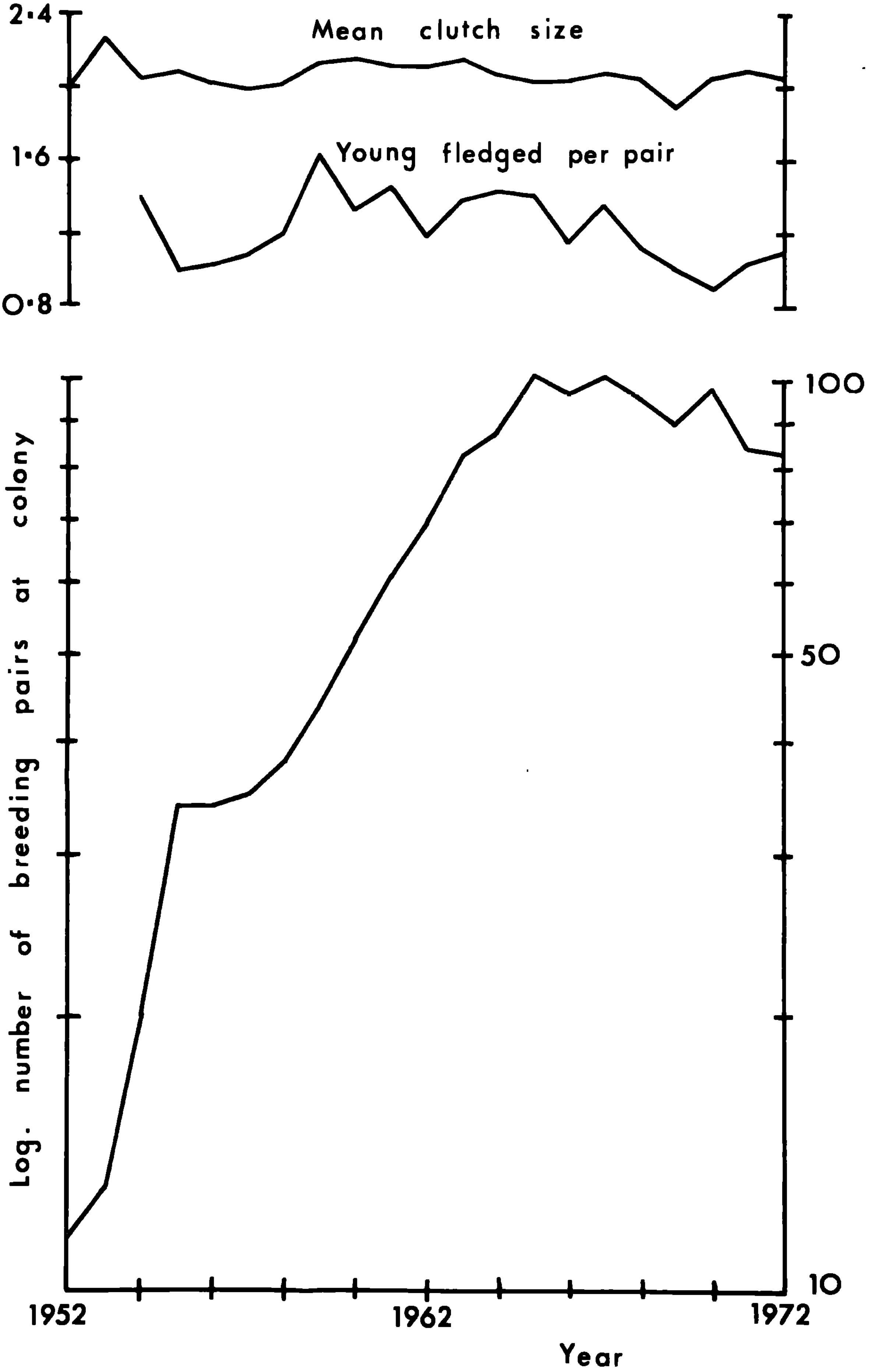
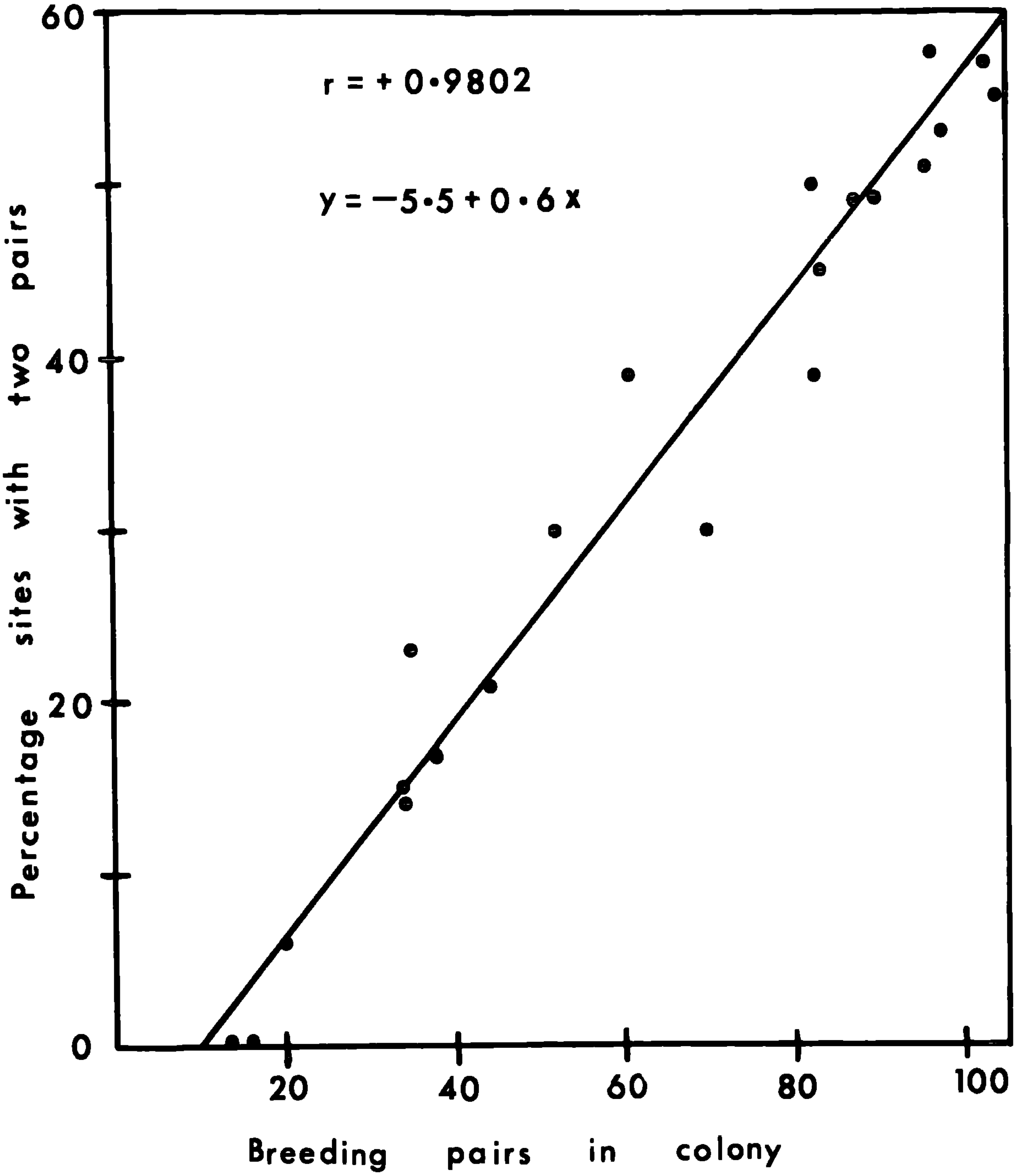

Colony
Roost
NORTH
SEA
N
Tynemouth
North
Shields
River Tyne
Newcastle
Marsden
1 mile

Figure 2. The growth and stabilisation of the North Shields Kittiwake population from 1952 - 1972. The mean annual clutch sizes and the mean number of young fledged per pair for these years are shown above.

Figure 3. The relationship between the annual size of the North Shields breeding colony and the proportion of occupied window-ledge sites which were used by two breeding pairs (1952 - 1972)


2·4
1·6
0·8
Mean clutch size
Young fledged per pair
Log. number of breeding pairs at colony
100
50
10
1952
1962
1972
Year


r = + 0•9802
y = −5•5 + 0 • 6 x
Percentage sites with two pairs
Breeding pairs in colony
0
20
40
60
20
40
60
80
100

lay earlier in the season than birds at the edge. Central males are also slightly heavier than males on more peripheral sites at the time of their recruitment to the population.

Most males breed for the first time at 4 years old, one year earlier than females. Both of the sexes often return to the colony in the year before they first breed (Fig. 4a). Males hatched on central sites breed for the first time at a significantly younger age than those from edge sites (Table 1, Fig. 4b), although they do not return to the colony at an earlier age. Birds breeding for the first time on central sites are not younger than similar birds on edge sites.

Once a male has acquired its initial site in either the central or edge areas of the colony it tends to change sites only within that area. Only very rarely do birds change to sites in the other category. This first site selection therefore is linked to the later reproductive success of the bird, and may itself be related to the quality of the bird concerned (Coulson 1968).

A similar situation was encountered by Tenaza (1971) among Adélie Penguins,[**] where birds which first bred on peripheral sites did not attempt, or were not able, to acquire more central positions. This avoids wastage of time and reproductive energy in possibly fruitless competition for better sites. Also, by returning to the same mate and site, albeit peripheral, in successive years, a bird produces more offspring.

[**] Specific names of animals mentioned in the text are listed in Appendix 8

Table 1. Age at time of first breeding and return to the colony of birds hatched on centre and edge sites

Hatched	First bred	Age when first bred (years)	Sample size
Centre	Centre	4.25 ± 0.41 **	20
Centre	Edge	4.57 ± 0.53	23
Edge	Centre	4.87 ± 0.55	15
Edge	Edge	5.00 ± 0.38	17

Only the first and last values differ significantly :

$t_{35} = 2.652; \quad P < 2\%$

Age at time of first breeding

Centre-hatched males	(N=43)	4.42 ± 0.34 years	$t_{78} = 2.149$
Edge-hatched males	(N=32)	4.94 ± 0.31 years	$P < 5\%$
All centre-hatched birds	(N=57)	4.58 ± 0.68	$t_{98} = 1.980$
All edge-hatched birds	(N=43)	5.00 ± 0.48	$P < 5\%$

Age when first seen at colony

Centre-hatched birds	(N=86)	3.88 ± 0.25 years	$t_{157} = 0.567$
Edge-hatched birds	(N=73)	3.99 ± 0.26 years	N.S.

Age of birds breeding for the first time

On centre sites	(N=44)	4.66 ± 0.33 years	$t_{93} = 0.759$
On edge sites	(N=51)	4.82 ± 0.29 years	N.S.

(similar results obtained for males only)

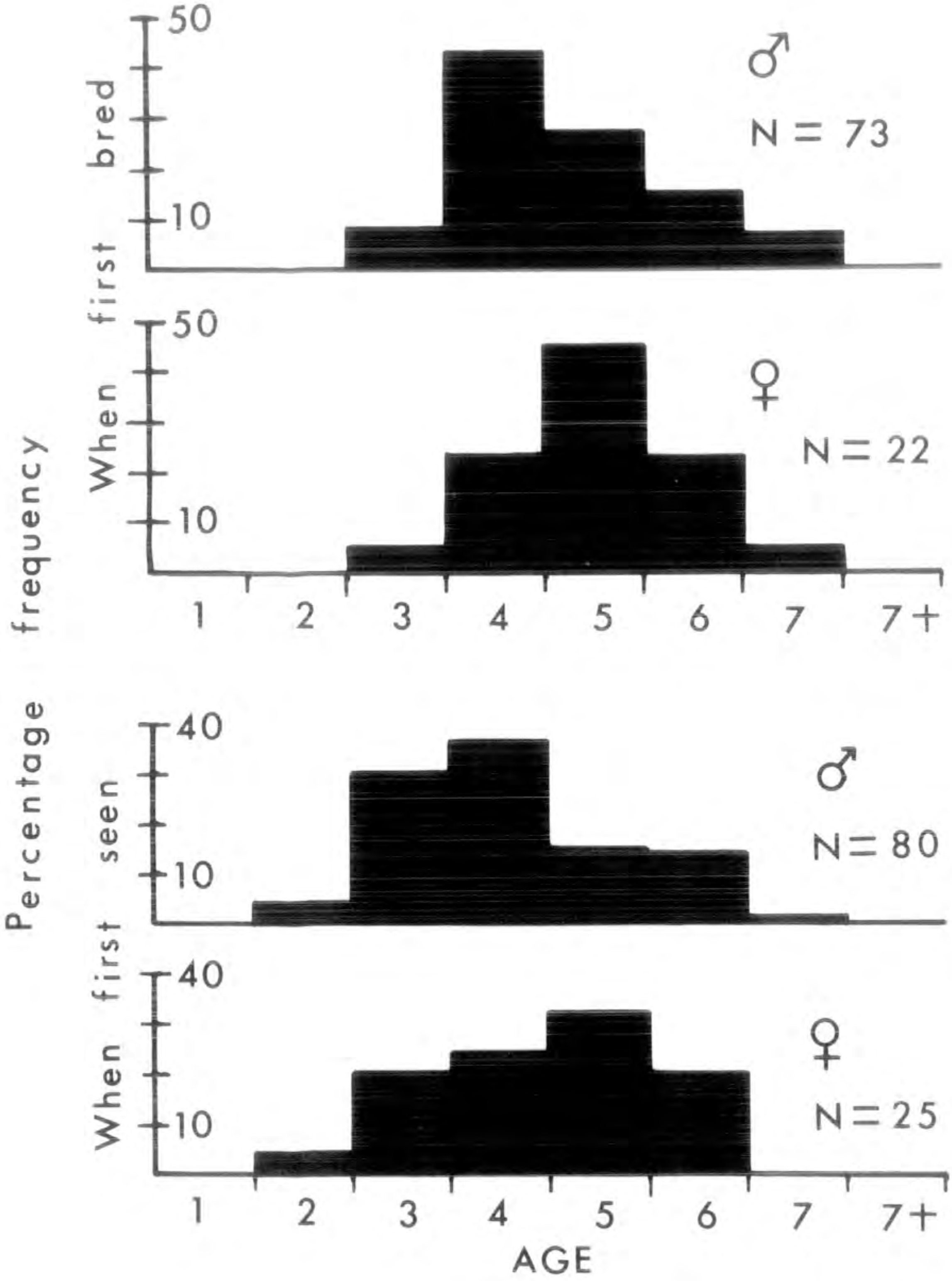
** Statistical note. Throughout, all means will be given ± 95% confidence limits (or 2 x S.E.) Degrees of freedom in statistical tests will be expressed as a numerical subscript. Thus t_{78} indicates t with 78 d.f. N.S. indicates non-significance in the test at the 5% level of probability.

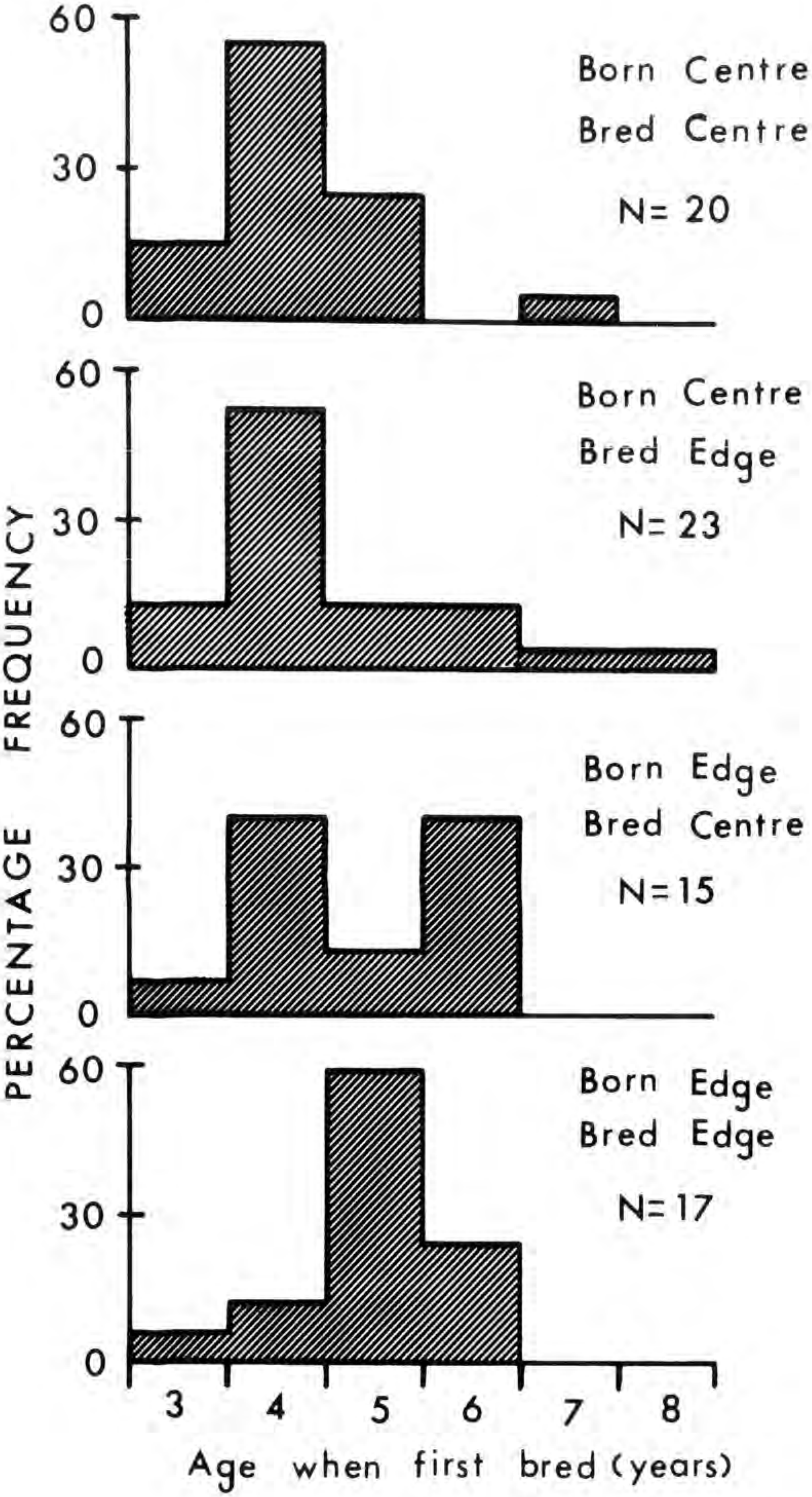
Figure 4a. Percentage frequency distributions of the ages at which males and females first bred, and their ages when first seen back at the North Shields colony.

Figure 4b. Percentage frequency distributions of the ages of males when they bred for the first time, for four categories. These represent males which originally fledged from sites in the centre or edge of the colony, and which returned to breed on either central or edge sites.

The centre of the colony has been arbitrarily taken (following Coulson 1968) as those sites occupied when the colony was half its present size.

Figures 4a and 4b are based upon information obtained from birds ringed as pulli at North Shields, which later returned to the colony to occupy breeding sites. Most of these are males and almost all have bred at the colony.


Percentage frequency
When first bred
50
10
♂
N = 73
50
10
♀
N = 22
1
2
3
4
5
6
7
7+
When first seen
40
10
♂
N = 80
40
10
♀
N = 25
1
2
3
4
5
6
7
7+
AGE


60
30
0
Born Centre
Bred Centre
N= 20
60
30
0
Born Centre
Bred Edge
N= 23
60
30
0
Born Edge
Bred Centre
N=15
60
30
0
Born Edge
Bred Edge
N=17
PERCENTAGE FREQUENCY
3
4
5
6
7
8
Age when first bred (years)

SECTION I

ANNUAL ATTENDANCE AND ACTIVITY

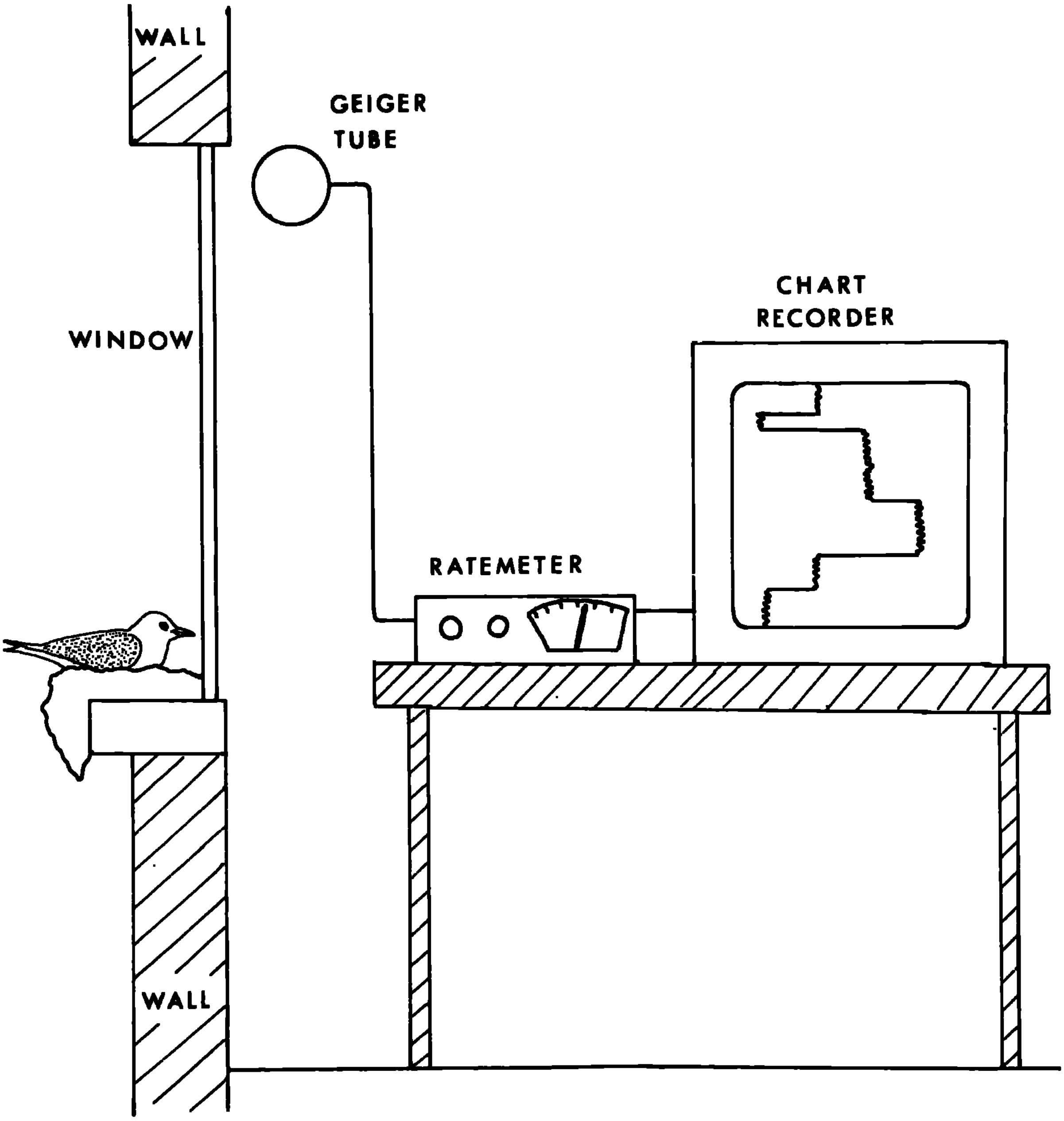
Method

Some pairs were fitted with radioisotope markers in the form of leg bands incorporating radioactive cobalt^{60}. A cobalt-nickel alloy (40% cobalt) was hammered thin and 1mm diameter discs were cut and cold-welded into aluminium rings which were then irradiated. Rings were made up with differing numbers of discs which gave a range of radiation levels and enabled individual members of pairs to be distinguished. Each disc had an initial activity of 1.905 µC and a maximum of six was used in any one ring. Cobalt^{60} has a half-life of 5.3 years and was chosen because it seemed appropriate to the need to study birds in several successive years.

The gamma radiation produced by the source was of sufficient energy (1.33MeV) to pass through a window and also through the body of a bird should it be sitting on its legs. However, the dosage level was low enough not to be a major hazard to the birds, and pairs bred for up to four years with no impairment of reproductive success.

The presence of a radioactively-ringed bird on a window ledge site was detected by a pair of Geiger-Muller tubes (20th Century Electronics B-6-H tubes) mounted behind the window. They were positioned above the site to nullify any movements of the bird about the ledge, and at a distance of about 50 cms from the source (Fig. 5).

Figure 5. Schematic section showing the arrangement used to monitor the presence of radioactively-ringed members of a breeding pair on their nest site


WALL
GEIGER
TUBE
WINDOW
CHART
RECORDER
RATEMETER
WALL

The Geiger tubes were energised at about 360 volts by an IDL 7030 Ratemeter. Using this instrument an integration time of 50 secs and a range of 0 - 10 counts/sec was found most satisfactory. The instrument also had facilities for the suppression of background radiation. The output from the ratemeter went to a Kent 100 mv strip-chart recorder which provided a continuous record of the output and hence of the presence of a radioactive bird on the site. The members of a pair could be distinguished by the different levels of the trace recorded. In any one year Kittiwakes remain strictly faithful to their site and it was only necessary to distinguish between the two mates.

Trials with different chart speeds (from 1 in/hour up to 8 ins/hour) showed that a rate of 2 ins/hour was most efficient and gave a resolution of considerably better than 1 minute. At this speed a 120 ft chart lasted one month and recorded all arrivals and departures of radioactive birds at the site.

This method provides information on the presence or absence of members of a pair, the frequency and duration of their visits to the site, and the times of these visits. It would also be possible to obtain some measure of the activity of a bird on the site from the amplitude of the trace recorded, but this was not attempted.

After a time-base had been placed on a chart the times of all arrivals and departures at a site were transferred to daily record sheets and all further analysis was carried out using these sheets.

Applicability of the method

Once set up, the arrangement used requires little attention other than changing the chart, and possibly the writing pen, once every month. It will provide continuous data over long periods of time - in this case ten months of each year. Unlike photographic methods, it is independent of light. It is also possible to distinguish a number of different individuals at any one location, although multiple levels may be difficult to interpret since different combinations of individuals could produce the same resultant level. In this study only two individuals occupied any one site and their levels of radioactivity were easily distinguished. Radioactive tagging has been used for tracking small mammals for many years (Godfrey 1954; Gerrard 1969), but it is only recently that it has been used for recording the activity of birds at their nests.

Simultaneously with this study Ward (1969), using tantalum^{182} sources of 100 and 50 µC, monitored the White-flanked Flycatcher and the tunnel-nesting Carmine Bee-eater. He rightly emphasizes the necessity of visual observations over several hours if the trace recorded is to be interpreted correctly.

Storteir & Palmgren (1971) used the method to study the daily activity of the Black Guillemot in the breeding season. They used sources of zinc^{65} with strengths of 2.5 µC and 10 µC. They point out that it gave a continuous and accurate picture of both incubating rhythm and feeding frequency, while reducing human interference to a minimum during the breeding season.

This method is applicable in a wide range of situations where activity at a nest, roost, or other specific location needs to be monitored. It would be especially useful for species which are nocturnal, or nest in holes, burrows and crevices. It might also be used for species nesting in inaccessible situations such as tall trees or cliff faces, as only an initial visit to install the detectors is required. It could also be helpful for studying species in which the sexes cannot be visually identified in the field.

As the equipment needs only minimal attention and can be sited at a considerable distance from the place being monitored, this method would be valuable in studying species which are particularly sensitive to disturbance.

Although a mains supply of electricity was used in this study, battery-operated versions of the equipment may easily be assembled, and were used in the two studies of birds cited above.

Selection of the pairs studied

Sufficient equipment was available to monitor up to 6 pairs in any one season. Initially the pairs selected were ones which had been together for several years. This was intended to provide a baseline of well-integrated activities which could be used in comparisons with less-experienced pairs. In later seasons pairs with less breeding experience, some breeding for the first time, were studied.

However, these young pairs may not be formed until the breeding season is well advanced. They may undergo several changes of apparent mate and site before finally settling down, and this makes it very difficult to mark and monitor them radioactively in the early part of the season. It would have been undesirable to ring large numbers of birds with radioisotope markers, both because of the stringent regulations governing their use, and because of the difficulty of identifying individuals from subsequent records.

Due to the reasons above, information during the period before egg laying was incomplete in eight cases. Six pairs were monitored from their arrival at the colony in January until their departure in October or November. Information was collected for the periods of egg laying, incubation and the remainder of the breeding season, from 1968 - 1972 for a total of 22 pair-years. Table 2 lists the year, site and individuals concerned, and the previous breeding histories of all these birds are shown in Table 3. The dates of laying of these pairs may be found in Appendix 1.

Five of the pairs remained unchanged in two successive years, and two pairs remained unchanged for three years. Two individuals have been followed for four out of the five years of the study. There have been changes of mate due both to "divorce" and to bereavement, and also changes of site.

Table 2. Composition of the radioactive pairs

	W1F		W1E		W1B		W1D		W1G		E1D		W1H/W21		S1CT	
	m	f	m	f	m	f	m	f	m	f	m	f	m	f	m	f
1968	a	j			d	m			c	l						
1969	a	j			e	n			c*	l	g*	r				
1970			b	j	f	n	e	q	c**	l	g	s				
1971			b*	j	f	n	e	q			g**	s	h	t		
1972			b	j	f	p	e	q					h**	t	i	v

* indicates failure to hatch eggs

** indicates disappearance (presumed dead) of one partner during the breeding season

m and f indicate male and female members of the pair

Table 3. Life-histories of radioactively ringed birds

Columns coded as follows :

A. Site and Year
B Individuals concerned. a to i are males; j to t females
C Number of previous years breeding experience
D Number of years had bred previously with this partner
E Number of previous years had bred on this site
F Number of previous partners
G Number of sites on which had bred previously
H Number of eggs laid previously
I Number of eggs hatched previously
J Number of young fledged previously

A	B	C	D	E	F	G	H	I	J
W1F 68	a	13	12	13	2	1	25	23	22
	j	13		13	2	2	25	23	22
W1F 69	a	14	13	14	2	1	27	25	24
	j	14		14	2	2	27	25	24
W1E 70	b	1	0	1	1	1	2	2	2
	j	15		0	2	2	29	27	26
W1E 71	b	2	1	2	2	1	4	4	4
	j	16		1	3	3	31	29	28
W1E 72	b	3	0	3	2	1	6	4	4
	k	4		0	4	3	8	7	5
W1G 68	c	6	1	4	4	2	11	10	10
	l	6		1	5	3	9	5	5
W1G 69	c	7	2	5	4	2	13	12	12
	l	7		2	5	3	11	7	7
W1G 70	c	8	3	6	4	2	14	13	12
	l	8		3	5	3	12	7	7
S1C 72	i	2	0	0	2	2	4	4	4
	v	3		0	2	2	6	2	1

Continued overleaf.....

Table 3. (Continued)

	A	B	C	D.	E	F	G	H	I	J
E1D	69	g	8	2	8	3	1	21	12	10
		r	2		2	1	1	6	6	4
E1D	70	g	9	0	9	4	1	22	12	10
		s	3		0	3	3	6	3	3
E1D	71	g	10	1	10	4	1	24	13	11
		s	4		0	4	4	8	4	4
W1B	68	d	6	6	6	1	1	17	14	13
		m	9		9	2	1	24	21	20
W1B	69	e	0	0	-	-	-	-	-	-
		n	0	0	-	-	-	-	-	-
W1B	70	f	0	0	0	-	-	-	-	-
		n	1		1	1	1	2	2	2
W1B	71	f	1	1	1	1	1	2	2	2
		n	2		2	2	1	4	4	4
W1B	72	f	2	0	2	1	1	4	3	3
		p	1		0	1	1	2	1	1
W1D	70	e	1	0	0	1	1	2	2	2
		q	1		0	1	1	2	2	2
W1D	71	e	2	1	1	2	2	4	2	2
		q	2		1	2	2	4	2	2
W1D	72	e	3	2	2	2	2	6	4	3
		q	3		2	2	2	6	4	3
W1H	71	h	6	4	0	3	4	12	7	7
		t	11		0	6	8	22	9	9
W2I	72	h	7	5	0	3	4	14	8	8
		t	12		0	6	8	24	10	10

Male a and female j were the most experienced and successful breeding pair in the colony.
Male b paired with female j after divorcing his mate.
Male e bred for the first time aged 4 years on W1B, then moved the following year to W1D.
Male f, who replaced him, also bred for the first time in 1970 aged 4.
Male i paired with female v after divorcing his mate. Her mate had disappeared (presumed dead) during the intervening winter.
Female k paired with male b, and female p with male f, both in 1972 after divorces from their mates. Female q also mated with male e in 1970 after a divorce.

Parameters used

The information was summarised as weekly totals, and the following parameters were taken :

1. Attendance. This was the percentage of the period concerned when the individual (or the pair) was present on the site. In some cases this was additionally calculated for the hours of daylight only. The attendance of an individual includes its attendance as a member of a pair as well as its attendance alone.
2. Activity. This was the number of arrivals at the site by the bird concerned. In the case of pair activity it was the number of times that one member of a pair arrived on the site to find its mate already present. This formation of the pair is often accompanied by a greeting ceremony.
3. The percentage of the weekly period that the site was left unoccupied, and hence undefended, by the radioactive pair was also calculated.

These weekly totals for male and female attendance and activity, pair attendance and activity, and the proportion of time that the site was unoccupied, are given for each pair-year in Appendix 2. Some of these figures are represented diagrammatically in Figs. 7 - 18 where they are shown relative to the date on which the first egg was laid.

Additional data for single birds

The female which had bred on site W1F in 1968 and 1969 also returned to the site in 1970. Records were made of her attendance while she awaited the return of her mate (Fig. 19). However, he did not return and had presumably died. This pair had bred together on this site for 13 years and was the most experienced breeding pair in the colony. Later in the year the female moved to an adjacent site where she paired and bred.

The female who bred on site W1G in 1968, 1969 and 1970 also returned to the colony in 1971 and 1972. She was deserted by her mate in 1970 and he has not been seen since and may be presumed dead. In 1971 she returned to the same site (W1G) as previously and although it was occupied intermittently by a breeding pair, she continued to visit the site occasionally when they were not present. Records were made of these visits from January to May (Table 12).

In 1972 she again returned to the site W1G where she was recorded from January to March but during this period she was also observed on other sites. Eventually she took up residence on an adjacent site where she spent a considerable amount of time during the second half of the season, and records were made of this (Table 13). In neither of these two latter years did she pair with a new mate.

Kestrel

Between 28 March and 28 April in 1969 a pair of Kestrels attempted to nest on the warehouse. During the period that these predators were present at the colony the attendance of the Kittiwakes was considerably disturbed and this is reflected in the records for 1969. The Kestrels were removed and the Kittiwakes rapidly resumed their normal pattern of attendance.

Time-lapse photography

Information was collected for some pairs using the time-lapse photographic method of Hodges (1969). Since this method does not necessitate catching individuals to mark them, it was used to study young pairs whose composition was uncertain, and which were particularly susceptible to disturbance. This method only provides information for the daylight hours, but does record the different activities performed by members of a pair during their presence on the site.

Generalised pattern of attendance and activity

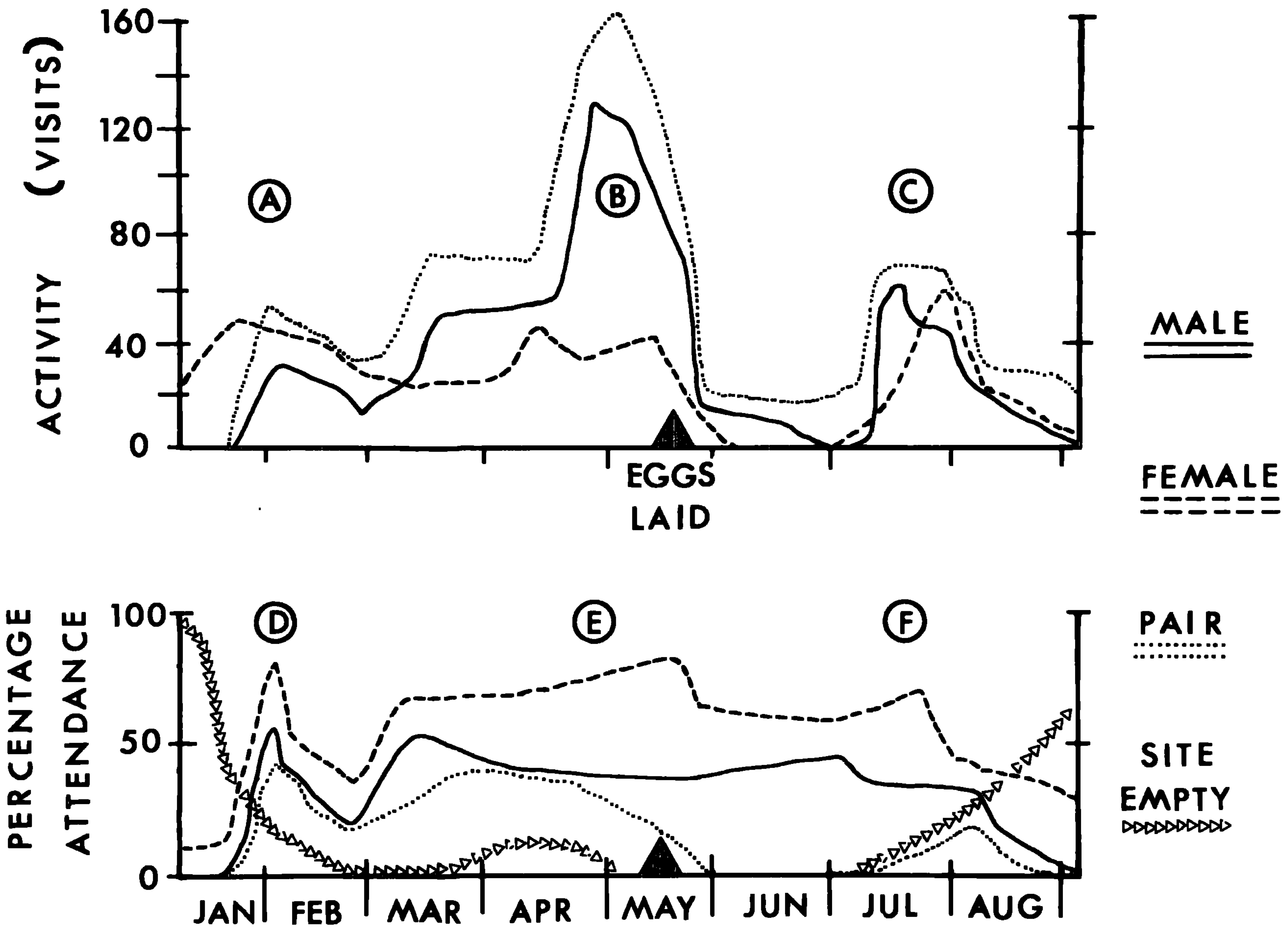
Although there is very considerable variation in the patterns of activity and attendance between the different pairs, and in different years, it is possible to build up a generalised pattern of these parameters throughout the breeding season. Such a pattern, intended to represent a well-integrated pair, is shown in Fig. 6.

After the birds return in January or February there is a peak of activity at the site (A) when the birds take possession of the site. At this point they may be nervous about coming to land after some months at sea. This is followed by a peak in attendance (D) when the birds

Figure 6. A generalised representation of the activity (top figure) and attendance (bottom figure) at their site during the breeding season, of the members of a well-integrated pair.

Activity refers to the number of visits to the site per week and attendance is the percentage of the week that the partners were present or that the site was left vacant (see page 16). The attendance and activity of male and female includes their attendance and activity as members of the pair.

The letters are reference points mentioned in the text, and a solid triangle indicates the date when the eggs were laid.


160
120
80
40
0
ACTIVITY (VISITS)
Ⓐ
Ⓑ
Ⓒ
EGGS LAID
MALE
FEMALE
100
50
0
PERCENTAGE ATTENDANCE
Ⓓ
Ⓔ
Ⓕ
PAIR
SITE EMPTY
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG

settle down to claim ownership of the site by occupying it intensively and regularly. Attendance at the site falls away before building up again in March. After this, the attendance of the male falls gradually, while that of the female builds up until by point (E) before laying the female level is about 80 % attendance and that of the male 40 %.

At this time the female remains on the site contributing largely, although not entirely, towards the building of the nest and being fed by the male. Meanwhile he indulges in bursts of activity either fishing or collecting nest material. This results in a large peak of pair activity (B) prior to laying of about 100 - 160 visits per week, mainly caused by the 80 - 100 visits per week to the site by the male.

The actual amount of time that the pair are together at this point (E) has fallen quite steeply to about 15 - 20 % or less, and it dies away almost completely during the incubation of the eggs when the birds only meet briefly to change over incubation duties - in which they take roughly equal shares.

During the brooding and care of the young both members of the pair again spend similar amounts of time on the site, and meet only at changeover times. About 6 - 10 weeks after egg-laying the pair finally begin to leave the site vacant for increasing lengths of time, and are often away from the site overnight.

After the young have departed there is a post-breeding resurgence of activity in July and August. At this point (C) the peak of male activity occurs a week before that of the female. Their activity is fairly high relative to their site attendance at this point (F) and there are some signs of sexual and territorial activity. This is discussed further in Section VII.

After this the birds spend less time on the site and their attendance tails away fairly rapidly until by September and October the site is virtually untenanted.

Daylight and overnight patterns of attendance have been calculated for pairs W1E and E1D in 1971 for comparison with the full profiles (Tables 4 and 5 in Appendix 3). The only major difference occurs early and late in the season when birds are absent overnight from the colony. The greater daylight attendance at this time is presumably necessary because this is when ownership of the sites is contested.

Comparisons of attendance and activity of different pairs

A very generalised picture of the attendance and activity of pairs at their nest sites has been drawn, but pairs differed in some respects in their patterns, although the same pair in successive years tended to have very similar patterns. Some of these patterns are represented in Figs. 7 - 18 and briefly considered below. A more detailed discussion of these pairs can be found in Appendix 4.

The most successful and experienced pair at the colony (Figs. 7 and 8) shows the high degree of integration attained after many seasons of shared activity. A progressive improvement in performance due to increasing individual breeding experience and previous experience with the same partner is shown in Figs. 9, 10 and 11.

Figures 7 - 18

These figures are based upon information given in Appendix 2 and each figure shows the seasonal attendance and activity profiles of pairs referred to briefly in the text, and discussed in more detail in Appendix 4.

Hatched kite diagrams represent changes in weekly activity and cross-hatched ones show weekly attendance. In each figure the diagrams from top to bottom show :

Male activity
Male attendance
Female activity
Female attendance
Pair activity
Pair attendance
Percentage time site left empty

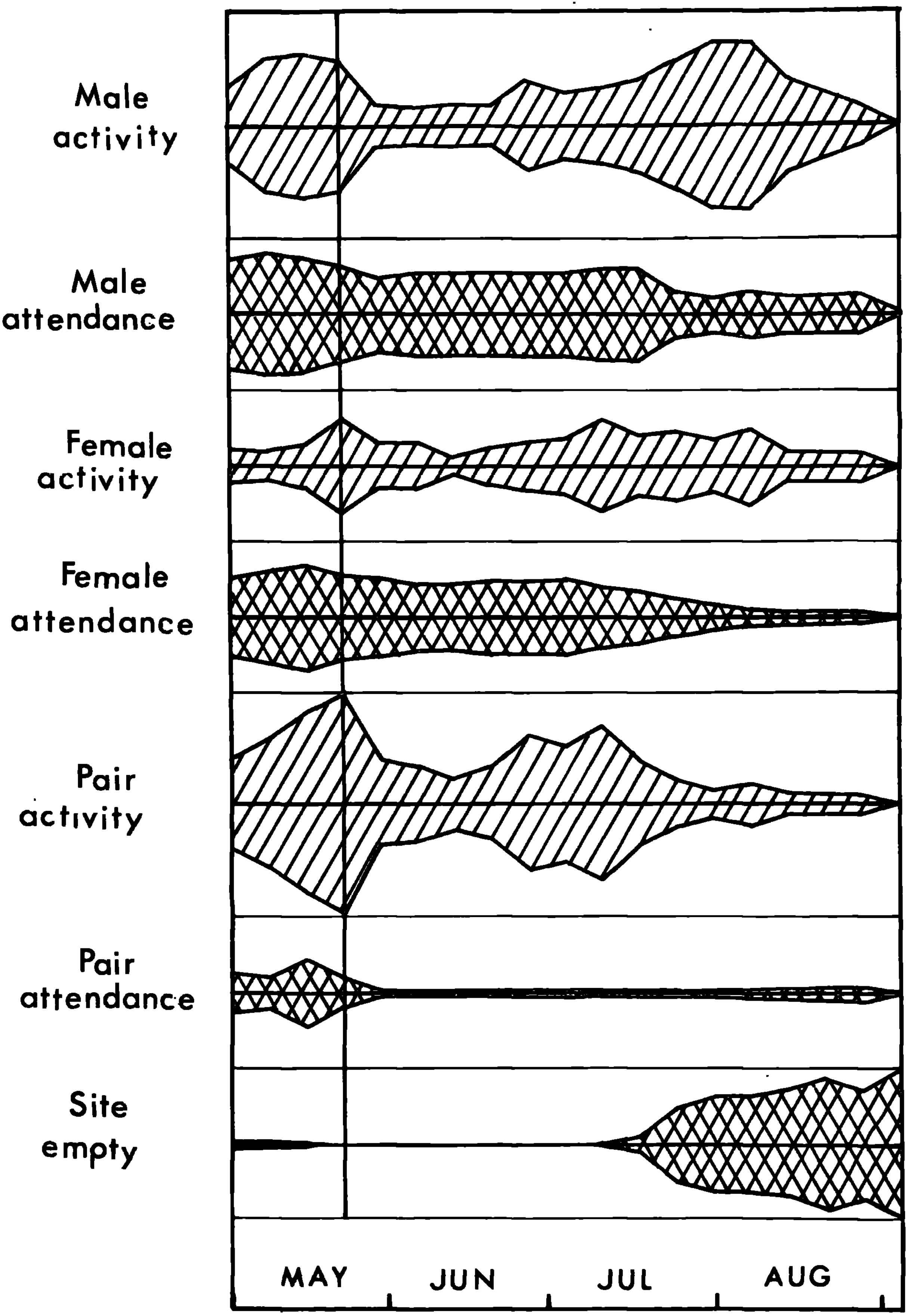
A vertical line during May shows the date on which the first egg was laid, and attendance and activity were calculated for weekly periods from this date.

Horizontal lines bounding attendance diagrams denote 100 % attendance, and a similar separation distance for lines enclosing activity profiles represents 100 visits per week. Some activity diagrams are delimited by lines denoting 150 visits/week.

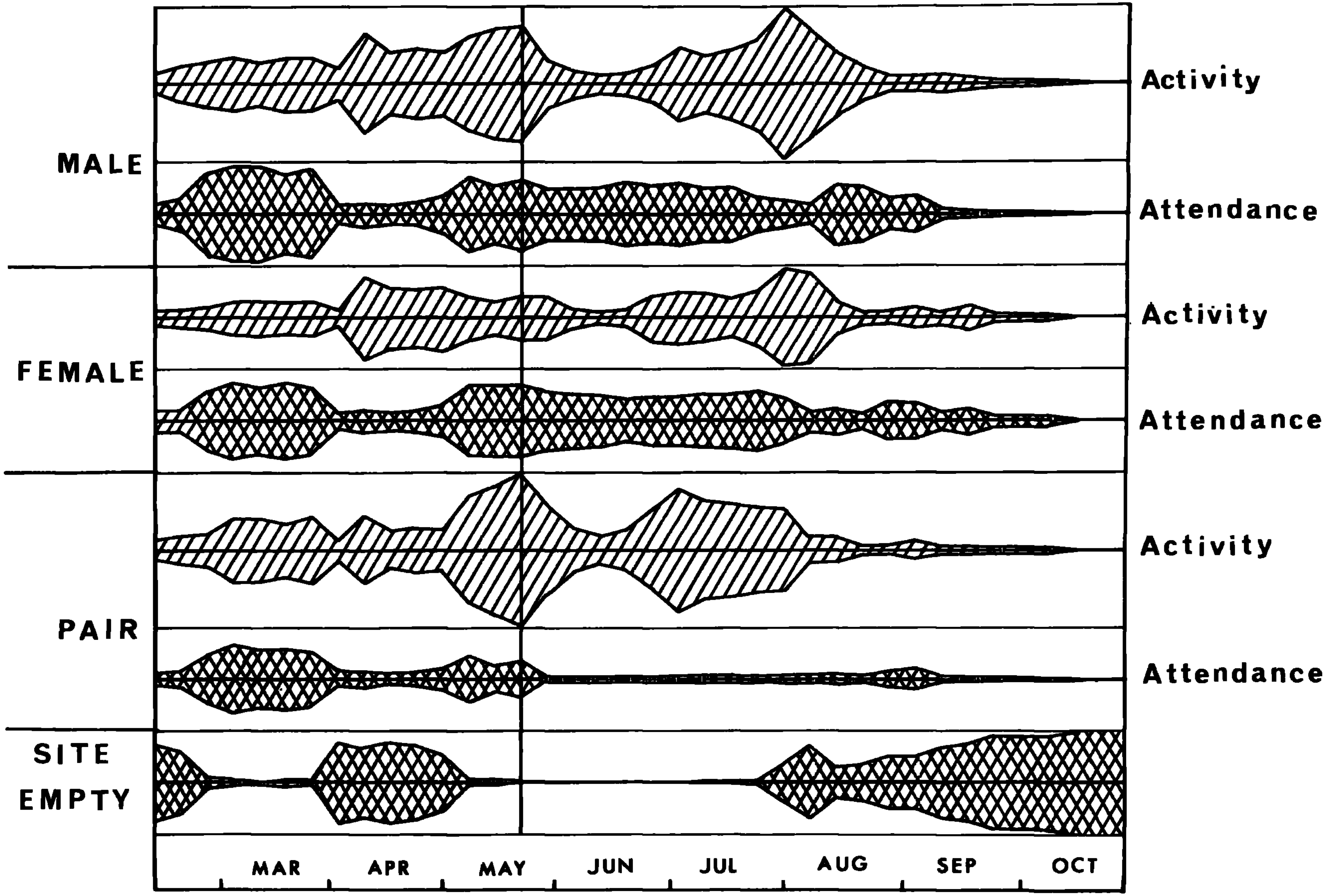
The figures represent the following pairs and years :

7	W1F	1968
8	W1F	1969
9	W1E	1970
10	W1E	1971
11	W1E	1972
12	W1G	1969
13	W1G	1970
14	E1D	1970
15	E1D	1971
16	W1B	1970
17	W1B	1971
18	W1D	1972

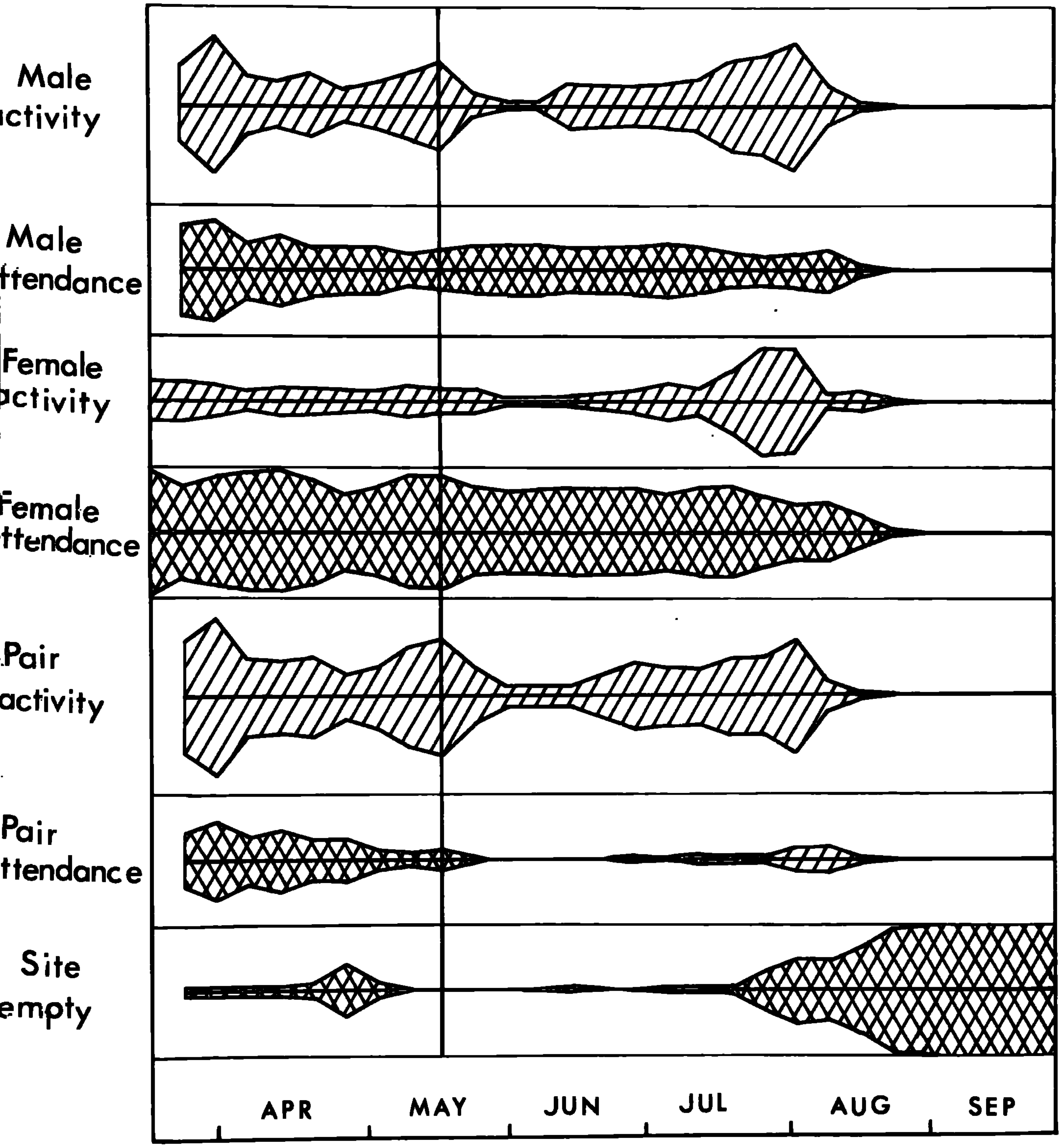
7

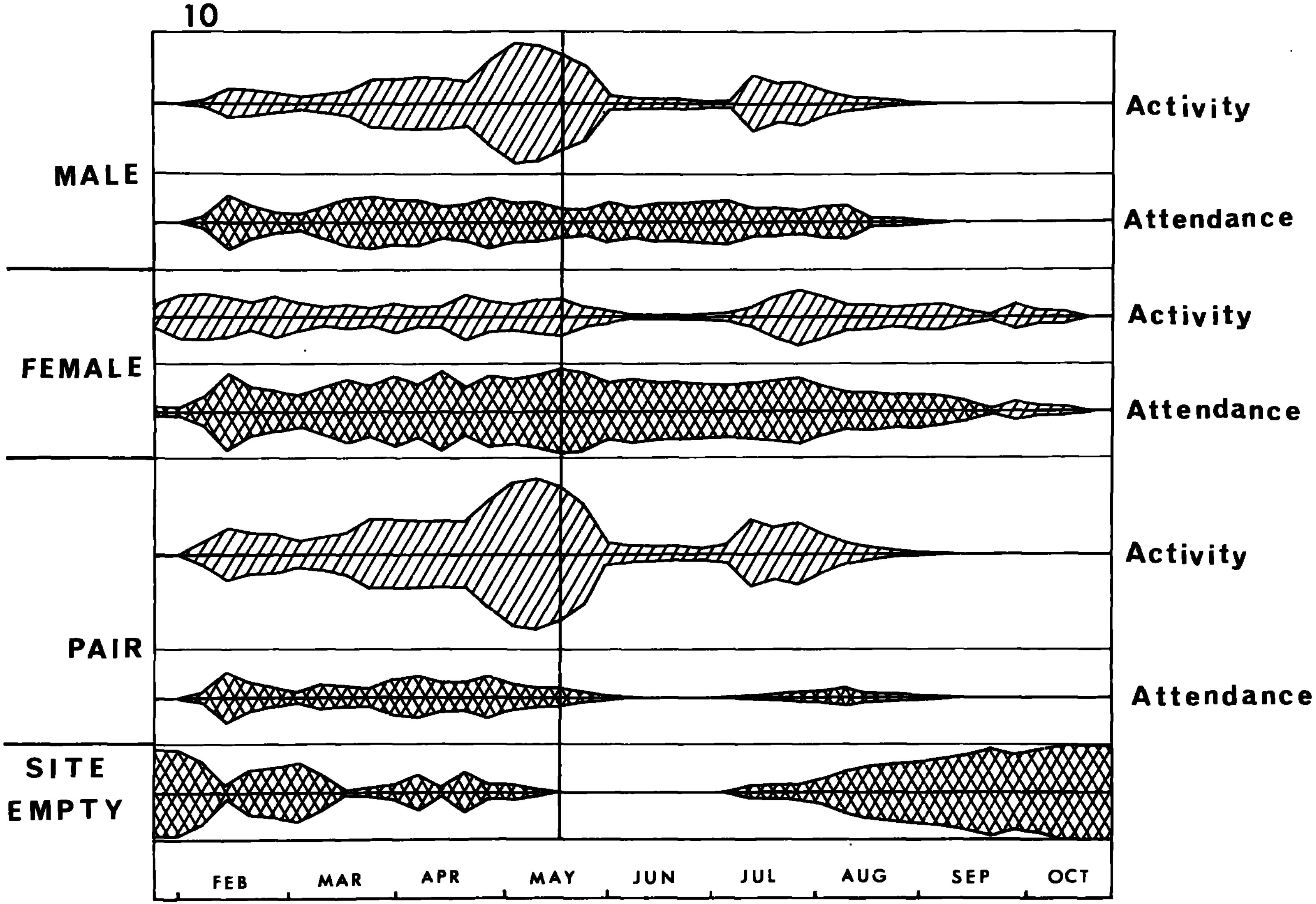

Male activity
Male attendance
Female activity
Female attendance
Pair activity
Pair attendance
Site empty
MAY
JUN
JUL
AUG

8

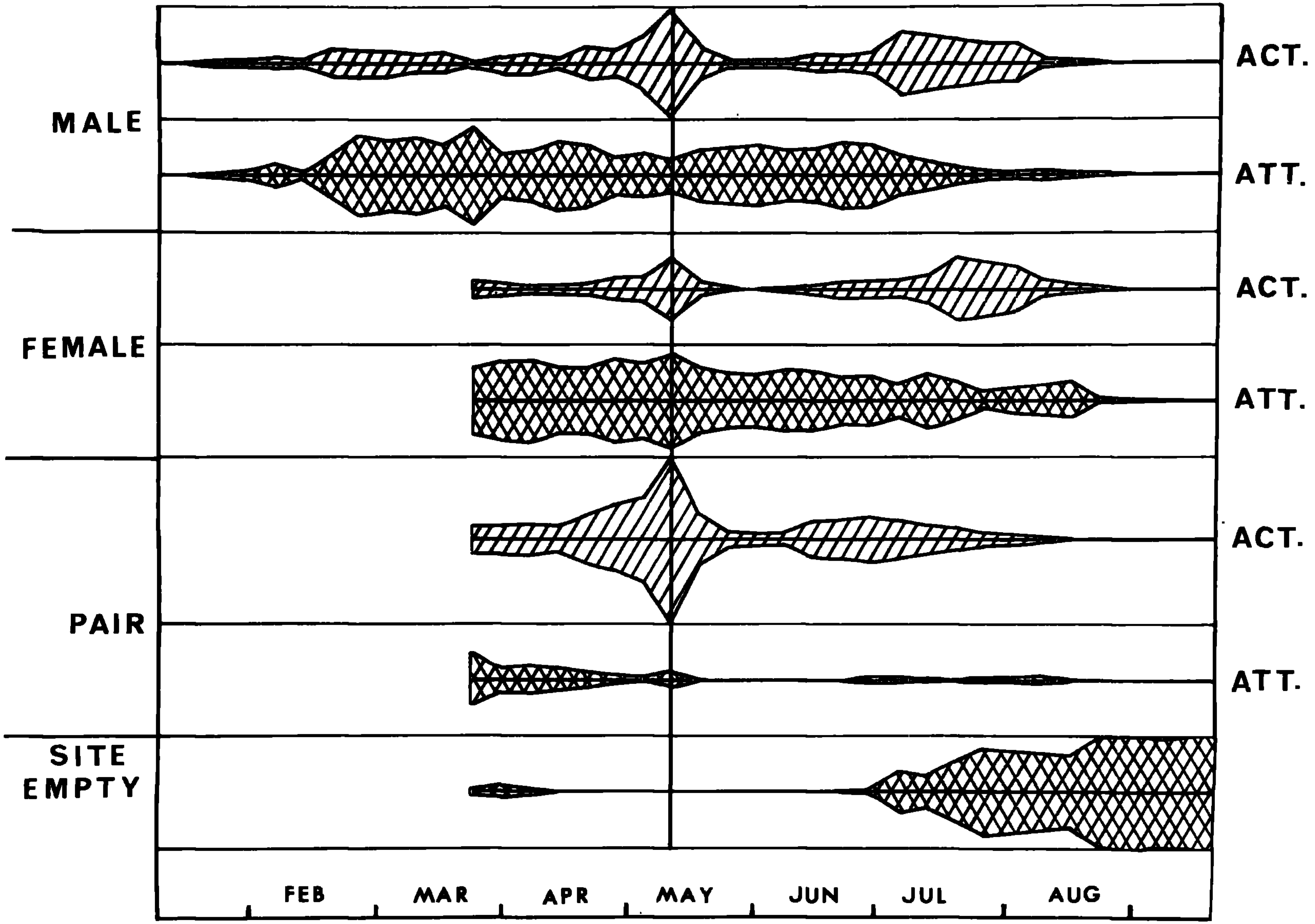

MALE
Activity
Attendance
FEMALE
Activity
Attendance
PAIR
Activity
Attendance
SITE
EMPTY
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT

9

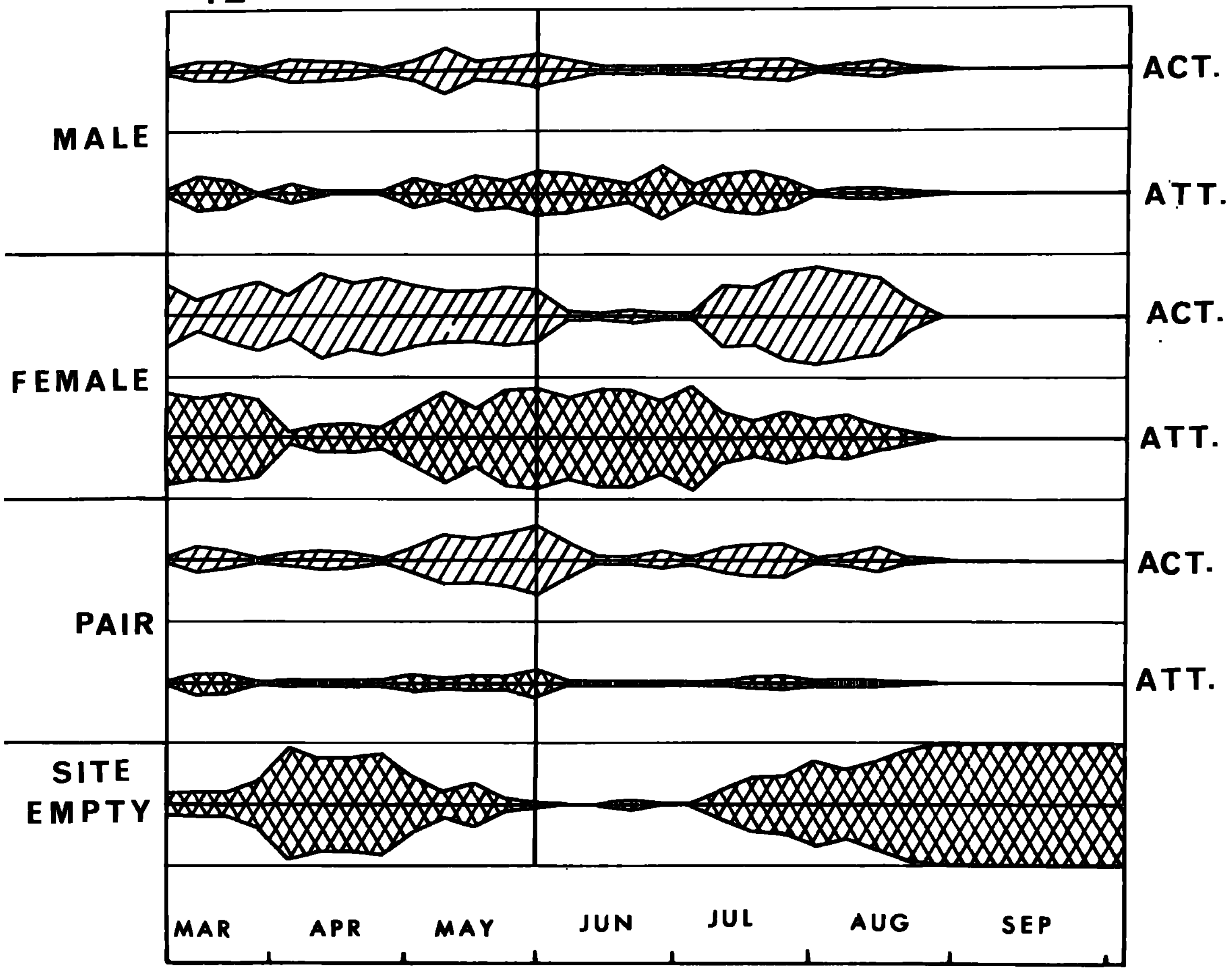

Male
ctivity
Male
ttendance
Female
ctivity
Female
ttendance
Pair
activity
Pair
ttendance
Site
empty
APR
MAY
JUN
JUL
AUG
SEP


10
MALE
Activity
Attendance
FEMALE
Activity
Attendance
PAIR
Activity
Attendance
SITE EMPTY
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT

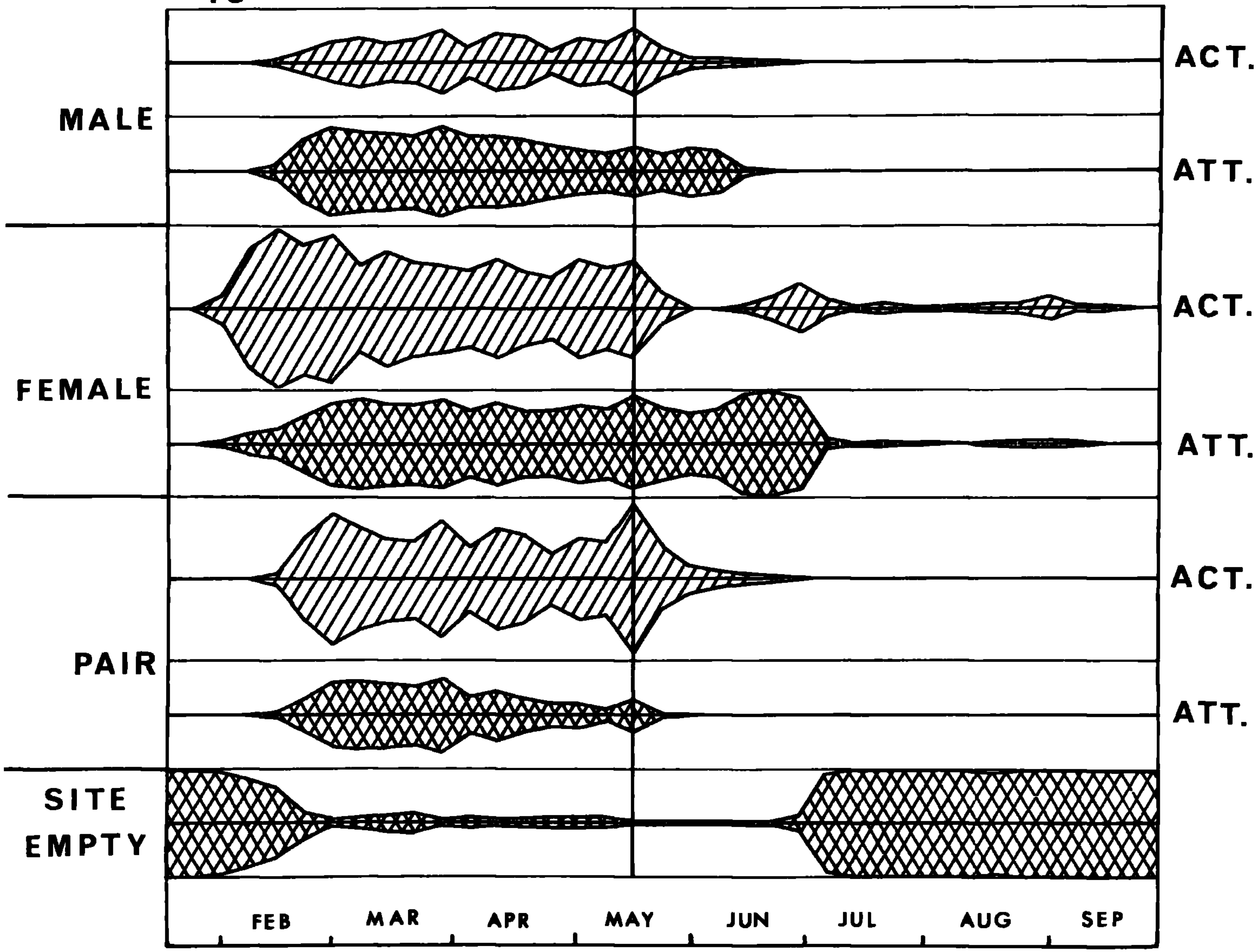
11


MALE
FEMALE
PAIR
SITE EMPTY
ACT.
ATT.
ACT.
ATT.
ACT.
ATT.
FEB
MAR
APR
MAY
JUN
JUL
AUG

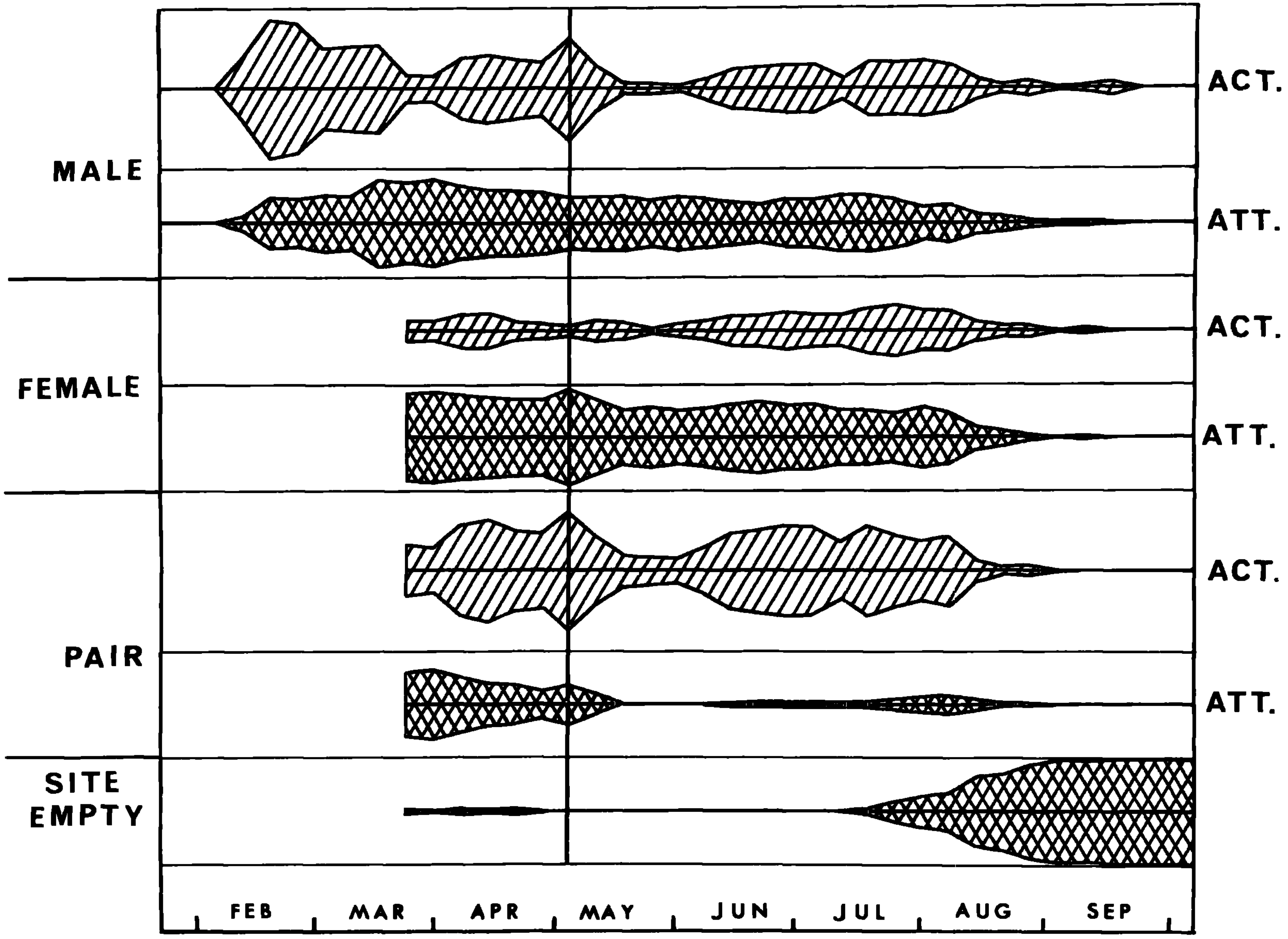
12


MALE
ACT.
ATT.
FEMALE
ACT.
ATT.
PAIR
ACT.
ATT.
SITE
EMPTY
MAR
APR
MAY
JUN
JUL
AUG
SEP

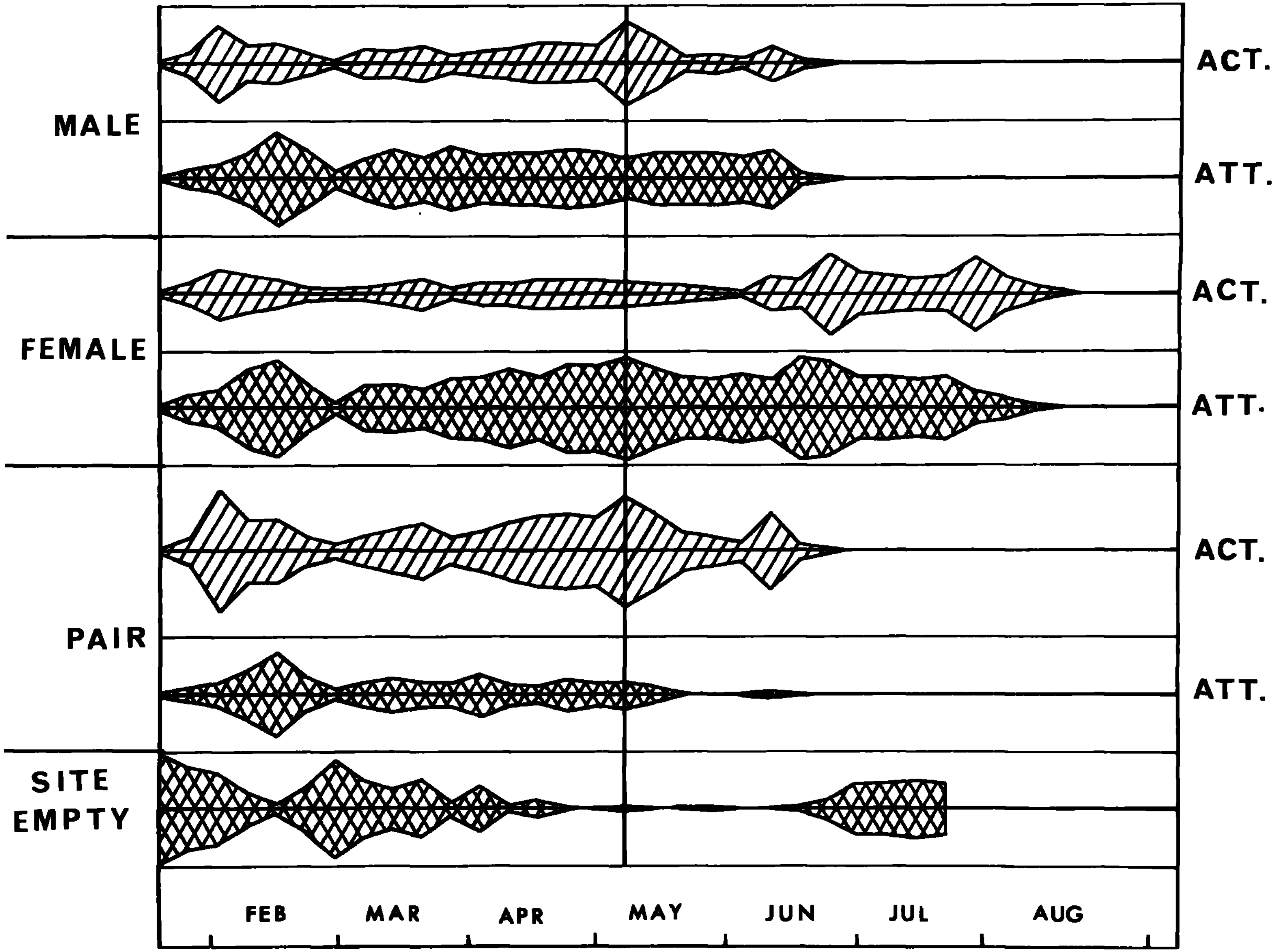
13


MALE
ACT.
ATT.
FEMALE
ACT.
ATT.
PAIR
ACT.
ATT.
SITE
EMPTY
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

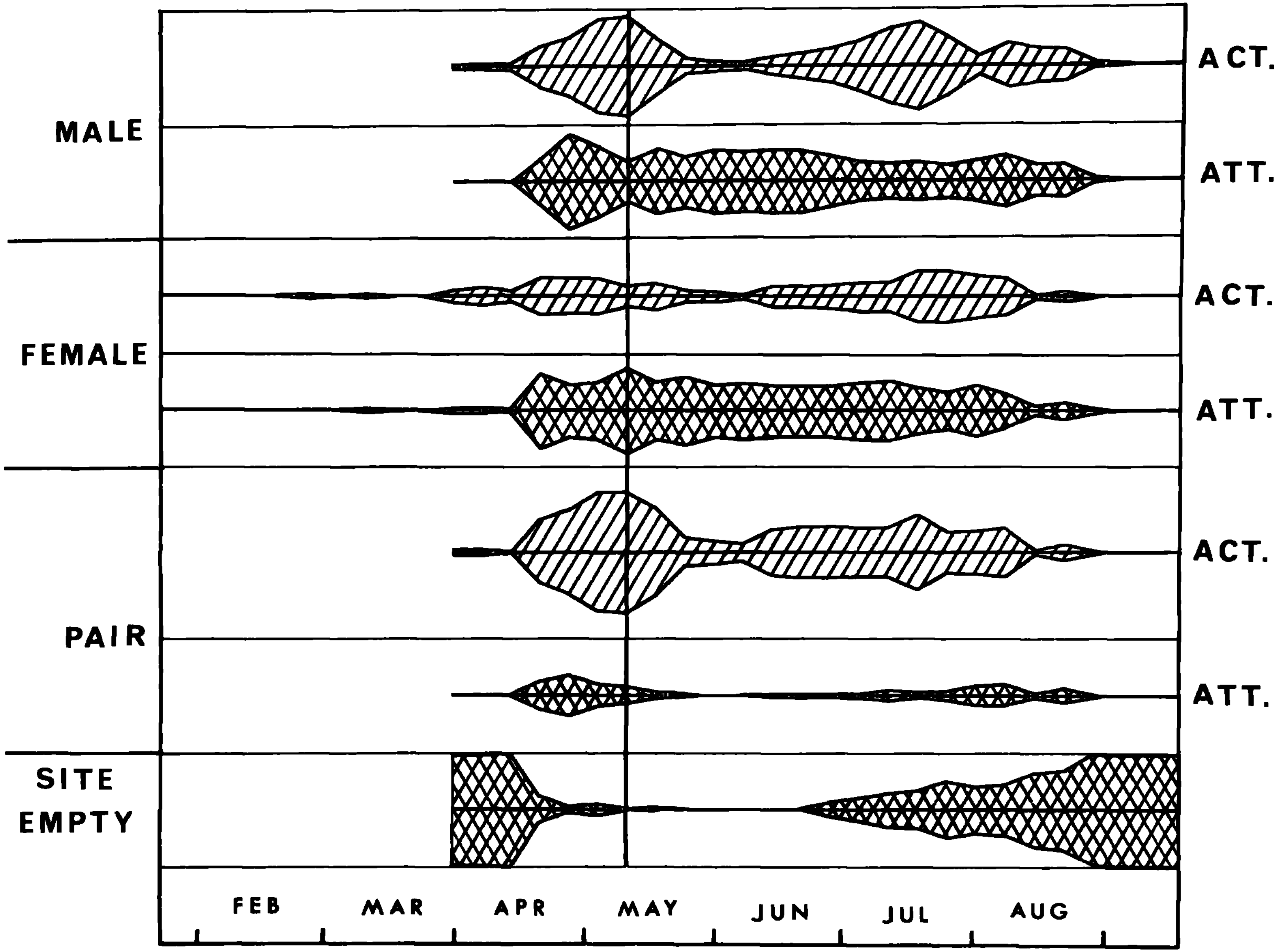
14


MALE
FEMALE
PAIR
SITE EMPTY
ACT.
ATT.
ACT.
ATT.
ACT.
ATT.
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

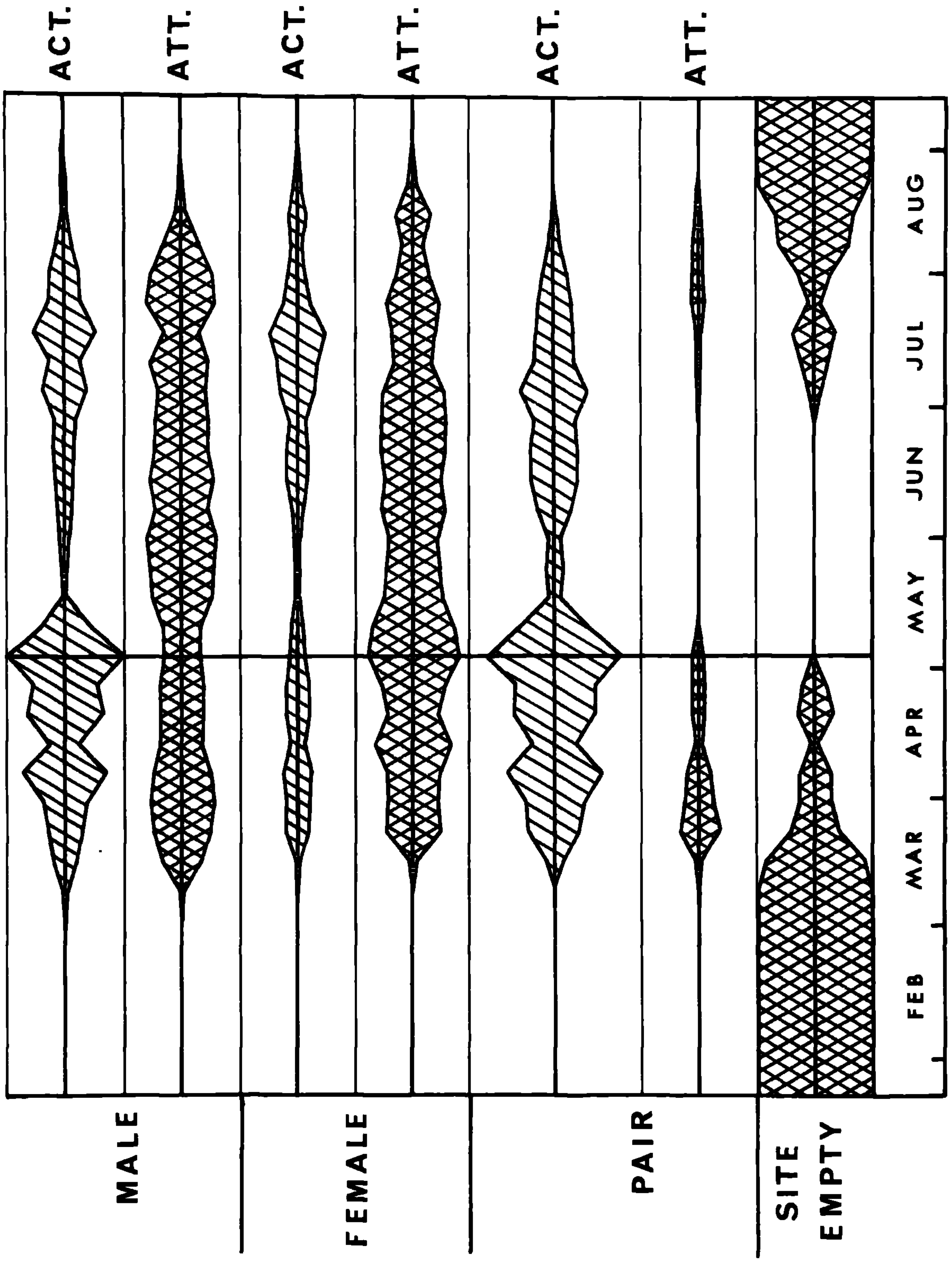
15


MALE
FEMALE
PAIR
SITE EMPTY
ACT.
ATT.
ACT.
ATT.
ACT.
ATT.
FEB
MAR
APR
MAY
JUN
JUL
AUG

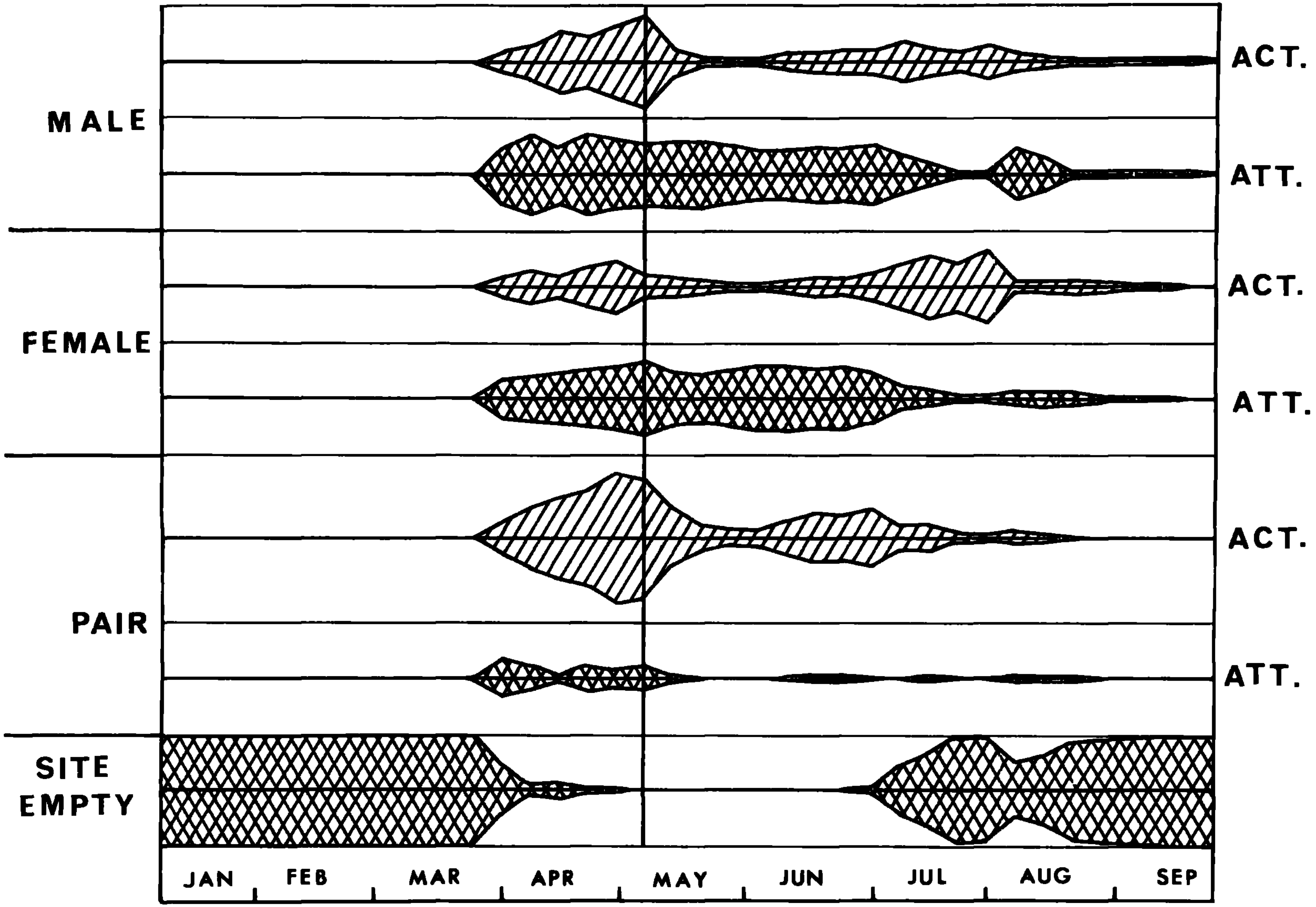
16


MALE
FEMALE
PAIR
SITE EMPTY
ACT.
ATT.
ACT.
ATT.
ACT.
ATT.
FEB
MAR
APR
MAY
JUN
JUL
AUG

17


MALE
ACT.
ATT.
FEMALE
ACT.
ATT.
PAIR
ACT.
ATT.
SITE EMPTY
FEB
MAR
APR
MAY
JUN
JUL
AUG

18


MALE
FEMALE
PAIR
SITE EMPTY
ACT.
ATT.
ACT.
ATT.
ACT.
ATT.
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

Conversely, co-ordination between even experienced partners may deteriorate to a point where they no longer breed successfully (Figs. 12 and 13). Low male breeding activity may often be responsible for such failure, although it sometimes produces a relatively weak pair bond which is still sufficient for breeding to be successful (Figs. 14 and 15).

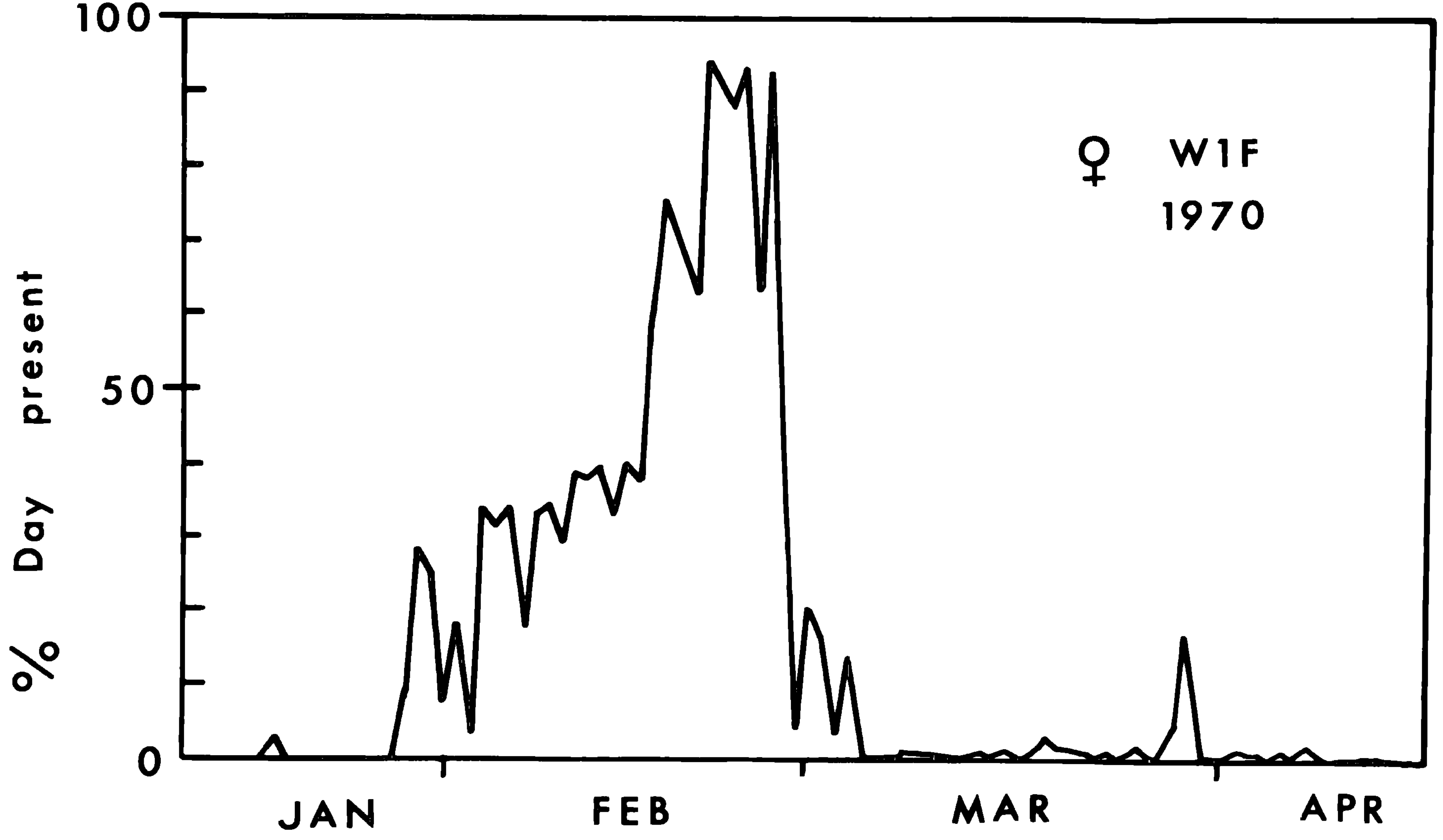
Inexperienced individuals breeding together for the first time may integrate their breeding activities very successfully (Fig. 18), but presumably some measure of compatibility between the partners is necessary for this to happen. More commonly, birds breeding for the first time record low levels of activity which increase considerably on the second occasion that they breed together (Tables 6 - 9 in Appendix 4).

A non-breeding pair monitored throughout two seasons showed a reversal of the normal pattern of site occupation (Tables 10 and 11 in Appendix 4), although this pair could not be regarded as typical of non-breeding pairs.

The male of one pair, in the second season monitored, attempted to retain two sites. Except during incubation and early brooding he alternated between the two sites (Tables 12 and 13 in Appendix 4).

The attendance of a female awaiting the return of her mate is illustrated in Fig. 19. Although this female paired with a new partner, some unmated females appear unable or unwilling to take a new mate. The attendance of one such individual in two successive years is given in Tables 14 and 15 (in Appendix 4), and in the latter year she recorded some very high attendance figures.

Figure 19. Percentage daily attendance on site W1F during early 1970 by a female unsuccessfully awaiting the return of a mate with whom she had bred previously for 14 seasons. During March she moved to an adjacent site and paired with a new partner.


♀ W1F
1970
% Day present
100
50
0
JAN
FEB
MAR
APR

Such attachment to a site alone suggests the possibility that some older females may develop as "matriarchs" although, as mentioned above, the oldest female at the colony readily took a new mate on a different site when it became apparent that her previous mate would not return. Females with more than about 6 years previous breeding experience are more likely to remain on the same site when remating after changing their mate (Table 16). Only about 30 % of younger females remain on their previous site after a mate change, but this proportion doubles in older females, suggesting behavioural changes among these latter birds.

Table 16. Site retention after a mate change by different aged females

Breeding experience (years)	Percentage females retaining same site after mate change	Sample size
1 - 3	29	200
4 - 5	30	79
6 - 7	44	45
8 and over	69	29

SECTION II

OCCUPATION OF THE COLONY

Annual return

The date on which the birds first arrive back at the colony after their "winter" away at sea has been steadily advancing. In 1952 they arrived on 27 February, in 1953 on 17 February and in 1954 on 4 February. More recently in 1971 the birds arrived on 8 January, in 1972 on 1 January and in 1973 on 2 January.

At a much larger colony 3 miles further south (Marsden Rock) the Kittiwakes have been returning at about the same time of year as they did twenty years ago.

This advance in arrival at North Shields may be due to a general trend such as climatic amelioration or easier availability of food in December and January. However, if this were true, one would expect the arrival at the Marsden colony to show a similar advance.

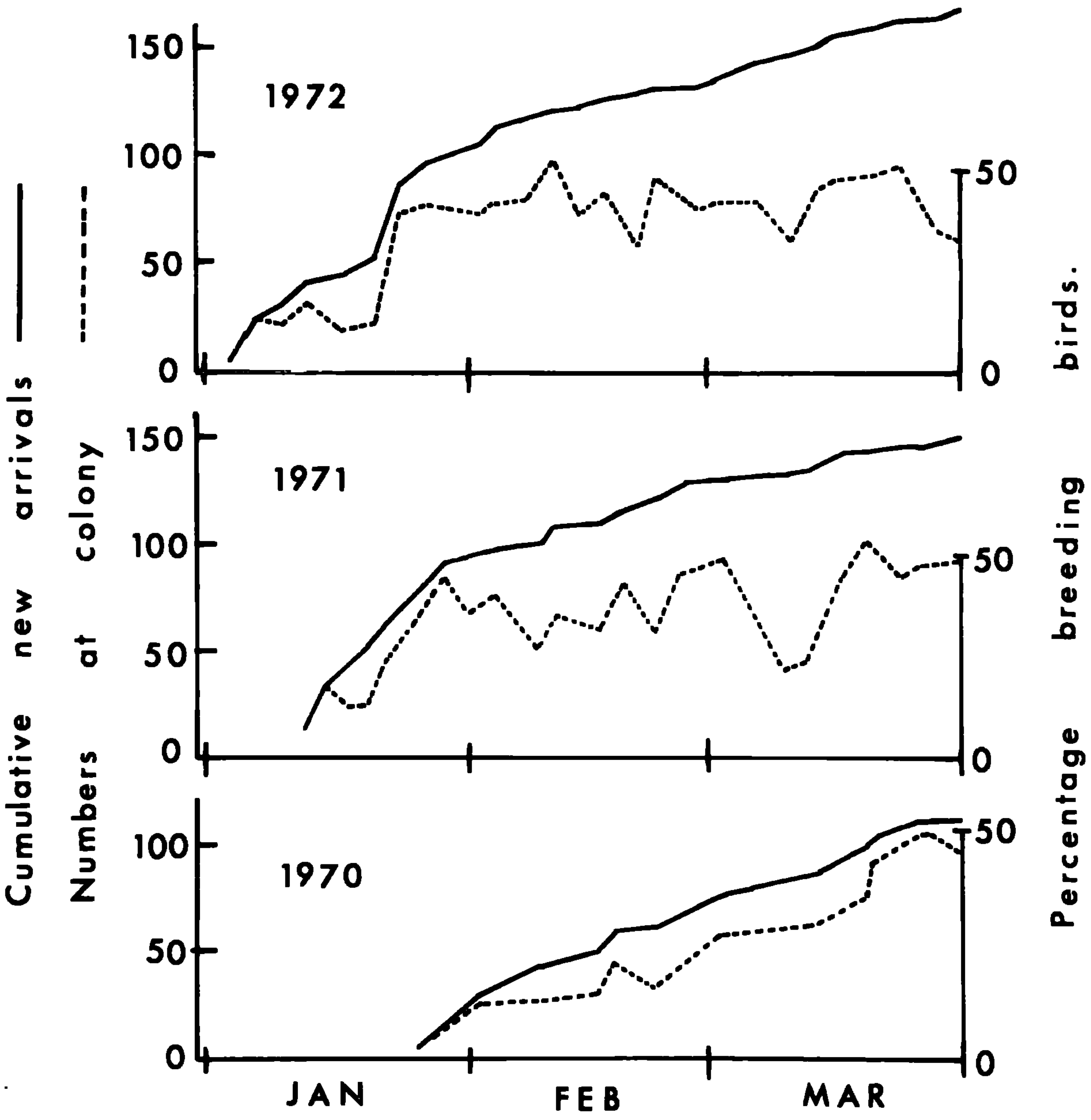
Another possibility is that as the colony has matured, competition for sites among older and more experienced individuals has increased, forcing them to return earlier to acquire suitable sites.

During the first three months of 1970 - 1972 the colony was visited twice each week and the build-up in the number of birds is shown for these years in Tables 17 a, b and c and in Fig. 20.

After an initially rapid rise in January the number of birds present at the colony in February and March

Figure 20. The numbers of birds at the North Shields colony during the first three months of 1970, 1971 and 1972, and the cumulative totals of these which had not been seen previously that year. The figure also illustrates the percentage of the annual breeding population (about 100 pairs) which was present on each visit to the colony.

Tables 17 a, b, and c give the information for these three years upon which this figure is based.



Cumulative new arrivals ——
Numbers at colony - - - - -
Percentage breeding birds.
1972
1971
1970
150
100
50
0
50
0
150
100
50
0
50
0
100
50
0
50
0
JAN
FEB
MAR

Table 17a. Arrival of birds at the North Shields colony in 1970

Date	a	b	c	d	e	f	g	h
26/1	11	6	55	6	11	55	-	17
2/2	29	24	83	30	40	73	97	33
9	28	13	46	43	68	56	65	42
16	31	8	26	51	99	45	61	43
18	45	8	8	59	144	35	76	46
23	33	2	6	61	177	29	54	48
2/3	59	17	29	78	236	27	76	49
13	64	10	16	88	300	24	73	52
19	76	12	16	100	376	22	76	51
20	93	5	5	105	469	20	89	50
25	106	6	6	111	575	17	95	51
26	107	1	1	112	682	14	96	51
2/4	90	1	1	113	772	12	80	50

Column headings :

a Number of birds at the colony on the date specified

b Number of these which had not been seen previously (new arrivals)

c Percentage of new arrivals on date concerned (viz. $\frac{b}{a}$ as %)

d Cumulative total of birds known to have returned to colony

e Cumulative total of all bird-visits to colony recorded

f Percentage of bird-visits to colony made by new arrivals (viz. $\frac{d}{e}$ as %)

g Percentage of birds known to have returned to the colony which were present on the date concerned (viz. $\frac{a}{d}$ as %)

h Cumulative percentage of all new arrivals which were made by females

Visits were made to the colony twice a week, although not at regular intervals, at differing times of day between 0900 and 1600.

Table 17b. Arrival of birds at the North Shields colony in 1971

Date	a	b	c	d	e	f	g	h
8/1	3	3						
12	16	13	81	13	16	81	-	40
15	36	21	58	34	52	65	-	46
18	24	11	46	45	76	59	53	44
20	25	6	24	51	101	51	49	43
22	45	11	24	62	146	42	73	47
26	66	16	24	78	212	37	85	47
29	84	14	17	92	296	31	91	50
1/2	67	3	5	95	363	26	71	50
4	75	3	4	98	438	22	77	50
9	51	2	4	100	489	20	51	50
12	67	8	12	108	556	19	62	49
16	60	2	3	110	616	18	55	49
19	82	6	7	116	698	17	71	48
23	58	6	10	122	756	16	48	49
26	87	7	8	129	843	15	67	50
2/3	94	2	2	131	937	14	72	51
9	42	2	5	133	979	14	32	50
12	46	2	4	135	1025	13	34	50
16	85	8	9	143	1110	13	59	50
19	102	2	2	145	1212	12	70	et seq.
23	85	2	2	147	1297	11	58	
25	91	0	0	147	1388	11	62	
31	94	6	6	153	1482	10	61	

Column headings as in Table 17a.

January	(8 observations)	92 new birds (31 %)
February	(8 observations)	37 new birds (7 %)
March	(8 observations)	24 new birds (4 %)

Table 17c. Arrival of birds at the North Shields colony in 1972

Date	a	b	c	d	e	f	g	h
4/1	4	4	100	4	4	100	100	0
7	25	21	84	25	29	86	100	42
10	22	6	27	31	51	61	71	46
13	32	11	34	42	83	51	76	47
17	19	3	16	45	102	44	42	48
21	22	8	36	53	124	43	42	52
24	73	34	47	87	197	44	84	51
27	78	10	13	97	275	35	80	50
2/2	73	8	11	105	348	30	70	50
4	77	8	10	113	425	27	68	et seq.
8	80	4	5	117	505	23	68	
11	97	4	4	121	602	20	80	
14	72	1	1	122	674	18	59	
17	83	4	5	126	757	17	66	
21	57	3	5	129	814	16	44	
23	89	2	2	131	903	15	68	
28	76	1	1	132	979	14	58	
1/3	79	4	5	136	1058	13	58	
6	79	7	9	143	1137	13	55	
10	60	4	7	147	1197	12	41	
13	84	4	5	151	1281	12	56	
15	89	5	6	156	1370	11	57	
20	91	4	4	160	1461	11	57	
23	96	3	3	163	1557	10	59	
27	66	1	2	164	1623	10	40	
30	61	4	7	168	1684	10	36	

Column headings as in Table 17a.

remains fairly stable, although during this period birds not seen previously at the colony that year continue to arrive.

There is no pronounced trend for one sex to arrive back earlier than the other, although in all three years considered males represented a higher proportion of first arrivals early in January. Since the males are the siteholders there may be greater pressure on them to return earlier to secure suitable sites. Any diurnality in the attendance of the sexes would bias this finding, but since the colony was covered during most of the hours that it was attended, this is thought unlikely.

Using the data for 1971 it was found that for males and females the date of return was significantly related to the number of years that the individual had bred at the colony :

Males $r_{47} = + 0.673$ $P < 0.1\ \%$ $y = 5.84 + 0.39x$

Females $r_{44} = + 0.583$ $P < 0.1\ \%$ $y = 5.74 + 0.40x$

(where y = weeks before 1 April that first seen at colony, and x = number of years breeding experience)

Since breeding experience and the number of years as a member of the same pair are closely related (males $r_{47} = + 0.823$; females $r_{44} = + 0.776$) it is not surprising that the longer a pair have been together, then the earlier they return :

Males $r_{47} = + 0.636$ $P < 0.1\ \%$ $y = 3.97 + 0.33x$

Females $r_{44} = + 0.582$ $P < 0.1\ \%$ $y = 3.56 + 0.31x$

(where y = weeks before 1 April that first seen at colony, and x = number of years that individual was member of same pair)

Not unexpectedly, the birds which returned earlier to the colony paid more subsequent visits to the colony over the three month period considered. They also appeared to be more frequent in their attendance (as determined by their presence or absence at the colony at the time of visit). Tables 18 and 19 .

These differences in regularity of attendance are not significant however. Nor could any relationship be demonstrated between the mean number of times per week that an individual was seen, and its date of return (r_{152} = + 0.1436 N.S.)

Table 18. Frequency of attendance at the colony after initial return in January to March 1971

Returned between :	12/1 - 20/1	22/1 - 1/2	4/2 - 19/3
Mean no. times seen at colony since return	12.5 ± 1.0	9.7 ± 1.0	4.1 ± 0.7
% visits when present at colony (after initial return)	66 %	64 %	59 %
Sample size	46	46	47

Table 19. Frequency of attendance at the colony after initial return in January to March 1972

	January	February	March
Mean visits per month when seen	4.7 ± 0.9	4.3 ± 1.3	3.6 ± 0.7
% visits when present at colony (after initial return)	52 %	47 %	40 %
Sample size	84	32	37

Individuals returning in January and in February differed significantly in the mean number of sites per month on which they were seen during February ($t_{115} = 2.1004$; $P < 5\ \%$) and during March ($t_{115} = 2.6191$; $P < 1\ \%$) (Table 20). Birds returning in March were seen on significantly more different sites during that month than January-returning birds ($t_{122} = 3.9401$; $P < 0.1\ \%$).

January-returning birds were seen on significantly fewer different sites during their first month back at the colony (viz. Jan.) than February-returning birds in their first month (Feb.) ($t_{114} = 2.4976$; $P < 2\ \%$) or March-returning birds during March ($t_{121} = 2.2971$; $P < 5\ \%$).

Thus birds returning earlier in the season were less prone to move around on different sites than later birds, both during their first month back at the colony, and indeed in subsequent months.

Table 20. Site faithfulness of birds returning in January February and March 1972

	Mean number of sites on which seen during			
	January	February	March	Sample size
Returned in January	1.262 ± 0.118	1.294 ± 0.133	1.145 ± 0.085	85
February	-	1.581 ± 0.275	1.393 ± 0.214	31
March	-	-	1.526 ± 0.223	38

Daily occupation of the colony

Since the radioactive-tagging method only provides information for a few pairs, and these may contain some pairs atypical in their behaviour, observations were made of a colony on the Brownsman, Farne Islands, in 1970, and to a lesser extent in 1971.

The numbers at this colony were counted from sunrise to sunset over a 14-day period just before the laying of the first eggs (3 May 1970). The figures illustrate the rapid build-up in numbers at the colony from first light until about 0900 (Table 21 and Fig. 21). The number of sites occupied changes hardly at all from this mid-morning level, but the number of birds continues to rise - with a consequent increase in the proportion of occupied sites with pairs. This trend continues until dusk.

A similar situation exists in the Gannet where Nelson (1965, p. 261) says "There is no significant daily rhythm, except early in the season when males and pairs are mainly in attendance late in the day".

The number of birds not on the cliff but in the roost at its base, or rafting and bathing nearby, also increases noticeably over this period. Many of these birds were in immature plumage, and possibly many of the others were non-breeding birds arriving at the colony later in the day.

As well as a diurnal change in the percentage of sites with pairs, this proportion is affected by the stage in

Figure 21. Changes in the number of occupied sites and birds present from dawn to dusk at a Kittiwake colony. The information was collected at the Brownsman colony on the Farne Islands during the fortnight before the first eggs were laid (see Table 21). The rise, throughout this daylight period, in the percentage of occupied sites with pairs present, is also shown.

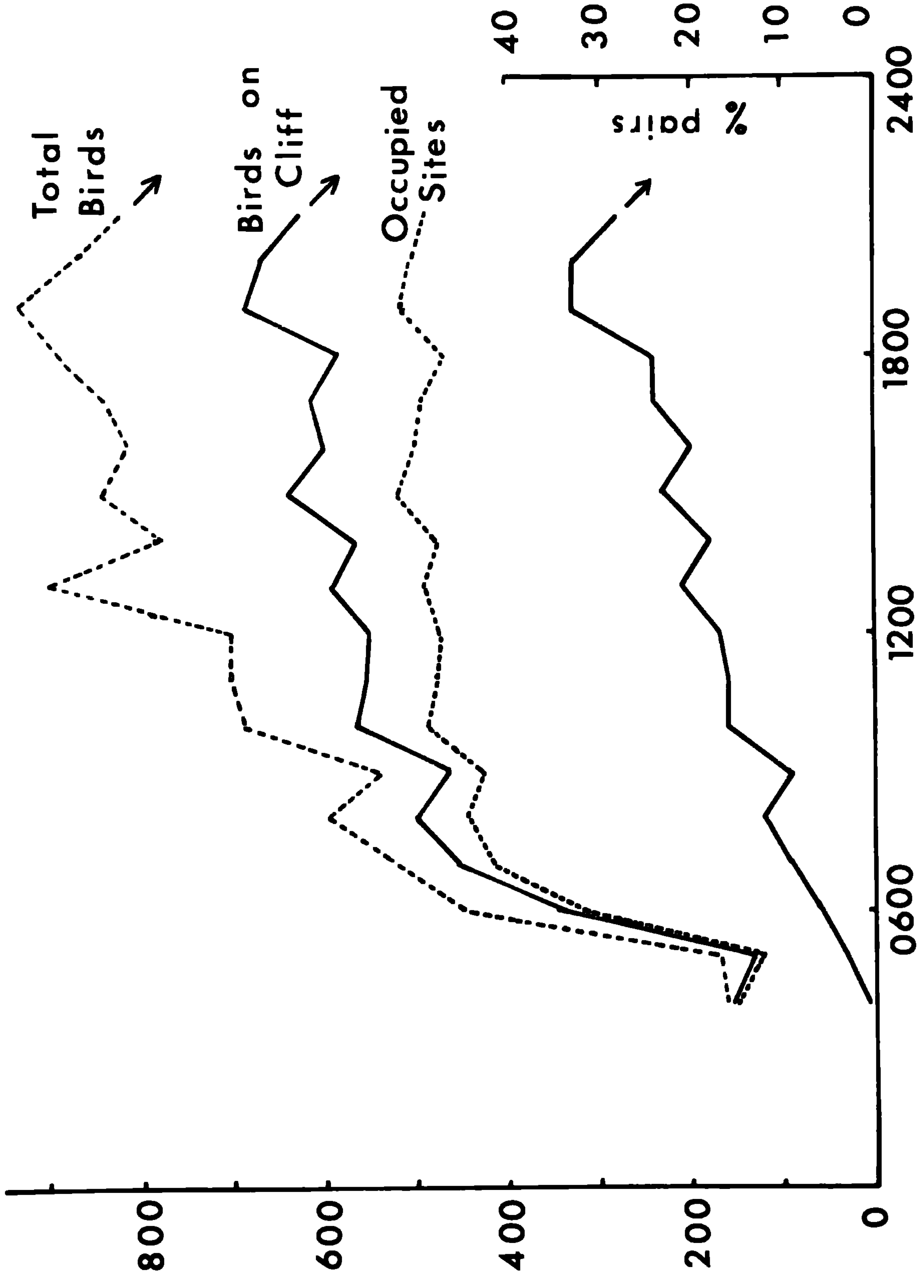

Total Birds
Birds on Cliff
Occupied Sites
% pairs
0
200
400
600
800
0
10
20
30
40
0600
1200
1800
2400

Table 21. Daily occupation of sites in the Brownsman colony, Farne Islands, during the fortnight before egg-laying, 1970

Hourly period ending	Days Observ-ations	Occupied sites (a)	Birds on cliff (b)	Birds at colony (c)	% sites with pairs (d)
0400	5	154	155	160	1
0500	6	125	132	168	3
0600	6	337	347	443	6
0700	8	417	455	523	9
0800	13	445	499	595	12
0900	13	427	466	537	9
1000	12	488	565	690	16
1100	11	477	552	704	16
1200	10	474	553	706	17
1300	13	490	592	901	21
1400	11	476	564	776	18
1500	12	518	638	839	23
1600	13	500	600	812	20
1700	13	493	613	839	24
1800	13	471	583	888	24
1900	12	515	687	931	33
2000	13	503	669	875	33
2100	12	490	625	820	28

Column a	records the mean number of sites on the cliff which were occupied
Column b	records the mean number of birds on the cliff
Column c	records the mean total number of birds at the colony (this includes those on the cliff + those roosting, rafting, bathing and flying close to the colony)
Column d	gives the percentage of occupied sites with pairs

All means were calculated from observations during the 14 days prior to the first eggs being laid on 3 May 1970 the breeding cycle. The cliff was divided for counting purposes into four sections corresponding to a beach cliff (1), an intermediate area (2), the main cliff (3), and a seaward cliff (4). No differences were found between these areas in the proportions of sites with pairs in April and early May. Later in the season counts were made at the end of May and in early June. At this time the proportion of well-built nests containing eggs was also recorded (Table 22). The proportion of pairs present was lower than earlier in the season, due to many pairs incubating eggs, when they meet only at the change-over of incubation duties. As more nests contain eggs, this proportion declines further.

Table 22. Percentages of sites on four sections of Brownsman Cliff, with pairs and with eggs

Section	24 May		2 June		6 June		10 June	
	Pairs	Eggs	Pairs	Eggs	Pairs	Eggs	Pairs	Eggs
1	12	74	7	93	6	91	3	95
2	17	52	12	76	7	82	7	81
3	8	92	13	100	8	98	4	94
4	11	84	7	100	4	100	4	94

The pairs column records the percentage of occupied sites with pairs present. The eggs column records the percentage of cup nests (370 counted) with eggs. All counts were made at midday.

For any date the differences in numbers of pairs reflects the numbers of pairs with eggs. It is interesting to note that the area where the nests were most dense (Section 3) was the one where the first eggs were laid, and also where the highest proportion of nests contained eggs. It was also the earliest-laying section. The least dense area (2) was the latest to lay and never reached as high a level of nests with eggs as the other areas. The other two sections were later than the main cliff, but still laid a high proportion of eggs.

The first eggs hatched between 6 June and 10 June, and the fall in percentage of nests with eggs at this time in the early-laying areas may be due to loss of eggs or chicks, or to an influx of late-laying or non-laying birds building new nests in these areas while the aggression of the incubating birds was at a low level.

Counts made in 1971 showed a similar pattern to that for 1970, the percentage of occupied sites with pairs rising from zero at dawn to a maximum at dusk. There was again very little difference between the four areas.

However, on 24 April a brief but violent storm washed all the nests off areas 2, 3 and 4 during the night. Early on the following morning there was a very high attendance at the colony, particularly in the sections where the nests had been lost (Table 23). The birds in these areas rebuilt their nests extremely rapidly, many finishing them within two days. A similar instance has been recorded by Maunder & Threlfall (1972) where 7 out of 8 nests destroyed by violent waves were rebuilt in 2 - 9 days.

Before the storm the nests in the denser areas (3 and 4) were more advanced than those in areas 1 and 2.

Table 23. Percentages of occupied sites with pairs present, before and after a storm on 24 April 1971

Farne Islands

Date	Cliff section :	1	2	3	4
22 April		20	18	15	13
23 April		18	24	16	17
24 April		13	most nests washed off cliff		
25 April		34	41	44	40
26 April		21	15	17	15
27 April		21	16	16	11

All values represent percentages (± 2 % for 95 % confidence limits) of occupied sites containing pairs, for the summation of all readings during a day (0700 - 2130)

After the storm one might have expected that the birds in the relatively unaffected area 1 would have become more advanced and hence the earliest to lay. However, within a few days most of the nests in sections 3 and 4 were once more at a further advanced stage, and this was maintained throughout the rest of the season.

There would thus appear to be no rigid period of time necessary to build a nest, and, indeed, it can be done very rapidly should this prove necessary. The state of the nests in an area would appear to be a good indicator of the stage in the breeding cycle which those birds have reached.

The birds returned after only a few days to their normal pattern of daily occupation of the colony, except that after the storm they tended to reach a peak in numbers earlier in the day, and then to decline in numbers up to sunset. Unfortunately, counts could not be continued long enough to see if this trend persisted.

First morning arrival or departure in relation to sunrise

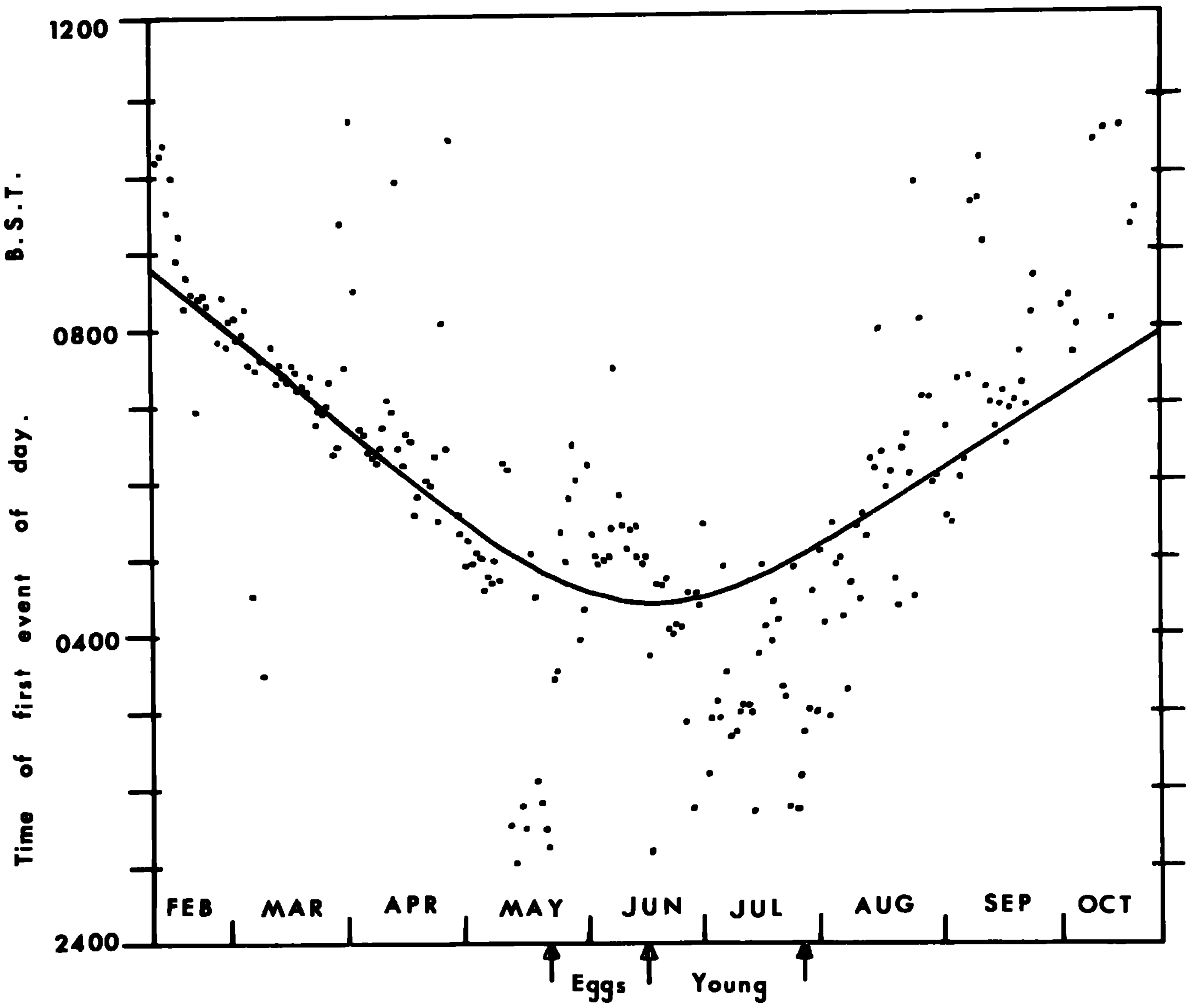
In the radioactively marked pairs the first event of the day was normally the arrival of a member of the pair onto the site. Early and late in the season the site is empty overnight, but in the middle of the breeding season its mate would normally be present, having spent the night on the site.

In about 9 % of cases, however, a bird which had been overnight on the site departed before the arrival of its mate, either to fly out to sea or on a series of short aerial circuits around the colony. This was also counted as the first event of the day. The times of these first events were plotted in relation to the time of sunrise throughout the season, and an example is given in Fig. 22a.

Early in the season (January and early February) the birds do not arrive at the colony until an hour or two after sunrise. This may be due to a relatively greater proportion of the short daylight period available at this time of year being needed for feeding. Alternatively, the attraction of the colony may be weak at this time of year. Possibly a sufficient number of birds need to gather before they provide adequate

Figure 22a. The relationship between the time of sunrise (the solid line) and the times of the first event of the day (dots) for pair W1F throughout the 1969 breeding season. This first event was normally the arrival of one member of the pair on the site.

The arrows indicate the dates when the first egg was laid and hatched, and when the young fledged.


1200
0800
0400
2400
Time of first event of day. B.S.T.
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
Eggs
Young

stimulation to overcome their fear of land after a winter spent at sea. Also the need to obtain and defend a site at this time, when only a few other birds are present at the colony, is minimal.

However, the time of arrival becomes earlier until by the second half of February the birds are arriving within 15 - 30 mins of sunrise. This situation persists, the arrival of the birds advancing by four hours in parallel with the advance in the time of sunrise, until early or mid May when laying takes place. This pattern is probably due to the need to acquire a site by constant attendance, and defend it during the daylight hours. During this period some pairs exhibited significantly greater deviation from sunrise in their arrival times than others (Table 24a, Fig. 22b).

Table 24a. Differences between pairs in the times of their first morning events in relation to sunrise

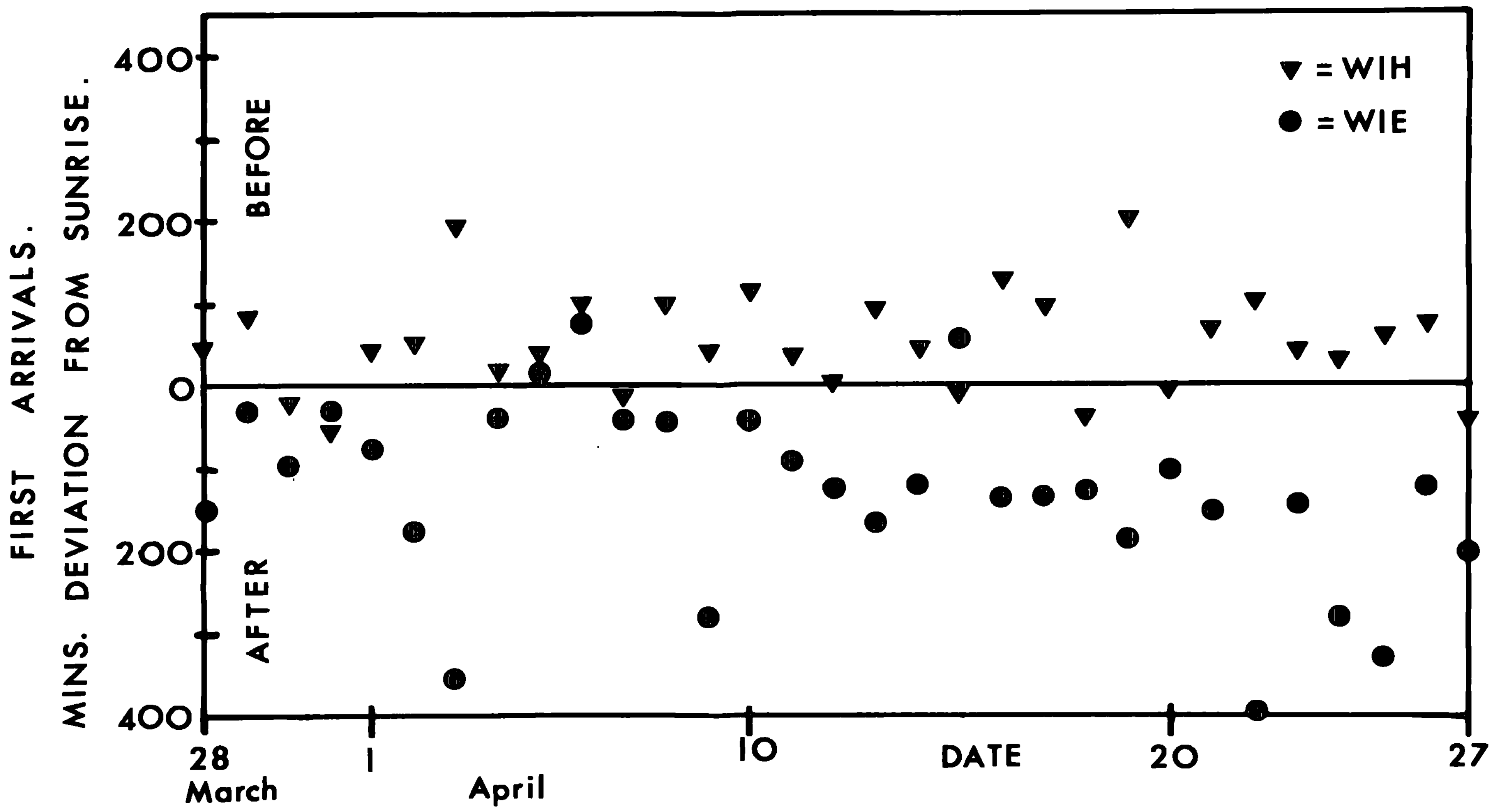
Information on deviation (in mins) from the time of sunrise for 4 pairs over 40 days (28 March to 6 May 1972)

Mean resultant deviation from sunrise :

W1H + 47 mins ± 23 (before sunrise)
W1E -131 mins ± 35 (after sunrise)
W1D - 74 mins ± 24 (after sunrise)
W1B - 97 mins ± 36 (after sunrise)

Thus, W1H is earlier than W1E $t_{78} = 3.8539$; $P < 0.1$ %
W1H is earlier than W1B $t_{78} = 2.1870$; $P < 5$ %
W1E is later than W1D $t_{78} = 2.6930$; $P < 1$ %

Figure 22b. The times of the first event of the day in relation to the time of sunrise, for two pairs during April 1972. Pair W1H (triangles) arrived consistently before sunrise, whereas pair W1E (circles) arrived after it.


FIRST ARRIVALS.
MINS. DEVIATION FROM SUNRISE.
400
200
0
200
400
BEFORE
AFTER
▼ = WIH
● = WIE
28
March
1
April
10
DATE
20
27

Once the changeover pattern has become established during incubation the relieving bird often does not arrive in the morning until an hour or more after sunrise. There is even a tendency for the morning arrival to become later as incubation proceeds, resulting in the observed slowing down of the changeover rate (Table 24b, Fig. 22c).

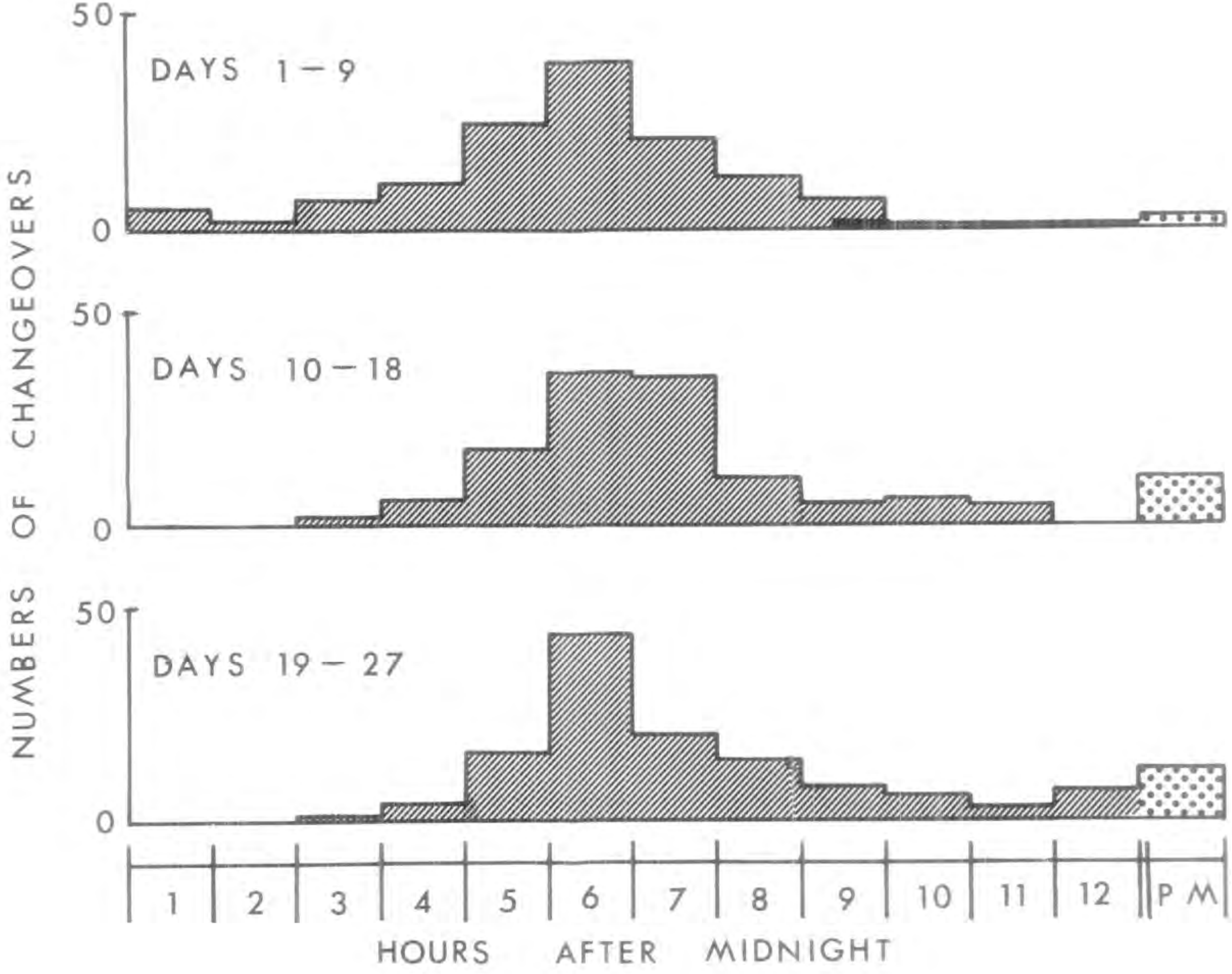
Table 24b. Mean hourly period (after midnight) of the first changeover of the day during early, middle and late incubation (for 15 pairs)

Period of incubation	Sample size	Mean hourly period of first changeover	
Days 1 - 9	135	5.72 ± 0.49	$t_{268} = 4.635$; $P < 0.1$ %
Days 10 - 18	135	7.20 ± 0.41	$t_{268} = 1.189$ N.S.
Days 19 - 27	135	7.56 ± 0.44	

After the chicks have hatched they require frequent feeding, and the first arrival of the day usually occurs long before sunrise. About 60 days (± 10) after laying, the parents begin to leave the site overnight for the first time since early in the season. Although at this point the first arrival is still before sunrise, it becomes rapidly later in the day - regressing far more quickly than the recession of sunrise - until by September the arrival time is at, or after, sunrise.

It becomes progressively later, so that around the time that the colony is vacated the birds are only present briefly in mid-morning, thus paralleling the situation early in the year.

Figure 22c. Distribution of the times that partners changed over incubation duties during the early, middle and late stages of incubation. The numbers represent totals of changeovers for 15 pairs during hourly periods after midnight.


50
DAYS 1 — 9
0
50
DAYS 10 — 18
0
50
DAYS 19 — 27
0
NUMBERS OF CHANGEOVERS
1
2
3
4
5
6
7
8
9
10
11
12
P M
HOURS AFTER MIDNIGHT

Occupation of the site at night

It is possible to establish when the radioisotope-marked pairs started to spend the night on their sites, and when this practice ended. There was wide variation in the time of year that a pair began to remain overnight on their site, ranging from February to April (Table 25).

This nightly occupation of the site follows shortly after the pair have come together on the site for the first time. In 7 out of the 12 cases considered the first overnight of the year took place on the same day that the pair were reunited (Column F in Table 25). Regular overnight occupation of the site was not undertaken by a single partner until its mate had also returned.

The sites are not contested for ownership as strongly early in the season, or at night. However, to enable a pair to occupy their site from dawn to dusk, when competition for sites takes place, it is advantageous for at least one member of the pair to spend the night on the site. There would be little advantage in a solitary bird attempting complete site defence in this manner - and indeed it would not be possible.

Overnight occupation of the site continues almost unbroken through the breeding season until about the second half of July. At this time the birds begin to leave the chicks alone on the site at night, although they continue to have the occasional overnight on the site throughout August. This post-breeding vacation of the site at night is discussed in more detail in Section VII.

Table 25. Overnight occupation of the site early in the season

Site	Year	A	B	C	D	E	F	G
1969	W1F	before 5/2	?	(8/2)	No data	20/2	No data	12
1970	W1B	5/3	F	13/4	13/4	17/4	0	4
	W1G	30/1	F	14/2	14/2	16/2	0	2
	E1D	4/2	M	9/2	12-14/2	16/2	3	7
1971	W1E	before 12/1	F	27/1	1/2; 14/2	5/3	5	37
	E1D	before 14/1	F	15/1	None	31/1	16	16
	W1B	23/1	M	14/3	14/3; 13/4	21/4	0	37
	W1D	22/2	M	27/3	27/3	4/4	0	8
1972	W1D	26/3	F	28/3	None	28/3	0	0
	W1B	8/3	M	10/3	None	10/3	0	0
	W1E	24/1	M	17/2	None	17/2	0	0
	W1H	before 7/1	M	27/1	None	20/2	23	23

Column headings :

A Date on which the first member of the pair returned

B Sex of the first bird back (M = male; F = female)

C First date on which the pair were together on the site

D Dates of isolated overnights on the site before the regular nightly occupation of the site

E Date on which regular nightly occupation of the site started

F Days between the pair coming together and the first overnight occupation of the site

G Days between the pair coming together and the site being occupied regularly at night

SECTION III

THE PRE-LAYING PERIOD

Male and female gonadal cycles

In the Kittiwake, as in many other birds, testis growth is maintained over a longer period than female follicle development (Swartz 1966, Belopol'skii 1961). The male is capable of fertilising the female over a wide period of time, but the female only completes the final, rapid stages of her gonadal development just prior to laying. No information on testis maturation and regression in the Kittiwake is available, but it is likely to be similar to that of other gulls.

Mills (1973) found that the testes of young Red-billed Gulls matured more slowly than those of older birds, producing a later onset of courtship activities. In the California Gull (Johnston 1956) the testes began to regress at about the time that the eggs were laid. Similarly, testis regression in the Fulmar began at the start of incubation (Marshall 1949).

The early, slow growth of the female gonads is probably a photoperiodic response, but the later stages may be related to factors at the nest site. Such factors may include the site itself, the mate, nest material and the state of the nest, vocalisations and activities such as copulation and courtship feeding taking place at the site.

External stimuli such as these may also rely on hormonal states for their effectiveness, and both of them may be modified by experience. The results obtained by the administration of hormones have been complex, and seem to differ with the species being studied.

Although internal states are important, as Slater (1970) points out, direct stimulation by external factors produces a more flexible system. Thus, when a nest is removed, as for example in the Brownsman Kittiwake colony referred to in Section II, building takes place immediately, whereas the removal of a mate leads to the cessation of building. In this instance only an appropriate response is evoked and this results in a more efficient system.

Slater (1970) found that both sexes of the Bengalese Finch showed all the patterns of building behaviour, but that males did more of the carrying, and females more of the building. This is also the situation in the Kittiwake. In the Bengalese Finch nest-building could not be induced by hormone treatment, suggesting a direct effect by the partner. The male was stimulated to carry material by the presence of the female, but obviously she could not build until he brought the material.

The males were most affected by the experience of bringing material to the nest box, and the actual building was relatively unimportant (Slater 1967). Lehrman (1959) suggested that in the Ring Dove the influence of nest material might be through its effect on the behaviour of the male, rather than directly on the female (Johnston 1963). In the canary, where the female does most of the building, Slater (1969) suggested that the nest material might directly stimulate ovarian development. He considered the Bengalese Finch to be intermediate between these two situations.

In the Kittiwake, the large number of collecting trips made by the male for nest material leads to many arrivals on the site with their consequent greeting ceremonies. These greeting arrivals also occur frequently without involving nesting material, and any stimulation of ovarian development is likely to be mediated through such ceremonies.

The presence of the completed nest was essential to "complete" maturation and ovulation in the House Sparrow (Polikarpova 1940) and to egg-laying in the canary (Hinde and Warren 1959) and the Ring Dove (Lehrman et al. 1961). This is not the case in the Kittiwake, since some birds lay their eggs in unfinished nests, and occasionally without any nest at all.

The peak of copulatory activity in the Kittiwake occurs in the week before laying (Tables 8 and 9) and the number of courtship feeds by the male to the female increases during the fortnight before laying. These activities appear to precede laying more closely than in other gulls.

The importance of the partner to female development is considerable. In Ring Doves no ovulation takes place without the mate (Lehrman et al. 1961), and indeed ovarian activity directly reflects the vigour of male courtship (Erickson & Lehrman 1964), in particular, his "nest soliciting" behaviour (Erickson 1970).

In the canary, reproductive development of the female is accelerated by stimuli from the male, but even females alone will lay (Warren & Hinde 1961, White & Hinde 1968). Oviduct growth in the House Sparrow was increased by the presence of a mate (Polikarpova 1940) and the ova of paired Starlings grew more quickly than those of isolated birds (Burger 1942).

In the Bengalese Finch (Slater 1969). copulation is not necessary for egg laying. Without copulation there is less ovulation in the Ring Dove (Lehrman et al. 1961). Copulation has been suggested as the key factor in stimulating ovulation in the Herring Gull (Brown 1967). In this latter species copulations began 30 days before laying and ended about 5 days before it. Brown further suggested that stimulation among the pairs produced locally-synchronous copulation and hence synchronous laying.

In the Gannet (Nelson 1965) the peak of copulatory activity occurs 10 - 14 days before laying. Such activity restarts soon after any egg loss, suggesting that an external stimulus stops it. The larger amount of time that the female spent at the nest during this period helped copulation and its associated activity of nest-gathering.

Courtship feeds to the female Red-billed Gull (Tasker 1970 in Mills 1973) increased about 20 days before laying, and reached a peak of about 4 feeds per day. This represented a large percentage of the total daily food intake of the female, and at this time she spent only 18 % of the daylight hours away from the territory. Similarly, Kittiwake females recorded attendances of over 80 % during the weeks before laying.

Vocalisations

In the Budgerigar, male vocalisations accelerate ovarian development in normal pairs (Ficken et al. 1960), isolated females (Vaugien 1951) and groups of females (Brockway 1965). Brockway (1964) has also shown that hearing the vocalisations of other males stimulates a male to vocalise more himself, and thus increases the intra-pair interactions.

Lott et al. (1967) have shown that in the Ring Dove stimulation from the surrounding colony produces ovarian development in addition to that induced by interaction with the mate. Such auditory stimulation may contribute to ovarian activity without any visual contact (Lehrman & Friedman 1969) but is more effective when combined with it (Lott et al. 1967). Similar stimulation may also exist in canaries (Warren & Hinde 1961). In the Zebra Finch, Bruen & Dunham (1973) found that sound alone from the female was not an effective stimulus for nest-building in the male. Sight and sound of a conspecific of either sex produced more nest-building than sound alone.

Thielcke (1970) has reviewed the social functions of bird vocalisations. Individual recognition of parents by their young has been demonstrated in the Adelie Penguin (Sladen 1958, Penney 1963), the Common Guillemot (Tschanz 1964, 1968) and several species of terns (Davies & Carrick 1962; Hutchison et al. 1968; Stevenson et al. 1970; Buckley & Buckley 1972). Such recognition has also been found in Herring Gulls (Goethe 1937), Ring-billed Gulls (Evans 1970a), Laughing Gulls (Beer 1970) and Black-billed Gulls (Evans 1970b). In this latter species Evans had shown that although calls vary between individuals and contexts, a call is consistent for a given bird in a given situation.

The same apparent display may be used in different contexts. In the Kittiwake an example of this is the "choking" of the male. This is probably agonistic towards other males but serves to attract potential mates to his site. Manley (1960) discussing such displays concluded that the recipient was capable of contextual interpretation. It is possible that "choking" in the Kittiwake indicates the willingness of the male to feed a female and would serve only to attract such females as were desirous of being fed.

Among seabirds, at least, it is possible that the calls of adults are structured in a manner similar to that demonstrated for the Little Auk (Ferdinand 1969). In this species all calls were found to be made up of two simple figures and the frequencies were almost constant. Moynihan (1962) also thought that all Larid calls were combinations of 4 basic rhythms and 2 - 3 basic tones.

The landing calls of adult Gannets have been examined in some detail (White & White 1970) and found to exhibit a temporal change in their amplitude envelopes. The characteristic shape of the first part of the call is probably an identifier for the individual, and may be time-coded. The second half, which is probably frequency-coded, may contain other information such as motivational state. Such temporal patterning would be useful in the considerable background noise found at seabird colonies, and amplitude coding does not suffer from the Doppler effect as does frequency.

Birds have a comparatively broad basilar membrane and it has been estimated that they may be as much as ten times more efficient than man at temporal resolution of sounds, but they probably have about the same absolute sensitivity and frequency discrimination (Thorpe 1961, p. 125). It has even been suggested that tonality is merely a by-product of such a time-intensity system.

It is relatively easy to examine the structure of calls, but far more difficult to judge their information content. If individual recognition is to take place, then the call must be highly variable within a population. However, it also needs to be species-specific, and hence highly stereotyped. Playback experiments are one way of investigating the functions of sound signals, but it is often difficult to gauge the reactions of the recipients accurately.

White (1971) in a further study on Gannet landing calls showed individual recognition of mates but not of immediate neighbours. She found the young to be less responsive than adults, but considered it possible that they could recognise their parents.

Emlen (1971, 1972), working with Indigo Buntings, found that males could distinguish between the familiar calls of neighbours and those of unfamiliar birds. In this case the greatest variability was in omissions and additions to the end of the song, and in its loudness. These differences he considered to reflect the motivational state of the bird.

The repertoire of calls in the Kittiwake has been reviewed by Paludan (1955), Tinbergen (1959) and by Moynihan (1962). The most common call is that from which the species derives its name, and which is given at most times when the pair comes together.

The calling of one pair often triggers off calling in neighbouring birds. In the denser, central areas of the colony, where pairs have more neighbours and arrivals are more frequent, the incidence of calling per pair is probably higher than on more peripheral sites (Coulson 1960, p. 75).

Recordings were made of the Kittiwake calls of different individuals in May when the birds are most vocal, and were analysed with a Sonagraph. Extensive analysis has not been made but the results obtained suggest some consistent individuality (Figs. 23 a, b, and c).

This situation is complicated by two factors, however. The full "kittiwake" call is often only part of a longer sequence involving incomplete versions of the call (Fig. 24). The sections used for the analysis of individuals were taken from such sequences after the birds had built up to a full-calling situation. The structures of these sequences probably reflect the changing motivational state of the individual.

Another factor involved may be the seasonal change in the calls of the bird. They sound more "hoarse" early and late in the season, presumably due to hormonal changes. These differences are illustrated in Fig. 25. Since the recordings analysed were taken from individuals at the same

Figures 23 - 25

All these figures show sonagrams of Kittiwake vocalisations referred to in the text. They were made on a Kay Sonagraph 6061B with contour display unit and scale magnifier. In all of the sonagrams, read frequency along the ordinate and time along the abscissa. Frequency markers show 0 - 8 kHz. except in Fig. 23b where specified otherwise. Baseline markers indicate 0.25 second intervals.

Figure 23a. Kittiwake calls from four different males (A - D). The structure of a single Kittiwake call is illustrated in sonagram A. Sonagrams C and D show 2 Kittiwake calls, and sonagram B gives 3 calls.

Figure 23b. Enlarged sonagrams of Kittiwake calls of males A - D showing the consistent individuality in greater detail. Two calls are given for each bird. Contour lines are 6dB apart.

Figure 23c. Kittiwake calls of four different females (E - H). Two calls are presented for each individual.

Figure 24. A complete calling sequence of a male Kittiwake. Read from top left to bottom right. The start of each full Kittiwake call in the sequence is starred.

Figure 25. Kittiwake calls of the same male at four different times in the year. From top to bottom the sonagrams illustrate calls in January, March, May and August.

Fig. 23a

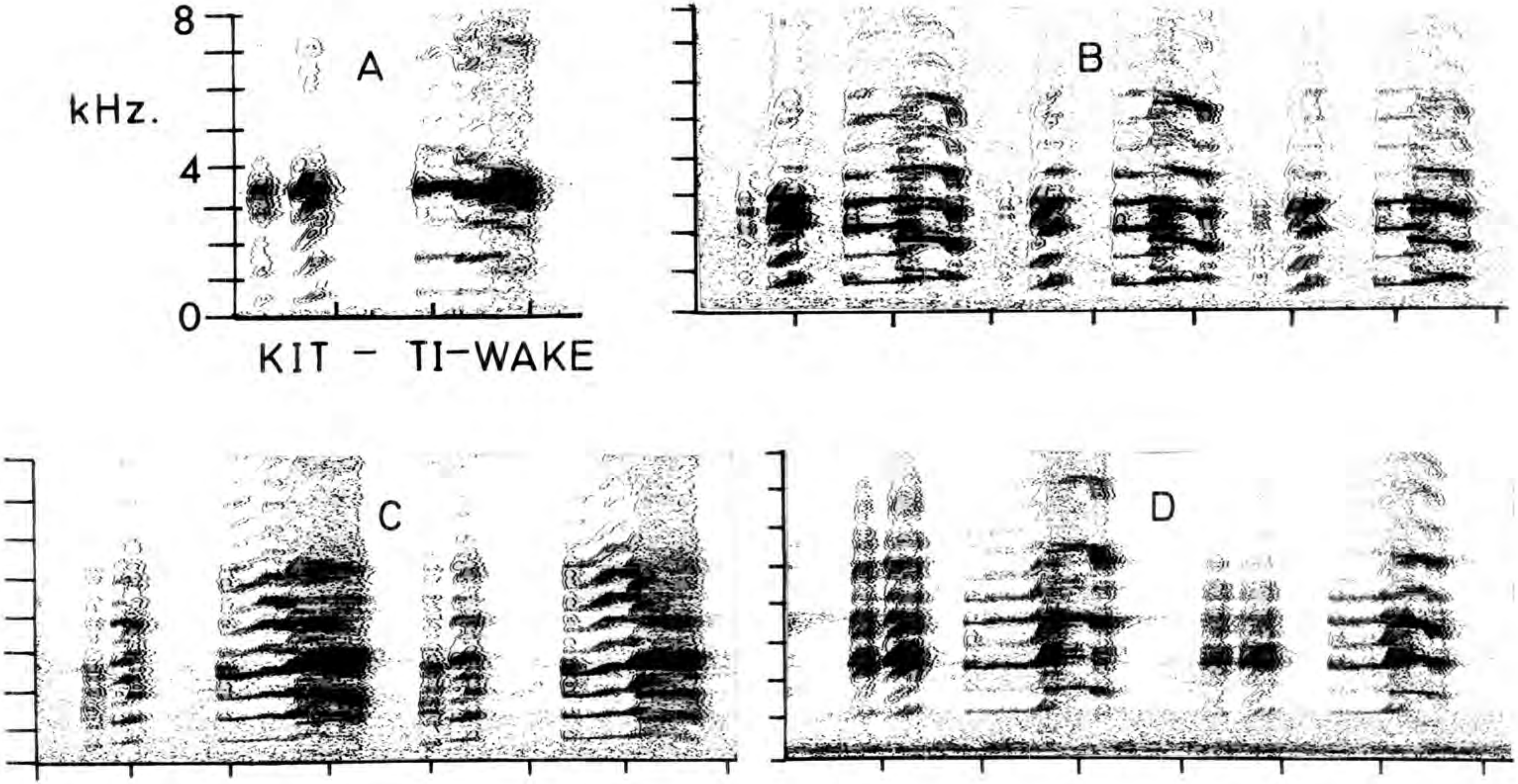


Fig. 23 b

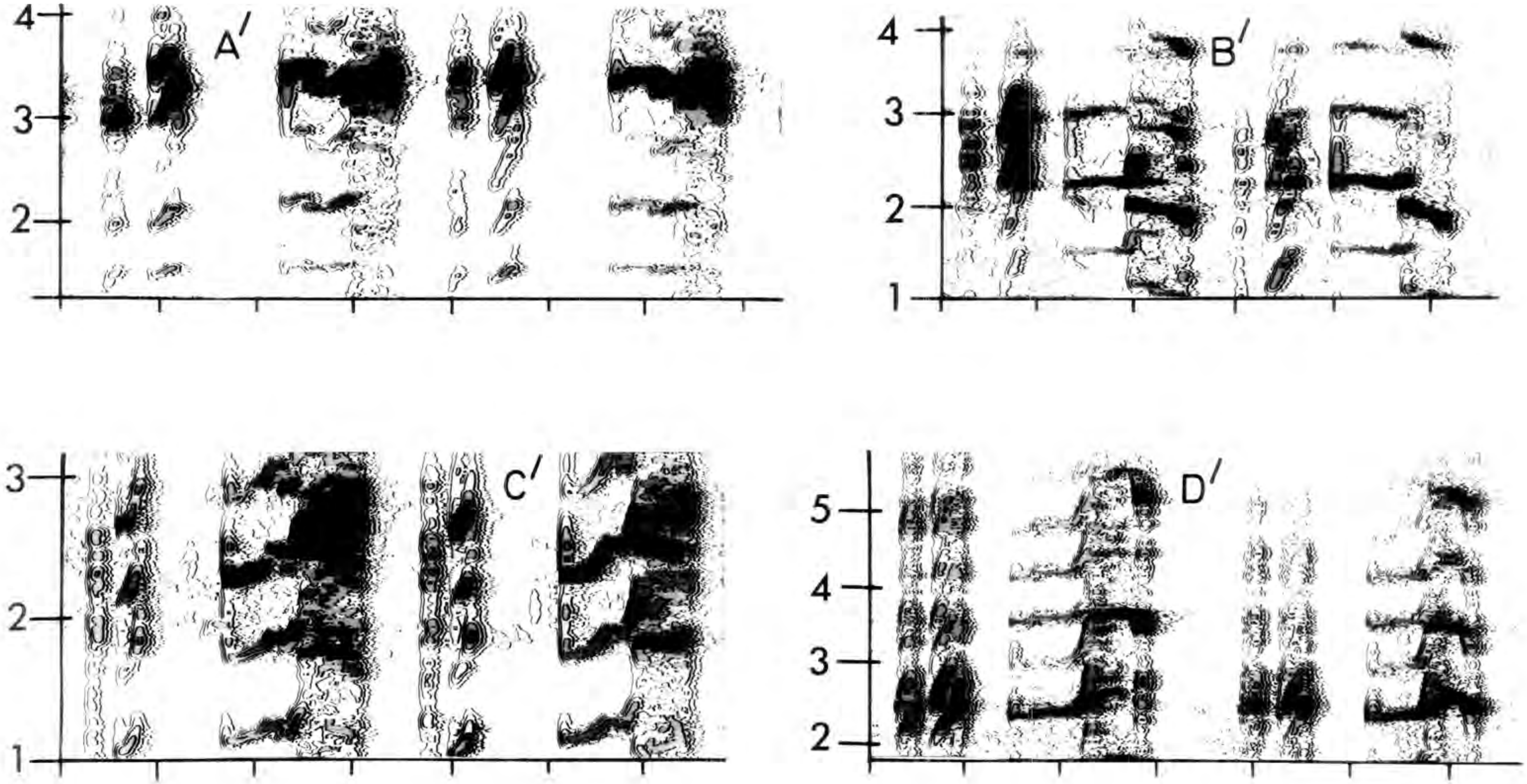


Fig. 23c

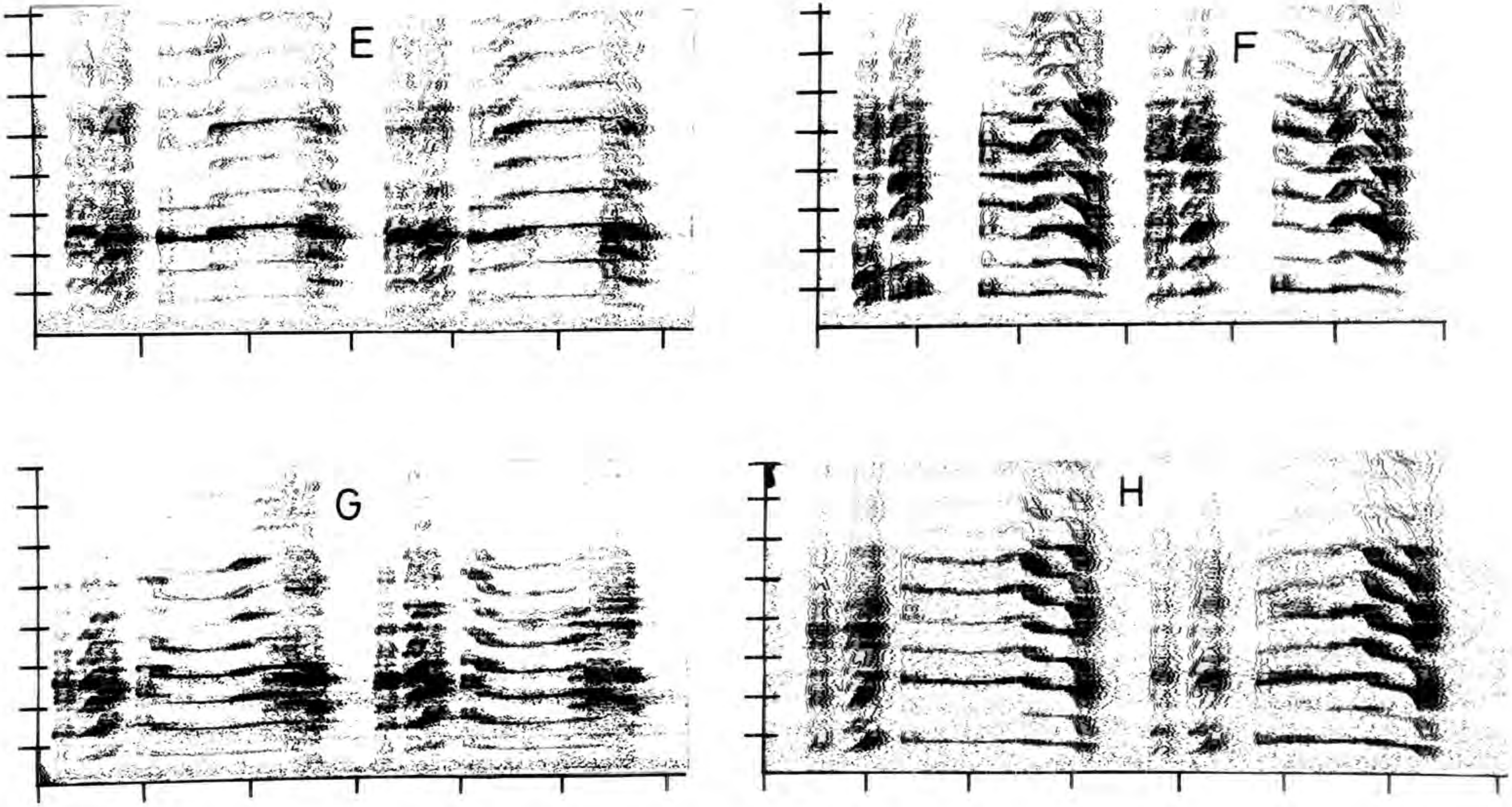


Fig. 24

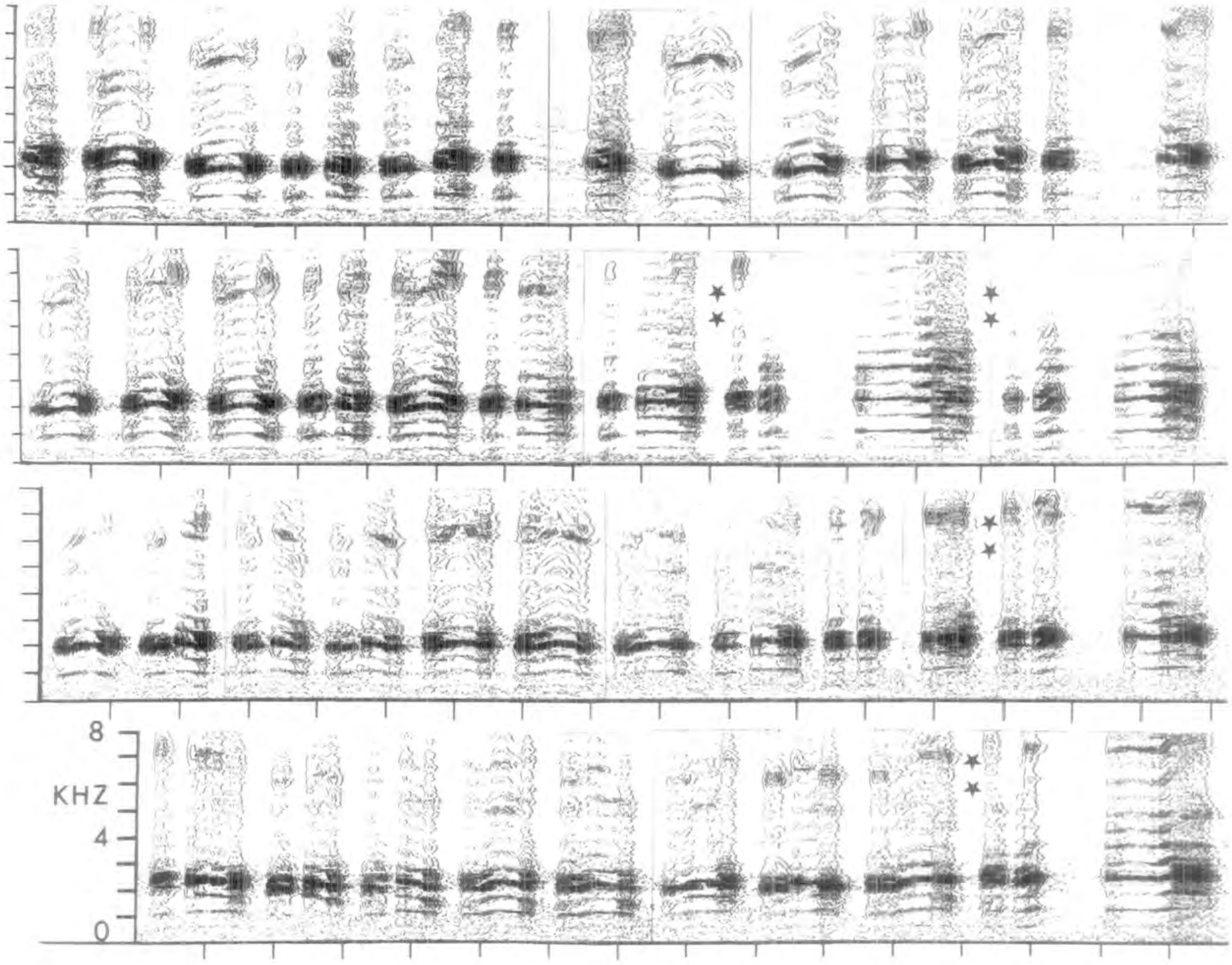
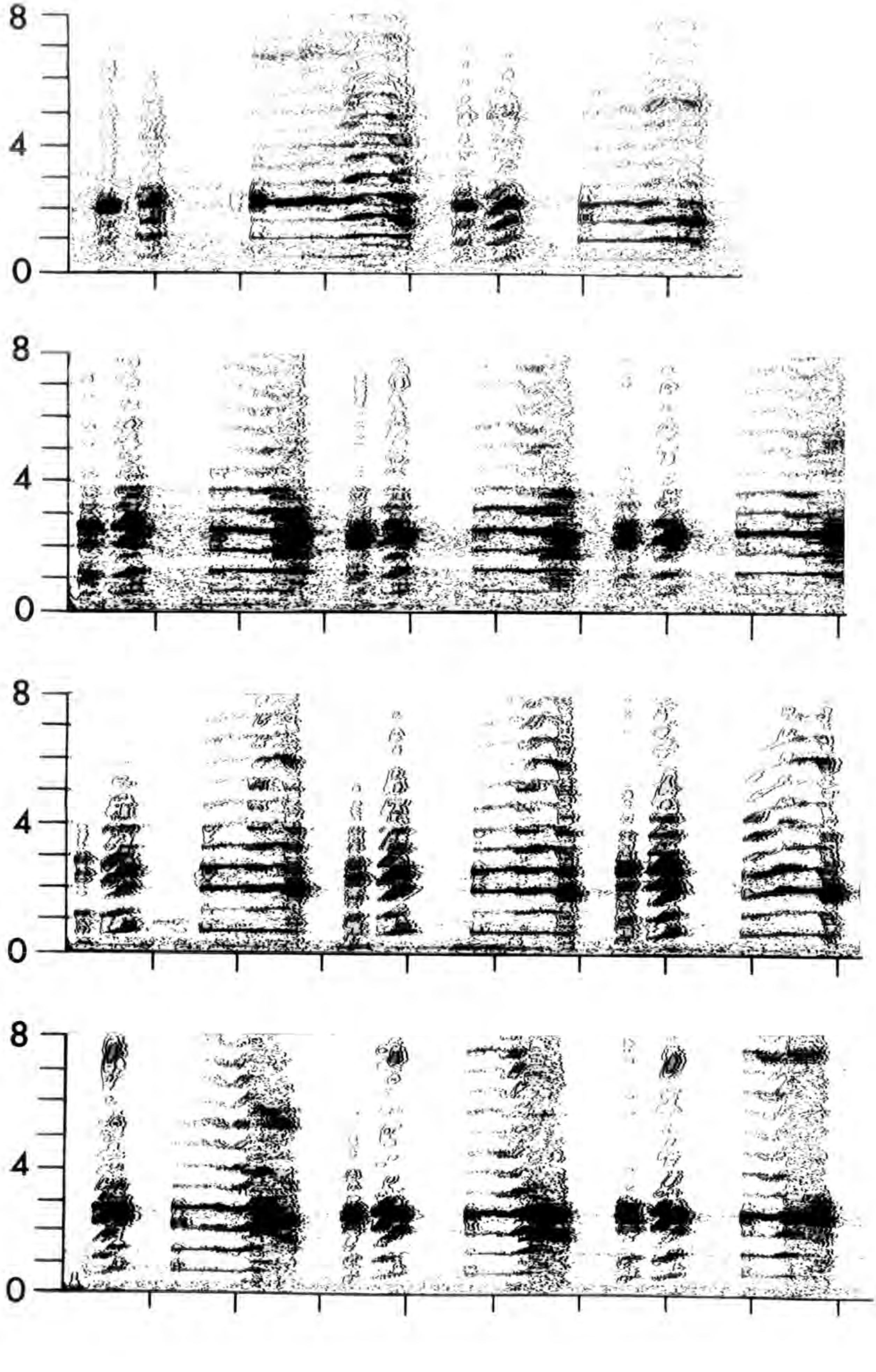


Fig. 25



stage in their reproductive cycles, the individual differences found are probably real. No attempt was made to investigate possible differences due to age, breeding experience, sex, motivational state or social context.

Preliminary attempts at playback experiments using the calls of known individuals showed that while it was possible to induce calling in the birds near the loudspeaker, this soon died away. In particular, the mate of the "calling bird" seemed to need visual reinforcement of its partner's presence. Since this could not be provided, these experiments were discontinued.

The number of times that the pair comes together rises to a marked peak before egg-laying. Since most arrivals of a bird result in the greeting ceremony between mates, involving the kittiwake call, it seems likely that such vocal greetings play an important part in stimulating ovarian development.

Later in the season it is believed (Hodges 1969) that food-begging pressure from the chicks drives the parents from the site. During the period before egg-laying the courtship food-begging of the female increases in frequency and intensity (Table 9), often occurring shortly after the pair come together. This build-up of begging pressure may contribute to the increased activity of the male forcing him to leave the site. This greater male activity leads to more arrivals, with their consequent greeting ceremonies and reinforcement of the pair bond, just before incubation, when the greatest strain is placed upon this bond.

The changeover system

A changeover is defined as an occasion when the arrival of one member of a pair on the site is followed by the departure of its mate (irrespective of the intervening period that the pair are together).

Although the number of times that the members of a pair come together on the site rises throughout the season to a marked peak just before laying, the proportion of these times that the partners change over remains fairly constant (Table 26). This is because the female remains more on the site with the male contributing more of the arrivals.

However, the percentage of these changeovers which are of 5 mins duration or less increases steadily towards laying and, indeed, after it. This is shown for pair W1E in 1971 (Fig. 26) and is true for the other pairs considered.

Once incubation is underway almost all changeovers are of one minute duration or less, and the birds meet only briefly on these occasions. It can thus be seen that the change to the system used during incubation is not quite as drastic as might have been supposed, the birds decreasing their changeover times as they phase into it gradually.

This decrease in changeover time as laying approaches may be partly the result of increasing food-begging pressure from the female, as outlined above.

Figure 26. The increase in the weekly percentage of pair changeovers which take less than 5 minutes. Pair W1E in 1971 (see Table 26) illustrates the rise in this percentage from their return to the colony in January until the incubation of their eggs in May

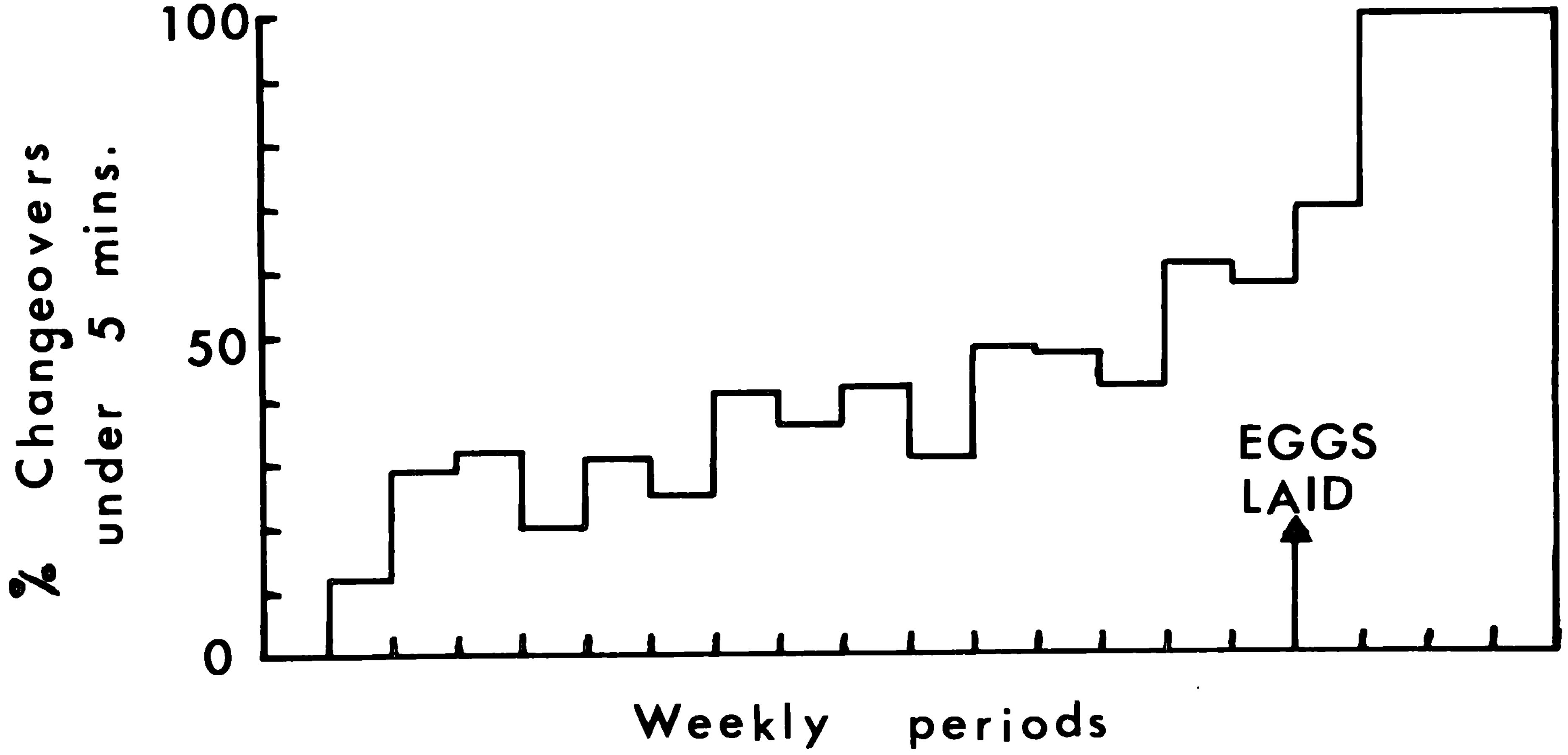

% Changeovers under 5 mins.
100
50
0
EGGS LAID
Weekly periods

Table 26. Seasonal decrease in the duration of changeovers (Pair on W1E in 1971)

Weekly period ending	Number of times per week			Percentage		
	Pair together (a)	Partners changed over (b)	Changeover took less than 5 mins (c)	Pair unions leading to changeovers $(\frac{b}{a})$	Pair unions leading to rapid changeovers $(\frac{c}{a})$	Changeovers less than 5 mins $(\frac{c}{b})$
31/1	24	7	29	0	0	0
7/2	54	17	31	2	4	12
14	43	17	40	5	12	29
21	41	19	46	6	15	32
28	28	10	36	2	7	20
7/3	35	16	46	5	14	31
14	43	24	56	6	14	25
21	73	34	47	14	19	41
28	72	33	46	12	17	36
4/4	67	26	39	11	16	42
11	69	32	46	10	14	31
18	70	29	41	14	20	48
25	117	43	37	20	17	47
2/5	153	31	20	13	8	42
9	160	56	35	34	21	61
16	143	57	40	33	23	58
EGG LAYING						
23	104	40	38	28	27	70
30	22	15	68	15	68	100
6/6	17	12	71	12	71	100

Nest-building

The process of nest-building in the Kittiwake has been described by Cullen (1957). As she noted, the collecting of mud for the early stages of the nest is often correlated with wet weather. This may result in considerable synchrony of nest-building for a colony, and the birds often collect material communally.

At this time the mud deposited is often "trampled" or "foot paddled". In a review of this type of behaviour Buckley (1966) thought it to be mainly a method of feeding, and considered it unlikely that it would be found to occur in such non-littoral larines as the Ivory Gull or the Kittiwake.

He recorded that gulls will paddle in grassy fields after rain but thought that this was unlikely to flush any earthworms or other invertebrates. Indeed, this was considered by Tinbergen (1962) to be an automatic response to a wet substrate. Rothschild (1962) found foot-paddling to be present in Black-headed Gull chicks as early as 12 days old, and Buckley considered it to be an innate pattern.

Cullen & Ashmole (1962) found trampling (called "side-stepping") to be present, although less marked, in the Black Noddy. They suggest that it is adaptive in the cliff-nesting Kittiwake and Black Noddy in fastening their nests on the cliffs, whereas it is virtually absent at the nest in the ground-nesting gulls and terns.

Later in nest-building, however, dry material may be trampled in dry conditions. Once a secure base has been established, straw and grass material is brought to make a raised platform. Eventually a cup-like nest is formed not long before the eggs are laid.

The technique used to form the cup is for the body to be tilted forward, and the legs braced backwards, with the breast pressed against the inside of the cup. This is called "bracing" and in a similar "scraping" movement the legs are used.

As noted by Cullen and Ashmole, both the Black Noddy and the Kittiwake depress their tail while bracing and scraping, although this is not encountered among the other gulls. Probably this results in a firmer and deeper cup than found among ground-nesting gulls, and helps to prevent eggs rolling out of the more vulnerable cliff nests.

The stealing of material from the nests of other birds is by no means uncommon in the Kittiwake. This behaviour is less often seen among the ground-nesting gulls where nest material is more readily available.

Possibly, as suggested by Hinde et al. (1963) for the domesticated canary, the selection of the type of material brought is in part controlled by the changing sensitivity of the brood patch. If tactile sensitivity to stimuli from the nest increased as laying approached, then changes in the nest material brought might well result.

In 1971 the states of nests at the North Shields colony were recorded daily. Two main stages were recognised; nests which consisted of a raised platform, and those which had a well-formed cup. The mean time taken from platform to cup nest was 10.2 ± 1.7 days, and the mean interval from the completion of the cup until the first egg was laid was

13.6 ± 2.1 days. The interval between the attainment of a platform nest and the laying of the first egg (y) is shorter the earlier in the season (x) that a pair lay :

$r_{61} = + 0.3813$; $P < 0.1\ \%$ $y = 10.5 + 0.5x$ (Fig. 27a)

The interval between cup completion and laying is also shorter in the early-laying pairs :

$r_{70} = + 0.3536$; $P < 0.1\ \%$ $y = 3.3 + 0.5x$ (Fig. 27b)

Thus, while it might be advantageous for pairs laying later in the season to take a shorter time over their nest-building, they are probably the younger, less-experienced pairs and are unable to do so.

This increase in the time taken to build a nest as the season progresses is the converse of the situation found in the Shag (Coulson et al. 1969). The nest-building interval in the Shag decreased from 33 days in mid April to 11 days in early June.

The relationship between nest-building and the laying of the first egg is not always a simple one, and laying is not necessarily related to the achievement of a nest.

In the three years 1970 - 1972 the same pair of Kittiwakes on site E2F at North Shields built an excellent cup nest and maintained it for over a month before laying their eggs. Although this is a peripheral site where little can be seen or heard of the birds in the colony, other pairs on this site have laid normally.

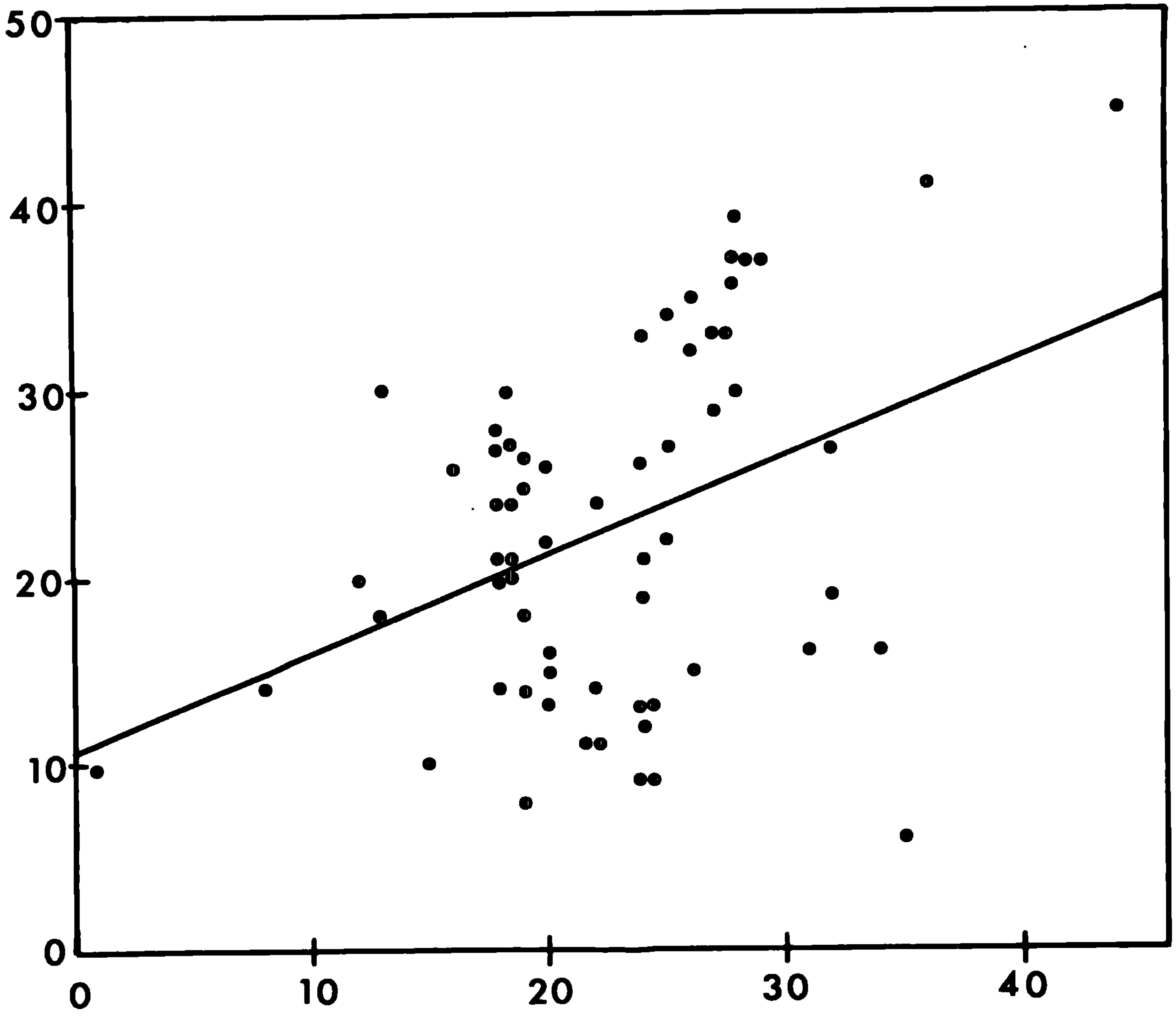
The converse of this situation is when a bird lays its eggs on a bare site, as happened five times at North Shields during this study. In addition, two pairs laid on very inadequate

Figure 27a and 27b

The relationship between the date on which the first egg was laid (in days after 22 April) and the number of days elapsing between the completion of the platform (Fig. 27a; unlabelled axes) or the cup nest (Fig. 27b) and the laying of this egg. In the unlabelled Figure 27a, the abscissa is the same as Fig. 27b and the ordinate is similar, except that the interval is taken from the platform nest stage.

The interval from nest completion (using either nest stage criterion) to laying is longer in those pairs which laid later in the season.

Fig.27a



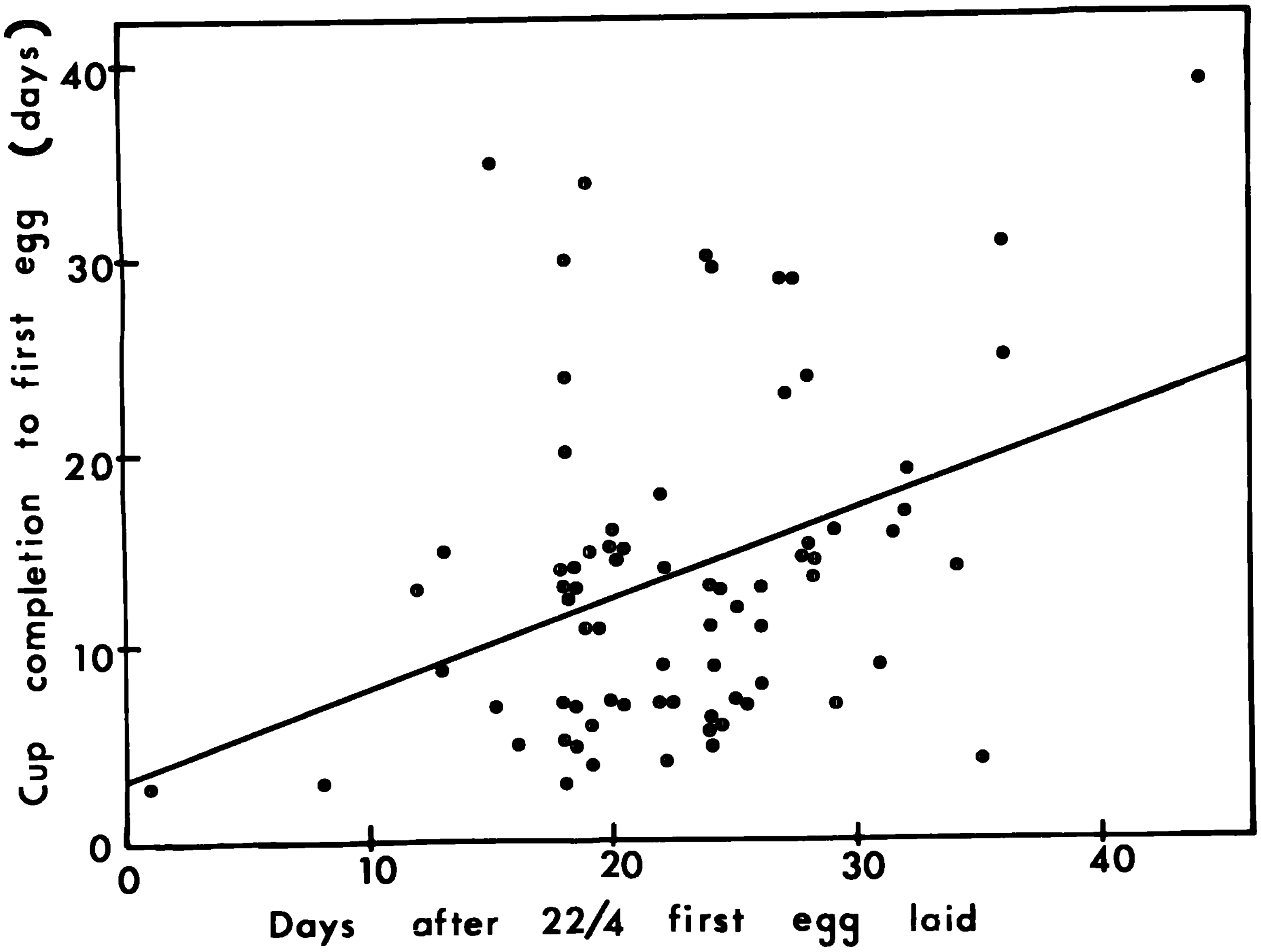

Cup completion to first egg (days)
40
30
20
10
0
0
10
20
30
40
Days after 22/4 first egg laid

Fig. 27b

nests. In all but one of these cases the eggs rolled off the site. In the remaining instance the pair built a normal nest around the eggs during the early part of incubation. Three cases similar to this are reported by Maunder & Threlfall (1972).

Although nest-building only occurs at a low level during incubation, if the nest loses its characteristic shape then extensive bouts of building may take place to restore it fairly rapidly. This also happens in the Herring Gull (Baerends & Drent 1970). Obviously it is adaptive for building to quickly reach a high level again should the need arise.

Nest-building activites during incubation are of two kinds. Collecting trips may occur at nest-relief and are performed by the incoming bird or by the bird just relieved. Sideways building usually takes place just after settling down to incubate, particularly after a nest relief. Moynihan (1953) and Beer (1965) record a similar pattern for the Black-headed and Black-billed Gulls.

In the Kittiwake, the proportion of settlings which were followed by this sideways building fell from about 35 - 45 % during the early part of incubation to just over 10 % later on. However, there were some exceptions to this, and one female was significantly more frequent in building than her mate (Table 27).

Baerends & Drent (1970) showed that in the Herring Gull 45 % of all settling sequences were followed within a minute by building, and that 66 % of all sideways building occurred within a minute of settling. They also note that sideways building often preceded a rising/settling movement (13.5 %) although most building movements (86.5 %) took place afterwards.

This sideways building behaviour and its relationship to sideways throwing and the formation of the nest in birds has been discussed in some detail by Harrison (1967).

Table 27. Proportions of settling sequences during incubation which resulted in nest-building within one minute. Information from time-lapse exposed film for two pairs in 1971

W1Da	Male		Female		Total	
Days 1 - 8	$\frac{60}{173}$	34%	$\frac{79}{175}$	45%	$\frac{139}{348}$	40%
Days 9 - 27	$\frac{25}{210}$	12%	$\frac{63}{249}$	25%	$\frac{88}{459}$	19%
Whole of incubation	$\frac{85}{383}$	22%	$\frac{142}{424}$	33%	$\frac{227}{807}$	28%

The building behaviour of the female was significantly ($P < 0.1\%$) greater than that of the male

W1Db	Male		Female		Total	
Days 1 - 8	$\frac{60}{133}$	45%	$\frac{48}{133}$	36%	$\frac{108}{266}$	41%
Days 9 - 27	$\frac{18}{190}$	10%	$\frac{15}{165}$	11%	$\frac{33}{355}$	9%
Whole of incubation	$\frac{78}{323}$	24%	$\frac{63}{298}$	21%	$\frac{141}{621}$	23%

For this pair there was no significant difference between the building behaviour of the female and that of the male

SECTION IV

INCUBATION

The roles of the sexes during incubation

Incubation is taken as the period from the laying of the first egg until it hatches. The relative amounts of time spent in incubation by the parents are shown in Table 28. Normally the roles of the sexes are about equal, with the female tending to incubate slightly more than the male. This difference is a significant one, however.

In pair c - 1 (on W1G) the female consistently performed over 60 % of the incubation during the three years considered. Female j was recorded for two years with one male and with a different male in the two successive years. Her performance with any one mate was consistent, but when she took a less experienced male she had to perform more of the incubation.

Although both sexes incubated during the night, females incubated significantly more often than males (Table 29), proportional with their higher total incubation percentages. Individual pairs were again fairly consistent in successive years.

Observations were made on the Farne Islands in 1970 on pairs at the edge of a colony. Twenty pairs were considered, and for 12 of these incubation proceeded normally throughout June (Table 30). There was variation in the shares of incubation undertaken by males and females, and this may be connected with the probable youth and inexperience of some of these peripheral pairs.

Once more the females performed significantly more than half of the incubation duties. There was a tendency for males to be incubating more in the mid-morning and late evening, and females more around midday and early afternoon. No observations were made before 0600, so that it is not possible to say whether males took over from females during the hours just after sunrise.

In other gull species a similar picture of the roles of the sexes during incubation emerges; that of roughly equal shares, with perhaps the female having a slight preponderance (Goethe 1956; Tinbergen 1953). Baerends & Drent (1970), studying 30 nests of the Herring Gull for 290 hours (on days 0 - 35) found the male present on 50.3 % and the female incubating 46.5 % of the time. Other attendance values are :

Black-headed Gull	male	53.5 %	Ytreberg 1956
	female	46.5 %	(652 hours)
Glaucous-winged Gull	male	47.5 %	Vermeer 1963
	female	52.5 %	(517 hours)

None of these three species showed any consistent trend during the course of incubation, but only fluctuations around the 50 % level. This is also true for the Kittiwake.

The Kittiwake does not leave its eggs unprotected, either while laying or incubating them. However, other gulls tend to leave the eggs during the hours of darkness (Baerends & Drent 1970; Beer 1967). This is almost certainly an anti-predator device in these more vulnerable ground-nesting gulls, and as such not necessary in the Kittiwake.

Table 28. Percentage attendances during incubation by males and females

Site	Year	Male	Female	% male	% female	
W1F	1968	a	j	53	47	
W1F	1969	a	j	51	49	
W1E	1970	b	j	35	65	
W1E	1971	b	j	38	62	*
W1E	1972	b	k	48	53	
W1G	1968	c	l	39	61	
W1G	1969	c	l	38	62	*
W1G	1970	c	l	38	62	**
W1B	1968	d	m	56	45	
W1B	1969	e	n	48	52	
W1B	1970	f	n	51	49	
W1B	1971	f	n	49	51	
W1B	1972	f	p	54	47	
W1D	1970	e	q	50	50	*
W1D	1971	e	q	45	55	
W1D	1972	e	q	52	49	
E1D	1969	g	r	41	59	*
E1D	1970	g	s	50	50	
E1D	1971	g	s	45	55	**
W1H	1971	h	t	55	47	
W2I	1972	h	t	55	47	**
S1Ct	1972	i	v	38	63	
			Mean	45.3	54.7	

* indicates that the eggs did not hatch

** indicates that one partner disappeared during incubation (percentage attendances for W1G 1970 calculated for shared incubation only)

Based upon complete information for attendance from the laying of the first egg until it hatched (or 27 days for the pairs which failed to hatch their eggs).

Table 29. Differences between male and female partners in the proportions of overnight incubation performed

Site	Year	Male	Female	Percentage overnights during incubation performed by male
W1F	1968	a	j	63
W1F	1969	a	j	50
W1E	1970	b	j	33
W1E	1971	b	j	21
W1E	1972	b	k	32
E1D	1969	g	r	33
E1D	1970	g	s	50
E1D	1971	g	s	31
W1B	1968	d	m	67
W1B	1969	e	n	29
W1B	1970	f	n	48
W1B	1971	f	n	61
W1B	1972	f	p	56
W1D	1970	e	q	31
W1D	1971	e	q	32
W1D	1972	e	q	64
W1G	1968	c	l	45
S1Ct	1972	i	v	22
W1H	1971	h	t	70
W2I	1972	h	t	61
(W1G	1969	c	l	12)
(W1G	1970	c	l	15)

For 26 days of incubation and the first 20 pairs (520 overnights)

Males performed 233 = 44.8 % ± 2 %

Females performed 287 = 55.2 % ± 2 %

$X^2 = 5.6076$

$P < 5\ \%$

Table 30. Proportions of incubation performed by male and female partners in twelve pairs during June 1970. Farne Islands

Pair	No. times recorded during incubation in June			Percentage attendance during incubation		
	Male	Female		Male	Female	
B	90	115		44	56	
C	81	98		44	54	(Pair 2 %)
D	44	136		24	76	
F	65	90		42	58	
G	80	87		48	52	
I	52	113		31	68	(Pair 1 %)
J	84	86		49	51	
L	109	50		69	31	
M	76	117		39	61	
Q	102	77		57	43	
S	47	117		29	71	
V	108	81		57	43	
Total	938	1167	Mean	44.6	55.4	

Testing difference between these proportions :

$$\chi^2_1 = 24.192; \quad P < 0.1\ \%$$

Diurnality in the sex of the incubating partner during June 1970. Inner Farne Island

Time period	No. observations		% male	% female	± male
0600 - 0800	250		52.4	47.6	+ 2.2
0800 - 1000	209		52.2	47.8	+ 2.4
1000 - 1200	241		55.6	44.4	- 1.0
1200 - 1400	230		57.4	42.6	- 2.8
1400 - 1600	306		59.5	40.5	- 4.9
1600 - 1800	275		52.7	47.3	+ 1.9
1800 - 2000	525		53.7	46.3	+ 1.1
2000 - 2300	342		53.8	46.2	+ 0.8
Total	2378	Mean	45.4	54.6	

The last column gives the deviation in the percentage attendance of the male from the overall (45.4 %) attendance.

Female attendance was significantly greater than that of the male :

$$\chi^2_1 = 19.985; \quad P < 0.1\ \%$$

Even after steady incubation has set in, the overall attendance of other gulls while incubating their eggs is less than the 99.7 % shown by the Kittiwake (99.9 % for the last three weeks of incubation).

Herring Gull	97.5 %	Baerends & Drent 1970
Black-headed Gull	97.3 %	Ytreberg 1956
Glaucous-winged Gull	95.8 %	Vermeer 1963
Lesser Black-backed Gull	92.1 %	Barth 1949
Common Gull	90.5 %	Barth 1949

If the relative amounts of time spent incubating by males and females are calculated separately for the hours of daylight, it will be seen (Table 31) that these are very similar to the values obtained for the total time. It will be noted that the daylight figures more closely approximate to equal sharing, presumably due to the greater amount of night incubation undertaken by the female.

Table 31. Comparison of the male and female contributions to daylight incubation and to the total incubation period

	MALE		FEMALE	
Pair & Year	Daylight incubation	Total incubation	Daylight incubation	Total incubation
E1D. 1971	48	45	52	55
W1E. 1971	39	38	61	62
W1Da.1971	49	45	51	55
W1Db.1971	48	42	52	58
Mean	46	43	54	57

All values are expressed as percentages

The individual overnight periods of incubation by females were also longer than those of males, although during the daytime males incubated for longer periods between change-overs (these periods will be termed "stints"). Table 32 gives the durations of these overnight and daytime stints during incubation.

Daytime incubation stints were shorter than those involving overnight periods of incubation, and daytime stints starting after 1100 were shorter than those starting before this time. The distributions of starting times of overnight and daytime stints are given in Appendix 5.

Table 32. Durations of overnight and daytime incubation stints performed by males and females

Mean male overnight stint = 808 ± 53 mins (N = 113)
Mean female overnight stint = 932 ± 55 mins (N = 154)
$t_{265} = 3.1367$
$P < 1\%$

N.B. An overnight stint was one during which the bird was incubating at midnight, and a daytime stint was any other period of incubation.

	Duration of daytime stint (mins) starting			
	before 1100		after 1100	
	Number	Mean	Number	Mean
Males	144	448 ± 37	73	257 ± 28
Females	113	393 ± 38	62	261 ± 36

There are no differences between males and females in the lengths of their daytime stints after 1100, but males have significantly longer morning daytime stints than females ($t_{255} = 2.071$; $P < 5$ %), the converse of the overnight situation.

Thus, a daytime incubating shift lasts about 4 - 8 hours and one involving an overnight on the site about 13 - 16 hours. However, if one partner fails to return when expected, the sitting bird will continue to incubate until it is relieved by its mate. A similar situation has been demonstrated for the Black-headed Gull (Beer 1961).

Figure 28 shows the numbers of hours each day that the parents incubated and demonstrates this compensatory mechanism. Pair A adhered to a fairly regular pattern, while pair B had a more irregular but still successful pattern. In pair C the male was very irregular in his incubation attendance, and the eggs did not hatch. Normally this compensation only involves extending a daytime shift overnight (see also Figs. 31 - 34).

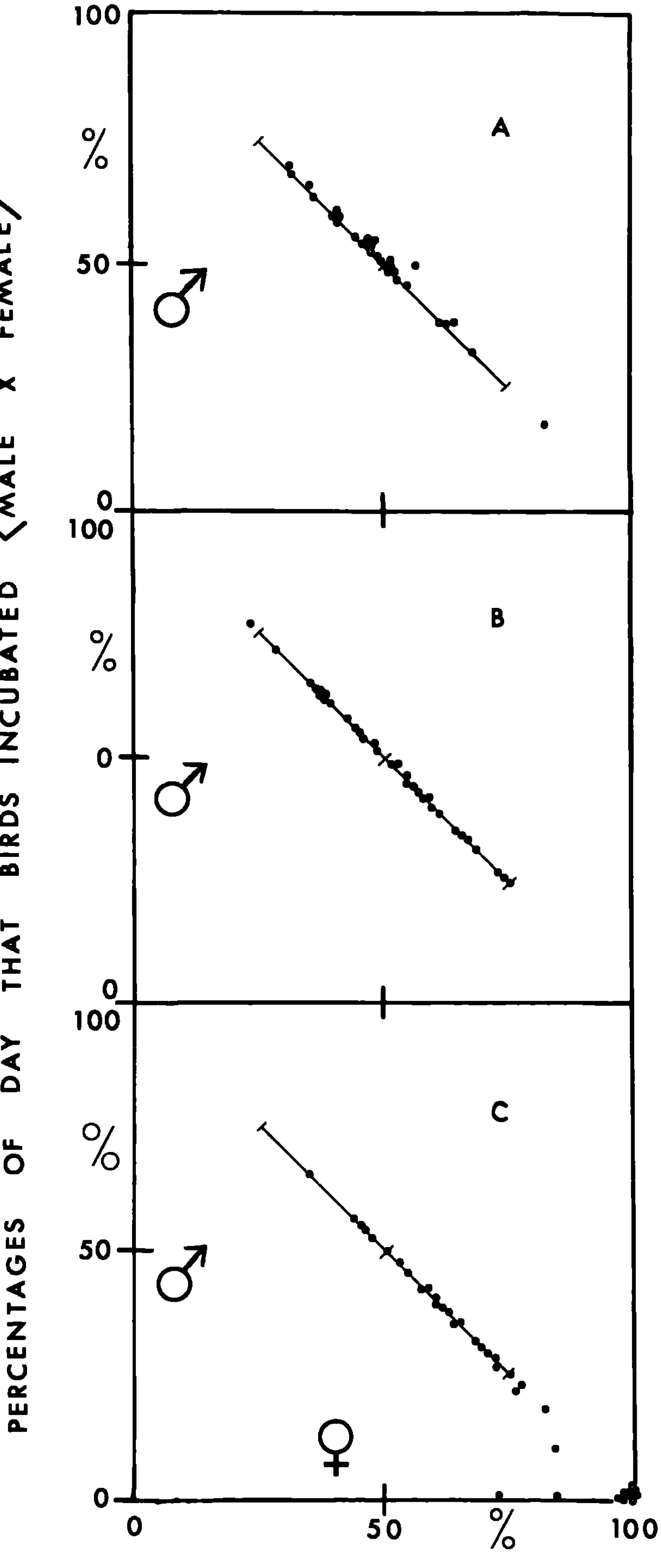
This mechanism is not confined to gulls, and Slater (1970) has demonstrated it in Bengalese Finches. In this latter species the sexes normally alternate during steady incubation with the male performing 44 % and the female 56 % of incubation. However, if a mate is removed or dies during incubation, then the other bird will remain on the eggs almost continuously, taking only occasional breaks to feed.

Holmes (1973), studying sandpipers (Calidris spp.), has suggested that equal dual incubation allows all breeding individuals a maximum time for feeding. In high latitudes where food may be scarce or unpredictable this would obviously be adaptive, and the system may have persisted into lower latitudes where food is more abundant.

Figure 28. The compensatory mechanism during incubation

The percentage of each day during incubation that the male partner incubated (vertical axes) has been plotted against that for the female (horizontal axes) for three pairs in 1969. Pair A was W1F, pair B was W1B, and the unsuccessful pair C was W1G.

The diagonal line drawn shows the theoretical line for total compensation, and its upper and lower limits represent 75% and 25% male incubation respectively.


PERCENTAGES OF DAY THAT BIRDS INCUBATED ⟨MALE X FEMALE⟩
A
B
C
100
%
50
♂
0
100
%
0
♂
0
100
%
50
♂
♀
0
0
50
%
100

Dual incubation provides little opportunity for pair interaction, but by retaining the commitment of both partners to the nest results in both parents caring for the vulnerable young.

The changeover rate during incubation

For the first few days after the first egg has been laid, while the clutch is being completed, the partners alternate frequently, handing over incubation duties up to 20 times a day. This high level of activity falls rapidly to a fairly stable level of about two changeovers per day (Fig. 29 and Appendix 6). There is a slight further drop in this level throughout the course of incubation.

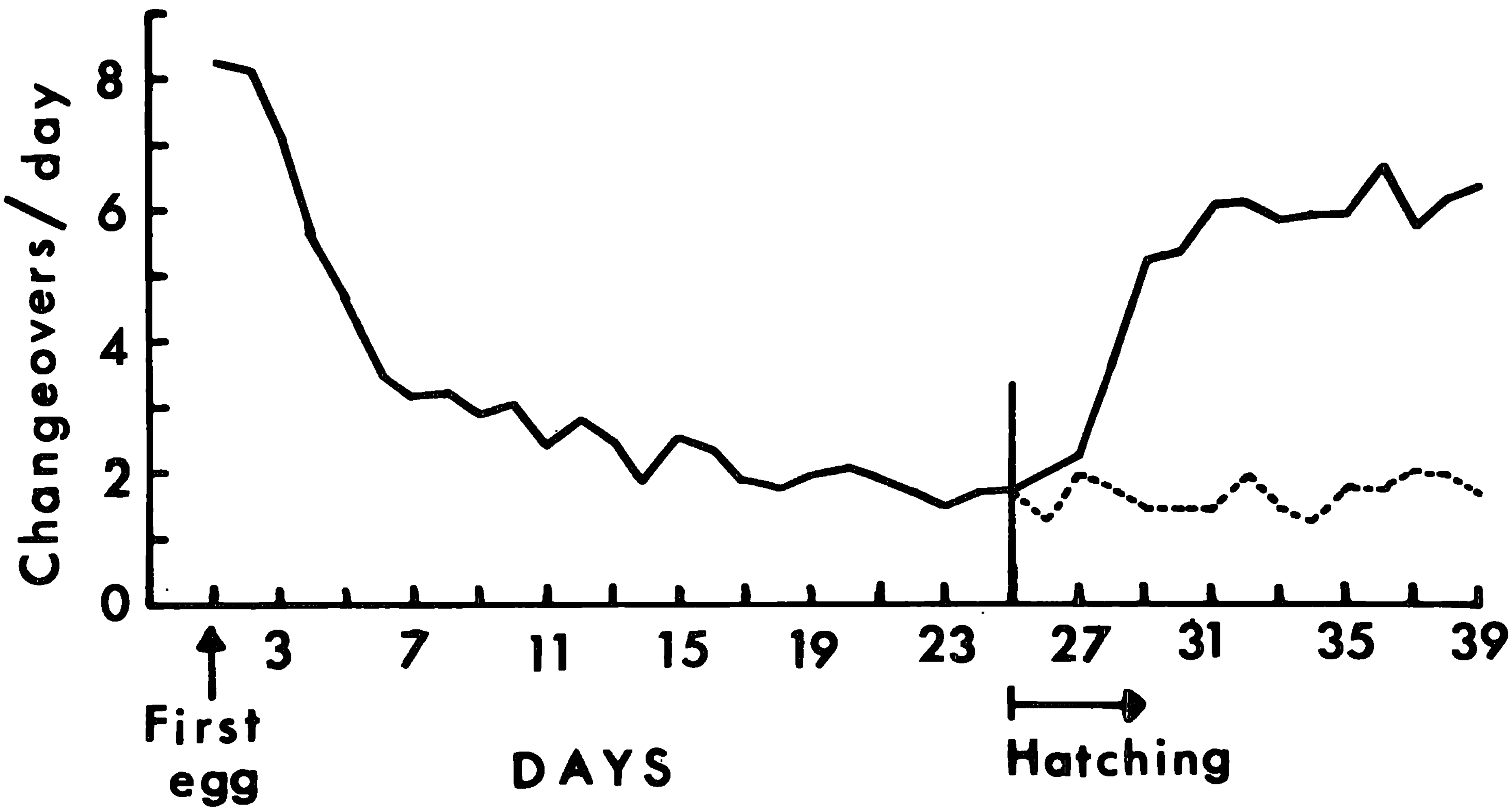
Once the eggs have hatched, the rate of changeover rises rapidly, although pairs whose eggs do not hatch continue the incubation pattern for a further 10 - 20 days.

The overall tendency is for a two shift/day system with one parent incubating from early evening until dawn on the following day, and the returning mate incubating during the day. Such a pattern is subject to considerable irregularity throughout incubation. This unevenness in the shift system is often produced by a bird returning after a shorter time away than might have been expected. Alternatively, the disruption may be caused by a partner not returning when expected, whereupon the sitting bird continues to incubate until the absent mate returns. It seems, therefore, that the length of an incubation shift is determined by the return of the non-incubating member of the pair to the site.

Figure 29. The number of times per day that the partners changed over parental duties during incubation and the early brooding of the chicks.

The mean daily changeover rate was calculated for 22 pairs from day 1, when the first egg was laid, until day 25 when some eggs started to hatch. Thereafter, changeover rates were calculated separately for the 17 pairs whose eggs hatched (solid line) and for the four pairs whose eggs failed to hatch (broken line).

95 % confidence limits lie between ± 25 - 45 % of all mean changeover rates.


Changeovers / day
0
2
4
6
8
First egg
3
7
11
15
19
23
27
31
35
39
DAYS
Hatching

Diurnality in the times of changeover

The times of day at which nest reliefs take place during incubation show a marked diurnality (Fig. 30 and Appendix 7). There is almost always a changeover in the hour after dawn, and there is a much less marked peak in the late afternoon and early evening.

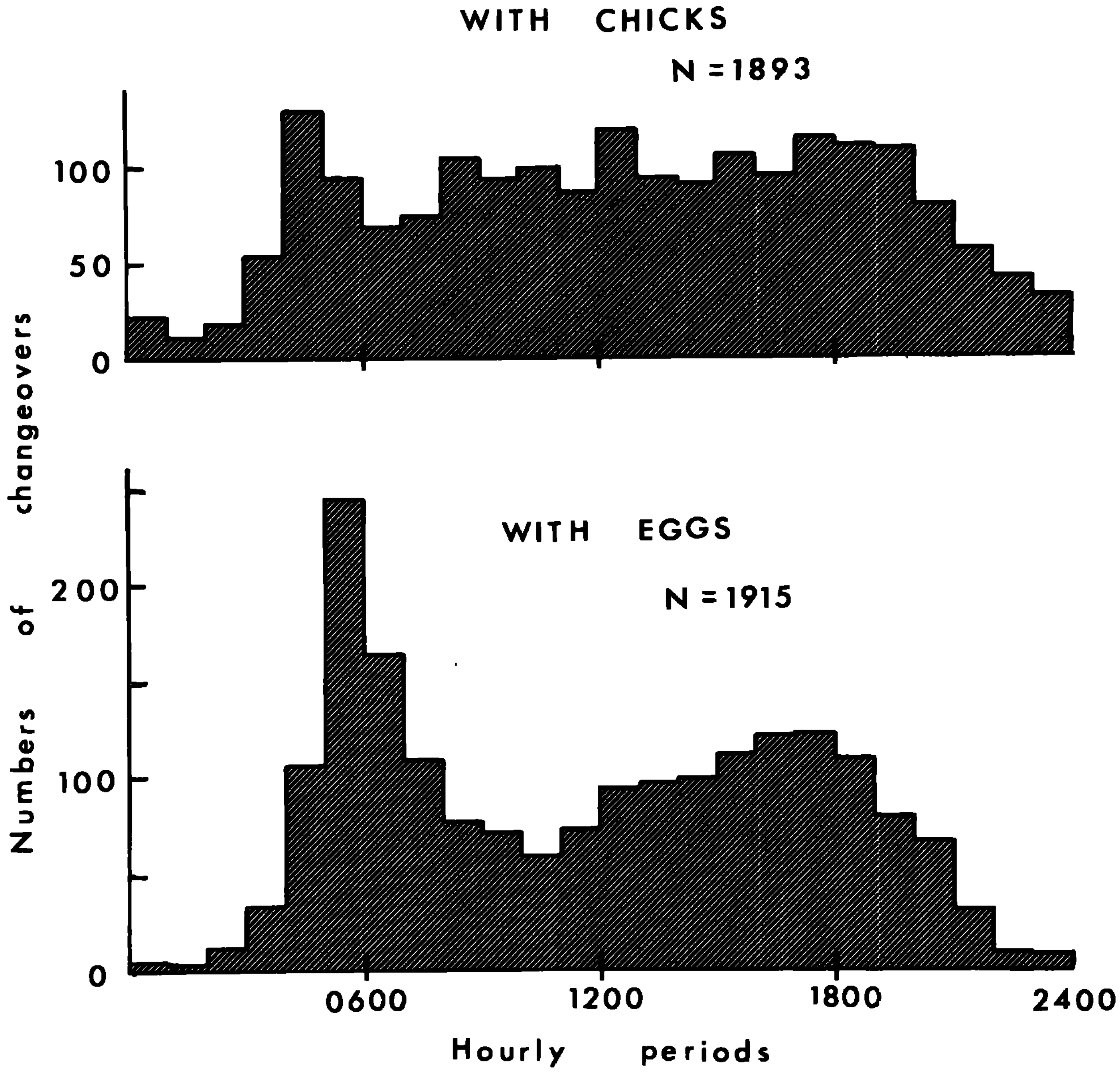
This post-dawn influx of birds is probably a carry-over from the pre-laying part of the season (see Section II). It is not known whether this is related to a feeding cycle, or whether the birds merely leave their sea roost at dawn to come to the colony.

Baerends & Drent (1970) note that during early incubation in the Herring Gull departure from the eggs is at the time of low water when the birds go off foraging. The influence of this foraging cycle was still noticeable later in continuous incubation when there was a marked peak in nest reliefs 1½ - 3½ hours after low water when the birds returned from the tidal flats.

Since the Kittiwake feeds far out to sea (Pearson 1968) it would not be expected to exhibit a feeding cycle such as this. Once the eggs have hatched, however, the chicks require to be fed frequently, and this probably accounts for the changed distribution of changeover times in this period (Fig. 30). There is a far less pronounced peak around dawn, and the birds return more often during the hours before dawn, as well as distributing their visits more uniformly throughout the daylight hours.

Figure 30. Hourly distribution of the times that partners changed over parental duties during the incubation of their eggs (lower histogram) and the brooding of their chicks (upper histogram).

Incubation was taken as the period from the laying of the first egg until it hatched, and brooding as the 20 days after the first egg had hatched. The numbers of changeovers are hourly totals for all 22 pair-years from 1968 - 1972.


WITH CHICKS
N = 1893
WITH EGGS
N = 1915
Numbers of changeovers
100
50
0
200
100
0
0600
1200
1800
2400
Hourly periods

It is not known whether adult Kittiwakes feed at night, but as Myres (1963) has pointed out, the prolonged twilight found in the arctic and high latitudes might permit feeding throughout the 24 hour period. Even in the British Isles, at the southern edge of the species breeding range, the summer twilight period is considerable and might allow the parents to feed before sunrise and after sunset.

Prolonged incubation

As mentioned earlier, if the eggs fail to hatch the birds will often continue to incubate them for twice the normal length of time.

In pair W1E in 1971 incubation was normal except that the female was off the eggs for 114 mins on day 3 of incubation, and off 8 times (total of 83 mins) on day 11. This second absence was sufficient to cause the death of the embryos, as determined by later examination of the eggs. Incubation proceeded, with a very regular 2 changeovers/day (Fig. 33) until day 52, when both birds started to leave the site at night. However, they continued to incubate the eggs by day until the 59th day after laying.

On E1D in 1969 the male showed intermittent desertion but once he returned incubation proceeded normally until day 47 when the birds left the site overnight. As with the pair cited above, they incubated the egg by day until this pattern also decayed.

The eggs of the pair on W1D in 1970 were infertile but were incubated until day 41 when the pattern began to break down. The longest unrelieved shift for this pair was performed by the male from day 17 until day 19, and lasted 2293 mins (38 hours).

Holcomb (1970) lists most of the recorded examples of prolonged incubation in birds, including the Herring Gull incubating for 56 - 75 days (two pairs) rather than the normal 27 days, and the Lesser Black-backed Gull for 36 - 58 days (5 pairs) rather than the usual 26 days. He also records two terns which normally incubate for 35 days sitting for over 60 days (White-capped Noddy Tern) and for over 64 days (Fairy Tern). Nelson (1966) notes that the Gannet, which normally hatches its egg in 44 days, may incubate for up to 102 days if the egg is infertile.

McFarland (1971) thought it possible that the tendency to incubate is self-reducing unless adequate feedback is available from the eggs. The alternative is Baerends' view (in Baerends & Drent 1970) that incoming feedback information from sitting on the clutch is checked against a preset expectancy value. In this case if the feedback is greater than the "expected" then the incubation tendency increases, whereas if it is less then it will decrease. It does not seem possible at present to decide which of these alternatives approximates most closely to the mechanism leading to prolonged incubation.

In the Kittiwake, young pairs will sometimes stop incubating long before hatching is due. The motivation of these individuals towards incubation is obviously very poorly developed by contrast with the prolonged incubation behaviour exhibited by other birds.

Patterns of changeover during incubation

The changeover patterns of several pairs are illustrated in Figs. 31, 32, 33 and 34. A hollow bar represents the presence of the female on the site and a solid bar represents the presence of the male. A vertical line separating these denotes a changeover. The dots indicate midnights and the distances between them are therefore 24 hour periods. The first day shown is that on which the first egg was laid.

Fig. 31a shows the great similarity in the patterns exhibited by the very experienced pair on W1F in successive seasons. In comparison, the rate of changeover of the less well-integrated pair on E1D in 1971 is considerably faster (Fig. 31b).

The progressive breakdown in the integration of the pair on W1G may be seen in Fig. 32. The failure of the male to perform his share of incubation was the cause of this disruption, and this instance is dealt with more fully in the following section.

The instance of prolonged incubation by pair W1E in 1971 is represented in Fig. 33, and has been discussed previously. It is worth noting the extremely regular nature of the pattern for a period towards the end of incubation. This may represent a fairly stable state which is rarely reached before the eggs hatch in normal incubation.

Figures 31 - 34

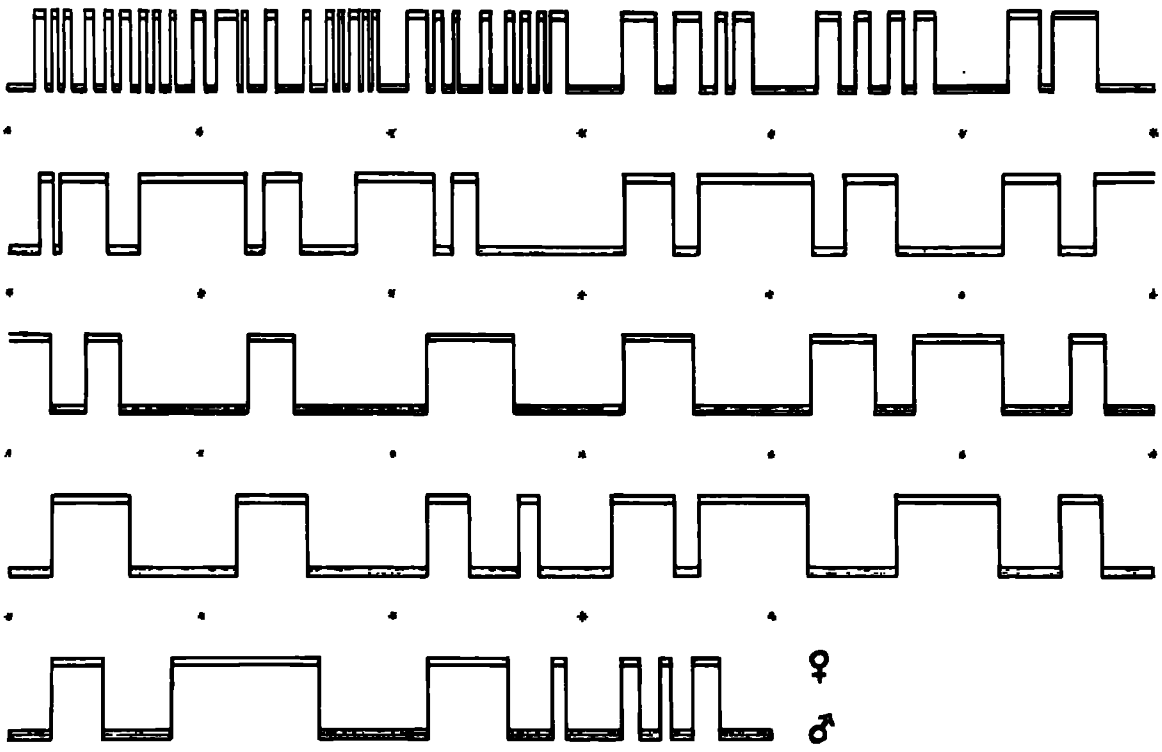
These figures represent patterns of changeover for the following pairs :

Fig. 31a	W1F in 1968 and 1969
Fig. 31b	E1D in 1971
Fig. 32	W1G in 1968, 1969 and 1970
Fig. 33	W1E in 1971
Fig. 34	W1D in 1972

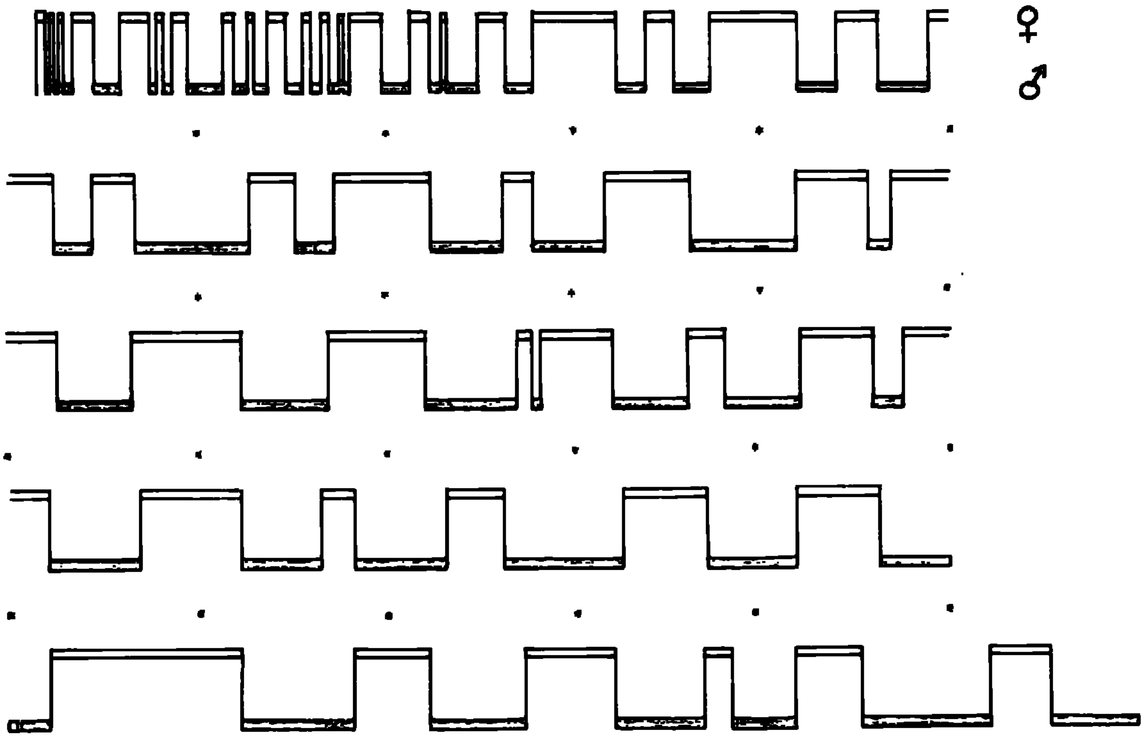
All these figures should be read linearly from top left to bottom right. A hollow bar represents the presence of the female on the site and a solid bar shows the presence of the male. A vertical line separating these denotes a changeover. The asterisks indicate midnights and the distances between them are therefore 24 hour periods. The first day shown is that on which the first egg was laid (except for W1G in 1968 which starts 7 days after laying).

Figures 31 and 32 terminate with the hatching of the first egg but figures 33 and 34 continue until the first break in the changeover pattern. Gaps in the upper hollow bars in Figures 32 and 33 indicate the occasions when the female left the eggs unattended.

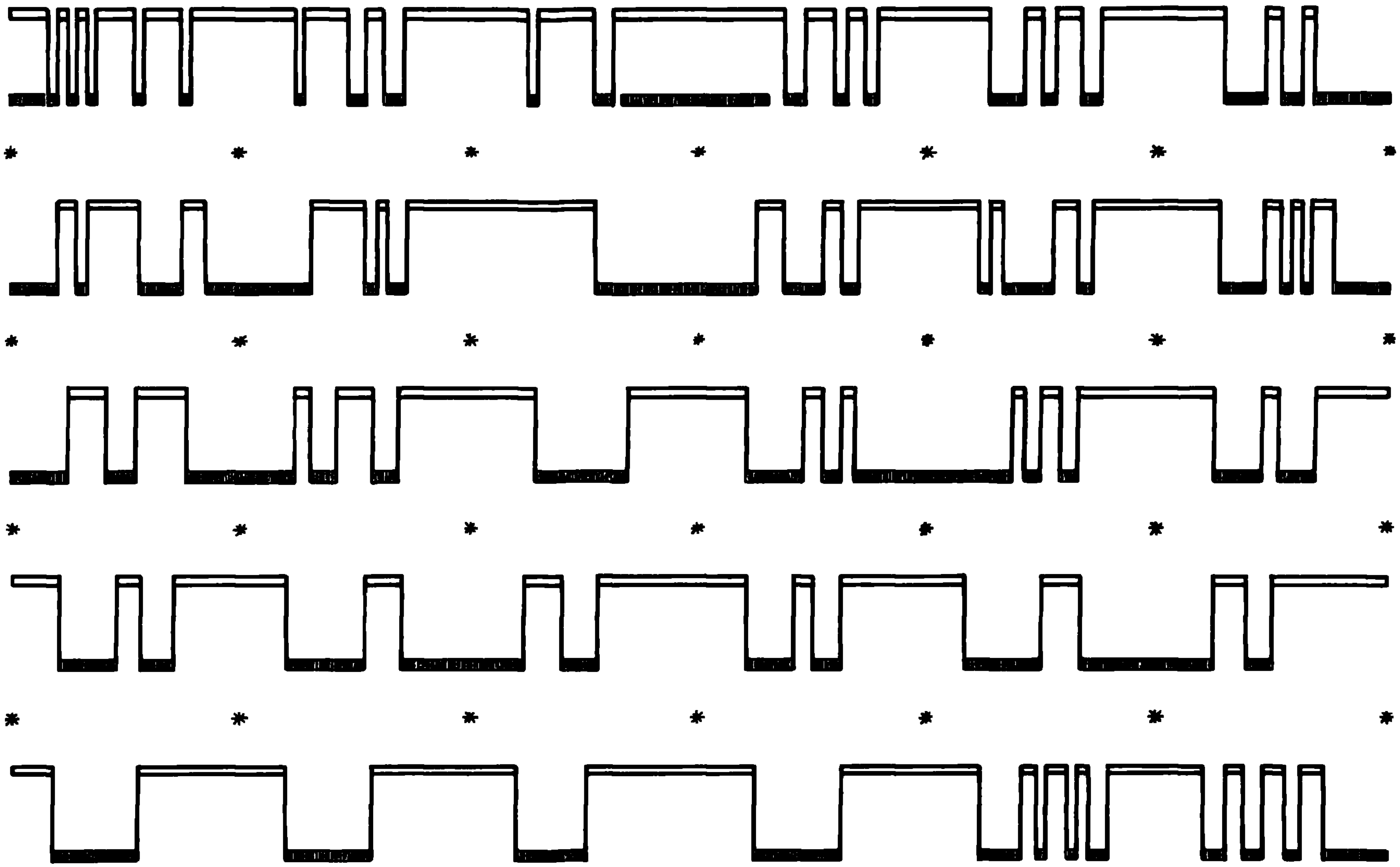
WIF 1968



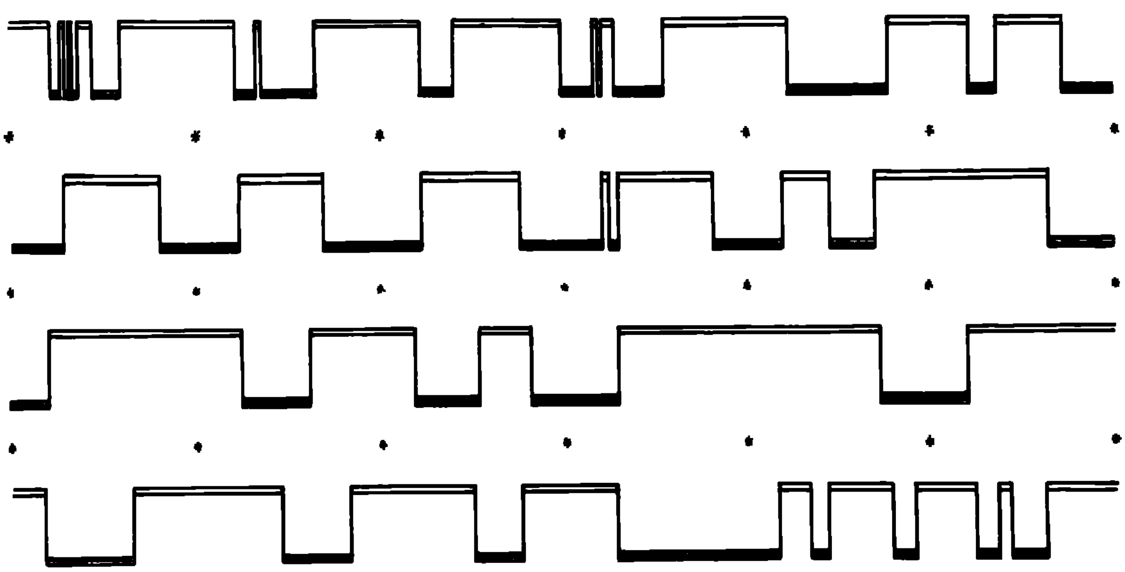
WIF 1969



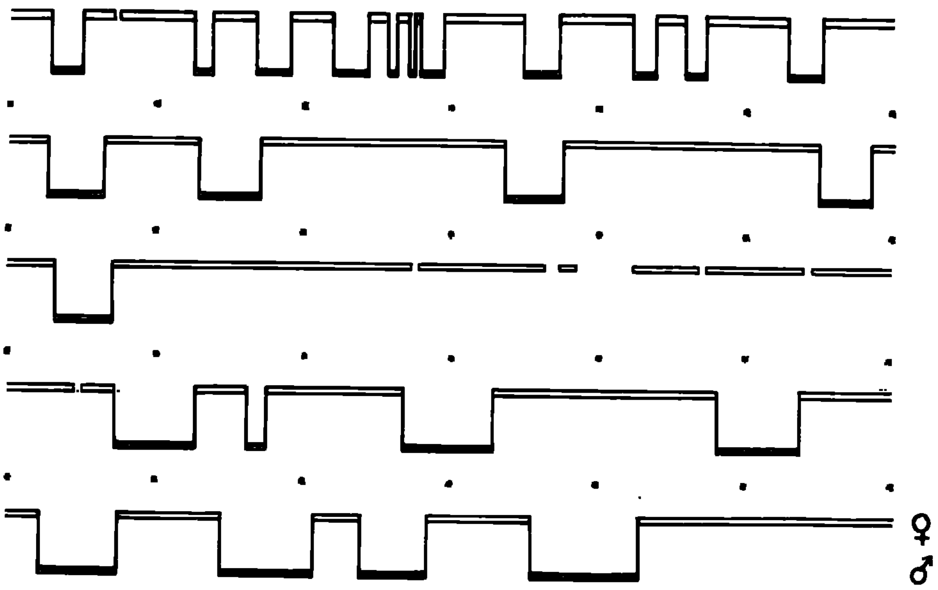
EID. 1971.



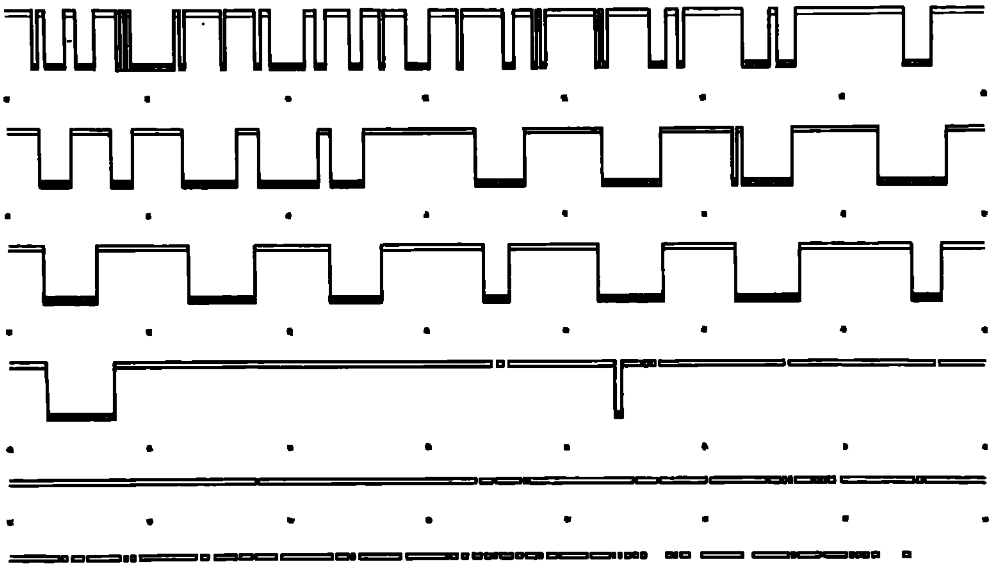
WIG 1968



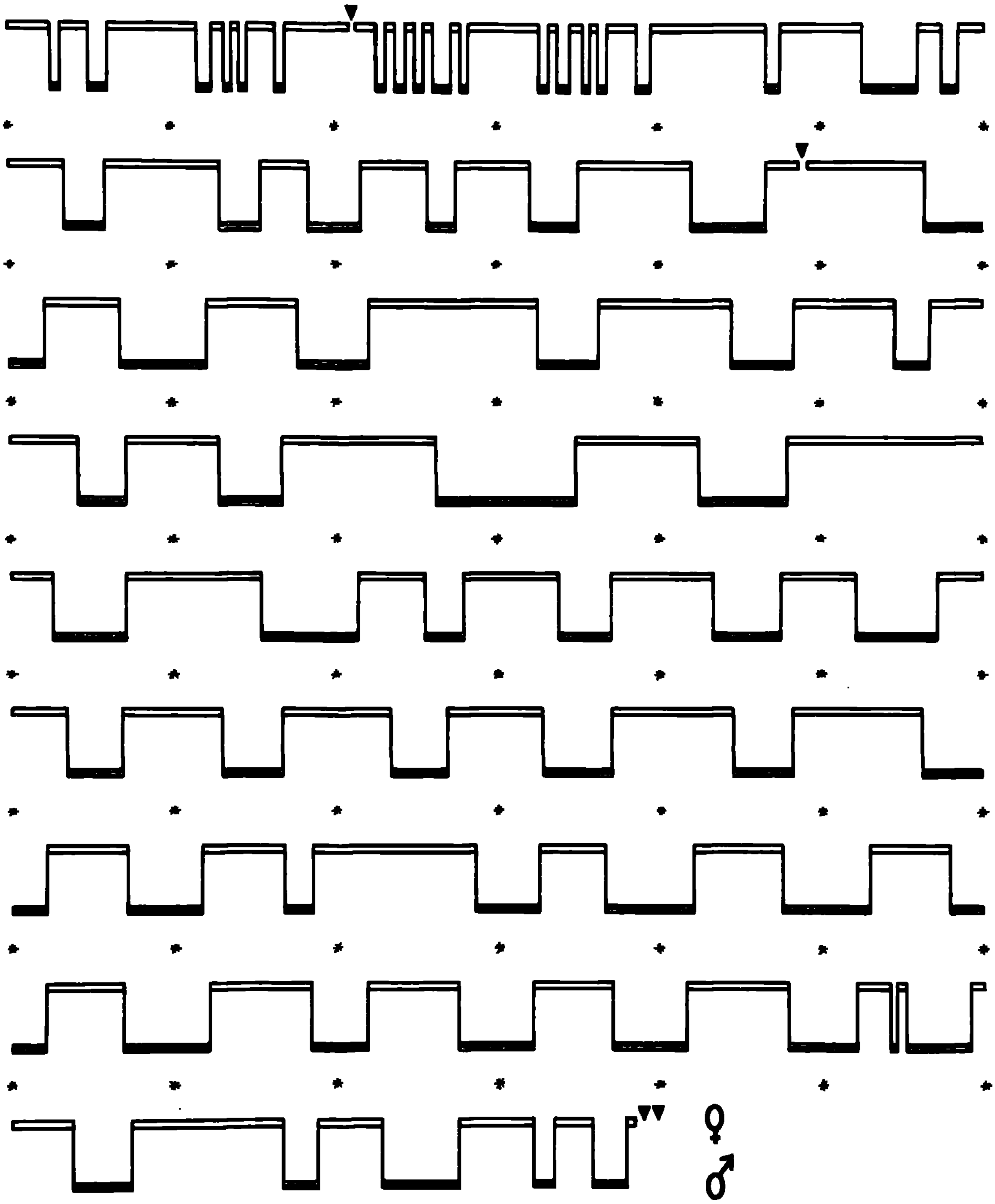
WIG 1969



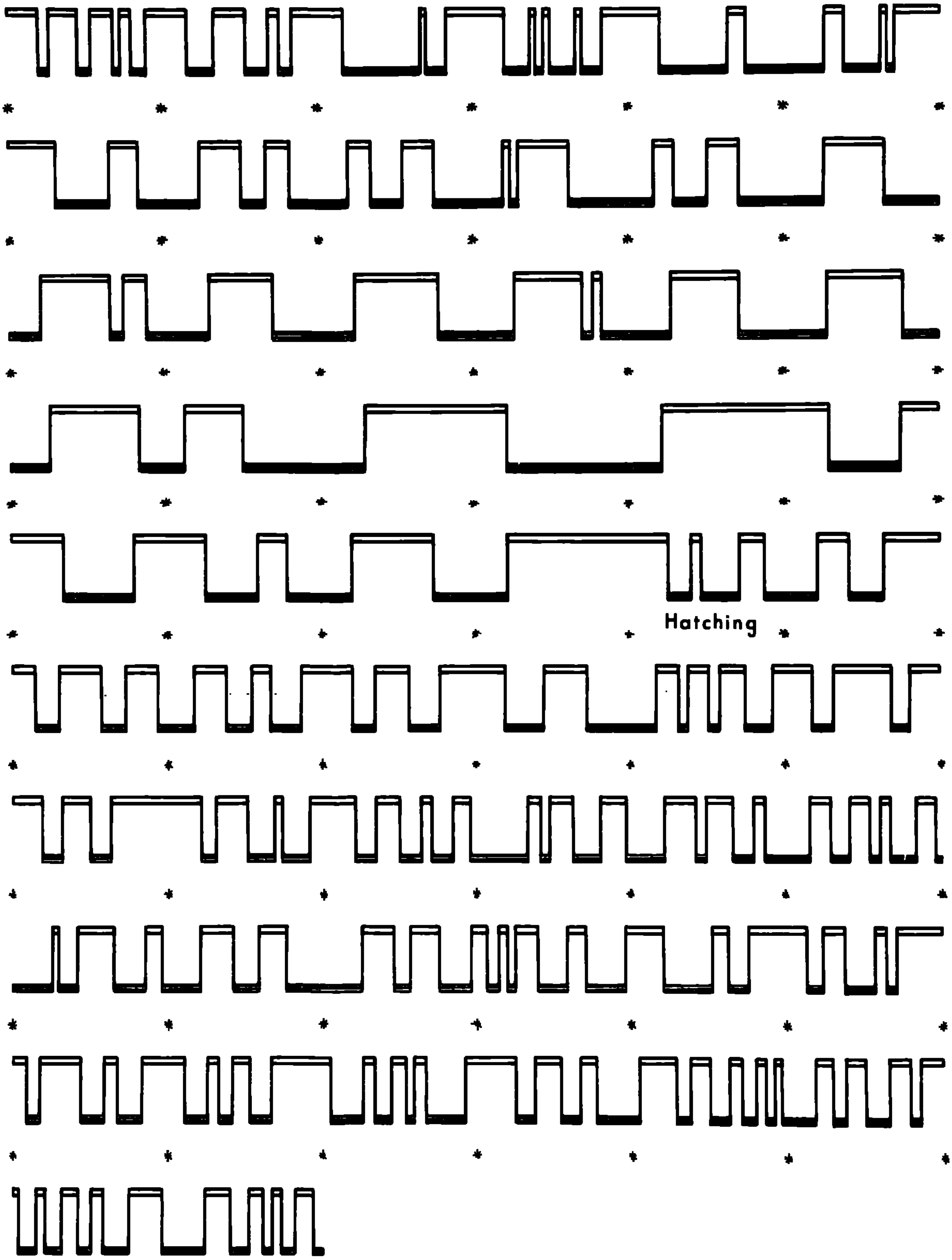
WIG 1970



W1E. 1971.



W1D. 1972.



The pattern after the eggs have hatched, as well as before, is illustrated in Fig. 34. The changeover routine continued unbroken in this pair for 28 days after hatching. The increase in the rate of changeover as brooding progresses may be clearly seen, and this is discussed in more detail at the end of Section V (Table 43).

Effectiveness of incubation

Defeathering of the brood patches in the Kittiwake takes place fairly rapidly (Swartz 1966) but refeathering of the patches after incubation occurs more slowly. These developments are similar in males and females. Jones (1971), reviewing incubation patches, concluded that gulls represent an intermediate case among birds in that either oestrogen + prolactin or androgen + prolactin may be effective in inducing defeathering and vascularisation of the brood patches.

Sitting continuously on the eggs protects them from predators and also from environmental fluctuations. The latter are probably more important in the Kittiwake, especially the factor of temperature.

Avian embryos have a narrow temperature optimum and are rather more resistant to chilling than to overheating (Baerends & Drent 1970). Many factors must be involved in transferring heat to the eggs, among them the size and shape of the brood patches relative to the eggs, their temperatures, and the insulation properties of the nest.

The reactions of incubating parents to variations in weather conditions are the normal ones which help them to maintain their body temperature. Since they are also sitting almost continuously on their eggs, this secondarily regulates egg temperatures.

Maunder & Threlfall (1972) found that in the Kittiwake the first few days of incubation were ineffective in maintaining a high egg temperature, although there was growth of some parameters even on the day of laying. Following this there was a rapid rise in temperature to a fairly stable level, and thereafter a slower temperature increase.

Initial development of the embryo was slow and it only attained 50 % of its maximum weight 22 days after the egg was laid - that is only 5 days before it hatched.

Batt & Cornwell (1972), working with Mallard embryos, showed hatchability to be little affected by exposure during the first few days after laying. They also found that embryos in larger eggs survived exposure to cold better than smaller ones, probably due to their greater metabolism and slower cooling rate.

In 1972 some data on the effectiveness of incubation were obtained from the pair on site W1Da.
An empty egg was filled with glycerine and a copper-constantan thermocouple, connected to a recorder, placed against the upper inside surface. The egg was fixed so that it could only rotate about its shorter axis.

The pair laid two eggs normally, and the artificial third egg was added on the day that the second egg was laid. The usual increase in temperature over the first 3 - 4 days, to a fairly steady state, was shown (Fig. 35). A similar pattern has been noted in the Herring Gull (Baerends & Drent 1970) and the Common Gull (Barth 1955).

In the Herring Gull the temperature of the body is 41.2°C, that of the brood patches 40 - 41°C, and the temperature at the interface between brood patch and upper egg surface 39.5°C. The lower surface of the egg and the nest floor was found to be 12°C lower, but this differential decreased to 4°C as incubation proceeded. An average brood patch covered 18 % of the egg surface, and without it the egg's upper surface was 35 - 36°C in Herring, Lesser Black-backed and Common Gulls, and the internal egg temperature was 38 - 39°C.

The eggs of the pair on W1Da started chipping on days 25 - 26 and by day 28 after laying, when the first chick emerged, the artificial third egg was out of contact with the brood patch for many short periods (Fig. 36). After the second chick hatched on day 29 the third egg was not incubated for much longer periods of time, and by day 36 it was receiving almost no incubation at all.

It seems likely that the increasing size and restlessness of the chicks forces the parents up off the eggs. Thus, unless the third egg hatches within a short period after the other eggs, it is unlikely to hatch at all since it will not receive adequate incubation.

Figure 35. The increase in temperature of an artificial third egg during the days after clutch completion by pair W1D in 1972. The shaded portion represents the temperature of a thermocouple at the upper inside surface of an egg fixed inside the nest. This third egg was added at the time that the second egg was laid

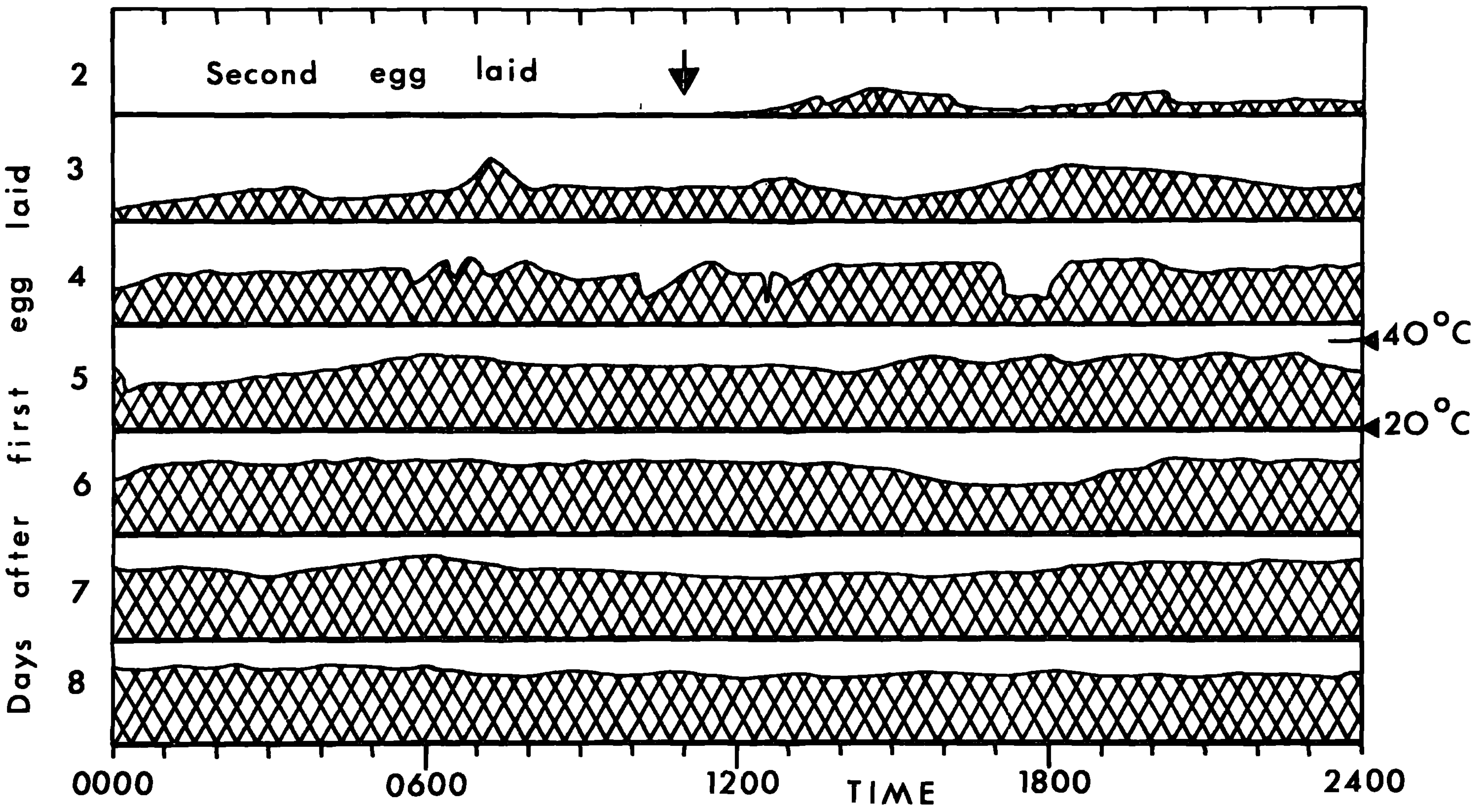
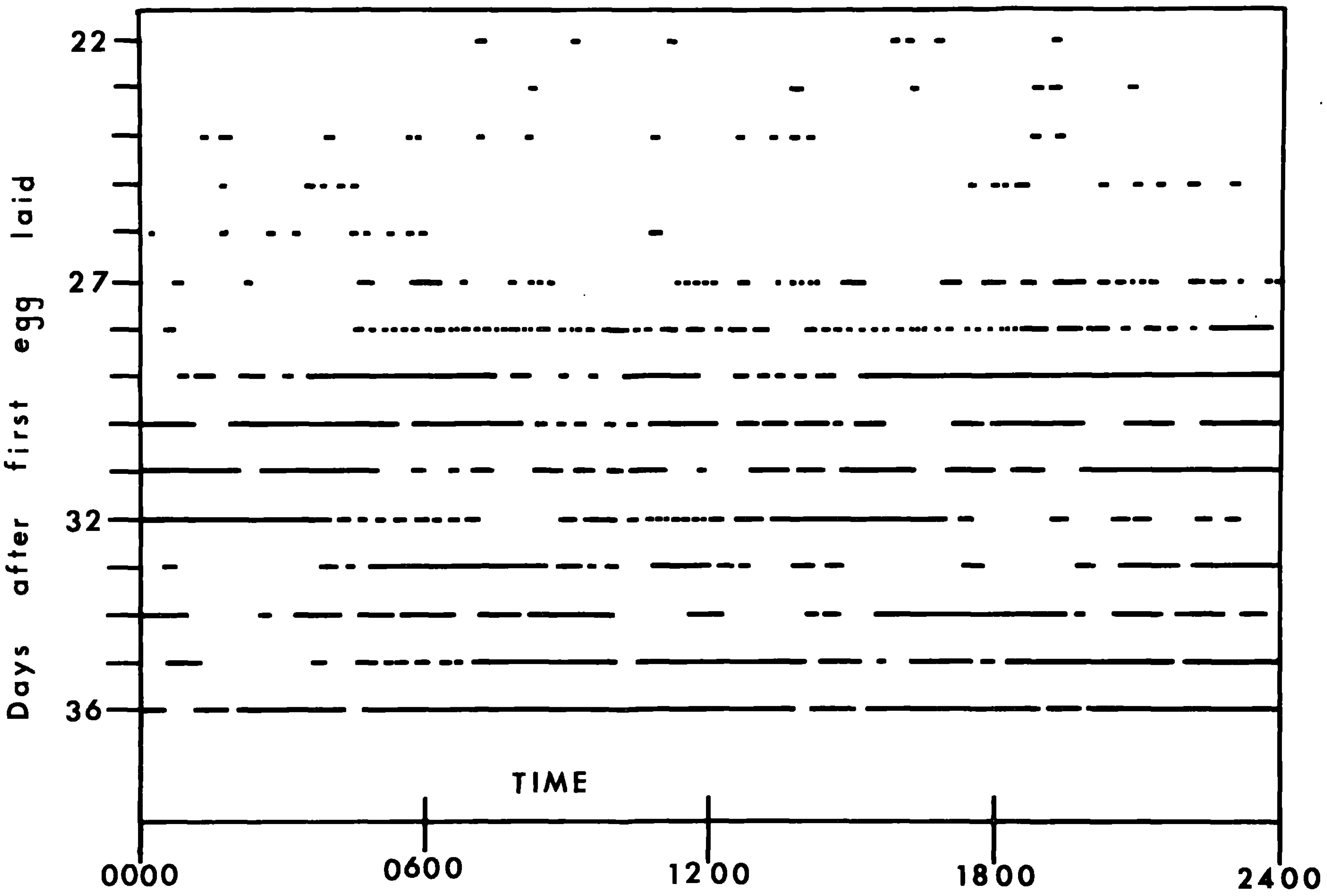

Second egg laid
2
3
4
5
6
7
8
Days after first egg laid
40°C
20°C
0000
0600
1200
1800
2400
TIME

Figure 36. The intermittent incubation of an artificial third egg after the hatching of the other two eggs.

Each day is represented linearly from left to right, and a solid line indicates when a thermocouple at the upper inside surface of the egg registered a temperature below 20°C.

The natural eggs started chipping 25 - 26 days after the first egg had been laid. The first chick hatched on day 28 and the second on day 29.


22
27
32
36
Days after first egg laid
TIME
0000
0600
1200
1800
2400

SECTION V

FLEXIBILITY OF THE INCUBATION AND BROODING SYSTEMS

Incubation by deserted females

An extreme example of the compensatory mechanism mentioned in Section IV occurs when one partner fails to return to the colony. In most of the cases encountered in this study it was the female who was left to compensate for the absence of the male.

The same pair on site W1G from 1968 - 1970 showed a progressive trend towards this situation (Fig. 32). In 1968 the pair incubated successfully using the two-shift pattern outlined previously. In 1969 the female was left alone for two periods of 40 hours. Later she incubated for 59 hours, went off the site overnight, and upon returning incubated for a further 58 hours. The male then returned and incubation proceeded normally although the eggs did not hatch.

In 1970 the decay in the pair's pattern occurred early in incubation when the female was left for 50 hours. Later in incubation the male deserted completely, whereupon she continued to incubate for over 20 days (a total of 456 hours on the site and 30 hours off), hatching the eggs successfully. During the first 11 days of this period (until the chicks were 6 days old) she left the site only 20 times for a total of 126 mins (max. period 12 mins). Tables 33 and 34 record her attendances after desertion in 1969 and 1970.

Table 33. Attendance at the nest during incubation by female of the pair on site W1G in 1970, illustrating compensatory attendance by a female during absence of the male partner

Days before and after desertion	% daily attendance	Number of times off site per day	Cumulative % attendance
- 5	63	0	
- 4	82	0	
- 3	55	0	
- 2	54	0	
- 1	79	0	
0 (deserted)	52	0	-
1	100	0	100
2	100	0	100
3	99	2	99.6
4	98	5	99.3
5	99	1	99.3
6	99	1	99.3
7	100	0	99.4
8	99	1	99.4
9	99	6	99.2
10	98	3	99.1
11	99	11	99.0
12	94	5	98.3
13	94	7	97.7
14	91	11	97.4
15	94	4	97.1
16	92	8	96.1
17	81	13	94.5
18	70	4	94.3
19	90	10	93.2
20	77	5	92.6
21	35	8	90.4
22	23	-	88.0
23	0	-	85.0
24	2	-	82.2
25	0	-	79.6

The male failed to return on day 22 of incubation leaving the female to incubate alone. Her initial period of unbroken attendance at the site was 3915 mins or 65 hours.

Table 34. Attendance at the nest during incubation by the female of the pair on site W1G in 1969, illustrating compensatory attendance by a female during the absence of the male partner

Days before and after desertion	% daily attendance	number of times off site per day	cumulative % attendance
- 5	58	0	
- 4	100	0	
- 3	61	0	
- 2	100	0	
- 1	65	0	
0 (Desertion)	60	0	-
1	100	0	100
2	100	1	100
3	85	3	95
4	73	1	89
5	97	1	91
6	73	2	88

Then followed a period when the male returned to incubate, but later he was absent again :

Days before and after desertion	% daily attendance	number of times off site per day	cumulative % attendance
0 (Desertion)	72	0	72
1	100	0	86
2	98	1	90
3	44	0	78
4	100	0	83
5	100	0	86
6	84	3	85

The initial unbroken period of attendance was 4251 mins (71 hours)

A similar attendance was recorded by the female on E1D in 1971 whose partner disappeared when the chicks were about 9 days old (Table 35). During 1969 this same male had left a different female on day 19 of incubation, returning on day 22. In the intervening period the female was only off the site for a total of 13 mins, and after the male returned the incubation pattern was resumed.

The longest unbroken attendances by females are those immediately after being deserted by their male partners, and all four values are remarkably similar :

4251 mins
3915 mins
3862 mins
4122 mins

Mean = 4038 ± 288 mins
or 67 ± 5 hours

Possibly this is the maximum length of time that the bird can go without drinking. Ensor & Phillips (1970, 1972) have shown that the high levels of prolactin during incubation help to offset the dehydration effects of being immobilised on the clutch. Nelson (1968) refers to boobies (Sula spp.) going for up to 5 days without drinking water in temperatures approaching 100°F.

The initial absences of the Kittiwakes were so short that it seems unlikely that they could have obtained food on these occasions. The fact that the Kittiwake does not have to leave the nest to excrete, as does the ground-nesting Herring Gull, may also assist it in remaining on the nest for almost three complete days.

Desertion by parents with chicks

Among the radioactively monitored pairs, one female (W2I in 1972) and one male (E1D in 1971) disappeared suddenly when they had chicks aged about 9 days. The subsequent attendance of their partners is shown in Table 35.

The E1D female acquired a new mate on the 10 - 13th day after desertion, and both fed the chicks thereafter. The new male continued to feed them for much longer than is normal - in one case until the chick was 12½ weeks old (2 September). The chicks were weighed shortly after desertion when aged 14 - 15 days, and found to be only 50 % (127 g) and 39 % (91 g) of the normal weight for chicks of this age.

The W2I male, who was a very experienced breeding bird, spent far more time off the site and continued to feed his two chicks alone. They both reached normal weight before fledging successfully at the usual age of 42 days.

In all the cases given so far, the cause of desertion is not known, although since none of the deserting birds have been seen since, sudden death may be presumed responsible. Three cases were recorded in 1971 when the mate is known to have died during the rearing of the young.

On site W2B the female of the pair was found oiled locally and died the following day. At this time the chicks were 10 - 14 days old. The male continued to care for them and no other bird was recorded on this site until they fledged (one at 36 days and one at 50 days). Throughout this period their weights were normal for their ages.

Table 35. Attendance at the nest with chicks by parents after the disappearance of their partners

Days after desertion	Cumulative % attendance		Number of times off site per day	
	E1D. 1971	W2I. 1972	E1D. 1971	W2I. 1972
0 (deserted)	-	-	0	0
1	100	97	0	7
2	100	79	0	37
3	99.5	73	2	46
4	99.1	69	4	39
5	98	70	4	27
6	97	71	14	36
7	95	71	12	43
8	94	68	13	55
9	93	65	14	17
10	90	61	16	36
11	89	61	4	34
12	89	59	11	38
13	88	57	8	38

In both of these cases the chicks were 8 - 10 days old when one parent failed to return. On E1D in 1971 the female was left by the male. On W2I in 1972 the male was left by the female. The initial unbroken periods of attendance on the site were :

E1D	female	4122 mins (69 hours)
W2I	male	1214 mins (20 hours)

On site S1Ct the chicks were deserted by the female when they were 16 and 19 days old. She was found dead locally three days later. Only the male was seen subsequently on the site, where he fed and reared the two chicks successfully until the last one fledged at about 44 days of age.

The male on site S2B died on the site, becoming tangled in a fishing line used for nest material, when the chicks were about 5 weeks old. During a 4 - 5 days period following his death a new male came onto the site, was accepted by the resident female and both new partners fed the chicks until they fledged successfully. This new pair stayed together for several weeks after the chicks had left. The incoming male had been a non-laying siteholder two years previously on the site, although not with the female involved in the above instance.

In three cases a male left alone was able to feed and raise two chicks successfully. In the other two cases deserted females took new mates who helped to feed and care for the young, although this is unlikely to happen often.

Possibly in the latter cases males arrived on the sites which were undefended, and, once established, took over the contents of the site - the incumbent female and her chicks. At this stage in the season there is always a number of non-breeding males at the colony, and some of these have had experience of raising chicks in previous breeding seasons.

Unfortunately no information is available on the ability of females to feed chicks unaided, but Hodges (in prep.) has shown that males are more responsive than females to the begging pressure of the chicks. The data from E1D in 1971 suggest that until the female took a new mate, the chicks were hardly growing at all.

It is worth recording that a converse situation to that of females taking two mates in a season was encountered on site W2D in 1971. The pair laid two eggs by 23 April and by 20 May had two chicks. The female disappeared and the chicks died by 24 May. A new female was seen regularly with the male after 27 May and on 13 June this female laid one egg. Both members of the newly-formed pair incubated this egg up to 25 June, but after this they merely stood on the site. Unfortunately, this egg was lost from the site and it is not known if it was fertile. The pair were seen together until the end of August, and the female until the end of September. This male was therefore responsible for the first and last clutches of the season at this colony.

Repeat laying

Not infrequently eggs are lost from the nest either as a result of the activities of a parent or due to the poor cup structure of the nest. As long as at least one egg remains the birds will continue to incubate. Should the whole clutch be lost, the bird may lay a replacement clutch after an interval of time. This repeat laying has been noted for the Kittiwake by Belopol'skii (1961) and Dement'ev & Gladkov (1969), and more recently by Maunder & Threlfall (1972).

In 1970 some trials were performed on the Farne Islands, and on a smaller scale at North Shields, to test the effect of removing complete clutches at different stages of incubation. The information from both colonies has been added together except where this seemed inappropriate.

In all, 81 complete clutches were removed and repeat laying resulted from 49 of these (60 %) (Table 36a).

There was a significant difference between clutches which were replaced and those which were not in their age when robbed (in days after the first egg had been laid) (Fig. 37 $t_{79} = 3.2470$; $P < 1$ %). There was no difference between the two categories in their mean laying dates for the first clutch ($t_{79} = 0.3794$; P = N.S.).

However, clutches were only removed over a limited time span and not throughout the laying period so that any seasonal effect may have been missed. Since there was no demonstrable relationship between the ages of clutches when robbed and their laying dates ($r_{47} = -0.154$; P = N.S.) it is unlikely that a seasonal effect is being lost by these two cancelling out.

There was no difference between the birds that relayed and the others in the deviation (± in days) of their laying dates from the mean for the colony (the same in both colonies in 1970) $t_{79} = 0.0138$; P = N.S.

Table 36a. Ages and dates of laying of clutches removed to produce repeat laying. 1970

	Sample size	Clutch age	Laying date	Deviation in laying date
	(see below for explanation of headings)			
Clutches replaced	49	4.1 ± 0.8	22 May ± 2.5	8.0 ± 1.6
Clutches not replaced	32	6.4 ± 1.6	21 May ± 2.5	7.5 ± 2.5

1. Clutch age : this is the age of the clutch when removed (in days after the first egg had been laid)
2. Laying date : the date on which the first egg of the first clutch was laid
3. Deviation in laying date : the deviation (± in days) of the laying date of a clutch from the mean annual laying date of the whole population

Considering the 49 repeat clutches, the mean interval between the loss of one clutch and the start of the next one was 12.4 days ± 1.4 days (range 10 - 17 days). Dement'ev & Gladkov (1969) record that the closely-related Red-legged Kittiwake will replace lost clutches after about 10 days.

This relay interval (y) was closely related to the age of the clutch when removed (x) :

$r_{47} = + 0.4571$; $P < 0.1$ % $\quad y = 11.09 + 0.25\,x$

However, the relay interval was not related either to the date of laying ($r_{47} = - 0.0670$) or to the deviation from the mean date of laying of the colony ($r_{47} = -0.2030$).

For a smaller number of individuals in the North Shields population the breeding experience of the females concerned is known.

Figure 37. The distribution of the ages of clutches when removed (in days after the first egg had been laid) for clutches which resulted in repeat laying and for those which did not.

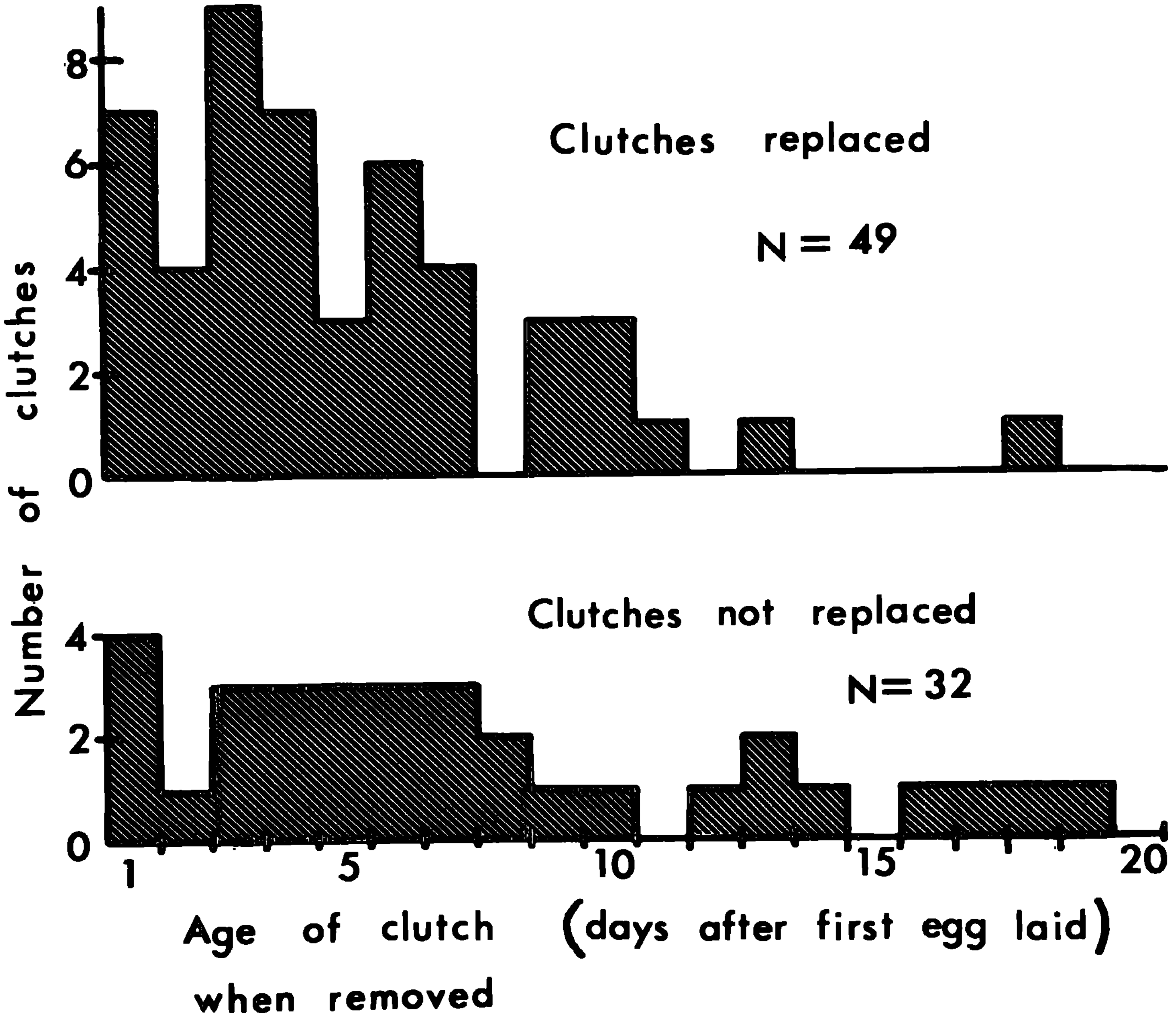

Clutches replaced
N = 49
Clutches not replaced
N= 32
Number of clutches
8
6
4
2
0
4
2
0
1
5
10
15
20
Age of clutch (days after first egg laid)
when removed

Table 36b. Ability of females with different breeding experience to replace lost clutches (Eggs removed within 2 days of clutch completion)

	Sample size	Breeding experience of female					Mean
		1	2	3	4	over 4 years	
Clutch replaced	13	0	1	3	2	7 cases	6.5 ± 2.0 years
Clutch not replaced	15	7	4	1	1	2 cases	2.6 ± 1.3 years
Percentage replacement	46	0	20	75	67	78 %	

The difference between the means of breeding experience for these two categories is a significant one ($t_{26} = 3.7240$; $P < 0.1$ %). However, the breeding experiences of females are not correlated significantly with their relay intervals ($r_{11} = + 0.4936$; P = N.S.). Since the age of the clutch when robbed has already been shown to affect the likelihood of its replacement, female breeding experience was compared with clutch age ($r_{26} = - 0.0247$; P = N.S.), the results indicating that these two factors were not correlated.

Earlier work (Coulson 1966) has shown that older, more experienced females breed earlier in the season, and the effect here attributed to female experience may be a seasonal one. In this small sample, however, no relationship could be demonstrated between female experience and either laying date ($r_{26} = + 0.3278$) or deviation from the mean laying date ($r_{26} = - 0.3457$).

It seems possible, therefore, that the breeding experience of a female may affect her ability to relay after losing her eggs, over and above any seasonal effect. Coulson (1963), studying the size of eggs, was able to show an increase due to the age of the female, as well as any seasonal effect.

Maunder & Threlfall (1972), working with a population of Kittiwakes in Newfoundland, noted that 6 out of 19 (32 %) of lost clutches were replaced, which is about half the replacement rate found in this study. This may be accounted for by the clutches being lost at a different time in the incubation period. They note that the tendency to replace a clutch and the success of the replaced eggs decreased as the time from the peak of laying activity increased. This may, however, have been due to the effect of clutch age rather than to any seasonal effect.

It is interesting that in all except one case their repeat clutches consisted of one egg, whereas in this study two-egg repeat clutches were normal. This may be related to the fact that in their population egg-laying occurred two weeks later than in the ones in this study. It is well-known that clutch size decreases as the season progresses (Coulson & White 1961), and that later-laying (more northerly) populations have smaller clutch sizes but larger individual eggs. It is possible that the Newfoundland single-egg replacements were larger than those in this study.

Parsons (1971) found that the mean time taken by 160 Herring Gulls to lay repeat clutches was 13.23 ± 0.12 days - one day longer than the Kittiwakes in this study.

He also analysed the relay intervals in pairs robbed immediately after laying, and after 15 days incubation, both early and late in the season, and concluded that any seasonal effect was greater than the incubation factor. He also found that the inability to relay increased as the season advanced (although the analysis did not separate seasonal and clutch-age effects) until eventually no more eggs were found.

Paludan (1951) also found that when complete clutches were removed, then repeat clutches were often laid by the Herring Gull (after 12 days) and the Lesser Black-backed Gull (11 days later; range of 9 - 14 days). Weidmann(1956), working with the Black-headed Gull, produced repeat clutches in 8 out of 25 complete clutches removed (32 %) after intervals of about 10 days (range 8 - 13 days).

Protracted laying

Parsons (1971), following Paludan (1951), found that in the Herring Gull, as long as there is always at least one egg in the nest, then any loss is not replaced. If the first egg is removed as it is laid, or the first two eggs removed within 24 hours of the laying of the second, then a fourth egg will be laid two days after the third. This is protracted laying. If all the eggs are removed later than 24 hours after the second egg, then there is no protracted laying, but repeat clutches may be produced as described above.

Weidmann (1956) produced protracted laying in the Black-headed Gull under the same conditions as those outlined for the Herring Gull above. He has suggested that protracted laying may have been overlooked in other species for which the "critical" period may be shorter. 2 - 2½ days incubation by the Black-headed Gull were not always enough to stop the fourth egg being produced, but 4 days (the interval between the first and third egg) was always enough. In this gull, as in others, no repeat or protracted laying results as long as at least one egg remains in the nest for the bird to incubate.

On the Farne Islands in 1970 attempts were made to induce protracted laying in the Kittiwake by removing eggs as they were laid (Table 37). The difficulty with this approach is knowing how many eggs the bird would have laid if left alone. In none of the 34 trials were any fourth eggs produced. There remains the possibility that some of the third eggs laid may have been induced by the removal of what would otherwise have been two-egg clutches, but this is considered unlikely.

Table 37. Trials to produce protracted laying by the removal of eggs as they were laid

Sequence of eggs in the nest **	Number of trials	Number of repeat clutches laid
0.0	14	8
1.0	5	4
1.2.0	4	3
0.0.0	2	2
0.1.0	3	0
0	6	5

** The convention for the sequence follows Weidmann (1956). Thus, 0.0 indicates that the first egg was removed when laid, and the second egg also removed when laid. 1.0 indicates that the first egg was left, and both eggs removed after the second egg had been laid. et seq.

Natural four-egg clutches have been reported by Belopol'skii (1961) for 1947 (two instances). A single case was encountered at the North Shields colony in 1972. In such cases there is always the possibility that two birds have laid their eggs in one nest, but this is deemed extremely unlikely. This fourth egg was similar in colour and size to the third egg and laid at a normal interval after it. Six days after it had been laid one of the four eggs disappeared from the nest and the remaining three were incubated normally.

Suppression of laying

Weidmann (1956) added artificial eggs to 60 nests of the Black-headed Gull before the eggs were laid. Some females were ready to sit on them for two weeks before laying. He thought that probably at least 7 - 8 days sitting on eggs prior to the time when the first egg would have been laid was necessary to stop laying. In many of these pairs laying was suppressed and some pairs incubated for up to two months without having laid any eggs themselves. In this species the fourth follicle degenerattes after the second egg is laid.

The Herring Gull will accept rather than reject foreign eggs for 9 days before the first egg (Paludan 1951). This coincides with the start of the final growth phase of the follicles. The fourth follicle degenerates after the laying of the second egg and before the third egg.

Although both of these species will accept eggs 8 - 10 days before laying, such a situation will only suppress the third follicle and not either of the first two. If suppression of the later follicles is mediated by feedback stimuli from the incubation of the eggs, then the cause may be the intermittent incubation of the first egg (Baerends & Drent 1970; Spaans 1971) or the relatively late development of the brood patches.

Smith (1966), studying the Iceland Gull, recorded that atresia of the remaining follicles did not begin until after the third egg was laid. In Thayer's Gull atresia of the "accessory" follicles occurred after the first egg had been laid. In eleven Kittiwakes which he examined (Ibid, p. 77) he found that follicular atresia was even more rapid than in Thayer's Gull.

As Smith suggests, it is likely that the delay in follicular atresia which occurs in some species may be adaptive in providing the possibility of egg replacement in the case of loss. Among the ground-nesting gulls where there is a higher early egg mortality this "insurance" mechanism is more evident than in the cliff-nesting Kittiwake and Thayer's Gulls. The Herring Gull leaves its eggs overnight and at other times during the first week of incubation (Spaans 1971; Baerends & Drent 1970) and the Common Gull is also an irregular incubator during laying (Barth 1955), but this does not happen in the Kittiwake.

In a series of trials at the North Shields colony eggs were added to empty cup nests before laying, and records made to see whether they were accepted. The results (Table 38) suggest that when two eggs are added, they are accepted during the seven days prior to the first egg being laid. However, a single egg is far less likely to be accepted.

The impression was gained that males were more willing to accept donated eggs than females. One male returning for a changeover after the eggs had been added, readily incubated and turned them 23 days before the pair's first egg. Slater (1967) has shown that in the Bengalese Finch the physiological condition of the male is more labile than that of the female.

In sixteen trials on the Farne Islands in 1970 single eggs were added to newly-laid first eggs, but in all cases a second egg was laid, and in two cases third eggs were also produced. Thus no suppression of the second egg could be induced, and it seems unlikely that any third eggs were suppressed either.

In gull clutches of three eggs the third egg is markedly smaller than the other two (Vermeer 1969). Parsons (1971) considered that the onset of incubation was responsible for the relatively smaller size of this third egg. He found that in the Herring Gull this third egg was not just a scaled down version of the earlier eggs, but that it had proportionately more yolk and less albumen than they did. Thus any depressive effect of incubation during the laying period affected the albumen and not the yolk.

The proportional decreases in volume between first and second eggs, compared with those between first and third eggs, are shown for several gull species in Table 39. The Kittiwake has the highest decrease between the first two eggs, this accounting for 36 % of the total decrease (between first and third eggs). By contrast, 93 - 95 % of this total decrease in the Herring and Lesser Black-backed Gull occurs between the last two eggs.

Table 38. Acceptance of eggs added to empty cup nests before laying. North Shields 1972

Days before laying that eggs added	Acceptance**	
	2 eggs	1 egg
1	yes	yes
1	yes	yes
1	yes	yes
1	yes	
2	yes	
3	yes	no
3	yes	no
4	yes	
5	no	no
5	yes	no
5	yes	
7	yes	no
8		no
9	no	
10		no
11	no	
11	no	
13	no	
15	no	
15	no	
23	no	

** Acceptance indicates that the egg(s) were regularly incubated by both members of the pair

Table 39. Decreases in egg volumes in gull clutches of 3 eggs

Species	Mean egg volumes (cc)			Percentage decreases		
	a	b	c	a - b	b - c	a - c
G.B.B.	96.95	98.21	94.93	+	3.3	2.1
H.G.	78.00	78.31	69.37	+	11.4	11.1
H.G.	90.18	89.58	81.40	0.7	9.1	9.7
L.B.B.	70.28	69.95	63.70	0.5	8.9	9.4
L.B.B.	71.21	71.18	67.16	0.04	5.6	5.7
C.G.	70.57	70.78	66.39	+	6.2	5.9
C.G.	69.78	68.66	62.36	1.6	9.2	10.6
R.B.G.	50.49	50.61	47.10	+	6.9	6.7
K.W.	44.63	43.47	41.38	2.6	4.8	7.3
L.G.	41.89	40.98	38.94	2.2	5.0	7.0
B.H.G.	33.86	33.63	31.92	0.7	5.1	5.7

(Data from Vermeer 1969, p. 103)

G.B.B. = Greater Black-backed Gull
L.B.B. = Lesser Black-backed Gull
R.B.G. = Ring-billed Gull
B.H.G. = Black-headed Gull
H.G. = Herring Gull
C.G. = California Gull
K.W. = Kittiwake
L.G. = Laughing Gull

This again suggests that in the Kittiwake the follicles regress very rapidly around the time of laying. This may well be related to its greater initial tenacity of incubation made possible by its cliff-nesting habit and the resulting freedom from predators. Probably the follicles also develop more quickly before laying, the whole process occurring over a shorter period due to little flexibility of egg replacement at this stage being required. Should a clutch be lost, however, it may be replaced after an interval similar to other gulls (12 days) being more frequently and more quickly replaced earlier in the season by the more experienced breeding birds.

Chick and egg substitutions

Little experimental disturbance could be undertaken at the North Shields colony without disrupting long-term studies, but some manipulations were performed to test the flexibility of the incubation and brooding systems.

1. Two chicks (3 and 5 days) were substituted for a repeat clutch (eggs ½ and 1½ days old). One chick died after 2 days, but the other was successfully raised to fledging.
2. One chick (3 days old) was substituted for the last, single-egg clutch of the season immediately after it had been laid. The chick was raised to fledging.
3. A one-day old chick was substituted for two infertile eggs which a pair had been incubating for 52 days (normal time 27 days). The chick was brooded and fed for two days, after which it was removed and the eggs replaced. They were again incubated regularly for a few days before incubation became intermittent.

4. One chick (3 days old) was substituted for two eggs still being incubated 39 days after laying. It was brooded and fed for two days. Then it was removed and the eggs replaced, whereupon they were incubated for a further week.

5. Two eggs were substituted for two chicks (3 and 5 days old). They were briefly and erratically incubated, but within 2 days had been deserted completely.

6. Two eggs were substituted for two chicks (1 and 3 days old). They were only incubated briefly and very intermittently, and later not at all. Two days later the chicks were replaced and subsequently raised successfully to fledging.

7. A 17-day old chick wandered onto an adjoining site where it was adopted by a pair incubating a 24-day old, two-egg clutch. Although often replaced on its original site the chick repeatedly returned to its foster parents who raised it to fledging.

8. A 4-day old chick wandering onto an adjacent site was adopted by a pair incubating a 27-day old, three-egg clutch. Once again when replaced on its original site it always returned to its adopted site where it was reared to fledging. Several examples of such behaviour have been recorded at the North Shields colony in previous years.

9. The pair concerned in this example built an isolated nest on a building near the warehouse colony, but it was destroyed on 11 May. On 6 June they occupied a site on the warehouse, 4 days after it had been vacated by a pair who had lost their nest and eggs.

Two eggs were added to this site on 13 June and immediately irregular incubation took place. After 2 days this incubation became regular, and after a further 3 days a cup-nest had been built around the hitherto unconfined eggs. Incubation was continued for 39 days after the eggs had been donated.

This last pair were therefore prepared to accept donated eggs on a site where they had only been in residence for a week, and where they had built no nest. This shows a considerable degree of flexibility in their behaviour.

From these admittedly very limited trials it appears that pairs are prepared to accept chicks in place of eggs at any stage between egg laying and day 52 of incubation. The age of the chick does not seem to matter, ranging from 1 - 17 days old.

Such acceptance must be qualified by noting that only one chick was added in most cases - the fate of two chicks is less certain. The trials were performed late in the season and involved relatively inexperienced birds, but presumably more experienced individuals would have accepted donated chicks even more readily. These late-laying pairs would not normally have hatched their eggs and therefore would not have had chicks.

The substitution of eggs for chicks is far less likely to result in successful incubation. Probably once the chicks have been brooded for about 3 days, the tendency to incubate has waned so far that the parents cannot revert to this behaviour.

Emlen & Miller (1969) found that Ring-billed Gull parents tolerated most exchanges, except those backwards from more advanced chicks. This appears to represent the same situation as encountered in the Kittiwake.

More recently Miller (1972) exchanged two newly-hatched chicks for two eggs in 24 clutches ranging from 3 - 20 days old. He found that until 8 days after laying the chicks were not accepted, but thereafter they were adopted.

In the Lesser Black-backed Gull, Paludan (1951) was able to obtain feeding of donated chicks as early as the last day of laying. Similarly Beer (1966) found that Black-headed Gull chicks substituted for eggs 1 - 2 weeks old were accepted, and that parents would brood and feed chicks even before they had completed their egg laying. It seems, therefore, that the appearance of chicks of any age leads to their acceptance during most of incubation. After this initial adjustment, the responses of the parents must be partly controlled by their interactions with the chicks. The influence of the chicks seems to be such that after 3 or 4 days the parents are no longer able to return to incubation behaviour.

Beer mentions several instances of birds ending incubation of their eggs when they adopted stray chicks. Instances of similar adoption at North Shields are not uncommon, but the broad, flat nesting ledges there may be unusual in allowing this. On the Farne Islands some chicks from higher up the cliff fall into nests below, but this is unlikely to happen often.

Among the ground-nesting gulls where the chicks may wander at an early age, some measure of hostility to the young of other birds no doubt helps to prevent premature termination of incubation. In the cliff-nesting Kittiwake, any chick which the parent encounters at its nest will almost invariably be its own, and thus it does not need to respond aggressively, but only parentally, to chicks.

Cullen (1957) exchanged Kittiwake broods of different ages and found that parents did not recognise their young up to 4 - 5 weeks of age, either by number or stage of development. She thought it possible that there was some discrimination of older chicks. She cites Paludan as recording that parents may attack young outside the nest, and suggests that recognition may be by location in the early stages. Later, when fledglings approaching the nest provoke more hostility than juveniles already present, the parent may be able to recognise the calls of its own young.

In the Herring Gull, Tinbergen (1953) considered that parents began to distinguish their young from strangers at about 5 days old. This is the time when they start to move around actively, so that individual recognition becomes desirable.

Changeover rates during incubation and brooding

The rates of changeover during the later, steady part of incubation do not differ from year to year as long as the same pair is involved (Table 40a). However, different pairs have rates significantly faster or slower than each other, and these differences tend to be consistent from year to year (Table 40b).

Although the processes of laying, incubating and hatching eggs follow one another in an unbroken manner, they were divided into a number of stages and these were compared (Tables 41a and 41b). The parameter used for the comparisons was the number of changeovers during the stage concerned, and also the pair activity peak during the week before laying.

The pattern of relationships established (Fig. 38) showed that the succeeding stages were related to one another except for a break at the point where the birds settled down to steady incubation.

It has been suggested by Emlen & Miller (1969) that the pace setting mechanisms of the breeding cycle switch from hormonal to external regulators early in the incubation phase. Slater (1970) modifies this and, while believing that external events exert ultimate control, concedes that they may rely more on hormonally-induced permissive states early in the cycle.

Once the eggs have hatched, the changeover system persists for varying lengths of time (mean 25 ± 6 days; range 8 - 42 days). The rise in the changeover rate occurs immediately upon the hatching of the first egg, rapidly reaching a level of about 6 - 8 changeovers/day.

This rate was lower during the first eight days of brooding than subsequently for almost all pairs. A situation parallel to that during later incubation was found, in that the same pairs had similar rates in successive years, with different pairs having dissimilar rates (Table 42).

As the course of brooding proceeds, the rate of changeover increases (Table 43). Pearson (1968) found that the mean number of feeds per day for single-chick broods was 5, and for two chicks was 8. This meant about 3 - 4 feeding trips per day for each parent. If the chicks are fed at every arrival of a parent, then these values agree well with the changeover rate.

The increase in the changeover rate after 5 days may represent the point at which the begging pressure of the chicks makes itself felt. The parents may then bring food at each arrival but only at the same intervals. Increasing pressure from the chicks may account for the observed increase in the rate. The final outcome of the further demands of the chicks is the breakdown of the changeover system, followed by erratic, little or even no feeding of the chicks. Such a scheme appears to fit in with the growth rates of Kittiwakes on the Farne Islands and elsewhere (see Section VI).

In the Ring-billed Gull, Emlen & Miller (1969) found a decline in the feeding rate after 5 - 6 days, as the chicks began to move away from the nest. They considered that this reflected a change from frequent small food deliveries to infrequent large ones.

Figure 38. The relationships between some consecutive phases in the breeding cycle of the Kittiwake

The upper part of this figure illustrates the lengths (in days) of the nest-building, incubation and fledging phases of breeding. Successive stages which are significantly related (see Tables 41a and 41b) are linked by arrows with solid heads. Incubation and brooding have each been subdivided into three stages.

The lower part of the figure (based upon Table 38) shows the period over which eggs added to empty cup nests are accepted. It also shows the time taken to lay a repeat clutch if the original one is lost.

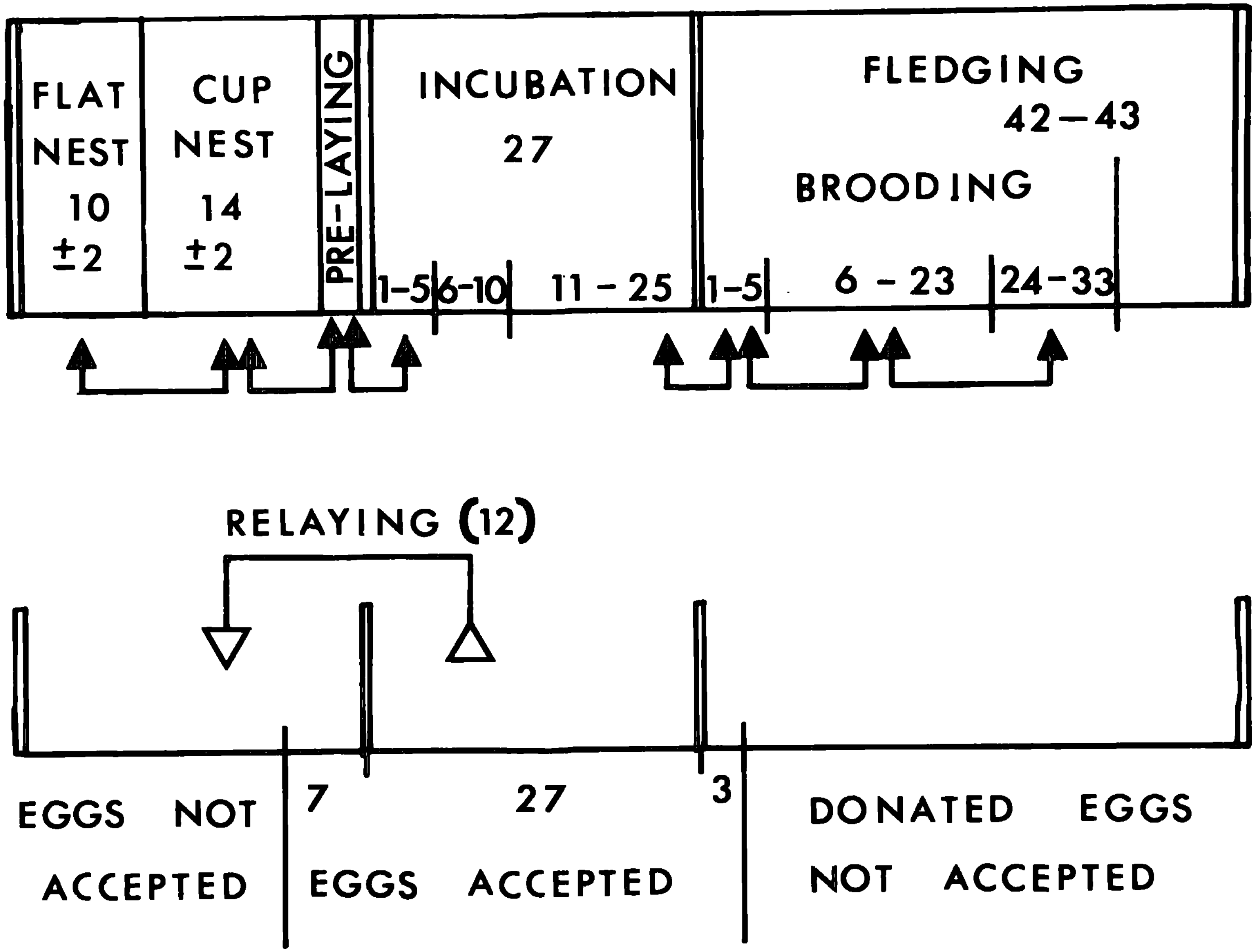

FLAT NEST 10 ±2
CUP NEST 14 ±2
PRE-LAYING
INCUBATION 27
FLEDGING 42—43
BROODING
1-5
6-10
11 - 25
1-5
6 - 23
24-33
RELAYING (12)
EGGS NOT ACCEPTED
7
EGGS ACCEPTED
27
3
DONATED EGGS NOT ACCEPTED

Table 40a. Changeover rates during the second half of incubation

Day of incubation	W1B		W1E		E1D		W1D			W1F		W1H/W2I	
	70	71	70	71	70	71	70	71	72	68	69	71	72
11	4	2	4	2	2	7	3	2	4	3	2	3	1
12	3	1	1	1	6	4	3	4	2	3	2	4	2
13	1	1	1	2	4	5	4	2	4	3	4	1	1
14	1	1	1	2	3	2	1	2	2	2	3	2	3
15	3	2	2	1	4	5	5	2	2	2	3	4	3
16	2	2	4	2	3	5	1	0	4	2	2	2	3
17	2	2	3	2	3	4	3	2	2	3	3	2	1
18	1	2	2	2	3	4	0	3	2	3	2	2	1
19	1	1	3	2	3	3	2	3	2	2	2	2	1
20	3	3	1	2	2	3	2	2	2	2	2	2	1
21	2	1	1	1	2	4	2	3	1	4	1	2	2
22	1	1	3	1	2	3	2	2	1	3	2	2	1
23	1	2	1	2	3	3	2	3	1	2	2	1	1
24	2	2	0	0	4	2	2	1	2	3	3	2	2
25	5	0	1	2	2	2	2	2	2	3	2	1	1
Mean	2.1	1.5	1.9	1.6	3.2	3.7	2.3	2.3	2.2	2.7	2.3	2.1	1.6
±	.6	.4	.6	.3	.6	.7	.6	.5	.5	.3	.4	.5	.4

Comparing the means for these same pairs in successive years :

W1B t = 1.603
W1E t = 0.741
E1D t = 1.174
W1F t = 1.362
W1H t = 1.675
W1D 1970 x 1971 t = 0
1971 x 1972 t = 0.281
1970 x 1972 t = 0.217

For all these t values (28 d.f.)
P > 10 %

Table 40b. Changeover rates during the second half of incubation

Using the same data as given in Table 40a this table gives the Student's t values for comparisons of the rates of changeover of different pairs in the same year

<u>1970 values</u>

	W1E	W1B	W1D
E1D	3.131**	2.506*	2.215*
W1D	0.888	0.298	
W1B	0.585		

<u>1971 values</u>

	W1E	W1B	W1D
E1D	5.423***	5.420***	3.368**
W1D	2.247*	2.342*	
W1B	0.266		

Symbols represent significance at

*	5 %	probability levels
**	1 %	
***	0.1 %	

Unmarked values are not significant at the 5 % probability level

Table 41a. Changeovers during different stages of incubation and brooding

Site	Year	Stage						
		1	2	3a	3b	4	5	6
W1G	1968	-	-	26	17	28	94	-
W1G	1969	59	20	14	10	No Hatching		
W1G	1970	134	44	26	14	Deserted		
W1F	1968	144	66	40	27	31	171	90
W1F	1969	148	43	35	21	34	185	83
W1E	1970	89	36	28	19	-	98	60
W1E	1971	143	32	24	16	No Hatching		
W1E	1972	153	27	23	15	20	92	-
W1B	1968	148	35	44	30	-	122	-
W1B	1969	-	-	35	19	23	133	85
W1B	1970	105	30	32	20	23	102	-
W1B	1971	115	22	23	16	22	95	-
W1B	1972	145	36	35	18	26	95	-
W1D	1970	-	31	34	18	No Hatching		
W1D	1971	-	33	34	22	25	85	58
W1D	1972	107	29	33	19	22	104	78
E1D	1969	-	-	17	10	No Hatching		
E1D	1970	110	36	47	27	34	150	162
E1D	1971	96	27	56	33	42	-	-
W1H	1971	-	24	32	18	36	100	-
W2I	1972	-	-	22	14	32	-	-
S1Ct	1972	-	33	27	18	27	106	-

For explanations of the different stages see Table 41b.

All figures represent the numbers of changeovers during the stage specified, except for stage 1 where they are the numbers of times that the pair came together during this stage.

Table 41b. Comparisons of different stages of incubation and brooding

The information used in making these comparisons is that contained in Table 41a.

Comparison	Correlation coefficient	Probability	Sample size
1 x 2	+ 0.5173	< 5 %	14
1 x 3a	+ 0.1521	N.S.	14
1 x 4	- 0.2224	N.S.	9
1 x 5	+ 0.3351	N.S.	10
2 x 3a	+ 0.2969	N.S.	18
2 x 4	+ 0.1859	N.S.	12
3a x 4	+ 0.6379	< 1 %	15
3a x 5	+ 0.5994	< 5 %	15
4 x 5	+ 0.5712	< 5 %	13
5 x 6	+ 0.4720	N.S.	7

Stages :

1.	Pre-incubation	Times pair together during the week before the first egg is laid
2.	Early incubation	Number of changeovers during days 1 - 5 of incubation
3a.	Late incubation	Days 11 - 25 of incubation
3b.	Late incubation	Days 16 - 25 of incubation
4.	Early brooding	Days 1 - 5 of brooding
5.	Late brooding	Days 6 - 23 of brooding
6.	Later brooding	Days 24 - 33 of brooding

Day 1 of incubation was the day on which the first egg was laid

Day 1 of brooding was the day on which the first egg hatched

Table 42. Changeover rates during brooding

Site	Year	Male	Female	Days 1 - 8		Days 9 - 28	
				Mean	±	Mean	±
E1D	1970	g	s	7.5	1.3	9.0	0.9
E1D	1971	g	s	9.1	1.0	-	-
W1F	1968	a	j	7.0	1.1	9.6	0.9
W1F	1969	a	j	8.0	1.6	9.7	1.1
W1E	1970	b	j	-	-	5.2	0.5
W1E	1972	b	k	4.6	0.8	5.1	0.7
W1B	1968	d	m	-	-	7.2	0.7
W1B	1969	e	n	5.6	1.7	7.9	1.2
W1B	1970	f	n	4.6	0.7	-	-
W1B	1971	f	n	4.4	0.7	5.2	0.6
W1B	1972	f	p	4.6	0.7	5.8	0.9
W1D	1971	e	q	5.1	0.5	4.9	0.5
W1D	1972	e	q	4.5	0.9	6.5	0.8
W1H	1971	h	t	6.9	0.9	-	-
W2I	1972	h	t	6.5	0.7	-	-
W1G	1968	c	l	5.9	0.7	-	-
S1Ct	1972	i	v	4.8	1.2	6.6	1.6

Day 1 of brooding was the day on which the first egg hatched. All figures represent the mean numbers of changeovers per day (± 95 % confidence limits) during the period of brooding specified.

Table 43. Changeover rates during different phases of brooding

Period :

Days 1 - 5 of brooding (N = 79)	Mean = 5.709 ± 0.36 changeovers per day
Days 6 - 23 of brooding (N = 238)	Mean = 6.609 ± 0.30
Days 23 - 33 of brooding (N = 50)	Mean = 7.475 ± 0.62

Comparing early brooding with middle brooding :

$t = 3.1416$; $P < 1\ \%$

Comparing middle brooding with late brooding :

$t = 2.5099$; $P < 2\ \%$

Thus the rate of changeover appears to increase significantly as the course of brooding proceeds.

SECTION VI

THE CHICK STAGE

Egg volume and chick weight

At hatching the weight of the chicks is largely determined by the size of the egg, with larger eggs producing heavier chicks (Fig. 39). The chicks were weighed just after hatching whilst still wet, and their weights (y) found to be closely related to the volumes of the eggs (x) from which they had just emerged (calculated from the formula 0.4866 x breadth^2 x length after Coulson 1963).

$$r_{74} = +\ 0.904; \quad y = 15.60 + 0.18\ x$$

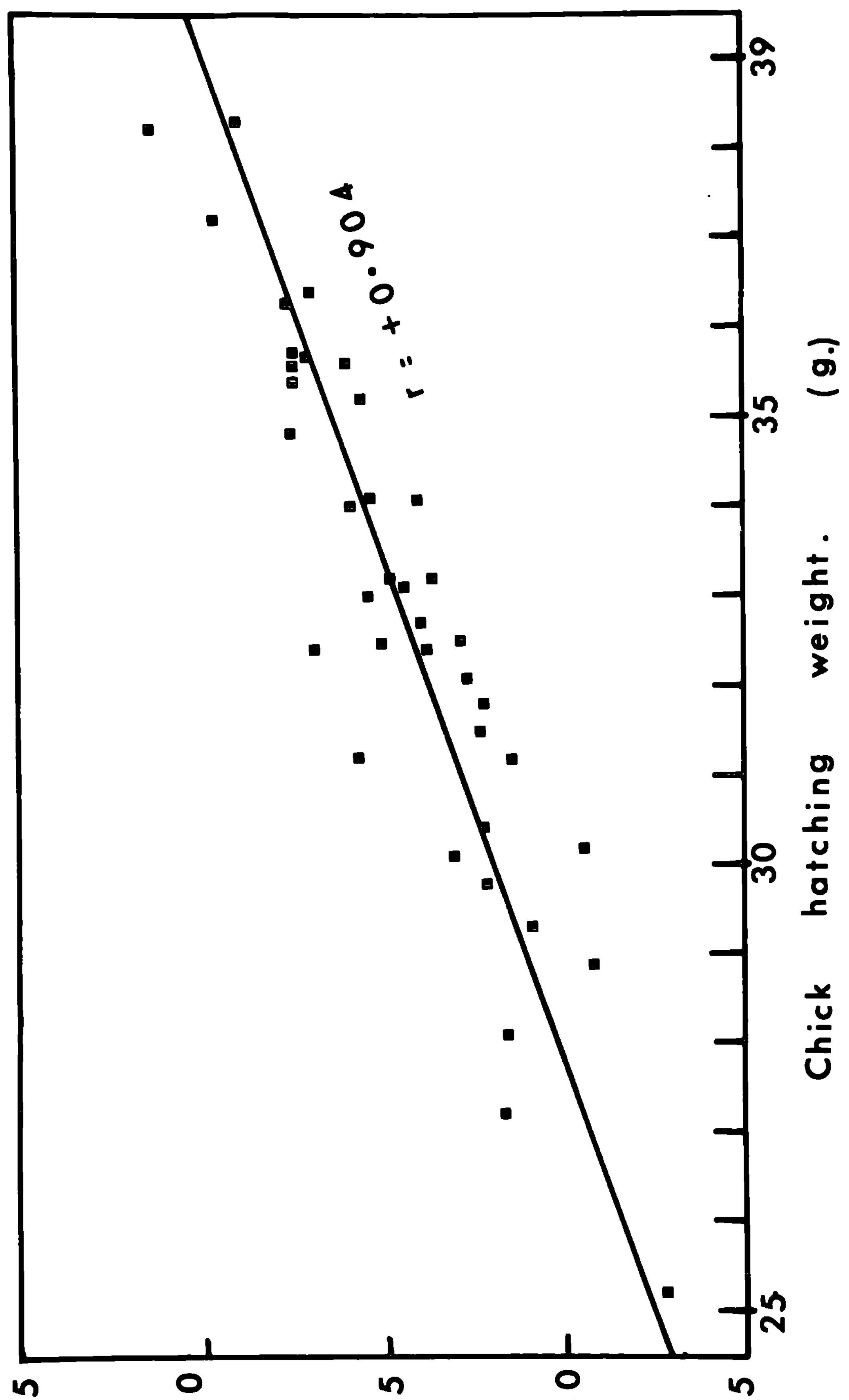
Parsons (1971) also established this relationship for the Herring Gull ($r = +\ 0.901$) and studies on poultry have yielded similar results. Parsons further found that egg volume and post-hatching chick mortality were strongly correlated for first, second and third eggs. The larger the egg was, then the higher the percentage survival, this being partly due to variation in lipid reserves. He concluded that the parent-chick relationship takes some time to develop and that food reserves are of importance in the early post-hatching days.

In this context it is interesting to note that Harris (1964) found a drop in weight of about 15 % in the Herring Gull chick at hatching. In the Kittiwake, Maunder & Threlfall (1972) found that the growth of the embryo/chick continues

Figure 39. The relationship between the volumes of Kittiwake eggs and the weights of newly-hatched chicks resulting from them.

Chicks were weighed just after hatching and while still wet. Volumes were calculated from the formula of Coulson (1963) :

$$0.4866 \times \text{breadth}^2 \times \text{length}$$


r = +0·904
Chick hatching weight. (g.)
25
30
35
39
Egg volume. (ccs.)
35
40
45
50
55

without interruption through the hatching. They also found that chicks only recently hatched had food in the foregut, and I have similar records for very young chicks on the Farne Islands. Thus, although the Herring Gull chick does not receive its first feed until about one day old, the Kittiwake chick may be fed very soon after hatching.

At hatching the emerging chick accounts for all but 11 % of the original egg weight (Table 44). The rest is made up of shell, membranes, and the remains of the yolk sac.

It was noted that weighing the chicks while they were still wet did not materially affect the results obtained. One chick when wet weighed 35.4 g and dry 35.2 g, a loss of weight through drying of only 0.5 %.

Chick growth

Growth rates in the Kittiwake have been determined by Belopol'skii (1961), Pearson (1968) and Maunder & Threlfall (1972). These studies have shown that weight increases without any interruption during and after hatching, to be followed by a period of steady growth.

A decline in the growth rate sets in at day 17 - 23, and by about day 27 there is zero weight increase per day. After day 31 the chick begins to lose weight and this lasts until fledging. The chicks reached adult weight at about 22 - 24 days of age in Pearson's work on the Farne Islands, but in the studies in Newfoundland and on the Murman coast the peak chick weights attained on days 29 - 33 were only 96 % of the adult weight.

Previous work has shown that the growth rates of chicks from different brood sizes do not differ (Pearson 1968), and that there are no differences between the growth rates of first and second hatched chicks (Coulson & White 1958a). There are no differences between the growth rates of chicks hatched early and late in the season.

The 38 chicks used to establish the relationship in Fig. 39 were weighed each day during the 10 days after they hatched. Pearson (1968) found this to be the period of most rapid growth. There appeared to be no difference between chicks starting at heavy, medium or light weights, although the sample sizes were small. Although the differential between heavy chicks and the others was maintained, the growth rates of all three categories were similar (Table 45).

All these results suggest that parents find little difficulty in feeding their young. This is borne out by the apparent ease with which parents deserted by their partners at the chick stage were able to raise two chicks alone (see Section V). However, these examples from North Shields are complicated by the considerable breeding experience of the birds involved, and the presence near the colony of the North Shields Fish Quay where the deserted parents might scavenge for food.

Since 1954, at the North Shields colony, 1868 eggs have hatched and 1632 of these young have fledged. This represents a fledging success of over 87 %. Since much of the mortality takes place during the first few days after hatching, this again lends support to the belief that parents experience little difficulty in feeding their chicks.

Table 44. Proportion of the total egg weight which is shell at the time of hatching

Weight of chick at hatching	Weight of shell at hatching	Weight of chick + shell	% total egg weight which is shell
33.1	3.6	39.7	9.1
34.0	4.7	38.7	12.1
36.4	5.4	41.8	12.9
27.2	3.2	30.4	10.5
35.4	4.9	40.3	12.2
28.1	3.3	31.4	10.5
37.2	5.6	42.8	13.1
38.3	4.3	42.6	10.1
32.1	3.2	35.2	9.1
34.5	3.7	38.2	9.7
31.8	3.4	35.2	9.7
31.5	3.5	35.0	10.0
35.6	4.2	39.8	10.6
36.3	4.2	40.5	10.4
32.5	4.6	37.1	12.4
39.4	4.4	43.8	10.1
g	g	g	

Thus, at hatching, the shell represents a mean 10.8 % of the total weight of the egg (embryo + shell + membranes). After the membranes and yolk sac have dried out, this shell weight drops to about 6 - 7 % of the total hatching weight.

Table 45. Mean weights of chicks from small, medium and large eggs

Days after hatching	Size category		
	Small	Medium	Large
At hatching	30.3	33.6	36.2
1	33.2	35.8	42.7
2	43.3	44.2	48.3
3	49.3	53.8	58.1
4	53.9	66.0	64.7
5	79.7	77.1	79.9
6	87.6	98.3	100.2
7	97.1	108.2	118.2
8	118.7	117.7	131.8
9	135.1	123.4	142.6
10	144.1	138.4	160.3

Ranges of initial weights used in categories :

Small	=	25 - 31 g	9 chicks
Medium	=	31 - 34.5 g	17 chicks
Large	=	34.5 - 39 g	12 chicks

All values given in the table represent the mean weights (g) of chicks in the three categories on the day specified.

All weighings were made between 0700 - 1000.

Artificially enlarged broods

Although all gulls have only three brood patches, it has been shown that some species can raise more than three young :

Herring Gull	not more than 3 to fledging	Harris &
Lesser Black-backed Gull	4 - 6 young to fledging	Plumb (1965)
Glaucous-winged Gull	4 - 6 young to fledging	Vermeer (1963)
Western Gull	4 - 7 young to fledging	Coulter (1966)

In the Swallow-tailed Gull, which is ecologically similar in some respects to the Kittiwake, Harris (1970) found that twins were raised to fledging as successfully as the normal single chick. Such twins had similar growth curves for weight and wing length when compared with single chicks, and also the same feeding frequencies and feed sizes.

In 1959 Coulson (in Lack 1966, p. 245) made up four broods of 4 Kittiwake chicks at North Shields and all the chicks fledged. Nelson (1964) found that Gannets had no difficulty in hatching two eggs or raising two chicks in place of their usual one. These last two instances Lack (1966) has attributed to highly favourable feeding conditions in the areas concerned.

It has been pointed out by Pearson (1968) that planktonic-feeding petrels cannot raise such artificially enlarged broods. He suggested that these species must spend a greater time in catching their smaller food organisms than gulls and gannets which can probably obtain an equivalent amount from a few large fish.

Parsons (1971) made up 78 Herring Gull clutches of four and five eggs, but found them to have a lower hatching success (37 %) than normal clutches (65 %). Indeed, the extra eggs confused the birds and resulted in incubation of the original eggs being less effective than normal.

On the Farne Islands in 1970 twelve Kittiwake clutches were made up to 4 eggs by adding eggs of similar age (about 20 - 22 days) to the last egg laid. This was a somewhat unnatural situation since any fourth egg would normally be 1 - 2 days younger than the third at laying. Three of these clutches resulted in all four eggs being hatched successfully, although hatching was probably more highly synchronised than would have occurred naturally. In the remaining instances incubation broke down (2 cases), the original eggs were infertile (2 cases), and one or two of the eggs received incubation inadequate for embryonic development (5 cases).

Among the four-chick broods produced, in one case a chick died on the first day, and in another the chick disappeared from the site within the first day after hatching. The remaining brood survived for 9 days before it too lost one chick. In this latter case the nest was on a very wide ledge, suggesting that initially at least there was sufficient room for the chicks.

Following this, 8 broods of four chicks were made up, half on normal nests and half on large, ledge nests. The chicks on these latter lasted longer before losses occurred, although in no case did more than three chicks survive to fledging.

The successful fledging of enlarged broods at North Shields mentioned earlier may be due to the very wide ledges afforded by the window ledges at this colony.

Cullen (1957) believed that chicks falling from nests represented at least as important a source of chick mortality as starvation. Indeed, the chicks which fall are not just the weaker, inadequately-nourished members of the brood, but often the older and more vigorous chicks.

McClannahan (1973) has investigated in some detail the behaviour of Kittiwake chicks, contrasting it with that of the young of ground-nesting Herring Gulls. She considered the nest structure of the Kittiwake to be similar to that of the Herring Gull, and to play little part in the differential retention of eggs and young. Chicks were brooded continuously for the first day, but thereafter more spasmodically. The chicks did not mind moving in the dark, so that brooding at night is obviously important. Kittiwake parents are less easily disturbed than Herring Gulls.

Kittiwake chicks rarely stand for long periods; they face towards and approach vertical walls, and only one chick at a time wing-flaps. Up to 10 days of age the chicks will only start to beg for food after a changeover, when the incoming parent is alone at the nest. They have a perfect avoidance response to a visual cliff, and a less perfect one to tactile cues of an edge.

All these findings of McClannahan represent adaptations to prevent the chicks being knocked or falling from the nest. However, in laboratory trials, 4 of her 5 chicks fell from the nest - although admittedly under abnormal conditions. All the chicks fell at night, and her lack of evidence for falling under natural conditions may be due to this occurring only at night. Falling tended to occur either when the chicks were very young or around 30 days when the chicks were actively wing-flapping.

She found ledge size to have no effect on the activity of the chicks. However, it seems possible that that might have some effect on the parents by enabling them to retreat from the begging pressure of the chicks. Time lapse photography of the pair on site W1D at North Shields revealed that the parents had different responses to the begging of their chicks. The female remained on or close to the nest, hiding her bill when pestered by the chicks. The male, under similar pressure, retreated into a chute which had been installed for photographic purposes. Since the chicks were unwilling to leave the proximity of the nest, this enabled him to escape the begging pressure of the chicks, while at the same time remaining on the site to defend it, and the young, if necessary. As the pair only met briefly at the times of nest relief, little opportunity existed for the female to learn this strategy by observing the male.

The inability of the normal Kittiwake nest to support more than two or three chicks as well as their parents may be at least as important a factor in chick mortality as the inability of parents to feed their young. Such a factor would be likely to take effect earlier than possible starvation.

Overnight absence after hatching

After breeding, the birds begin to leave the site at night in July when they still have chicks. In each year there appears to be considerable similarity between the pairs considered in the time of these overnight departures. Indeed, apart from 1972, they all started to stay away overnight in the second half of July. However, they continued to have the occasional overnight on the site throughout August.

Table 46 gives the dates of the first overnight absences for each pair and the time that the partners regularly began to stay away from the colony overnight. These dates are very similar for all pairs in any given year (although the annual overnight departure date varies by at least three weeks). The consequence of this is that pairs which lay early in the season spend more nights with their chicks than later-laying pairs (Fig. 40). Since it is the more experienced breeding birds which lay earliest (Coulson 1966), it is the young of these individuals which receive greater protection from falls during their fledging period.

Table 46. Overnight absences from the site after hatching

Year	Site	A	B	C	D	E	F	G	H	x	y
1968	W1F	a	j	21/7	m	2	21/7	60		+ 2	- 5
	W1G	c	l	15/7	m	2	20/7	57	58	- 1	- 7
	W1B	d	m	20/7	f	2	20/7	58		0	- 3
1969	W1F	a	j	22/7	f	5	22/7	62		+ 9	+ 3
	*W1G	c	l	8/7	f	7	8/7	38		-15	- 7
	*E1D	g	r	13/7	f	5	13/7	45	53	- 8	- 4
	W1B	e	n	24/7	m	-	24/7	66		+ 13	+ 6
1970	W1E	b	j	18/7	f	4	18/7	62		- 7	- 1
	W1B	f	n	27/6	m	11	15/7	66		- 3	+ 6
	**W1G	c	l	30/6	(f)	-	-	-	69		
	E1D	g	s	16/7	m	5	21/7	79		+10	+13
1971	W1B	f	n	8/7	f	4	27/7	86		+ 9	+13
	*W1E	b	j	9/7	f	24	28/7	73		- 4	- 2
	**E1D	g	s	25/7	(f)	-	25/7	79	77	+ 2	+ 6
	W1D	e	q	12/7	f	6	26/7	76		- 1	+ 5
	W1H	h	t	14/7	f	6	25/7	72		- 5	0
1972	W1D	e	q	2/7	f	6	7/7	62		+ 7	+ 9
	W1B	f	p	29/6	m	3	2/7	48		- 7	- 2
	W1E	b	k	1/7	m	9	10/7	60	55	+ 5	+ 3
	**W2I	h	t	3/7	(m)	-	14/7	41		-14	- 9
	S1Ct	i	v	16/7	f	14	16/7	63		+ 8	0

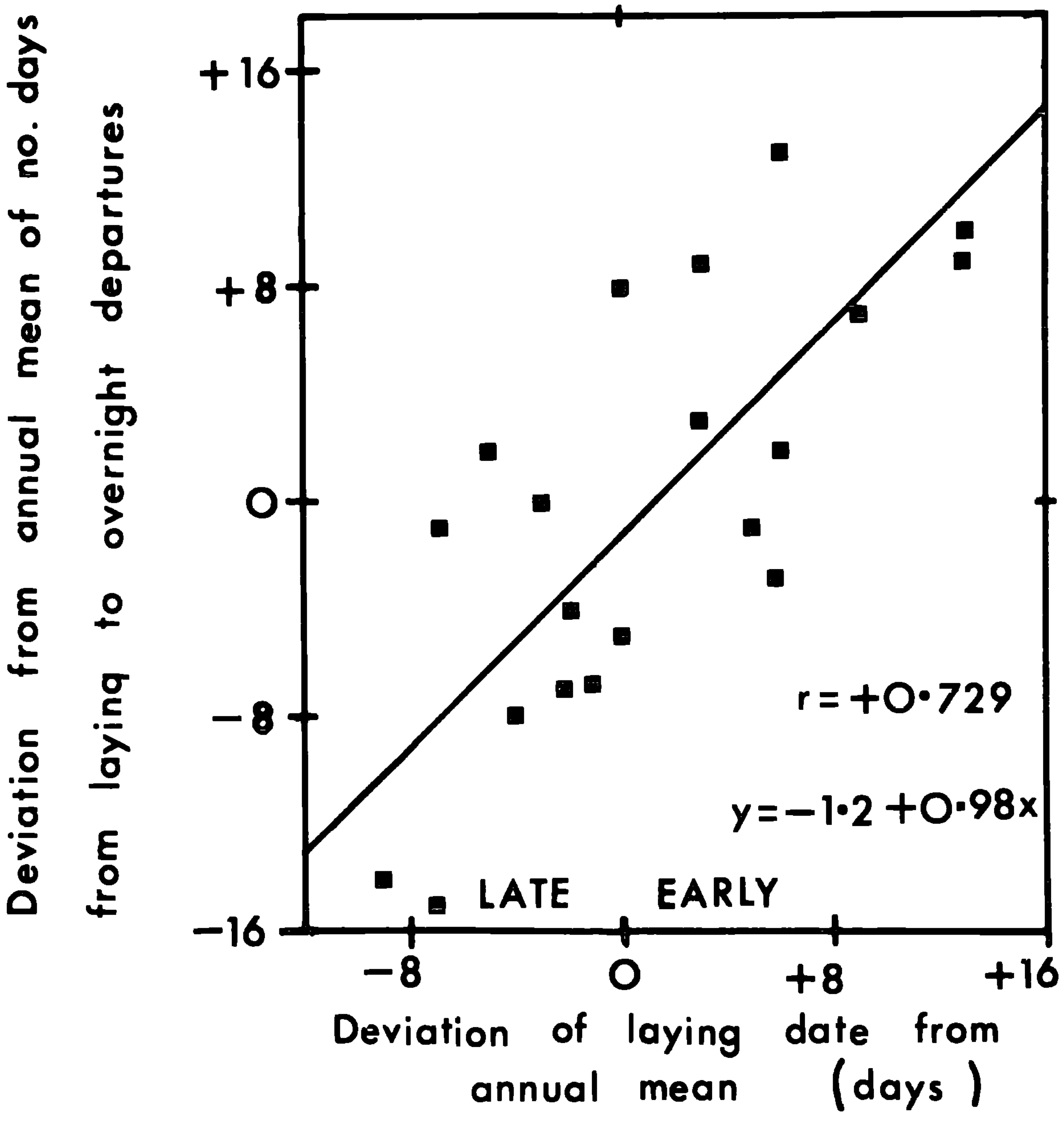
Column headings :

A & B	Male and female members of the pair
C	Date on which the site was first left vacant at night
D	Sex of the bird first leaving the site vacant overnight
E	Days after C when the other partner stayed away overnight
F	Date after which the site was regularly left vacant at night
G	Number of days between the laying date of the first egg and the start of regular overnight vacation of the site
H	Annual mean values for intervals in column G
x	Deviation of values in G from annual mean (H) ± in days
y	Deviation of laying date of the pair from the colony mean annual laying date (positive values indicate early-laying and negative values late-laying pairs)
*	indicates no hatching; ** indicates one partner disappeared

Figure 40. This figure shows the relationship between the date of laying and the length of regular overnight brooding of the young.

In each year studied, an annual mean was calculated for the pairs monitored of the number of days elapsing between the laying date of the first egg and the date on which the parents regularly began to leave the site unattended at night. The deviation (in days) of each pair from this annual mean comprised the values on the vertical axis (column x in Table 46).

These values have been plotted against the deviation of the laying date for each pair (in days) from the annual mean laying date for the colony, on the horizontal axis (column y). Positive values indicate early-laying pairs and negative values late-laying ones.


Deviation from annual mean of no. days from laying to overnight departures
+16
+8
0
−8
−16
−8
0
+8
+16
Deviation of laying date from annual mean (days)
r = +0·729
y = −1·2 +0·98x
LATE
EARLY

SECTION VII

DEPARTURE FROM THE COLONY

Post-breeding activity

As has been mentioned in Section I, there is a post-breeding resurgence in the activity of breeding pairs after the young have departed from the colony in July and August. At this time there are also signs of territorial and sexual behaviour. Nelson (1965) has recorded a similar situation in the Gannet which exhibits a late flowering of territorial activity. Coombs (1960) also found considerable activity in the Rook in Autumn. In the latter species the sexual resurgence involved displays and activities as intense and frequent as those in spring. Coombs considered these to be important in pair-formation as well as establishing and maintaining territory.

It seems likely that the post-breeding activity peak in the Kittiwake serves a similar function in strengthening the pair-bond between members of an established pair. The higher level of activity among these pairs may also contribute to the earlier return of experienced birds to the colony at the start of the following season.

This is also the time when birds which have not bred previously prospect for sites and mates to which many of them return the following season. Breeding pairs which have been unsuccessful often split up at this time, and while some leave the colony soon after failure, others remain to take new sites or mates to which they also return at the beginning of the next season. This familiarisation of a bird with a potential site or mate may confer upon it a marked advantage in the ensuing competition for nest sites and partners.

Mate changes due to divorce and bereavement

Birds which change their mate while their former mate is still present at the colony will be termed divorced birds, while those whose mate has died will be called bereaved birds.

Coulson (1972) has shown that the delay in the date of laying brought about by a mate change is shorter in divorced birds than bereaved ones, although this difference is not significant. There is also a suggestion that divorced birds lay slightly larger clutches than bereaved birds. The latter had a significantly lower breeding success and fledged fewer young per pair than divorced birds.

This lesser effect of divorce compared with bereavement may be due to differences in the time that they take effect. A bird whose mate dies during the winter may return to the colony and wait for its mate for several weeks (see Fig. 19) before attempting to secure a new mate or site. During this time the potential number of mates and sites decreases since pair-formation and site-ownership proceed throughout the fruitless wait.

In contrast, a pair which have been unsuccessful in some aspect of breeding may split up soon after failure.

This allows them to look for a new mate or establish themselves on a new site during the post-breeding period of activity. On their return the following year they go to their new site, or pair immediately with their new mate. Even if neither of these are possible, they will look for new ones without delay - unlike a bird whose mate has died.

Nelson (1965) records that the attitude of male Gannets towards females as potential mates goes through a receptive period at the beginning of the season, becomes highly selective later, and then goes through a second receptive phase towards the end of the season. As mentioned earlier, the Gannet also shows a marked period of post-breeding activity. If the Kittiwake went through a similar phase of receptivity to potential mates during its post-breeding resurgence of activity, then this might contribute to the success of divorced birds in finding a new mate for the following season.

Primary moult

Birds examined from February to early May showed no signs of moult. This first appeared in the latter half of May and in June, shortly after the start of egg laying. During June and July the breeding birds looked at had about 6 - 8 old primaries, and in August about 3 - 5 old primaries remained. In September, when the colony was vacated, the few individuals inspected still had 2 - 3 old primaries. The major part of this annual moult is thus accomplished between egg laying and the time that the birds leave their colony to overwinter at sea.

Departure from the colony

The departure of individuals from the colony in 1971 is shown in Table 47, and was similar in the other years considered. The rate of departure accelerated towards the end of the season, but there was no difference between males and females in the last date on which they were seen (t_{112} = 0.2718).

The greater the number of years that an individual had bred at the colony (x), then the later was the date on which it was last seen (y; in weeks after 24 July) :

Males $r_{54} = + 0.4912$ $P < 0.1\ \%$ $y = 3.69 + 0.37\ x$

Females $r_{56} = + 0.4833$ $P < 0.1\ \%$ $y = 3.78 + 0.40\ x$

Similarly, the members of old-established pairs remained at the colony later in the season than others :

Males $r_{54} = + 0.2834$ $P < 5\ \%$ $y = 4.71 + 0.47\ x$

Females $r_{56} = + 0.2553$ $P < 5\%$ $y = 4.83 + 0.52\ x$

This follows from the finding, mentioned when discussing the occupation of the colony, that such established pairs are composed of the more experienced breeding individuals.

Table 47. Departure of birds from the North Shields colony

1971

Date	A.	B	C	D.	E.	F	G
28/7	80	2	3	2	80	3	9 %
31	30	1	3	3	110	3	
3/8	120	12	10	15	230	7	
6	88	13	15	28	318	9	
9	40	8	20	36	358	10	15 %
12	39	1	3	37	397	9	
16	63	6	10	43	460	9	
19	70	17	24	60	530	11	
24	34	2	6	62	564	11	13 %
27	15	2	13	64	579	11	
31	44	2	5	66	623	11	
2/9	39	11	28	77	662	12	
6	18	1	6	78	680	12	33 %
9	24	7	29	85	704	12	
13	38	18	47	103	742	14	
16	3	1	33	104	745	14	
23	19	6	32	110	764	14	47 %.
28	24	13	54	123	788	16	
30	20	8	40	131	808	16	
4/10	16	10	63	141	824	17	

Column headings :

A	The number of birds at the colony on the date shown
B	The number of these which were seen for the last time on the date shown
C	The percentage of birds at the colony which were seen for the last time (viz. $\frac{B}{A}$ as %)
D	Cumulative total of birds seen for the last time that year
E	Cumulative total of all bird-visits to colony recorded
F	Cumulative percentage of birds visiting the colony for the last time (viz. $\frac{D}{E}$ as %)
G	Percentage of visits to the colony during fortnightly periods which were made by birds visiting it for the last time that year

DISCUSSION

Cullen (1957), in her classic study of the Kittiwake, showed how it differed in many behavioural and morphological aspects from gulls which still retained the ancestral ground-nesting habit. More recently McClannahan (1973) has continued and extended this comparison, examining the adaptive behavioural complex of the young in relation to the cliff nest.

Similarities in behaviour also exist between the Kittiwake and other gulls which nest on cliff sites, such as the Swallow-tailed Gull (Hailman 1965) and Thayer's Gull (Smith 1966). The Gannet, which also breeds on cliffs, shows considerable behavioural similarity to the Kittiwake despite the two species being phylogenetically very different (Nelson 1967). This is presumably due to convergent evolution, although Nelson believes that the Gannet was ancestrally a cliff-nester and has only recently used flatter ground.

The patterns of Kittiwake behaviour emerging from this study also reflect its adaptation to cliff-nesting as well as the concomitant relaxation of predation pressure. The limited number of suitably safe cliff sites - especially those near other Kittiwakes - results in intense competition for such sites, and this is reflected in the many aggressive elements to be found in Kittiwake behaviour.

Individuals cannot move gradually onto such sites but must land on them unreservedly, and once on the site the birds must perforce stand close together. This results in appeasement displays also being well-developed. Thus the protracted greeting ceremony performed upon the arrival of a bird at the site may serve to reduce aggression between members of the pair. Once a pair has been formed, some measure of individual recognition may serve to lower hostility towards an arriving mate, and this may also apply to neighbours.

Pair members also indulge in allopreening (Cullen 1962) when standing together on the site. This behaviour is also found in the cliff-nesting Black Noddy (Cullen & Ashmole 1963) and it may help to decrease aggression when the birds are close together. In view of the preference of the Kittiwake for red rather than yellow (Cullen & Cullen 1962) it is interesting to note that most allopreening takes place around the eye and at the base of the bill - both of which are red.

Many Kittiwakes have bright red orbital rings when they return to the North Shields colony in January. These persist until laying but fade rapidly thereafter, until by July they are almost black again. Young, non-breeding birds arriving at the colony late in the season have red orbital rings, in marked contrast to the darker rings of the breeding birds. The implications of this difference and its underlaying endocrine mechanism are not understood but it is clearly linked with gonadal development.

The greeting ceremony may serve a dual function, in that as well as lessening aggression it may also serve to strengthen the pair bond. Thus when during the period that the pair is being formed the male frequently leaves the site to perform short aerial circuits of the colony, this may strengthen the pair bond and also accustom the female to remain on the site after the departure of the male. Once again a parallel exists in the behaviour of the Gannet (Nelson 1965, p. 274).

It has been shown that during the period before egg laying there are a large number of repeated arrivals by the male. This may serve to bring the female into ovulatory condition, and also to reinforce the pair bond just before shared incubation places the greatest strain on it.

The hormonal basis of the reproductive cycle in birds is complex and imperfectly understood. It is probable that ecological factors such as photoperiod and temperature act through the hypothalamus and anterior pituitary to influence the growth of the gonads, and to determine breeding at an appropriate time of year.

Within this breeding season the successive reproductive phases involve complex interactions between stimuli from the environment and internal changes in endocrine condition. This study has shown successive stages of the Kittiwake breeding cycle to be related, with a break early in incubation where the relative influence of external events may become greater. Experiential and social factors may also modify behavioural development and the response to external stimuli, but the interactions of all these factors are as yet uncertain.

Seasonal differences in behaviour, and differences between individuals, may be due to differential sensitivity as well as different levels of hormones. The greater lengths of reproductive phases late in the breeding season, as demonstrated for nest-building in the Kittiwake, may be due to hormonal levels changing more slowly at this time.

Much more work needs to be done on these aspects and also on the hormonal differences between birds breeding early and late in the season, and between naive and experienced breeding individuals. The hormonal state of non-breeding individuals is also worthy of investigation, since some of them have been shown to exhibit high attendance at the colony although they make no attempt to breed. It would also be most interesting to know the underlying endocrine mechanism for the post-breeding resurgence of sexual activity seen in the Kittiwake and other birds (e.g. Coombs 1960, Nelson 1965), since at this time the gonads are in a regressed state.

In mammals reproduction is centred around the female, who has an oestrus cycle of limited receptivity. She alone carries the developing embryo and in most species the male contributes little to the care and feeding of the young. Thus the oestrus cycle is fundamental to mammalian reproductive co-ordination and there is little need for elaborate courtship.

In birds however the roles of both sexes are often considerable and in the Kittiwake they are almost equal. Co-ordination between pair members extends from territory establishment early in the year, through nest-building, copulation, laying and incubation, to brooding and feeding of the young. In avian species the more complex and highly elaborated courtship behaviour probably helps to ensure a strong pair-bond and successful co-ordination.

Although this study has restricted itself to the heterosexual interactions between pair members, this almost certainly represents a considerable simplification in the case of such an intensely colonial animal as the Kittiwake. Complications are likely to be afforded by the relationships between parents and their offspring, and between adults and other conspecifics.

For instance Butterfield (1970) has studied the pair bond in the Zebra Finch, which pairs for life, using operant techniques. She found that although the mate provided the highest reinforcing efficacy, other members of the group also appeared to have some reinforcing value. Thus the effects of sexual motivation by the mate, involving courtship and consummation, may be combined with social motivation provided by the mate and other conspecifics. It seems likely that in the social Kittiwake, neighbours and other members of the breeding colony exert a considerable effect upon an individual, in addition to effects induced by its mate.

Any pair bond functions to promote reproductive success by enhancing sexual tendencies and repressing aggressive ones. In addition, bonds maintained over successive breeding seasons may produce a progressive improvement in performance. A strong nest-site and mate tenacity develops in long-lived seabird species such as the Kittiwake Gull, penguins (Richdale 1957) and albatrosses (Richdale & Warham 1973) where breeding associations may last for up to 15 years.

In the Kittiwake, Coulson (1966a) has shown that it is the retention of the mate rather than actual age which leads to older individuals breeding earlier and with greater success. Indeed a change of mate may have a prolonged and directly depressive effect upon breeding success even two years after the change has taken place.

In other seabirds, older parents have been shown to be more efficient than younger ones (Richdale 1957, Nelson 1964) but such older birds have usually bred previously. Only in the White Stork (Ciconia ciconia) has it been shown (in Lack 1966) that age may have some effect on breeding performance in addition to any previous experience.

In primates and other mammals, experienced animals usually exhibit greater maternal care than primiparous ones. However it is not known whether this is due to age per se, to experiential factors, or to the animal having been through the endocrine changes associated with breeding.

Ainley & Schlatter (1972) showed that while adult Adélie Penguins were able by 3 - 4 years old to feed themselves and their young, they raised increasingly more and heavier chicks up to 6 years of age. In addition they found that previous breeding experience did not increase the ability of birds to raise heavier chicks. This led them to suggest that as the birds aged, their improved ability to raise fledglings was due to accumulated experience at sea rather than to experience with mates, chicks and eggs during breeding.

In the Kittiwake, chick mortality is low, adults require only a short period each day to acquire food, and parents have little difficulty in feeding their young - even when one parent has to do so alone. The species is expanding rapidly, like some other seabird species, and it seems likely that food is readily available during the breeding season, even to inexperienced breeders.

Indeed the failure of these latter individuals takes place during the incubation of their eggs and they are as successful as older parents in raising young (Coulson 1966a). This situation has also been found in the Gannet (Nelson 1964). Predation pressure on the Kittiwake is virtually absent and infertility is likely to be about the 6 - 7 % suggested for the Herring Gull and the Gannet (Baerends & Drent 1970).

It therefore seems likely that the poorer reproductive success of younger birds results from their inability to co-ordinate their breeding activities, especially during incubation. Since 80 % of females breeding for the first time do so with similarly inexperienced males (Coulson 1966a) it is hardly surprising that integration among these individuals is less efficient.

However the pair bond is a reciprocal arrangement and through learning processes the relationship may well be modified and indeed specialised during the years that it continues. Thus although young birds lack the experience of older ones, they may compensate for this in part by having greater behavioural flexibility in adapting to a new partner.

One interesting feature to emerge from this study is the very considerable way in which one member of a pair can compensate for the failings of its mate. Among the admittedly few cases considered, the male appeared to be more prone to fail in his breeding duties. Since only interactions at the breeding colony were examined, it is always possible that they were only the consequences of interactions elsewhere. It is thought unlikely however that for instance a failure to perform incubation duties was related to a difficulty in finding food. Such failure is more likely to be related to a weak level of motivation.

Despite the marked degree of flexibility exhibited within the incubation and brooding systems, in a species like the Kittiwake where both sexes contribute almost equally towards breeding duties, poor co-ordination between partners will frequently result in failure.

It has been shown in this study that the more experienced birds return to the colony earlier than others and most birds mate with individuals of similar breeding experience. This differential return and mating has also been demonstrated in the Adelie Penguin (LeResche & Sladen 1970).

In a slowly-maturing species such as the Kittiwake, not all individuals reach the same stage at the same time. In the population studied some birds bred for the first time aged 3, whereas others did not breed until 7 years old. Deferred maturity and its relationship to the dynamics of avian species has been widely discussed, and will only be dealt with briefly here.

Lack (1966) has suggested that breeding imposes a strain on young birds, increasing their mortality rate, such that selection produces a delay in breeding. In some species of birds, younger individuals have been shown to have a less efficient foraging ability (Orians 1969, Recher & Recher 1969, Dunn 1972) and this might mean that they find difficulty in finding enough food to support themselves and their young. In addition, younger birds may compensate for their lower fishing success by foraging longer, with a consequent reduction in the time available for competing with more experienced birds for mates and sites at the colony.

In contrast Wynne-Edwards (1962) has proposed that delayed breeding regulates population size by holding back a reservoir of potentially mature but non-breeding adults. In colonial seabirds this might be accomplished by conventional limitation of breeding sites. Thus the length of adolescence would be individually variable and governed by social competition.

Intermittent breeding, which has been encountered among the members of the Kittiwake population studied, would be due to conventional social pressures under the Wynne-Edwards model, and he believes that such a scheme could only operate in species such as long-lived seabirds where mortality rates are low.

In the North Shields population, males bred for the first time at an earlier age than the females. This is the reverse situation to that found in the Yellow-eyed Penguin (Megadyptes antipodes) where males start breeding on average one year older than females (Richdale 1957).

These differences may reflect the reproductive loads of the sexes in these species, the one with the heavier task having its breeding retarded more.

The role of the female Kittiwake in forming and laying the eggs imposes an obvious breeding strain. However the male must undertake the major share of site defence as well as feeding the female during courtship, and shares with her the incubation of the eggs and the feeding of the young. It would be difficult to decide which breeding role demands most effort.

In many seabirds, such as the Kittiwake and the Adélie Penguin (LeResche & Sladen 1970), young individuals come to the breeding colonies in the year before they first breed. Frequently they occupy sites, form pairs and even build nests, but do not lay any eggs. This "prospecting" experience is likely to be an advantageous and even necessary prelude to successful courtship and breeding.

It is probable that young birds lack experience, not just in feeding, but in other modes of behaviour, and are able to explore breeding colonies and feeding areas during the year before they breed. In a species with a low mortality rate it might be better to forfeit a breeding attempt when young rather than endanger a potentially long and more productive breeding life. However the physiological state of these young birds is not known, and it may be that their gonadal and endocrine development is inadequate for breeding.

Birds are probably more dependent on gonadal hormones for their interaction patterns than mammals, and in the latter learning and experience may be of increased importance. In primates, for example, some social behaviour may be traditional and passed on through individual and social learning processes, so that, for instance, roles in a hierarchy may be transferred from ageing animals to younger ones.

Although to be successful an individual must adapt to the behavioural norms of the group in which it reproduces and survives, within any population there is often a considerable degree of behavioural lability. Indeed perhaps the most surprising finding of this study was the amount of heterogeneity in behaviour shown by pairs and individuals within the limits of tolerance imposed by the dynamics of the population and the ecology of the species. Factors such as predation and the availability of food and sleeping and breeding sites probably mould these limits, but within them, variations in social structure between populations may occur in the same way as individual differences within a population.

The adaptations of cliff- and ground-nesting gulls have been dealt with earlier, and primates also show widespread levels of adaptation to forest, tree savannah, grassland and arid environments. The latter also show extensive intraspecific variation in their social organisations related to differences in environment, as exemplified by arboreal forest primates and those of the savannah. Unrelated primates living in similar environments may have similar social systems and the avian parallel between the Kittiwake and the Gannet has also been mentioned earlier.

Since it was found that some inexperienced breeding individuals integrated their activities very successfully on their first attempt, whereas some experienced individuals did not, it is suggested that some measure of compatibility must exist between potential and actual mates for any degree of breeding success to be achieved. This idea is consistent with the considerable heterogeneity of individual behaviour encountered in the population studied.

Individuals monitored throughout several consecutive years revealed that consistently successful birds exhibited high levels of activity even if they had to change mate or site. In particular, the long-established pairs showed great similarity in their breeding patterns in successive years. Indeed they may become so specialised that, although experienced, they may have difficulty in adjusting their behaviour to a new mate after several years with a previous partner. It is obvious that much more work will need to be done before such effects can be separated within a relatively complex pattern of breeding.

SUMMARY

Some aspects of the breeding biology of the Kittiwake gull were studied at a colony nesting on a riverside building in North Shields, Northumberland from 1969 - 1972. This colony has been studied since its formation in 1949 and since 1965 has consisted of about 100 breeding pairs.

Birds ringed as young at North Shields return to the colony in the year before they first breed. Most males breed for the first time at about 4 - 5 years old, one year earlier than females. Males hatched from sites in the centre of the colony breed for the first time at an earlier age than those from edge sites.

A technique is described which was used to monitor the attendance and activity of radioisotope-marked members of breeding pairs at their sites. The characteristic profile of attendance and activity for breeding pairs throughout the season is described, and comparisons made between the profiles of established and newly-formed pairs, and experienced and naive birds.

Older, more experienced breeding individuals and established pairs showed higher levels of activity (and often attendance) than less experienced birds. Naive individuals showed a marked improvement in their breeding activity in their second year together.

Some inexperienced breeding individuals integrate their activities very successfully on the first occasion that

they are paired, whereas some experienced individuals do not. It is suggested that some measure of compatibility may be necessary for successful co-ordination of breeding activities.

Non-breeding pairs differ markedly from breeding pairs in their attendance and activity. Low male activity appears to be most frequently the cause of disjunction in the co-ordination of a breeding pair. Some females, although unmated, exhibit high attendance at the colony, and, since after a mate change older females change site less often than younger ones, it is possible that their behaviour alters with age.

The first birds return to the colony in January, 15 - 20 weeks before most laying takes place (in mid-May). The initially rapid occupation of the colony slows down by late February and March. Males and females return at the same time. The more experienced breeding individuals and members of established pairs return before the less experienced birds (about 3 days earlier for each year of experience). Birds returning later in the season change site more often than early arrivals.

Prior to laying, the number of birds at a colony builds up rapidly after dawn and during the early morning but then slows down. Birds continue to arrive at the colony throughout the day, many of them non-breeding birds, and the proportion of sites with pairs present increases steadily from dawn to dusk.

Early in the season birds arrive at the colony well after dawn. During February, March and April they arrive just before or after sunrise. Some pairs arrive consistently earlier or later than others. After the young have left the colony, the bird's arrivals become later, so that by the time they vacate the colony their arrivals are once more well after sunrise. Overnight occupation of the site only starts when the pair first come together each season, and continues until the latter half of July.

A scheme is proposed whereby the high activity of the male before laying (collecting nest material or on aerial circuits of the colony) leads to many display arrivals. These serve to strengthen the pair bond and bring the female into ovulatory condition. The Kittiwake calls given at the greeting arrivals appear to show consistent individuality and may provide a basis for recognition of mates and neighbours. Breeding partners phase gradually into the shared incubation phase by shortening the time taken to change round on the site, until it is less than one minute.

From a flat nest-base to a cup nest takes about 10 days and from cup completion to the laying of the first egg is a further 14 days. Nests destroyed at this stage are rapidly replaced. Pairs laying earlier in the season take a shorter time to build their nests than later-laying pairs.

The sexes share the incubation of the eggs, with the males taking 45 % and the females 55 %, although some pairs show consistent differences from these proportions. The proportions of the shared overnight incubation are the same. The eggs are attended for 99.7 % of the time - the highest figure so far recorded for any gull.

If one partner fails to return, the sitting bird will continue to incubate until relieved. When not relieved, a bird will incubate for nearly 3 days before first leaving the eggs briefly unprotected. One female incubated 97 % of the 2 weeks (and 90 % of the 3 weeks) after her partner had disappeared.

While the eggs are being laid, the partners alternate incubation duties frequently but this rate of changeover rapidly falls to two changeovers/day. Some pairs show a consistently higher rate of changeover than others. One changeover occurs in the hour after dawn and the other in the late afternoon or early evening.

Birds whose eggs do not hatch continue to incubate for up to twice the normal period of 27 days. After hatching, the changeover rate increases to about 6 changeovers/day, and this rate continues to rise throughout the brooding of the chicks.

Egg temperature reaches a steady state about a week after the clutch has been completed. Asynchronous hatching of the eggs leads to the first chicks forcing the parents up off any third egg, which receives incomplete incubation just before hatching.

Single eggs lost from clutches are not replaced, but complete clutches lost may be replaced after about 12 days. Clutches which have only been incubated for a few days are more likely to be replaced than those incubated for longer. Clutches are more frequently and more rapidly replaced earlier in the season by the more experienced breeding birds.

Most egg and chick exchanges are tolerated except those backwards from advanced chicks. Donated eggs are accepted and incubated about 7 days before laying, and for about 3 days after the eggs have hatched. Pairs will accept chicks (up to 3 weeks old) in place of eggs at any stage of incubation, and raise them successfully to fledging.

Successive stages of laying, incubation and brooding are related to one another except for a break at the point where birds begin steady incubation. This may reflect an increased reliance on external, rather than hormonal, regulators after this point.

Eggs with larger volumes produce heavier chicks at hatching. No differences have been found in growth rates between early and late, first and second, heavy and light chicks, or those from one- and two-chick broods. Parents are able to feed and raise two chicks successfully to fledging, even when they have to do so alone. This, coupled with a fledging success of over 87 %, and trials with artificially enlarged broods, suggests that it is principally the small size of the breeding site that restricts the brood size, rather than the inability of parents to feed their young.

After the chicks have hatched there is a post-breeding resurgence of sexual and territorial activity. It is suggested that the lesser detrimental effect of a mate change due to "divorce" rather than "bereavement" may be due to the changes taking place at different times in the year.

In any one year most pairs first leave their sites vacant overnight at the same time. This means that experienced breeding pairs, which lay earlier in the year, spend more nights on the site with their chicks. Experienced breeding individuals and members of established pairs remain at the colony until later in the season than less experienced birds.

APPENDICES

1. Dates of laying of the first egg for radioactive pairs

2. Weekly activity and percentage attendance of radioactive pairs

3. Total, daylight and overnight attendance by two pairs in 1971

4. Comparisons of attendance and activity of different pairs

5. Percentage hourly distribution of the start of incubation stints

6. Number of times per day that partners alternated incubation duties during the course of incubation (changeover rate)

7. Diurnality in times of changeover during and after incubation

8. Common and specific names of animals mentioned in the text

Appendix 1.

Dates of laying of the first egg for radioactive pairs

(All dates are in May)

Year	Site							
	W1F	W1E	W1B	W1D	W1G	E1D	W1H/W21	S1CT
1968	22	-	23	-	24	-	-	-
1969	21	-	19	-	31	29	-	-
1970	-	17	10	23	17	3	-	-
1971	-	16	2	11	-	7	14	-
1972	-	11	15	6	-	-	23	14

APPENDIX 2. Weekly attendance and activity of members of radioisotope-monitored pairs

All values have been calculated for weekly periods before and after the date on which the first egg was laid. The attendance figures represent the percentage of the week that the individual (or the pair) was present on the site, or the percentage of the week that the site was left empty. The attendances of males and females included their attendances as members of the pair.

All activity figures are the number of visits to the site during the weekly period, or, in the case of the pair, it is the number of times per week that the pair came together on the site.

The following symbols are used in the tables :

*	indicates a value of less than 1 % attendance
**	indicates that the pair failed to hatch their eggs
***	shows that one partner disappeared during the breeding season
******	indicates the date on which the first egg was laid
-	is used to show that the site was not monitored during the week indicated, or that the individual was not marked with a radioisotope leg band

Only 21 pair-years are included in this Appendix. The remaining pair (W1H/W2I in 1972) is dealt with in more detail in Appendix 4, and their attendance and activity data is listed in Tables 12 and 13 in Appendix 4.

Male attendance :

Weeks before and after laying	W1F	W1F	W1E	W1E	W1E	W1G	W1G	W1G	S1Ct	W1H
	68	69	70	71	72	68	69	70	72	71
19	-	-	-	-	0	-	-	-	-	-
18	-	-	-	0	0	-	-	0	-	-
17	-	-	-	0	1	-	-	0	-	-
16	-	-	-	12	5	-	-	0	-	-
15	-	19	-	57	20	-	-	0	-	-
14	-	31	-	34	6	-	-	14	-	-
13	-	78	-	22	40	-	3	60	-	-
12	-	89	-	18	71	-	28	80	-	-
11	-	88	-	36	63	-	23	73	-	-
10	-	75	-	51	68	-	*	70	-	-
9	-	84	68	55	56	-	15	65	-	-
8	-	18	75	48	84	-	3	79	-	-
7	-	23	42	47	41	-	1	64	-	-
6	-	17	53	34	45	-	1	64	-	-
5	-	21	39	37	60	-	22	58	-	-
4	72	36	35	52	54	-	11	48	-	-
3	80	71	36	41	33	-	28	40	-	-
2	76	55	26	40	38	-	22	34	-	-
1	63	67	29	33	30	-	35	44	-	-
*******										
1	50	49	34	28	44	-	32	34	39	-
2	56	50	38	41	50	-	22	44	44	54
3	56	51	37	32	53	39	14	37	31	59
4	54	60	32	38	44	37	42	7	39	53
5	54	54	-	39	47	42	14	0	41	56
6	55	58	36	43	57	29	30	0	45	54
7	61	50	40	45	54	19	36	0	41	39
8	61	49	36	30	35	20	24	0	46	24
9	29	33	26	30	25	2	1	0	46	44
10	23	24	20	26	16	1	7	0	32	36
11	29	18	26	33	7	1	8	0	25	32
12	24	58	32	34	6	0	2	0	6	16
13	-	52	9	10	8	-	0	0	32	8
14	26	29	0	9	3	-	0	0	32	7
15	1	35	0	2	0	-	0	0	13	3
16	-	10	0	*	0	-	0	0	2	2
17	-	6	0	0	0	-	0	0	4	0
18	-	1	0	1	0	-	0	0	1	5
19	-	-	0	0	0	-	0	0	6	1
20	-	3	0	0	-	-	-	0	8	2
21	-	0	0	0	-	-	-	0	4	3
22	-	0	-	0	-	-	-	-	1	1
23	-	-	-	-	-	-	-	-	0	0
24	-	-	-	-	-	-	-	-	0	-
				**			**	***		

<u>Male attendance</u> (Contd.)

Weeks	W1D 70	W1D 71	W1D 72	E1D 69	E1D 70	E1D 71	W1B 68	W1B 69	W1B 70	W1B 71	W1B 72
19	-	-	-	-	-	-	-	-	-	-	0
18	-	-	0	-	-	-	-	-	-	-	0
17	-	0	0	-	-	1	-	-	-	-	0
16	-	0	0	-	0	16	-	-	-	0	0
15	-	0	0	-	0	25	-	-	-	0	0
14	-	0	0	-	0	46	-	-	-	0	0
13	-	0	0	-	13	81	-	-	-	0	0
12	-	*	0	-	47	51	-	-	-	0	0
11	-	0	0	-	45	14	-	-	-	0	0
10	-	2	0	-	53	35	-	-	-	0	74
9	-	*	0	-	50	51	-	-	-	*	78
8	-	0	0	-	80	32	-	-	-	33	73
7	-	14	0	-	76	54	-	-	*	48	59
6	-	57	48	-	81	42	-	-	*	54	59
5	-	64	69	-	68	44	-	-	*	49	48
4	-	45	48	-	62	44	-	-	40	35	50
3	-	55	70	-	61	51	65	-	83	37	42
2	-	48	61	-	57	46	62	-	59	38	68
1	-	49	55	-	48	34	60	-	35	31	66
*******											
1	54	42	57	-	49	45	61	-	54	32	55
2	45	51	58	-	49	46	58	46	42	50	57
3	59	43	51	75	43	46	49	56	56	56	53
4	43	46	42	57	51	40	-	43	52	59	51
5	41	46	43	64	46	49	55	48	56	45	49
6	-	45	48	60	40	9	51	51	54	54	48
7	-	38	47	43	36	0	52	36	43	44	32
8	51	48	52	34	45	0	44	47	32	44	8
9	26	40	34	41	44	0	18	40	29	39	13
10	51	24	19	26	53	0	13	-	33	46	5
11	52	32	2	11	53	0	25	-	28	29	6
12	46	31	2	8	45	0	7	-	34	57	3
13	43	16	46	7	31	0	0	-	46	53	0
14	32	16	29	2	34	0	-	0	27	30	0
15	13	18	4	6	21	0	-	0	28	8	0
16	9	11	3	1	15	0	-	0	3	*	0
17	1	9	4	3	8	0	-	0	0	0	0
18	3	10	1	*	3	0	-	0	0	0	0
19	*	-	1	*	4	0	-	-	0	0	0
20	-	-	0	*	2	-	-	-	-	0	-
21	-	-	-	0	0	-	-	-	-	-	-
22	-	-	-	0	0	-	-	-	-	-	-
23	-	-	-	0	0	-	-	-	-	-	-
	**			**		***					

Male activity

Weeks before and after laying	W1F	W1F	W1E	W1E	W1E	W1G	W1G	W1G	S1CT	W1H
	68	69	70	71	72	68	69	70	72	71
19	-	-	-	-	0	-	-	-	-	-
18	-	-	-	0	0	-	-	0	-	-
17	-	-	-	0	2	-	-	0	-	-
16	-	-	-	6	4	-	-	0	-	-
15	-	22	-	30	8	-	-	0	-	-
14	-	36	-	27	4	-	-	4	-	-
13	-	43	-	21	24	-	2	21	-	-
12	-	51	-	14	38	-	14	22	-	-
11	-	43	-	20	22	-	13	45	-	-
10	-	52	-	25	14	-	3	35	-	-
9	-	49	60	50	17	-	17	40	-	-
8	-	33	105	52	3	-	15	58	-	-
7	-	97	45	54	13	-	12	29	-	-
6	-	59	36	51	18	-	3	52	-	-
5	-	68	47	47	10	-	16	48	-	-
4	52	63	24	90	27	-	35	22	-	-
3	91	91	34	126	23	-	16	43	-	-
2	93	105	51	120	48	-	20	38	-	-
1	86	110	68	99	95	-	26	59	-	-
********										
1	29	46	20	78	25	-	16	28	46	9
2	24	25	4	13	4	-	4	9	6	12
3	27	17	5	10	4	4	3	8	7	41
4	24	21	35	9	4	3	6	5	8	18
5	58	34	-	9	15	19	2	5	13	33
6	44	71	30	1	13	17	11	0	13	34
7	49	55	32	5	19	17	15	0	27	127
8	58	67	39	58	54	19	18	0	36	75
9	86	88	70	41	48	21	1	0	26	37
10	109	145	75	44	40	0	7	0	40	28
11	110	103	97	25	33	0	12	0	93	65
12	59	58	31	16	33	0	2	0	13	36
13	-	31	5	10	3	-	0	0	22	11
14	24	16	0	6	2	-	0	0	31	7
15	2	13	0	5	0	-	0	0	15	3
16	-	17	0	1	0	-	0	0	2	7
17	-	11	0	0	0	-	0	0	11	0
18	-	3	0	1	0	-	0	0	2	6
19	-	-	0	0	0	-	0	0	20	3
20	-	6	0	0	-	-	-	-	19	2
21	-	0	0	0	-	-	-	-	27	8
22	-	0	-	0	-	-	-	-	4	3
23	-	-	-	-	-	-	-	-	0	0
24	-	-	-	-	-	-	-	-	0	-
				**			**	***		

Male activity (Contd.)

Weeks	W1D	W1D	W1D	E1D	E1D	E1D	W1B	W1B	W1B	W1B	W1B
	70	71	72	69	70	71	68	69	70	71	72
19	-	-	-	-	-	-	-	-	-	-	0
18	-	-	0	-	-	-	-	-	-	-	0
17	-	0	0	-	-	5	-	-	-	-	0
16	-	0	0	-	0	21	-	-	-	0	0
15	-	0	0	-	0	66	-	-	-	0	0
14	-	0	0	-	0	31	-	-	-	0	0
13	-	0	0	-	59	35	-	-	-	0	0
12	-	2	0	-	129	21	-	-	-	0	0
11	-	0	0	-	119	6	-	-	-	0	0
10	-	7	0	-	74	26	-	-	-	0	15
9	-	4	0	-	78	23	-	-	-	1	26
8	-	0	0	-	82	31	-	-	-	21	32
7	-	2	0	-	24	16	-	-	1	31	16
6	-	56	17	-	23	22	-	-	2	37	17
5	-	50	29	-	56	26	-	-	4	69	12
4	-	108	52	-	63	36	-	-	34	26	58
3	-	58	44	-	56	33	45	-	49	65	52
2	-	69	66	-	50	30	76	-	80	55	48
1	-	61	81	-	95	73	83	-	85	99	114
*******											
1	40	30	25	-	41	45	34	-	47	45	54
2	12	8	4	-	10	13	12	13	12	1	12
3	3	7	1	7	11	17	15	7	8	1	3
4	-	3	5	11	6	8	-	2	6	7	1
5	13	14	14	6	18	30	19	8	15	13	15
6	-	14	17	8	37	7	25	21	22	15	12
7	-	14	20	13	41	0	43	19	30	18	41
8	23	14	21	33	45	0	79	29	45	17	23
9	23	16	34	70	44	0	66	27	64	38	34
10	23	15	26	91	21	0	30	-	75	27	22
11	33	19	18	81	50	0	30	-	49	53	27
12	55	15	28	39	48	0	9	-	18	27	27
13	53	12	16	19	51	0	0	-	37	24	0
14	33	9	9	36	42	0	-	0	30	13	0
15	7	12	2	7	19	0	-	0	27	5	0
16	4	8	2	22	7	0	-	0	2	1	0
17	1	11	4	6	14	0	-	0	0	0	0
18	1	14	2	2	2	0	-	0	0	0	0
19	3	-	1	6	5	0	-	-	0	0	0
20	-	-	0	3	13	-	-	-	-	0	-
21	-	-	-	0	0	-	-	-	-	-	-
22	-	-	-	0	0	-	-	-	-	-	-
23	-	-	-	0	0	-	-	-	-	-	-
	**			**		***					

Female attendance

Site and year

Weeks before and after laying	W1F	W1F	W1E	W1E	W1E	W1G	W1G	W1G	S1CT	W1H
	68	69	70	71	72	68	69	70	72	71
18		-	-	9	-	-	-	0	-	-
17	-	-	-	8	-	-	-	0	-	-
16	-	-	-	30	-	-	-	3	-	-
15	-	19	-	80	-	-	-	19	-	-
14	-	21	-	49	-	-	-	24	-	-
13	-	58	-	43	-	-	75	50	-	-
12	-	74	-	34	-	-	68	75	-	-
11	-	64	-	51	-	-	72	82	-	-
10	-	75	96	67	-	-	64	73	-	-
9	-	66	71	56	-	-	10	73	-	-
8	-	16	84	75	61	-	23	81	-	-
7	-	22	90	58	70	-	23	62	-	-
6	-	17	92	85	76	-	17	74	-	-
5	-	21	80	53	59	-	46	63	-	-
4	53	31	57	74	60	-	76	60	-	-
3	37	69	68	71	75	-	48	71	-	-
2	69	70	83	77	68	-	78	66	-	-
1	56	68	84	88	83	-	82	79	-	-
*******										
1	51	54	67	82	58	-	68	67	65	44
2	45	52	62	61	50	-	79	57	56	46
3	45	51	64	68	47	61	79	64	69	47
4	48	41	67	62	56	63	59	93	62	49
5	47	47	-	61	53	58	85	98	59	54
6	47	47	66	57	43	71	42	85	55	47
7	41	53	58	55	46	67	30	9	59	53
8	33	53	68	60	31	36	41	*	52	63
9	23	58	69	65	48	5	31	3	53	54
10	16	46	55	71	36	9	37	1	42	43
11	11	20	42	52	17	9	19	*	42	43
12	11	26	45	40	22	*	9	1	53	30
13	-	14	23	41	26	-	0	5	45	28
14	7	37	6	36	32	-	0	3	30	16
15	0	36	0	36	2	-	0	5	24	23
16	-	17	0	30	0	-	0	1	3	8
17	-	24	0	20	*	-	0	*	4	19
18	-	11	0	4	0	-	0	0	7	5
19	-	-	0	20	0	-	0	-	4	6
20	-	12	0	10	-	-	-	-	5	5
21	-	0	0	9	-	-	-	-	0	7
22	-	0	-	0	-	-	-	-	0	1
23	-	-	-	-	-	-	-	-	0	0
24	-	-	-	-	-	-	-	-	0	0
				**			**	***		

Female attendance (Contd.)

Week	Site and year										
	W1D	W1D	W1D	E1D	E1D	E1D	W1B	W1B	W1B	W1B	W1B
	70	71	72	69	70	71	68	69	70	71	72
18	-	-	0	-	-	-	-	-	-	-	-
17	-	-	0	-	-	4	-	-	0	-	-
16	-	-	0	-	-	24	-	-	0	0	-
15	-	-	0	-	-	32	-	-	0	0	-
14	-	-	0	-	-	68	-	-	0	0	-
13	-	-	0	-	-	84	-	-	0	0	-
12	-	-	0	-	-	43	-	-	*	0	-
11	-	-	0	-	-	10	-	-	0	0	-
10	-	-	0	-	-	40	-	-	1	0	-
9	-	-	0	-	-	42	-	-	0	0	-
8	-	-	0	-	-	34	-	-	0	7	-
7	-	-	0	-	82	53	-	-	6	46	-
6	-	-	35	-	85	56	-	-	4	43	-
5	-	-	39	-	79	69	-	-	1	45	-
4	-	-	43	-	76	56	-	-	64	65	-
3	-	-	51	-	72	78	65	-	46	43	32
2	-	-	53	-	69	75	61	-	51	56	46
1	-	-	64	-	90	90	73	-	75	78	58
******											
1	-	59	47	-	70	71	41	-	49	69	48
2	-	49	42	-	51	54	43	54	59	50	45
3	-	57	49	25	57	53	51	44	44	45	47
4	-	55	58	43	49	61	-	57	49	41	49
5	-	54	57	36	55	53	45	52	45	55	52
6	-	55	53	40	63	90	49	49	46	47	54
7	-	62	56	44	68	83	45	64	46	56	52
8	-	53	46	38	59	55	43	53	50	56	28
9	-	56	23	45	61	55	30	60	52	53	31
10	-	48	16	55	50	51	16	-	40	33	16
11	-	39	3	44	50	55	4	-	32	38	5
12	-	37	5	63	46	30	2	-	44	44	11
13	-	22	9	37	57	20	0	-	30	27	23
14	-	19	13	47	48	4	-	0	7	18	14
15	-	9	11	6	22	0	-	0	16	30	6
16	-	8	3	10	14	0	-	0	0	4	1
17	-	7	1	7	6	0	-	0	0	0	0
18	-	9	*	14	0	0	-	0	0	0	0
19	-	-	0	3	1	0	-	-	0	0	0
20	-	-	0	1	0	-	-	-	-	0	-
21	-	-	-	0	0	-	-	-	-	-	-
22	-	-	-	0	0	-	-	-	-	-	-
23	-	-	-	0	0	-	-	-	-	-	-
	**			**		***					

Female activity

Weeks before and after laying	Site and year									
	W1F	W1F	W1E	W1E	W1E	W1G	W1G	W1G	S1CT	W1H
	68	69	70	71	72	68	69	70	72	71
18	-	-	-	25	-	-	-	0	-	-
17	-	-	-	44	-	-	-	0	-	-
16	-	-	-	48	-	-	-	23	-	-
15	-	15	-	41	-	-	-	109	-	-
14	-	17	-	32	-	-	-	145	-	-
13	-	20	-	43	-	-	51	119	-	-
12	-	32	-	29	-	-	26	134	-	-
11	-	36	-	20	-	-	42	78	-	-
10	-	30	29	25	-	-	55	106	-	-
9	-	33	30	20	-	-	36	86	-	-
8	-	16	23	28	16	-	67	80	-	-
7	-	80	15	21	12	-	55	70	-	-
6	-	58	19	23	7	-	63	88	-	-
5	-	55	20	47	9	-	50	67	-	-
4	23	62	14	33	10	-	42	58	-	-
3	21	39	16	27	19	-	41	88	-	-
2	28	32	22	34	23	-	48	76	-	-
1	58	39	18	39	53	-	43	87	-	-
*********										
1	28	39	18	21	14	-	6	27	23	11
2	31	17	3	13	3	-	4	3	3	9
3	11	10	4	0	0	4	10	0	0	8
4	25	16	7	1	1	-	5	6	2	6
5	32	43	-	0	11	19	5	20	16	21
6	36	49	18	5	14	10	50	44	13	16
7	60	44	27	8	15	32	48	14	37	53
8	40	37	21	21	14	41	72	2	56	58
9	43	52	46	44	25	82	80	8	37	31
10	34	94	83	57	54	65	71	3	83	20
11	48	88	81	46	48	19	63	1	146	28
12	18	33	11	27	40	23	25	3	125	64
13	-	13	14	25	15	-	0	6	87	49
14	18	12	3	20	7	-	0	11	46	14
15	0	18	0	26	1	-	0	21	36	22
16	-	13	0	27	0	-	0	4	7	18
17	-	23	0	16	1	-	0	5	17	23
18	-	7	0	6	0	-	0	0	26	6
19	-	-	0	28	0	-	0	-	19	14
20	-	8	0	14	-	-	-	-	18	11
21	-	0	0	12	-	-	-	-	0	17
22	-	0	-	0	-	-	-	-	0	3
23	-	-	-	-	-	-	-	-	0	0
24	-	-	-	-	-	-	-	-	0	-
				**			**	***		

Female activity (Contd.)

Weeks	W1D	W1D	W1D	E1D	E1D	E1D	W1B	W1B	W1B	W1B	W1B
	70	71	72	69	70	71	68	69	70	71	72
18	-	-	0	-	-	-	-	-	-	-	-
17	-	-	0	-	-	4	-	-	0	-	-
16	-	-	0	-	-	20	-	-	0	0	-
15	-	-	0	-	-	42	-	-	0	0	-
14	-	-	0	-	-	33	-	-	0	0	-
13	-	-	0	-	-	24	-	-	0	0	-
12	-	-	0	-	-	12	-	-	1	0	-
11	-	-	0	-	-	9	-	-	0	0	-
10	-	-	0	-	-	12	-	-	1	0	-
9	-	-	0	-	-	18	-	-	0	0	-
8	-	-	0	-	-	27	-	-	0	2	-
7	-	-	0	-	19	8	-	-	11	19	-
6	-	-	18	-	18	19	-	-	14	18	-
5	-	-	27	-	31	20	-	-	8	23	-
4	-	-	20	-	32	26	-	-	32	13	-
3	-	-	35	-	17	25	22	-	31	19	31
2	-	-	46	-	14	23	30	-	30	20	39
1	-	-	20	-	9	21	24	-	17	13	49
*******											
1	-	9	17	-	19	17	28	-	23	8	48
2	-	3	12	-	14	14	10	8	9	1	12
3	-	8	6	9	5	9	8	4	7	5	6
4	-	1	4	8	12	3	-	1	2	4	5
5	-	17	10	6	17	29	21	8	18	10	14
6	-	14	18	9	27	24	22	21	17	18	18
7	-	10	14	21	28	70	21	19	21	17	26
8	-	17	24	29	34	38	36	25	24	14	56
9	-	21	39	50	30	33	39	26	25	30	57
10	-	32	56	47	28	28	33	-	44	36	61
11	-	52	44	33	42	30	5	-	46	48	71
12	-	22	64	42	47	66	2	-	37	22	56
13	-	27	11	35	37	29	0	-	32	15	21
14	-	23	12	30	37	14	1	0	5	8	14
15	-	9	12	8	17	0	-	0	7	14	3
16	-	15	7	12	11	0	-	0	0	5	1
17	-	17	2	6	11	0	-	0	0	0	0
18	-	14	2	11	0	0	-	0	0	0	0
19	-	-	0	3	4	0	-	-	0	0	0
20	-	-	0	1	0	-	-	-	-	0	-
21	-	-	-	0	0	-	-	-	-	-	-
22	-	-	-	0	0	-	-	-	-	-	-
23	-	-	-	0	0	-	-	-	-	-	-
	**			**		***					

Pair attendance

	Site and year									
Weeks before and after laying	W1F 68	W1F 69	W1E 70	W1E 71	W1E 72	W1G 68	W1G 69	W1G 70	S1CT 72	W1H 71
18	-	-	-	0	-	-	-	0	-	-
17	-	-	-	0	-	-	-	0	-	-
16	-	-	-	10	-	-	-	0	-	-
15	-	12	-	53	-	-	-	0	-	-
14	-	15	-	29	-	-	-	2	-	-
13	-	47	-	19	-	-	2	30	-	-
12	-	65	-	13	-	-	17	61	-	-
11	-	54	-	26	-	-	16	64	-	-
10	-	57	-	22	-	-	*	59	-	-
9	-	52	41	18	-	-	4	54	-	-
8	-	13	59	37	45	-	3	68	-	-
7	-	14	38	43	22	-	1	36	-	-
6	-	10	47	32	25	-	1	43	-	-
5	-	12	31	31	19	-	13	28	-	-
4	25	21	32	43	14	-	8	19	-	-
3	19	44	16	28	8	-	10	23	-	-
2	44	26	9	20	6	-	10	9	-	-
1	20	35	13	21	13	-	22	27	-	-
*********										
1	2	3	1	11	1	-	*	2	4	-
2	1	1	*	3	*	-	*	*	*	*
3	1	*	*	*	*	*	*	*	*	6
4	1	1	*	*	*	*	*	*	1	2
5	2	1	-	*	*	1	*	*	*	1
6	2	3	1	*	*	*	1	0	*	1
7	2	2	1	*	1	*	10	0	1	5
8	2	4	5	2	1	*	11	0	2	5
9	*	3	2	6	*	0	*	0	6	9
10	3	7	4	11	1	0	2	0	4	2
11	4	6	18	11	3	0	2	0	6	5
12	6	11	22	17	3	0	1	0	1	3
13	-	4	*	6	4	-	0	0	16	2
14	7	14	0	5	0	-	0	0	13	4
15	0	21	0	2	0	-	0	0	6	2
16	-	2	0	*	0	-	0	0	0	1
17	-	4	0	0	0	-	0	0	1	0
18	-	1	0	0	0	-	0	0	0	*
19	-	-	0	0	0	-	0	0	2	*
20	-	3	0	0	-	-	-	-	3	0
21	-	0	0	0	-	-	-	-	0	1
22	-	0	-	0	-	-	-	-	0	1
23	-	-	-	-	-	-	-	-	0	0
24	-	-	-	-	-	-	-	-	0	-
				**			**	***		

Pair attendance (Contd.)

Weeks	W1D 70	W1D 71	W1D 72	E1D 69	E1D 70	E1D 71	W1B 68	W1B 69	W1B 70	W1B 71	W1B. 72
18	-	-	0	-	-	-	-	-	-	-	-
17	-	-	0	-	-	1	-	-	-	-	-
16	-	-	0	-	-	13	-	-	-	0	-
15	-	-	0	-	-	20	-	-	-	0	-
14	-	-	0	-	-	43	-	-	-	0	-
13	-	-	0	-	-	73	-	-	-	0	-
12	-	-	0	-	-	31	-	-	-	0	-
11	-	-	0	-	-	9	-	-	-	0	-
10	-	-	0	-	-	23	-	-	-	0	-
9	-	-	0	-	-	29	-	-	-	0	-
8	-	-	0	-	-	22	-	-	-	6	-
7	-	-	0	-	59	21	-	-	*	33	-
6	-	-	29	-	66	38	-	-	*	24	-
5	-	-	19	-	53	19	-	-	0	21	-
4	-	-	4	-	40	15	-	-	25	5	-
3	-	-	22	-	37	28	30	-	35	10	11
2	-	-	15	-	26	21	24	-	19	9	42
1	-	-	19	-	37	24	33	-	15	8	44
******											
1	-	*	5	-	19	16	2	-	4	1	14
2	-	*	*	-	*	*	*	*	1	*	1
3	-	*	*	*	*	*	*	*	*	*	*
4	-	*	*	*	*	*	-	*	*	*	*
5	-	*	*	*	*	2	1	*	1	*	1
6	-	*	1	*	2	*	1	*	1	*	2
7	-	*	4	1	5	0	*	*	1	*	1
8	-	1	1	4	4	0	1	*	2	*	1
9	-	1	*	6	5	0	*	*	11	2	1
10	-	1	1	5	3	0	*	-	5	2	*
11	-	6	*	4	6	0	0	-	8	3	*
12	-	5	*	1	9	0	*	-	17	10	0
13	-	4	3	2	15	0	0	-	20	7	0
14	-	3	3	1	18	0	-	0	2	7	0
15	-	1	2	*	9	0	-	0	13	3	0
16	-	1	0	1	1	0	-	0	0	0	0
17	-	1	0	*	2	0	-	0	0	0	0
18	-	3	0	2	0	0	-	0	0	0	0
19	-	-	0	0	0	0	-	-	0	0	0
20	-	-	0	0	0	-	-	-	-	0	-
21	-	-	-	0	0	-	-	-	-	-	-
22	-	-	-	0	0	-	-	-	-	-	-
23	-	-	-	0	0	-	-	-	-	-	-
	**			**		***					

Pair activity

Weeks before and after laying	Site and year									
	W1F	W1F	W1E	W1E	W1E	W1G	W1G	W1G	S1CT	W1H
	68	69	70	71	72	68	69	70	72	71
18	-	-	-	0	-	-	-	0	-	-
17	-	-	-	0	-	-	-	0	-	-
16	-	-	-	24	-	-	-	0	-	-
15	-	20	-	54	-	-	-	0	-	-
14	-	27	-	43	-	-	-	11	-	-
13	-	31	-	41	-	-	3	75	-	-
12	-	63	-	28	-	-	20	120	-	-
11	-	59	-	35	-	-	13	93	-	-
10	-	52	-	43	-	-	3	75	-	-
9	-	65	86	73	-	-	9	71	-	-
8	-	20	119	72	24	-	16	107	-	-
7	-	66	57	67	25	-	9	60	-	-
6	-	37	54	69	27	-	2	93	-	-
5	-	42	59	70	23	-	21	82	-	-
4	61	41	36	117	43	-	39	48	-	-
3	84	106	47	153	58	-	35	75	-	-
2	121	123	78	160	76	-	43	67	-	-
1	144	147	89	143	153	-	56	134	-	-
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1	56	85	43	104	46	-	27	56	74	-
2	51	42	14	22	14	-	6	25	16	25
3	34	28	16	17	11	12	6	16	14	56
4	48	37	17	16	12	4	13	7	17	31
5	89	77	-	16	33	35	4	5	35	59
6	77	118	50	13	34	26	22	0	35	56
7	103	96	46	20	39	13	26	0	59	138
8	56	91	43	68	33	5	24	0	64	85
9	30	82	57	56	25	0	2	0	37	64
10	19	80	58	65	19	0	10	0	25	36
11	27	26	87	39	10	0	20	0	16	53
12	12	26	22	22	9	0	2	0	7	28
13	-	8	2	12	2	-	0	0	24	12
14	11	8	0	6	0	-	0	0	31	6
15	0	17	0	2	0	-	0	0	18	3
16	-	7	0	1	0	-	0	0	0	3
17	-	7	0	0	0	-	0	0	6	0
18	-	3	0	0	0	-	0	0	0	2
19	-	-	0	0	0	-	0	0	9	1
20	-	6	0	0	-	-	-	-	12	0
21	-	0	0	0	-	-	-	-	0	4
22	-	0	-	0	-	-	-	-	0	3
23	-	-	-	-	-	-	-	-	0	0
24	-	-	-	-	-	-	-	-	0	-
				**			**	***		

Pair activity (Contd.)

Weeks	W1D	W1D	W1D	E1D	E1D	E1D	W1B	W1B	W1B	W1B	W1B
	70	71	72	69	70	71	68	69	70	71	72
18	-	-	0	-	-	-	-	-	-	-	-
17	-	-	0	-	-	5	-	-	-	-	-
16	-	-	0	-	-	23	-	-	-	0	-
15	-	-	0	-	-	105	-	-	-	0	-
14	-	-	0	-	-	54	-	-	-	0	-
13	-	-	0	-	-	56	-	-	-	0	-
12	-	-	0	-	-	25	-	-	-	0	-
11	-	-	0	-	-	12	-	-	-	0	-
10	-	-	0	-	-	26	-	-	-	0	-
9	-	-	0	-	-	37	-	-	-	0	-
8	-	-	0	-	-	48	-	-	-	14	-
7	-	-	0	-	48	23	-	-	1	42	-
6	-	-	31	-	40	35	-	-	1	49	-
5	-	-	56	-	84	50	-	-	0	83	-
4	-	-	72	-	96	62	-	-	55	38	-
3	-	-	85	-	76	65	72	-	72	70	57
2	-	-	114	-	70	60	108	-	103	68	77
1	-	-	107	-	110	96	114	-	105	115	145
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1	-	30	50	-	66	67	69	-	76	61	79
2	-	17	23	-	31	33	27	29	26	9	30
3	-	19	14	17	26	26	30	16	19	14	16
4	-	11	16	13	23	18	-	10	15	10	14
5	-	38	31	13	42	66	45	23	40	30	36
6	-	35	43	22	71	14	30	35	45	40	35
7	-	31	41	30	77	0	31	42	45	39	33
8	-	38	49	47	85	0	51	61	43	34	9
9	-	37	22	99	82	0	11	45	43	57	19
10	-	17	24	78	54	0	10	-	64	34	2
11	-	28	7	60	86	0	0	-	34	32	2
12	-	20	1	27	67	0	2	-	38	30	0
13	-	11	8	20	56	0	0	-	42	20	0
14	-	10	6	23	65	0	-	0	2	8	0
15	-	4	1	3	19	0	-	0	14	4	0
16	-	4	0	9	7	0	-	0	0	0	0
17	-	7	0	2	9	0	-	0	0	0	0
18	-	11	0	9	0	0	-	0	0	0	0
19	-	-	0	0	0	0	-	-	0	0	0
20	-	-	0	0	0	-	-	-	-	0	-
21	-	-	-	0	0	-	-	-	-	-	-
22	-	-	-	0	0	-	-	-	-	-	-
23	-	-	-	0	0	-	-	-	-	-	-
	**			**		***					

Site empty

Weeks before and after laying	W1F	W1F	W1E	W1E	W1E	W1G	W1G	W1G	S1CT	W1H
	68	69	70	71	72	68	69	70	72	71
18	-	-	-	91	-	-	-	100	-	-
17	-	-	-	92	-	-	-	100	-	-
16	-	-	-	68	-	-	-	97	-	-
15	-	73	-	16	-	-	-	81	-	-
14	-	60	-	47	-	-	-	64	-	-
13	-	11	-	53	-	-	17	20	-	-
12	-	2	-	62	-	-	21	6	-	-
11	-	1	-	38	-	-	21	10	-	-
10	-	7	-	5	-	-	37	15	-	-
9	-	2	6	7	-	-	89	17	-	-
8	-	78	-	15	*	-	78	6	-	-
7	-	68	6	37	11	-	78	10	-	-
6	-	78	2	8	4	-	83	6	-	-
5	-	72	12	41	*	-	45	7	-	-
4	1	56	39	16	*	-	22	11	-	-
3	3	4	12	15	0	-	34	11	-	-
2	0	3	*	3	*	-	11	9	-	-
1	0	*	*	*	*	-	5	2	-	-
******										
1	0	0	*	1	0	-	*	1	-	0
2	0	0	0	1	0	-	0	*	0	*
3	0	0	0	0	0	0	7	*	0	0
4	0	0	2	0	0	0	0	1	0	0
5	0	0	*	0	0	0	1	2	0	0
6	0	0	*	0	0	1	26	15	0	*
7	*	*	3	0	*	14	44	92	2	13
8	8	1	1	13	34	44	46	100	4	18
9	48	1	6	12	27	93	69	98	7	11
10	63	35	29	14	50	90	57	99	29	23
11	64	68	50	26	78	90	72	100	39	31
12	71	30	45	44	75	100	89	99	42	57
13	85	36	68	56	70	-	100	95	39	67
14	72	49	94	60	65	-	100	97	51	67
15	99	51	100	64	98	-	100	95	69	76
16	-	68	100	70	100	-	100	99	95	91
17	-	74	100	80	100	-	100	100	93	81
18	-	89	100	92	100	-	100	100	92	91
19	-	-	100	80	100	-	100	-	91	93
20	-	88	100	90	-	-	-	-	90	93
21	-	100	100	91	-	-	-	-	96	92
22	-	100	-	100	-	-	-	-	99	99
23	-	-	-	-	-	-	-	-	100	100
24	-	-	-	-	-	-	-	-	100	-
				**			**	***		

<u>Site empty</u> (Contd.)

Weeks	W1D	W1D	W1D	E1D	E1D	E1D	W1B	W1B	W1B	W1B	W1B
	70	71	72	69	70	71	68	69	70	71	72
18	-	-	100	-	-	-	-	-	-	-	-
17	-	-	100	-	-	96	-	-	-	-	-
16	-	-	100	-	-	73	-	-	-	100	-
15	-	-	100	-	-	63	-	-	-	100	-
14	-	-	100	-	-	29	-	-	-	100	-
13	-	-	100	-	-	9	-	-	-	100	-
12	-	-	100	-	-	37	-	-	-	100	-
11	-	-	100	-	-	85	-	-	-	100	-
10	-	-	100	-	-	49	-	-	-	100	-
9	-	-	100	-	-	36	-	-	-	100	-
8	-	-	100	-	-	50	-	-	-	86	-
7	-	-	100	-	2	13	-	-	94	39	-
6	-	-	46	-	*	39	-	-	96	27	-
5	-	-	11	-	4	6	-	-	99	27	-
4	-	-	13	-	2	15	-	-	22	6	-
3	-	-	1	-	4	0	*	-	6	30	36
2	-	-	1	-	0	0	*	-	10	20	27
1	-	-	0	-	0	1	0	-	*	*	21
******											
1	-	0	0	-	0	*	0	-	1	*	11
2	-	*	0	-	0	*	0	1	*	0	*
3	-	*	0	*	0	1	0	*	*	0	0
4	-	0	0	*	*	0	0	*	0	*	0
5	-	0	0	*	0	0	0	*	0	0	0
6	-	0	0	0	0	1	0	*	*	0	*
7	-	0	0	14	0	17	3	*	12	*	17
8	-	0	2	32	*	45	14	1	20	*	64
9	-	5	43	20	0	45	52	*	30	10	57
10	-	30	65	20	*	49	71	-	32	23	79
11	-	35	95	34	3	45	67	-	48	37	90
12	-	37	93	27	18	-	92	-	39	9	86
13	-	67	48	57	28	-	100	-	44	27	77
14	-	68	61	47	36	-	-	100	66	60	86
15	-	73	87	92	66	-	-	100	69	65	94
16	-	83	93	86	72	-	-	100	97	96	99
17	-	85	95	92	88	-	-	100	100	100	100
18	-	84	98	85	97	-	-	100	100	100	100
19	-	-	99	97	95	-	-	-	100	100	100
20	-	-	100	99	98	-	-	-	-	100	-
21	-	-	-	100	100	-	-	-	-	-	-
22	-	-	-	100	100	-	-	-	-	-	-
23	-	-	-	100	100	-	-	-	-	-	-
	**			**		***					

APPENDIX 3

Table 4. Total, daylight and overnight attendance for E1D in 1971

Male			Female			Pair together			Site empty		
Total	Day	Night	Total	Day	Night	Total	Day	Night	Total	Day	Night
1	6	0	4	23	0	1	6	0	96	77	100
16	48	*	24	71	1	13	40	*	73	21	99
25	66	3	32	87	3	20	51	3	63	1	97
46	37	49	68	79	62	43	33	49	29	12	38
81	61	93	84	61	99	73	42	93	9	20	1
51	63	43	43	50	38	31	27	34	37	14	52
14	32	1	10	21	1	9	19	1	85	66	99
35	75	2	40	65	19	23	50	1	49	10	80
51	80	25	42	48	37	29	34	25	36	7	63
37	73	2	34	68	2	22	43	1	50	2	97
54	78	30	53	45	62	21	26	15	13	4	23
42	78	1	56	92	15	38	70	1	39	0	85
44	66	17	69	65	75	19	33	2	6	2	10
44	56	29	56	69	37	15	26	0	15	*	35
51	57	42	78	63	100	28	19	42	0	0	0
46	48	34	75	69	84	21	22	18	0	0	0
34	46	13	90	84	99	24	31	12	1	1	0
******											
45	46	44	71	65	81	16	11	24	*	*	0
46	44	52	54	57	48	*	*	0	*	*	0
46	54	28	53	45	72	*	*	0	1	1	0
40	50	15	61	50	85	*	*	*	0	0	0
49	51	43	53	51	58	2	2	*	0	0	0
9	12	*	90	88	97	*	*	*	1	*	*

MALE DISAPPEARED FROM THE COLONY

All figures represent weekly percentages of the time that individuals or the pair were present on the site, or the time that the site was left empty. Male and female attendances include their attendance as members of the pair.

Other conventions are those used in the preceding Appendix 2.

Table 5. Total, daylight and overnight attendance for W1E in 1971

Male			Female			Pair together			Site empty		
Total	Day	Night	Total	Day	Night	Total	Day	Night	Total	Day	Night
0	0	0	9	33	0	0	0	0	91	67	100
0	0	0	8	24	0	0	0	0	92	76	100
12	47	0	30	80	3	10	40	0	68	14	97
57	48	62	80	86	77	53	39	62	16	5	23
34	41	30	49	81	28	29	33	26	47	12	68
22	44	6	43	87	13	19	37	5	53	6	87
18	40	*	34	76	2	13	30	*	62	14	98
36	56	20	51	88	20	26	49	6	38	6	66
51	29	71	67	79	55	22	19	26	5	11	0
55	41	70	56	83	28	18	19	11	7	*	13
48	56	39	75	81	68	37	38	36	15	1	29
47	83	5	58	93	16	43	77	2	37	1	80
34	58	14	85	76	96	32	45	15	8	10	6
37	29	48	53	47	62	31	20	47	41	43	37
52	62	38	74	85	58	43	47	37	16	*	41
41	45	34	71	75	66	28	32	19	15	13	19
40	38	43	77	86	62	20	24	14	3	0	9
33	49	*	88	82	100	21	32	*	*	1	0

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Continued overleaf......

Table 5 (Contd.)

Male			Female			Pair together			Site empty		
Total	Day	Night	Total	Day	Night	Total	Day	Night	Total	Day	Night
28	38	7	82	73	94	11	16	1	1	5	0
41	39	47	61	63	53	3	2	7	1	*	0
32	40	11	68	60	86	*	*	0	0	*	0
38	44	22	62	58	73	*	*	0	0	2	0
39	54	0	61	47	100	*	*	0	0	0	0
43	31	75	57	70	25	*	*	0	0	0	0
45	32	81	55	68	20	*	*	0	0	*	0
30	41	2	60	53	75	2	3	1	13	8	24
30	34	19	65	68	56	6	9	1	12	7	25
26	36	6	71	65	84	11	15	4	14	14	14
33	39	21	52	61	32	11	15	3	26	15	50
34	48	11	40	50	21	17	26	2	44	30	70
10	14	2	41	52	21	6	9	1	56	43	79
9	13	1	36	57	4	5	7	*	60	37	96
2	4	0	36	52	11	2	3	0	64	47	89
*	*	*	30	48	5	*	*	0	70	52	95
0	0	0	20	33	3	0	0	0	80	67	97
1	1	0	4	7	1	0	0	0	92	92	99
0	0	0	20	38	*	0	0	0	80	62	100
0	0	0	10	21	*	0	0	0	90	79	100
0	0	0	9	9	0	0	0	0	91	91	100
0	0	0	0	0	0	0	0	0	100	100	100

All conventions used are those detailed at the start of Appendix 2

This site was monitored from 11 January until 3 October

Appendix 4.

Comparisons of attendance and activity of different pairs

W1F in 1968 and 1969 Figs. 7 and 8

This pair was breeding on this site for the 13th and 14th successive seasons, and was the most experienced breeding pair in the colony. Their pre-laying and post-breeding peaks of activity were higher than for any other pair studied. Also their steady and approximately equal attendance continued longer after laying than for other pairs (8 - 10 weeks). They obviously represent a highly-integrated pair.

In 1969 the "Kestrel depression" referred to in Section I occurred in April. The post-breeding resurgence of activity in this year was greater than in 1968, but no reason other than a climatic one can be suggested for this.

W1E in 1970, 1971 and 1972 Figs. 9, 10 and 11

The first two of these years involved the same pair (the female coming from the pair discussed above), but in the third year the female did not return and the male took a new mate.

In 1970 the very experienced female recorded a very high level of attendance throughout the season and indeed had been present on site W1F earlier awaiting the return of her mate (see Fig. 19). The activity of the male prior to laying was not very pronounced and hence the activity of the pair was fairly low. This male had only bred once before and this was the first time that the pair had been together.

The post-breeding peaks of activity of this pair were much higher than the pre-laying ones, suggesting that the pair were becoming adjusted to one another. This seems borne out by the data for 1971. The female again recorded a high level of attendance, although not as high as the previous year. The activity of the male built up much earlier and to a far higher level than the previous season, producing a massive pre-laying activity peak for the pair.

In the next year the male had to take a new mate. His peak of activity occurred only just before laying, although it reached a high level. This suggests that although the pair were still becoming integrated, the breeding experience which he had accrued from previous seasons was improving his performance.

The female had bred for four seasons previously (one year more than him) and recorded a normal attendance pattern. The post-fledging activity peaks were also standard.

W1G in 1968, 1969 and 1970 Figs. 12 and 13

The same pair was involved in all three years on this site. Only limited information is available for 1968, but it is noticeable that there was no post-breeding activity.

In 1969 the activity of the male was extremely feeble throughout the season. Normally a pair are together more than 100 times in the week before laying, but in this pair the peak was reduced to less than 60 times per week. The male deserted during incubation and although he later returned to continue incubating, the eggs did not hatch. Once again there was no post-breeding peak of activity.

Early in 1970, before the arrival of her mate, the female exhibited intense activity at the site. This might be due to her uncertainty or to searching for a male.

The activity of the male was again low and although the pre-laying peak was attained, this was mainly due to the activity of the female (the male only reaching 60 visits/week). Later the male disappeared during incubation and has not been seen since. The female, after very high site attendance attempting to compensate for the absent male, rapidly deserted the site.

Thus, although the members of this pair were experienced breeding birds even before they came together in 1967, their co-ordination suffered progressive deterioration. This was due in large measure to the male, and although the female was able to compensate for some of his absences, there was probably little she could do to stimulate him to greater activity.

E1D in 1970 and 1971 Figs. 14 and 15

The activity of the female of this pair was very similar in both years (around 20 visits/week), as was her attendance (rising to 90 % prior to laying). In 1970 male attendance was also high during the two months before laying, and his activity was quite normal.

The following year, however, after a high peak of initial pair activity in late January, the activity of the male was at a level considerably lower than in 1970. This produced a poor pre-laying peak for the pair.

The male attended regularly throughout incubation but he disappeared 6 weeks after laying, leaving the female with two chicks. He has not been seen since and has presumably died. The female successfully compensated for the absence of the male, recording very high levels of attendance, until she took a new mate 10 days after being deserted, whereupon her attendance dropped to more normal levels.

The impending desertion of the male may have been indicated by his low activity before laying if it was due to his loss of "breeding drive". Alternatively, he may have been ailing physically and eventually have died at sea.

This pair were unusual in that they were together 16 % and 19 % of the first week of incubation in the two years, whereas normally members of a pair only meet at the times they change parental duties during this period. Also, they consistently recorded a high rate of changeover during incubation (see Tables 40a and 40b). Both of these observations may suggest that the pair-bond was relatively weak, requiring regular reinforcement to withstand the strain of incubation.

W1B in 1970, 1971 and 1972 Figs. 16 and 17

The male concerned in all three years was hatched at the colony and bred for the first time, aged 4 years, in 1970. After breeding with the same female in the first two years he took a new mate in 1972 when she failed to return.

Although the male was a first-breeder and his mate had only bred once before, the pair's records for attendance and activity were normal, although they started regular occupation of their site only a few weeks before laying.

The following year the pair occupied the site only about 7 weeks before laying, returning within a few days of each other. Occupation of the site was immediate, with each bird spending about 40 % of their time on the site during the week after arrival.

The records for 1971 do not suggest any marked improvement in the performance of the pair, despite the male now having bred before and the pair being more used to each other. This is perhaps not surprising in view of the very successful co-ordination achieved by the pair at their first attempt. Some measure of compatibility is likely to be necessary between the partners before this can happen.

The male once more returned late in the season in 1972 (about 10 weeks before laying) and had to take a new mate. This new female had only bred once before and appeared nervous on the site. The male had to spend more time than normal on the site before laying, possibly to encourage the female also to remain on the site. The pair eventually bred quite successfully in that season.

W1D in 1970, 1971 and 1972 Fig. 18

This male was also hatched at the North Shields colony and bred first aged 4 years on W1B in 1969 (for which some data exist). The next year he transferred to site W1D where he bred with a female of one year's breeding experience. This pair then bred for two further years on the same site.

The performance of the pair was quite successful in the first instance and did not appear to improve radically. This parallels the case on site W1B mentioned above. A further parallel exists in the late return to their sites of both pairs.

On W1D the pair did not take up permanent occupation of the site until as late as only 6 weeks before laying. The partners tended to return within a few days of each other. Despite their late return the pair bred normally.

Such late-returning pairs, although apparently successful, are uncommon among the population. They do, however, show that it is possible for inexperienced birds breeding together for the first time to successfully integrate their activities over a short period of time.

W1C in 1970 and 1971

Information for this inexperienced breeding pair was collecting, using time-lapse photography. Both members of the pair bred for the first time in 1970 and for the second time together in 1971.

In 1970 (Table 6) they occupied the site only 5 - 6 weeks before laying their eggs, but despite this they managed to raise two young to fledging. Their pattern of attendance was a normal one.

Table 6. Weekly attendance of a pair breeding for the first time

W1C 1970

Weekly period ending	Percentage of daylight spent on site by			Percentage daylight that site empty
	Male	Female	Pair	
15/4	0	0	0	100
22	0	0	0	100
29	0	15	0	85
6/5	7	24	1	70
13	34	33	14	47
20	57	54	44	33
27	43	56	16	17
3/6	39	70	12	3
**** E				
10	45	67	12	0
17	52	48	*	0
24	29	71	*	0
1/7	51	49	*	0
**** H				
8	51	50	*	0
15	56	44	*	0
22	54	43	*	3
29	46	31	*	23
5/8	32	9	*	59
12	18	4	*	78
19	23	1	0	76
**** F				
26	14	6	*	80
2/9	3	1	0	96
9	0	0	0	100
16	0	0	0	100
23	0	0	0	100
30	0	0	0	100

*** E indicates egg-laying date; H = hatching date; F = fledging date

* indicates present on site but attendance less than 1 %

The attendance of male and female partners includes their attendance as members of the pair

Table 7. Weekly attendance of a pair breeding for the second time

W1C 1971

Weekly period ending	Percentage of daylight spent on site by			Percentage daylight that site empty
	Male	Female	Pair	
20/3	7	3	3	93
27	82	91	75	2
3/4	81	71	54	2
10	74	85	59	*
17	67	58	25	*
24	69	72	44	3
1/5	66	60	26	*
8	55	59	14	0
15	38	80	18	0
**** E				
22	52	49	1	0
29	37	62	*	0
5/6	49	51	*	0
EGGS STOLEN			EGGS STOLEN	
12	37	30	2	35
19	19	11	0	70
26	9	5	2	88
3/7	28	24	4	52

**** E indicates the date of egg-laying

* indicates that the bird(s) were present or absent but the value was less than 1 %

The attendance of male and female partners includes their attendance as members of the pair

Table 8. Pair activity and nest-building before egg laying in a pair breeding for the first time

W1C 1970

Weekly period ending	Weeks before laying	Pair activities				Nest-building activities									
						A		B		C		D		E	
		Cops	Begs	Feeds	Calls	m	f	m	f	m	f	m	f	m	f
15/4	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6/5	5	0	0	0	0	0	0	2	0	0	0	0	0	0	0
13	4	0	5	0	2	0	0	4	0	1	0	0	0	0	0
20	3	2	2	0	5	0	0	3	0	0	2	0	0	0	0
27	2	3	13	3	2	3	13	0	0	1	3	0	3	0	2
3/6	1	13	8	1	1	20	35	2	2	1	0	0	1	0	24

Column headings :

Cops = copulation attempts

Begs = food-begging attempts

Feeds = successful courtship feeds

Calls = mutual calling between pair members

A = sideways and frontal building

B = pecking at the nest

C = manipulating nest material

D = paddling (also called trampling)

E = bracing/scraping (forming the nest cup)

m and F indicate that the activity was performed by the male or the female respectively

Information obtained by time-lapse photography and hence the weekly totals above are for the daylight period only

Table 9. Pair activity and nest-building before egg-laying in a pair breeding for the second time

W1C 1971

Weekly period ending	Weeks before laying	Pair activities				Nest-building activities									
						A		B		C		D		E	
		Cops	Begs	Feeds	Calls	m	f	m	f	m	f	m	f	m	f
20/3	9	0	4	0	3	0	0	0	0	2	0	0	0	0	0
27	8	1	3	0	6	0	0	3	3	2	0	0	0	0	0
3/4	7	1	10	1	17	0	0	1	12	0	0	0	0	0	0
10	6	5	4	1	14	0	1	3	13	1	1	0	0	0	1
17	5	1	8	0	7	1	2	6	7	2	1	0	0	0	0
24	4	2	3	0	13	0	2	5	12	3	0	1	1	0	0
1/5	3	5	10	1	9	3	12	4	6	0	2	2	1	3	6
8	2	11	36	3	5	Large percentage of the daylight period									
15	1	13	48	16	8										

Column headings :

Cops = copulation attempts

Begs = food-begging attempts

Feeds = successful courtship feeds

Calls = mutual calling between pair members

A = sideways and frontal building

B = pecking at the nest

C = manipulating nest material

D = paddling (also called trampling)

E = bracing/scraping (forming the nest cup)

m and f indicate that the activity was performed by the male or female respectively

Information obtained using time-lapse photography and hence the weekly totals above are for the daylight period only

The following year (Table 7) they occupied the site much earlier and recorded much higher attendances. The two eggs were laid normally but stolen by vandals three weeks after laying. This immediately resulted in the site being left vacant for much of the time, and although the pair were present together for a further 5 - 6 weeks, thereafter only the male was seen occasionally.

The very low levels of pair activity and nest-building activity in 1970, prior to egg-laying (Table 8), may well be linked to the lack of breeding experience of the two partners.

In 1971, not only do these activities start much earlier, but they reach much higher levels (Table 9). It is interesting to note that the number of copulation attempts just before laying was the same in both seasons.

E1C in 1970 and 1971

The male non-breeding pair bred first aged 5 years in 1966 on site E1C and bred there until 1968. From 1969 to 1971 he occupied the site with a mate, but the pair did not lay any eggs.

The female bred from 1963 to 1967 on the adjacent site. From 1968 until 1971 she was paired (from 1969 with the male above) but did not lay.

Information was collected using the time-lapse photographic method in 1970 and 1971. In 1970 the pair occupied the site early and regularly, remaining together on the site for much of the time. Thereafter, however, they showed a reversal of the normal trend and left the site almost unoccupied at the peak laying time for the population. After another period of site occupation the pair deserted the site in June and July.

In 1971 the pair again returned early to the site and spent much time on it together. However, about 5 weeks before the mean laying date for the colony the male attendance decreased and eventually the female also disappeared from the site almost entirely. Regular checks in both years ensured that the pair were not present elsewhere in the colony.

The pair returned to their site at the time when chicks were present at the colony and they remained late into the season. This late attendance recorded in 1971 was not seen in 1970 although the earlier part of the season was similar in both years.

In the following year the pair once more returned to the site early in the season, but the male was shot by vandals on 21 February. The female then moved to an adjacent site where she paired and bred successfully.

Examination of the male revealed that a fish-hook had perforated his gut and encysted, displacing the testes and kidneys. This may well have accounted for his poor breeding performance in recent years, despite previous breeding success.

In both years pair activities were few, consisting mainly of mutual calling. No copulation attempts were recorded and no attempt was made in either year to build a nest. The pair spent most of their time on the site just standing, either alone or together.

Table 10. Attendance of the non-breeding pair on site E1C in 1970 (Information obtained for the daylight period only, using the time-lapse photographic technique)

Weekly period ending	Percentage of daylight spent on site by			Percentage daylight that site empty
	Male	Female	Pair	
5/3	64	62	36	10
12	82	59	44	3
19	62	67	34	5
26	66	63	33	4
2/4	54	56	29	19
9	60	64	31	7
16	62	53	23	8
23	40	35	11	36
30	33	7	1	61
7/5	35	46	10	29
14	3	2	1	96
********				
21	41	25	4	38
28	66	56	26	4
4/6	47	24	3	32
11	24	3	2	75
18	4	2	1	95
25	0	0	0	100
2/7	0	0	0	100
9	3	0	0	97
16	0	0	0	100
23	0	0	0	100
30	6	*	*	94
6/8	0	0	0	100
13	0	0	0	100
20	0	0	0	100
27	0	0	0	100

Percentage attendances of male and female include their attendance as part of the pair

******** indicates the mean laying date for the colony.

* indicates present at the site but less than 1 % attendance

Table 11. Attendance of the non-breeding pair on site E1C in 1971
(Information obtained for the daylight period only, using the time-lapse photographic technique)

Weekly period ending	Percentage of daylight spent on site by			Percentage daylight that site empty
	Male	Female	Pair	
19/2	49	44	28	35
26	38	48	29	43
5/3	38	58	31	35
12	62	77	48	9
19	32	42	18	44
26	21	47	2	34
2/4	29	63	3	11
9	19	65	2	19
16	6	33	1	62
23	15	22	4	66
30	15	38	13	60
7/5	3	24	13	60
14	3	10	1	88
********				
21	1	16	0	83
28	0	*	0	99
4/6	0	0	0	100
11	0	*	0	99
18	*	0	0	99
25	0	0	0	100
2/7	29	19	14	75
9	28	20	13	65
16	22	18	9	69
23	52	15	10	43
30	46	21	11	44
6/8	25	21	10	64

Percentage weekly attendance of male and female include their attendance as part of the pair

******** indicates the mean laying date for the colony

* indicates present at the site but less than 1 % attendance

W1H in 1971 and W2I in 1972

The male of this pair was ringed as a chick at the Dunbar colony in East Lothian, Scotland, in 1960 and bred first at North Shields in 1965. The female bred first in 1960 and has bred with the male above since 1967.

In 1967 and 1968 the pair bred on site W2I, the male having moved down one window from site W1H and the female from the adjacent W2H site. They moved up again to W1H where they bred in 1969, but down the following year to breed on site W2J. They were radioactively ringed in 1971 when they bred on W1H in a manner normal for a well-integrated pair. The male was only once recorded on site W2I during this season.

Upon their return in 1972 the pair spent most time on W1H early in the year but were also recorded regularly on W2I where they had bred some seasons previously. The activity of the male was very high as he alternated between the two sites, but the female remained more on W1H (Tables 12 and 13).

This unwillingness of the male to remain on one site appeared to unsettle the female. She started to build nests on both sites but only the one on W2I was completed two weeks before laying. At this point the female transferred to W2I where she eventually laid her eggs, and although the male regularly visited W1H, once incubation had started he confined his visits to the colony to site W2I.

The female disappeared during the second week after hatching, leaving the male to raise and fledge two chicks successfully. His activity at this time was extremely high and he was often present on W1H displacing an unmated female which had occupied this site (see Table 15). Possibly this enabled him to escape from the begging pressure of the chicks while still remaining close enough to defend them if necessary.

Thereafter his attendance at the colony waned rapidly, although he continued to frequent both sites. Such behaviour could only occur on edge sites since the more intense competition for sites in the centre of the colony would make defense of more than one site extremely difficult.

Much of the pre-laying behaviour of this pair was, therefore, carried out on a site where they did not lay their eggs. The pair was, however, a well-established one consisting of experienced individuals, and laid on a site where they had bred before. This suggests that the site may only be important as a focal point for the activities of the pair.

The attendance of unmated females

Female j on site W1F in 1970

This female returned in 1970 to the site where she had bred with the same male since 1956. He failed to return but she spent an increasing amount of time on the site during February, culminating in a week of almost total attendance (Fig. 19 in Section I).

She then moved to an adjacent site where she paired and bred successfully with another male in 1970 and 1971. The very high attendance recorded while awaiting the return of her mate probably reflects the strength of a pair-bond established over 14 breeding seasons.

Female 1 on sites W1G in 1971 and W1H in 1972

The deterioration of the pair c - 1 on site W1G from 1968 to 1970 has been discussed earlier, and resulted in the disappearance of the male in 1970. In the following year the female returned to W1G where the pair had bred for four years. Although the site was already occupied and defended by a pair which eventually bred there, records show her present very intermittently on the site from January through to April (Table 14). She was not subsequently seen at the colony that year.

In 1972 she returned to W1G which was again occupied by a breeding pair. After unsuccessfully attempting to establish herself there, she occupied a number of sites briefly before settling on site W1H.

Initially she was frequently scared off the site by a male which was defending this site as well as site W2I, but once he became caught up in the care of eggs and chicks on his breeding site she was able to occupy site W1H firmly (Table 15). Indeed, during this undisturbed period she recorded over 80 % attendance, and even when the male began again to displace her from the site, she was present regularly throughout August and intermittently into October.

This behaviour is probably only possible on edge sites since competition for sites in the centre of the colony is more intense. The apparent attachment of an unmated female to a site suggests the possibility that some older females may develop as "matriarchs", and this is discussed further in Section I.

Table 12. Weekly attendances by a pair occupying two sites (Pair h - t on sites W1H and W2I in 1972)

Weekly period ending	Male		Female		Pair		Site empty	
	W1H	W2I	W1H	W2I	W1H	W2I	W1H	W2I
18/1	20		4		2		78	
25	22		11		9		75	
1/2	37		44		19		38	
8	35		13		6		60	
15	24		22		12		66	
22	39		50		33		44	
29	49		63		36		24	
7/3	34		55		20		32	
14	54		48		35		32	
21	38		13		11		60	
28	42		16		12		55	
4/4	19		1		0		81	
11	39		30		15		46	
18	59		30		15		26	
25	54	22	18	51	6	9	34	18
2/5	22	6	9	12	1	0	70	82
9	20	2	29	8	6	1	57	89
16	36	-	34	-	20	-	50	-
23	19	-	9	-	2	-	49	-
****** E								
30	3	-	0	-	0	-	30	-
6/6	-	59	-	45	-	4	-	0
13	-	51	-	50	-	1	-	0
20	0	55	0	45	0	0.5	18	0
27	0	57	0	45	0	2	15	0
4/7	3	70	0	12	0	0.4	37	18
11	7	56					31	44
18	9	23		FEMALE			30	77
25	8	6					53	94
1/8	0	4		DISAPPEARED			16	96
8	1	15					48	85
15	0	0		FROM			45	100
22	2	4					66	96
29	2	1		COLONY			74	99
5/9	2	0					92	100
12	0	0					98	100
19	1	*					96	99
26	0	*					100	99
3/10	0	0					100	100
10	0.3	*					99	99
17	0	0					100	100
24	0	0					100	100
31	0	0					100	100

****** E indicates the date of egg-laying for this pair (on W2I).

* indicates presence but at very much less than 1 % attendance

All figures represent percentage weekly attendances, and the attendances of male and female include their attendance as members of the pair. A dash indicates that no information was available for that week, and there are no records for site W2I before 19/4.

Table 13. Weekly totals of visits to sites W1H and W2I in 1972 by the members of a pair occupying both sites

Weekly period ending	Male		Female		Pair	
	W1H	W2I	W1H	W2I	W1H	W2I
18/1	43		21		4	
25	52		14		24	
1/2	67		18		40	
8	74		21		29	
15	66		38		35	
22	82		34		66	
29	80		29		51	
7/3	121		45		46	
14	120		11		44	
21	164		7		3	
28	178		14		14	
4/4	114		1		0	
11	142		22		38	
18	177		35		78	
25	166	131	46	29	47	90
2/5	96	34	32	44	7	0
9	119	32	37	46	81	6
16	60	-	28	-	71	-
23	109	-	11	-	30	-
****** E						
30	28	-	0	-	0	-
6/6	-	57	-	10	-	66
13	-	23	-	6	-	29
20	0	9	0	5	0	14
27	0	32	0	26	0	57
4/7	72	149	0	16	0	31
11	100	255				
18	77	248				
25	46	163		FEMALE		
****** F						
1/8	0	66		DISAPPEARED		
8	3	50				
15	0	0		FROM		
22	7	12				
29	3	2		COLONY		
5/9	2	0				
12	0	0				
19	2	1				
26	0	2				
3/10	0	0				
10	1	2				
17	0	0				
24	0	0				
31	0	0				

All figures represent the number of visits per week, and in the case of the pair it is the number of times per week that the pair came together on the site.

****** E indicates the date of egg-laying and F that of fledging of the chicks. A dash indicates that no data were available.

Table 14. Visits of an unpaired female to site W1G in 1971

Weekly period ending	Number of mins spent on site	Number of visits made to site
19/1	32	1
26	155	11
2/2	54	9
9	0	0
16	38	5
23	63	3
2/3	36	4
9	27	2
16	0	0
23	0	0
30	0	0
6/4	107	2
13	0	0
20	0	0
27	0	0
4/5	0	0

This site was occupied regularly by the pair which eventually bred there in 1971, from the last week in January onwards. Most of the visits to the site, recorded above, were made by the unmated female in the early morning (around dawn) or just after sunset.

Table 15. Attendance and activity at site W1H in 1972 by an unmated female and by the breeding male from W2I

Weekly period ending	Unmated female		Breeding male		Site empty
	Attendance (%)	Visits	Attendance (%)	Visits	
23/5	25	57	19	109	56
30/5	67	43	3	28	30
No information available during the intervening period					
20/6	82	63	0	0	18
27	85	124	0	0	15
4/7	60	80	3	72	37
11	63	67	7	100	31
18	61	59	9	77	30
25	40	104	8	46	53
1/8	64	68	0	0	16
8	50	70	1	3	48
15	55	41	0	0	45
22	32	26	2	7	66
29	24	17	2	3	74
5/9	6	10	2	2	92
12	2	6	0	0	98
19	3	11	1	2	96
26	0	0	0	0	100
3/10	0	0	0	0	100
10	0.3	3	0.3	1	99.4

The unpaired female was first seen at the colony on 24 January, and subsequently on a number of different sites. She was first recorded on this site on 21 April but did not occupy it regularly until 13 May.

The male bred successfully on site W2I, but his mate disappeared on 1 July when the chicks were 8 - 10 days of age. He subsequently raised both chicks to fledging alone.

Neither individual was seen after 10 October, and monitoring of the site was discontinued on 6 November.

APPENDIX 5. Percentage hourly distribution of the start of incubation stints

Hour stint started	Stints lasting overnight			Daytime stints		
	Male	Female	Total	Male	Female	Total
0001-0100	0	0	0	0	0	0
-0200	0	0	0	0	1	0.25
-0300	0	0	0	1	1	1
-0400	0	0	0	3	4	3
-0500	1	4	3	9	10	10
-0600	2	5	4	23	23	23
-0700	1	4	3	11	10	11
-0800	2	1	1	7	5	7
-0900	1	1	1	5	4	5
-1000	4	1	2	8	6	7
-1100	2	0	1	4	4	4
-1200	4	1	2	6	3	5
-1300	4	4	4	6	6	6
-1400	10	6	7	5	4	4
-1500	7	6	7	4	5	5
-1600	11	11	11	2	6	4
-1700	6	13	10	1	4	2
-1800	12	12	12	3	1	2
-1900	10	9	9	1	2	1
-2000	12	8	10	1	0	0.5
-2100	5	10	8	0	1	0.25
-2200	4	4	4	0	0	0
-2300	2	1	1	0	0	0
2301-2400	2	1	1	0	0	0
Sample sizes	113	154	267	217	175	392

An overnight stint was one during which the bird was incubating at midnight (2400). A daytime stint was any other period of incubation.

APPENDIX 6. Number of times per day that partners alternated incubation duties during the course of incubation (changeover rate)

Day of incubation	Mean rate
1	8.29
2	8.17
3	7.11
4	5.56
5	4.67
6	3.53
7	3.19
8	3.19
9	2.86
10	3.05
11	2.43
12	2.81
13	2.52
14	1.90
15	2.55
16	2.41
17	1.95
18	1.82
19	2.00
20	2.09
21	1.95
22	1.77
23	1.50
24	1.73
25	1.77

Hatching starts

	Rates	
Day	Hatched	Failed to hatch
26	2.00	1.3
27	2.31	2.0
28	3.76	1.8
29	5.29	1.5
30	5.41	1.5
31	6.13	1.5
32	6.13	2.0
33	5.88	1.5
34	5.94	1.3
35	5.94	1.8
36	6.67	1.8
37	5.69	2.0
38	6.19	2.0
39	6.40	1.7

95 % confidence limits lie between ± 25 - 45 % of mean rates

The first egg was laid on day 1 of incubation. Means calculated for 22 pairs up to day 25 when hatching started. Thereafter for 17 pairs whose eggs hatched, and separately for 4 pairs whose eggs failed to hatch.

APPENDIX 7. Diurnality in times of changeover during and after incubation

Hourly period	Number of changeovers	
	During incubation	After hatching
0001-0100	5	22
0101-0200	4	12
0201-0300	12	19
0301-0400	33	54
0401-0500	116	128
0501-0600	245	94
0601-0700	164	68
0701-0800	109	74
0801-0900	77	104
0901-1000	71	93
1001-1100	59	99
1101-1200	73	86
1201-1300	94	118
1301-1400	97	93
1401-1500	99	90
1501-1600	112	105
1601-1700	121	95
1701-1800	122	114
1801-1900	109	110
1901-2000	79	108
2001-2100	66	79
2101-2200	31	56
2201-2300	9	41
2301-2400	8	31
Totals	1915	1893

During incubation : from the day on which the first egg was laid until the day before it hatched

After hatching : the 20 days after the first egg had hatched

Totals are for all 22 pair-years from 1968 - 1972.
Mean of 87 changeovers/pair/years during the incubation period.

APPENDIX 8 Common and specific names of animals mentioned

Common name	Specific name	
Adelie Penguin	Pygoscelis adeliae	Hombron & Jacquinot
Bengalese Finch	Lonchura striata	
Black Guillemot	Cepphus grylle	L.
Black Noddy	Anous tenuirostris	Temminck
Budgerigar	Melopsitacus undulatus	Shaw
Canary	Serinus canaria	L.
Carmine Bee-eater	Merops nubicoides	
Common Guillemot	Uria aalge	Pontoppidan
Common Tern	Sterna hirundo	L.
Crested Tern	Sterna bergii	Lichenstein
Fairy Tern	Gygis alba	Sparrman
Fulmar	Fulmarus glacialis	L.
Gannet	Sula bassana	L.
Gulls :		
Black-billed	Larus bulleri	
Black-headed	L. ridibundus	L.
California	L. californicus	Lawrence
Common	L. canus	L.
Glaucous-winged	L. glaucescens	Naumann
Greater Black-backed	L. marinus	L.
Herring	L. argentatus	Pontoppidan
Iceland	L. glaucoides	Meyer
Ivory	Pagophila eburnea	Phipps
Kittiwake, Black-legged	Rissa tridactyla	L.
Kittiwake, Red-legged	Rissa brevirostris	Bruch
Laughing	Larus atricilla	L.
Lesser Black-backed	L. fuscus	L.
Red-billed	L. novaehollandiae scopulinus	Forster
Swallow-tailed	Creagrus furcatus	Neboux
Thayer's	Larus thayeri	Brooks
Western	L. occidentalis	Audubon
House Sparrow	Passer domesticus	L.
Indigo Bunting	Passerina cyanea	
Kestrel	Falco tinnunculus	L.
Little Auk	Plotus alle	L.
Mallard	Anas platyrhynchos	L.
Ring Dove	Streptopelia risoria	L.
Rook	Corvus frugilegus	L.
Royal Tern	Sterna m. maxima	Boddaert
Sandwich Tern	Sterna sandvicensis	Latham
Shag	Phalacrocorax aristotelis	L.
Starling	Sturnus vulgaris	L.
White-flanked Flycatcher	Batis molitor	
Zebra Finch	Poephila guttata	

REFERENCES

AINLEY, D.G. & SCHLATTER, R.P. 1972. Chick raising ability in Adélie Penguins. Auk 89 : 559-566.

ASHMOLE, N.P. & TOVAR, S.H. 1968. Prolonged parental care in Royal Terns and other birds. Auk 85 : 90-100.

BAERENDS, G.P. & DRENT, R.H. (Eds.). 1970. The Herring Gull and its egg. Behaviour, Suppl. 17.

BARTH, E.K. 1949. Redetemperaturer og rugevaner. Naturen (Bergen) 73 : 81-95.

BARTH, E.K. 1955. Egg-laying, incubation and hatching of the Common Gull (Larus canus). Ibis 97 : 222-239.

BATT, B.D.J. & CORNWELL, G.W. 1972. The effects of cold on Mallard embryos. J. Wildl. Mgmt. 36(3) : 745-751.

BEER, C.G. 1965. Clutch size and incubation behaviour in Black-billed Gulls (Larus bulleri). Auk 82 : 1-18.

BEER, C.G. 1966. Incubation and nest building behaviour in Black-headed Gulls. V : The post-hatching period. Behaviour 26 : 189-214.

BEER, C.G. 1970. On the response of Laughing Gull chicks (Larus atricilla) to the calls of adults.
I. Recognition of voices of parents
II. Age changes and responses to different types of call.
Anim. Behaviour 18(4) : 652-660, 661-677.

BELOPOL'SKII, L.O. 1961. Ecology of sea colony birds of the Barents Sea. Jerusalem; Israel Program for Scientific Translations.

BROCKWAY, B.F. 1964. Ethological studies of the budgerigar : reproductive behaviour. Behaviour 23 : 294-324.

BROCKWAY, B.F. 1965. Stimulation of ovarian development and egg laying by male courtship vocalisation in budgerigars. (Melopsittacus undulatus). Anim. Behav. 13 : 575-578.

BROWN, R.G.B. 1967. Courtship behaviour in the Lesser Black-backed Gull (Larus fuscus). Behaviour 29 : 122-153.

BRUEN, K. & DUNHAM, D.W. 1973. Effects of social stimuli on nest building in the Zebra finch (Poephila guttata). Anim. Behav. 21 : 183-190.

BUCKLEY, P.A. 1966. Foot paddling in Four American Gulls with comments on its possible functions and stimulation. Z. Tierpsychol. 23 : 395-402.

BUCKLEY, P.A. & BUCKLEY, F.G. 1972. Individual egg and chick recognition by adult Royal Terns (Sterna maxima maxima). Anim. Behav. 20 : 457-462.

BURGER, J.W. 1942. The influence of some external factors in the ovarian cycle of the female starling. Anat. Rec. 84 : 518.

BUTTERFIELD, P.A. 1970. The Pair Bond in the Zebra Finch. in CROOK, J.H. (Ed.). Social Behaviour in Birds and Mammals. London.

COOMBS, C.J.F. 1960. Observations on the Rook Corvus frugilegus in south-west Cornwall. Ibis 102 : 394-419.

COULSON, J.C. 1963. Egg size and shape in Rissa and their use in estimating age composition of populations. Proc. Zool. Soc. Lond. 140 : 211-227.

COULSON, J.C. 1966a. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull. J. Anim. Ecol. 35 : 269-279.

COULSON, J.C. 1966b. The Movements of the Kittiwake. Bird Study 13(2) : 107-115.

COULSON, J.C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217 : 478-479.

COULSON, J.C. 1971. Competition for breeding sites causing segregation and reduced young production in colonial animals. in Den Boer & Gradwell (Eds.). Proc. Adv. Study Inst. Dynamics Number Popul. (Oesterbeek, 1971) : 257-268.

COULSON, J.C. 1972. The significance of the pair-bond in the Kittiwake. Proc. 15th Int. Ornithol. Congr. : 424-433.

COULSON, J.C., POTTS, G.R., & HOROBIN, J. 1969. Variation in the eggs of the Shag (*Phalacrocorax aristotelis*). Auk 86 : 232-245.

COULSON, J.C. & WHITE, E. 1956. A Study of colonies of the Kittiwake. Ibis 98 : 63-79.

COULSON, J.C. & WHITE, E. 1958a. Observations on the breeding of the Kittiwake. Bird Study 5 : 74-83.

COULSON, J.C. & WHITE, E. 1958b. The effect of age on the breeding biology of the Kittiwake. Ibis 100 : 40-51.

COULSON, J.C. & WHITE, E. 1959. The post-fledging mortality of the Kittiwake. Bird Study 6 : 97-102.

COULSON, J.C. & WHITE, E. 1960. The effect of age and density of breeding birds on the time of breeding of the Kittiwake. Ibis 102 : 71-86.

COULSON, J.C. & WHITE, E. 1961. An analysis of the factors influencing the clutch size of the Kittiwake. Proc. Zool. Soc. Land. 136 : 207-217.

COULTER, M. 1969. Mortality rates in different sized broods of Western Gulls. Pt. Reyes Bird Obs. Bull., 12 : 16-18.

CRAMP, S. 1971. Gulls nesting on buildings in Britain and Ireland. British Birds 64 : 476-483.

CULLEN, E. 1957. Adaptations in the Kittiwake to cliff-nesting. Ibis 99 : 275-302.

CULLEN, J.M. 1962. Allo-, auto- and hetero-preening. Ibis 105 : 121.

CULLEN, J.M. & ASHMOLE, N.P. 1963. Black Noddy on Ascension Island. II. Behaviour. Ibis 103b : 423-446.

CULLEN, E. & CULLEN, J.M. 1962. The pecking response of young Kittiwakes and a Black-headed Gull foster chick. Bird Study 9 : 1-16.

DAVIES, S.J.J.F. & CARRICK, F. 1962. On the ability of Crested Terns (Sterna bergii) to recognize their own chicks. Australian J. Zool. 10 : 171-177.

DEMENT'EV, G.P. & GLADKOV, N.A. 1969. Birds of the Soviet Union, Vol. 3. Jerusalem : Israel Program for Scientific Translations.

DUNN, E.K. 1972. Effect of age on the fishing ability of Sandwich Terns, Sterna sandvicensis. Ibis 114 : 360-366.

EMLEN, S.T. 1971. The role of song in individual recognition in the Indigo Bunting. Z. Tierpsychol. 28 : 241-246.

EMLEN, S.T. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. Behaviour 41 : 130-171.

EMLEN, J.T. & MILLER, D.E. 1969. Pace-setting mechanisms of the nesting cycle in the Ring-billed Gull. Behaviour 33 : 237-261.

ENSOR, D.M. & PHILLIPS, J.G. 1970. The effect of salt loading on the pituitary prolactin levels of the domestic duck (Anas platyrhynchos) and juvenile Herring or Lesser Black-backed gull (Larus argentatus or L. fuscus). J. Endocr. 48 : 167-172.

ENSOR, D.M. & PHILLIPS, J.G. 1972. The effect of dehydration on salt and water balance in gulls (Larus argentatus and L. fuscus). J. Zool. Lond. 168 : 127-137.

ERICKSON, C.J. 1970. Induction of ovarian activity in female ring doves by androgen treatment of castrated mates. J. comp. physiol. Psychol. 71 : 210-215.

ERICKSON, C.J. & LEHRMAN, D.S. 1964. Effect of castration of male ring doves upon ovarian activity of females. J. comp. physiol. Psychol. 58 : 164-166.

ERICKSON, C.J. & MORRIS, R.L. 1972. Effects of mate familiarity on the courtship and reproductive success of the Ring Dove. Anim. Behav. 20 : 341-344.

EVANS, R.M. 1970a. Imprinting and mobility in young Ring-billed Gulls (Larus delawarensis). Anim. Behav. Monogr. 3 : 195-248.

EVANS, R.M. 1970b. Parental recognition and the "mew call" in Black-billed Gulls (Larus bulleri). Auk 87 : 503-513.

EVANS, R.M. & MATTSON, M.E. 1972. Development of selective responses to individual maternal vocalisations in young Gallus gallus. Can. J. Zool. 50 : 777-780.

FERDINAND, L. 1969. Some observations of the behaviour of the Little Auk (Plotus alle) on its Breeding Ground, with special reference to voice production. Dansk. orn. foren. Tidsskr. 63 : 19-45.

FICKEN, R.W., van TIENHOVEN, A., FICKEN, M.S. & SIBLEY, F.C. 1960. Effect of visual and vocal stimuli on breeding in the budgerigar. Anim. Behav. 8 : 104-106.

GERRARD, M. 1969. Tagging of small animals with radioisotopes for tracking purposes. Isot. Radiat. Technol. 6 : 200-204.

GODFREY, G.K. 1954. Use of radioactive isotopes in small mammal ecology. Nature 174 : 951-952.

GOETHE, F. 1937. Beobachtung und Untersuchungen zur Biologie der Silbermöwe (*Larus a. argentatus*) auf der Vogelinsel Memmertsand. J. Orn. 85 : 1-119.

GOETHE, F. 1956. Die Silbermöwe. Brehm. Bücherei (Wittenberg).

HAILMAN, J.P. 1965. Cliff-nesting adaptations of the Galapagos Swallow-tailed Gull. Wilson Bull. 77 : 346-362.

HARRIS, M.P. 1964. Aspects of the breeding biology of the gulls *Larus argentatus*, *L. fuscus* and *L. canus*. Ibis 106 : 432-456.

HARRIS, M.P. 1970. Breeding ecology of the Swallow-tailed Gull (*Creagrus furcatus*). Auk 87 : 215-243.

HARRIS, M.P. & PLUMB, W.J. 1965. Experiments on the ability of Herring Gulls and Lesser Black-backed Gulls to raise larger than normal broods. Ibis 107 : 256-257.

HARRISON, C.J.O. 1967. Sideways-throwing and sideways-building in birds. Ibis 109 : 539-551.

HINDE, R.A. 1966. Animal Behaviour. McGraw-Hill. London.

HINDE, R.A., BELL, R.Q. & STEEL, E. 1963. Changes in sensitivity of the canary brood patch. Anim. Behav. 11 : 553-560.

HINDE, R.A. & WARREN, R.P. 1959. The effect of nest building on later reproductive behaviour in domesticated canaries. Anim. Behav. 7 : 35-41.

HODGES, A.F. 1969. A time lapse study of Kittiwake incubation rhythms. Ibis 111 : 442-443.

HOLCOMB, L.C. 1970. Prolonged incubation behaviour of the red-winged blackbird incubating several egg sizes. Behav. 36 : 74-83.

HOLMES, R.T. 1973. Social behaviour of breeding western sandpipers (Calidris mauri). Ibis 115 : 107-123.

HUTCHISON, R.E., STEVENSON, J.G. & THORPE, W.H. 1968. The basis for individual recognition by voice in the Sandwich Tern. Behaviour 32 : 150-157.

JOHNSTON, D.W. 1956. The annual reproductive cycle of the California Gull. II. Criteria of age and the testis cycle. Condor 58 : 134-162.

JOHNSTON, R.F. 1963. Stimuli for ovulation in the Rock Dove. Condor 65 : 58-69.

JONES, R.E. 1971. The incubation patch of birds. Biol. Rev. 46(3) : 315-340.

LACK, D. 1966. Population Studies of Birds. Oxford.

LACK, D. 1968. Ecological adaptations for breeding in birds. London.

LEHRMAN, D. 1959. Hormonal responses to external stimuli in birds. Ibis 101 : 478-496.

LEHRMAN, D.S., BRODY, P.N. & WORTIS, R.P. 1961. The presence of the mate and of nesting material as stimuli for the development of incubation behaviour and for gonadotrophim secretion in the Ring Dove (Streptopelia risoria). Endocrinol. 68 : 507-516.

LEHRMAN, D.S. & FRIEDMAN, M. 1969. Auditory stimulation of ovarian activity in the Ring Dove (Streptopelia risoria). Anim. Behav. 17 : 494-497.

LEHRMAN, D.S. & WORTIS, R.P. 1960. Previous breeding experience and hormone-induced incubation behaviour in the Ring Dove. Science 132 : 1667-1668.

LEHRMAN, D.S. & WORTIS, R.P. 1967. Breeding experience and breeding efficiency in the ring dove. Anim. Behav. 15 : 223-228.

LeRESCHE, R.E. & SLADEN, W.J.L. 1970. Establishment of pair and breeding site bonds by young known-age Adélie Penguins. Anim. Behav. 18 : 517-526.

LOTT, D.F. & COMERFORD, S. 1968. Hormonal initiation of parental behaviour in inexperienced ring doves. Z. Tierpsychol. 25 : 71-75.

LOTT, D., SCHOLZ, S.D. & LEHRMAN, D.S. 1967. Exteroceptive stimulation of the reproductive system of the female ring dove by the mate and by the colony milieu. Anim. Behav. 15 : 433-437.

MANLEY, G. 1960. Some aspects of social communication in Black-headed Gulls. Anim. Behav. 8 : 234.

MARSHALL, A.J. 1949. The function of the interstitium of the testis in the sexual cycle of a wild bird (Fulmanis glacialis). Quart. J. micr. Sci. 90 : 265-280.

MAUNDER, J.E. & THRELFALL, W. 1972. The Breeding biology of the Black-legged Kittiwake in Newfoundland. Auk 89 : 789-816.

McFARLAND, D.J. 1971. Feedback mechanisms in Animal Behaviour. London : Academic Press.

McLANNAHAN, H.M.C. 1973. Some aspects of the ontogeny of cliff nesting behaviour in the Kittiwake (Rissa tridactyla) and the Herring Gull (Larus argentatus). Behaviour 44 : 36-88.

MILLER, D.E. 1972. Parental acceptance of young as a function of incubation time in the Ring-billed Gull. Condor 74(4) : 482-484.

MILLS, J.A. 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull (Larus novachollandiae scopulinus). J. Anim. Ecol. 42 : 147-162.

MORRIS, R.L. & ERICKSON, C.J. 1971. Pair-bond maintenance in the Ring Dove. Anim. Behav. 19 : 398-406.

MOYNIHAN, M. 1953. Some displacement activities of the Black-headed Gull. Behaviour 5 : 58-80.

MOYNIHAN, M. 1962. Hostile and sexual behaviour patterns of South American and Pacific Laridae. Behaviour, Suppl. 8.

MYRES, M.T. 1963. Observations with radar of the feeding flights of Kittiwakes. Bird Study 10 : 34-43.

NELSON, J.B. 1964. Factors influencing clutch size and chick growth in the North Atlantic Gannet. Ibis 106 : 63-77.

NELSON, J.B. 1965. Behaviour of the Gannet. British Birds 58 : 233-288, 313-336.

NELSON, J.B. 1966. Breeding biology of the Gannet on the Bass Rock. Ibis 108 : 584-626.

NELSON, J.B. 1967. Colonial and cliff-nesting in the Gannet. Ardea 55 : 60-90.

NELSON, J.B. 1968. Galapagos. London; Longmans.

ORIANS, G.H. 1969. Age and hunting success in the Brown Pelican (Pelecanus occidentalis). Anim. Behav. 17 : 316-319.

PALUDAN, K. 1951. Contributions to the breeding biology of Larus argentatus and L. fuscus. Viddensk. Medd. Dansk. Naturh. Foren 114 : 1-128.

PALUDAN, K. 1955. Some behaviour patterns of Rissa tridactyla. Viddensk. Medd. Dansk. Naturh. Foren 117 : 1-21.

PARSONS, J. 1971. The Breeding Biology of the Herring Gull (Larus argentatus). Ph.D. Thesis, University of Durham.

PEARSON, T.H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37 : 521-552.

PENNEY, R.L. 1963. Territorial behaviour and social interactions by the Adélie Penguin. Doctaral Dissertation, University of Wisconsin.

POLIKARPOVA, E. 1940. Influence of external factors upon the development of the sexual gland of the sparrow. Compt. Rend. Acad. Sci. U.R.S.S. 26 : 91-95.

RECHER, H.F. & RECHER, J.A. 1969. Comparative foraging efficiency of adult and immature Little Blue Herons. Anim. Behav. 17 : 320-322.

RICHDALE, L.E. 1957. A Population Study of Penguins. Oxford.

RICHDALE, L.E. & WARHAM, J. 1973. Survival, pair bond retention and nest-site tenacity in Buller's Mollyhawk. Ibis 115 : 257-263.

ROTHSCHILD, M. 1962. Development of paddling and other movements in young Black-headed Gulls. British Birds 55 : 114-117.

SLADEN, W.J.L. 1958. The pygoscelid Penguins. Falkland Is. Depend. Survey, Sci. Rep., No. 17.

SLATER, P.J.B. 1967. External stimuli and readiness to incubate in the Bengalese Finch. Anim. Behav. 15 : 520-526.

SLATER, P.J.B. 1969. The stimulus to egg laying in the Bengalese Finch. J. Zool., Lond. 158 : 427-440.

SLATER, P.J.B. 1970a. Nest building in the Bengalese Finch. I. External factors affecting it and its relation to other behaviour early in the breeding cycle. Behaviour 36(4) : 300-319.

SMITH, N.G. 1966. Adaptations to cliff-nesting in some Arctic gulls (Larus). Ibis 108(1) : 68-83.

SPAANS, A.L. 1971. On the feeding ecology of the Herring Gull in the northern part of the Netherlands. Ardea 59 : 73-188.

STEVENSON, J.G., HUTCHISON, R.E., HUTCHISON, J.B., BERTRAM, B.C.R., & THORPE, W.H. 1970. Individual recognition by auditory cues in the Common Tern. Nature 226 : 562-563.

STORTEIR, S. & PALMGREN, A. 1971. Long term recording of incubating rhythm and feeding frequency with the aid of radioactive tagging. Ornis fenn. 48 : 33-35.

SWARTZ, L.G. 1966. Seacliff birds of Cape Thompson in Wilimovsky and Wolfe (Eds.). Environment of Cape Thompson Region, Alaska. Oak Ride, Tennessee, U.S. Atomic Energy Comm.

TASKER, C.R. 1970. Reproductive behaviour of the Red-billed Gull. unpubl. M.Sc. Thesis, University of Canterbury, New Zealand.

TENAZA, R. 1971. Behaviour and nesting success relative to nest location in Adelie penguins (Pygoscelis adeliae). Condor 73 : 81-92.

THIELCKE, G. 1970. Die Socialen Funktionen der Vögelstimmen Vogelwarte 25 : 204-229.

THORPE, W.H. 1961. Bird-Song. Cambridge University Press.

TINBERGEN, N. 1953. The Herring Gull's World. Collins, London.

TINBERGEN, N. 1959. Comparative studies of the behaviour of gulls (Laridae); a progress report. Behaviour 15 : 1-70.

TINBERGEN, N. 1962. Foot-paddling in gulls. British Birds 55 : 117-120.

TSCHANZ, B.B. 1964. Beobachtungen und Experimente zur Entstehung der "persönlichen" Beziehung zwischen Jungvogel und Eltern bei Trottellumen. Verh. schweiz. natur. Ges. 211-216.

TSCHANZ, B. 1968. Trottellumen. Die Entstehung der persönlichen Beziehung zwischen Jungvogel und Eltern. Z. Tierpsychol. Beiheft 4 : 1-103.

VAUGIEN, L. 1951. Ponte induite chez la Perruche ondulée maintenue à l'obscurité et dans l'ambience des volières. C.R. Hebd. Seanc. Acad. Sci. Paris 232 : 1706-1708.

VERMEER, K. 1963. The breeding ecology of the Glaucous-winged Gull (<u>Larus glaucescens</u>) on Mandark Island, B.C. Occ. Pap. B.C. Prov. Mus., 13 : 1-104.

VERMEER, K. 1969. Egg measurements of California and Ring-billed Gull eggs at Miquelon Lake, Alberta in 1965. Wilson Bull. 81 : 102-103.

WARD, P. 1969. The continuous recording of bird nesting visits using radioactive tagging. Ibis 111 : 93-95.

WARREN, R.P. & HINDE, R.A. 1961. Roles of the male and the nest cup in controlling the reproduction of female canaries. Anim. Behav. 9 : 64-67.

WEIDMANN, U. 1956. Observations and experiments on egg-laying in the Black-headed Gull (<u>Larus ridibundus</u>). Brit. J. Anim. Behav. 4 : 150-161.

WHITE, S.J. 1971. Slective responsiveness by the gannet to played-back calls. Anim. Behav. 19(1) : 125-131.

WHITE, S.J. & HINDE, R.A. 1968. Temporal relations of brood patch development, nest-building and egg-laying in domesticated canaries. J. Zool., Lond. 155 : 145-155.

WHITE, S.J. & WHITE, R.E.C. 1970. Voice recognition in Gannet. Behaviour 37 : 40-54.

WYNNE-EDWARDS, V.C. 1962. Animal Dispersion in Relation to Social Behaviour. Edinburgh.

YTREBERG, N.J. 1956. Contribution to the breeding biology of the Black-headed Gull (Larus ridibundus) in Norway. Nytt. Mag. Zool. 4 : 5-106.