A study on the biology of the kittiwake (rissa tridactyla)

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A STUDY ON THE BIOLOGY
OF THE
KITTIWAKE
(RISSA TRIDACTYLA)

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being a thesis presented in candidature for the degree
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ABSTRACT

The attendance and behaviour of successfully breeding kittiwake adults and their chicks at the breeding site was monitored both by a time-lapse filming technique and spot observations over 3 successive breeding seasons.

The orientation of adults at the site was shown to reflect the changing requirements of protection for eggs and brood through the cycle.

The attendance pattern similarly reflected variation according to the requirements of pair-bonds, egg and chick-care and although on average adults shared the duties, in particular cases pairs could take unequal shares. The early stages were co-ordinated and consistent but after early chick-care individual attendance patterns lost these properties due to the avoidance of the brood so that individual broods received individual patterns of guarding. Throughout the rest of the cycle adults increasingly avoided their broods as these developed. The form and amount of avoidance depended upon the restrictions of the nest site, brood size and the 'quality' of the adult.

While chicks were not killed by non-breeding adults visiting unguarded nest sites, their fledging patterns may well have been disrupted at the time when waterproofing and independant foraging skills were least developed. Those chicks left unattended relatively early were over-represented in the substantial mortality (mainly by drowning) during the fledging stage.

Adult behaviour showed cliff-nesting adaptations and was similar in form in all individuals. Avoidance of the attention of well-grown chicks was pronounced.

Chick behaviour (itself not affected by whichever adult of the pair attended) showed a progressive independance of the attention of the adults, although the chicks were not freely mobile over the ledge until after the first flight. Chicks' begging interactions, responsible for the avoidance by the parents, were not simply related to the amount of feeding. The possible consequences of this are discussed.

INTRODUCTION

It is well known that many sea-bird species are long lived. Mead & Hudson (1973) gave longevity records, from ringing to date of recovery, for the gannet (*Sula bassana*) 12.11, herring gull (*Larus argentatus*) 16.11, black-headed gull (*Larus ridibundus*) 19.11 and kittiwake (*Rissa tridactyla*) 15.00 - (all ages in years, months). This high survival rate means that birds can re-mate with partners of a previous year and in this way a pair-bond can become established that may bestow advantages not found in short-lived species. Longevity may also give physiological advantages associated with age and also advantages of previous experience in breeding.

Coulson and White (1958a) and Coulson (1960 and 1966) showed that both the age and the previous breeding experience of the individuals of a pair affected the breeding biology of the kittiwake gull. Like many other species of birds, young adult kittiwakes breed later in the breeding season than older birds (Coulson and White, 1958a) but this does not mean that this arises as a direct result of the increased age or breeding experience of the birds influencing the annual development of the gonads. Coulson (1966) showed that the retention by a female of a mate from the previous breeding season enabled the females to lay their eggs earlier than comparable individuals which had taken another mate. This effect, together with a tendency for few birds to change mate as their breeeding experience increased, was sufficient to account for the earlier breeding of older individuals.

The change of mate slightly lowered the clutch size but despite this the proportion of eggs producing fledged young was decreased. Birds changing mates were 13% less successful than those retaining their mates and this difference was due almost entirely to a failure to hatch eggs; there was no indication that the young were reared less effectively. A change of mate from one year to the next had a direct and depressive effect on the breeding biology of the pair that was shown to last for two years after the change. Established pairs were obviously more productive if they remained together. Pairs that failed to hatch a clutch in one year were found to be three times more likely to split up and form a new pair in the next breeding season than pairs that were successful. This suggested an incompatibility between certain individuals which made it an advantage for them to split up in the hope of finding a more compatible mate. It was suggested that birds of a newly formed pair were less well adjusted to one another and did not stimulate one another to such a high level of reproductive drive and thus did not co-ordinate their incubation pattern as well as established pairs.

Morris and Erickson (1971) showed that in the Ring dove, (Streptopelia risoria) individual females recognised their former mates. Their pairing relationships were retained even when physical contact was prevented and when the individuals were isolated for extended periods (even though the original pairings were determined by the experimenter. Working on the same species (Lehrman (1959) determined that the synchronization of behaviour of the mated pair was necessary for effective reproduction and that this synchronization was achieved by hormonal changes which were induced or facilitated by changes of stimuli arising in the external environment at different stages of the breeding cycle. These changes in hormonal secretions induced changes in behaviour that could themselves be a source of further stimulation. The two members of a breeding pair underwent a complicated reciprocal relation between the effects of the presence and behaviour of one mate on the endocrine system of the other and the effects of the presence and behaviour of the second bird (including those aspects of its behaviour induced by those endocrine effects) back on the endocrine system of the first.

Later work by Coulson (1968) on the birds breeding in the centre and edge of a kittiwake colony indicated that there was a high selection for better (in terms of survival and breeding success) and more vigorous males in the centre of the colony. These males were slightly heavier than those recruited to the edge of the colony and it was shown that subsequent survival of adults was partly related to the body weight at the time of recruitment. Other aspects of the breeding biology of kittiwakes in the two areas showed significant differences. There was a larger mean clutch size, higher hatching success and more young hatched and fledged per pair in the centre of the colony and also fewer birds changed their mate. The difference in the reproductive rate were ascribed to the direct or indirect results of variations in the quality of the males (and females) recruited in different parts of the colony, with the intense competition for nest sites in the centre resulting in very high selection for vigorous males with less severe selection towards the edge of the colony.

Lill and Wood-Cush (1965) showed that within an inbred strain of Brown Leghorn fowl (Gallus domesticus) preferential mating occurred as measured by female solicitation of the male. Females crouched at different rates to individual males; part of this difference was ascribed to the more vigorous courtship of the different males.

Coulson (1972) illustrated the interaction of age, nest position and pair status in the kittiwake and showed how the pair-bond resulted in more successful breeding when this relationship had been established for more than one year. He concluded that experience of the same mate resulted in a complex pair relationship that became more efficient through individual experience of a mate as successful rearing of young involved a great deal of co-operation between the members of a pair that shared incubation and care of the young.

In these previous population studies of the kittiwake, the mechanisms and degree of co-operation were largely inferred from the end results of numbers of eggs, young or fledglings produced.

AIMS

One of the aims of this study, therefore, was to elucidate the fine structure of the co-operation of behaviour between the two members of successful breeding pairs of kittiwakes in an attempt to shed light on the way that a pair bond could operate. It was of special interest that established pair bonds were shown particularly to affect facets of breeding up to the time shortly after hatching of the eggs and that once hatched, chicks appeared to be reared equally well by pairs of different status (Coulson 1966) such that the overall fledging success is 86% (Coulson and White 1958b). This present study also set out to investigate those features of chick-rearing which made it less open to disruption than the previous stages of breeding.

Coulson (1972) using a radio-active tagging method for monitoring adult attendance at the nest site during incubation, showed that the behaviour of pairs of kittiwakes was more variable than was first believed. He believed that the variability might be generally true amongst animals with a complex pattern of breeding. Thus, the possibility of general variation in the organisation of behaviour between individuals and pairs throughout successful breeding cycles merited consideration.

Cullen (1957) and McLannahan (1973) revealed how kittiwake adults and chicks show a great many alterations of behaviour from those shown by typical ground-nesting gulls. These differences were interpreted as adaptations to the cliff-nesting habit. The former study showed that kittiwake young have a much lower mortality than the young of ground-nesting gulls and Cullen presumed that this difference arose from the different nesting habits that protected them from predation and the disturbances that went with this.

Beer (1961, 1962, 1963a, 1966a 1963b) produced a detailed study of the organisation of behaviour throughout the breeding cycle of the black-headed gull, (*Larus ridibundus*) a ground-nesting species, and this provided a comparison for a study of the organisation of behaviour in the kittiwake. Such a comparison might indicate how the different nesting environments may modify the behavioural organisation and could confer an advantage during chick rearing to the cliff-nesting species.

The studies reported above indicated that the behaviour of individuals, and especially the co-ordination of behaviour between individuals, had a profound effect on breeding and, further, that the particular form of this behaviour in the kittiwake differed from the more typical ground-nesting gull due to the cliff-nesting habit.

The colony studied was one consisting of colour-ringed individuals nesting on the window ledges of a riverside warehouse in North Shields, Northumberland, described by Coulson and White (1958b). The special features of this colony allowed records to be collected of the activity of adults and young during the 3 breeding seasons 1968 - 70.

It was hoped that these records would provide insight into the behavioural strategies adopted by successful breeding pairs and of the external factors that affected them.

THE TIME-LAPSE METHOD

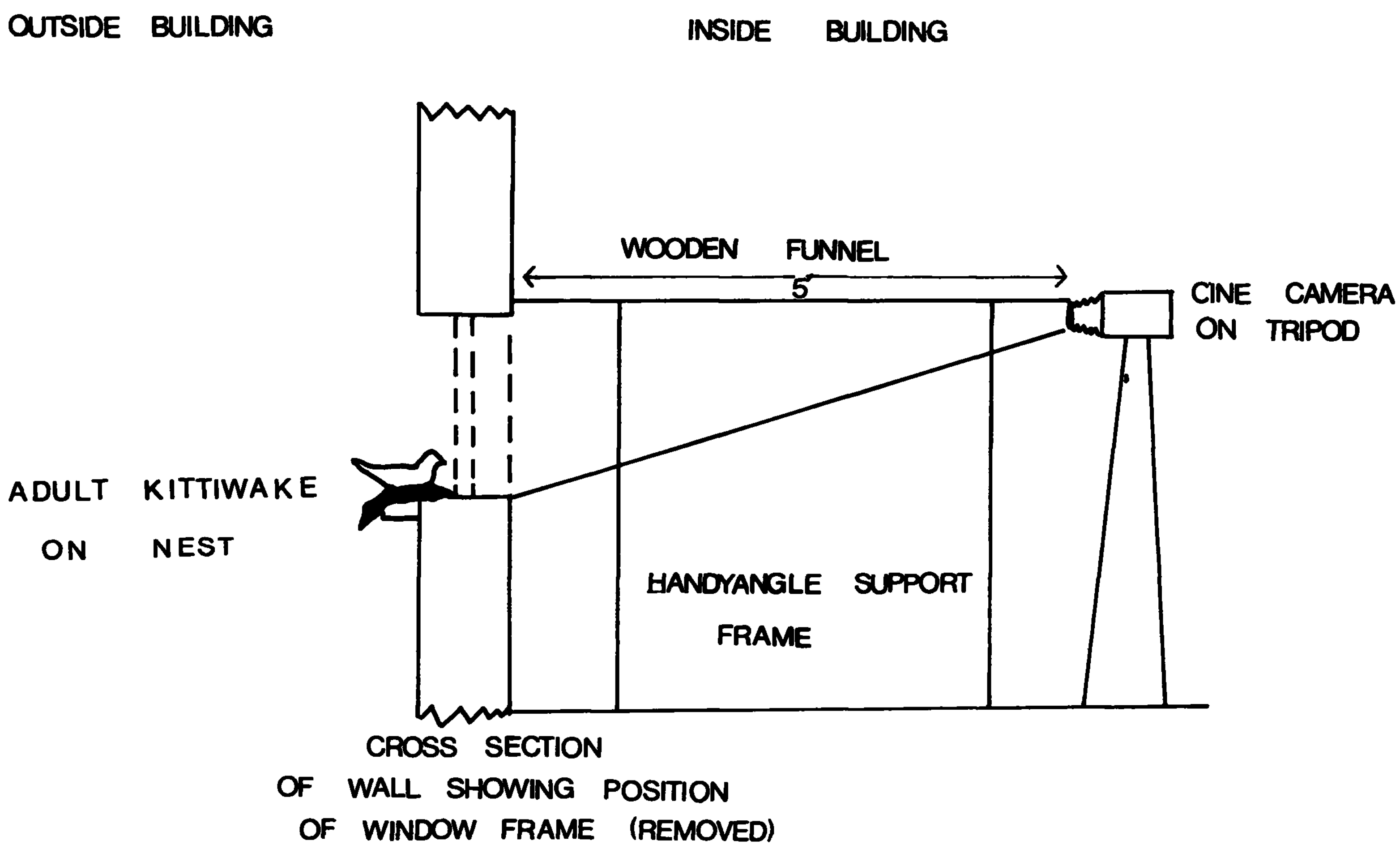
APPARATUS

Because birds of the North Shields colony nest on the window ledges of the riverside warehouse, 16mm Bolex H16 Reflex cine-cameras, fitted with Varioswitar 86EE Zoom lenses incorporating automatic exposure meters, could be mounted behind the nest sites of sexed pairs of known breeding experience. For the lens employed, the shortest focal length was five feet and the camera was mounted as shown in Fig. 1. The site was modified by removal of the window and the mounting of a five foot long wooden funnel behind the nest site. This reduced the disturbance of the breeding birds by the observers. The wooden funnels were constructed from 7mm Marine Plywood and Handy Angle which formed a waterproof apparatus that was heavy enough to stop the wind moving them when in position.

The advantage of the warehouse site was that the camera apparatus was weatherproofed and free from interference and could be powered by the stable mains electricity supply. Earlier attempts to use this apparatus in the field were hampered with problems of finding a dependable and robust power supply.

The cameras were fitted with modified Mk II Pelling and Cross Synchrolapse Timer units that triggered Pelling and Cross Mk IV Actuators so that one frame was exposed for 1/30th second at predetermined intervals, from 10 to 320 seconds; at 320 seconds per frame a 100 foot roll of film lasted about 14 days. The apparatus was run continuously throughout the 24 hour cycle, (making the timing of filmed events easier), although only the results from

Fig. 1. Side elevation of apparatus used for the time-lapse photography of Kittiwake nest sites.


OUTSIDE BUILDING
INSIDE BUILDING
WOODEN FUNNEL
5'
CINE CAMERA ON TRIPOD
ADULT KITTIWAKE ON NEST
HANDYANGLE SUPPORT FRAME
CROSS SECTION OF WALL SHOWING POSITION OF WINDOW FRAME (REMOVED)

the daylight hours, about 10 minutes after sunrise until 10 minutes before sunset, could actually be discerned. Because of the dull light conditions a fast film was required which had good contrast. The negative films, Kodak 4-X Type 7224 and Ilford HPS 16mm Negative, were found to give the best results. The film, after processing, was projected at short range using a Spectro 16mm projector with single frame presentation. Each frame was then coded as to time of exposure, date, presence or absence and behaviour of adults and chicks and the orientation of the parents.

PROCEDURE

In this way observations were made on four pairs of birds, One pair was filmed from their arrival at the nest site to their abandonment after breeding and the other three were filmed from a time soon after the chicks had hatched until their final abandonment. The film provided a long series of instantaneous observations of the nest site so that the number of times an event was recorded by the camera could be related to the amount of time the birds were engaged in that activity. In this way behaviour and attendance could be expressed as percentages of available time and the sequences of changes in behaviour and attendance, within a day and through the breeding season could readily be illustrated.

PROBLEMS OF TIME-LAPSE METHOD - Time-lapse filmed information suffers from the disadvantage of being discontinuous. Its interpretation must therefore depend upon correlated field observation. After observing the behaviour in the field and studying the complementary time-lapse data it was found to be relatively easy to recognise the categories of behaviour used in this analysis. Actual descriptions of the behaviour are not necessary for the initial purposes of this study and appear in a further section. The efficiency of any time-lapse method of observation, whether by camera or human observer, will depend on the length of the lapse between observations and the type of problem studied. Generally the longer the lapse length and the more erratic the nature of the behaviour studied the less accurate will be the measurements.

In the present study six lapse times were available; 320, 160, 30, 40, 20 and 10 seconds but each successive shortening of the time lapse represented a doubling of the resulting filmed information with an increase both in the cost of the film required and the time taken to analyse it. In order to decide which was the longest available time-lapse that would accurately measure kittiwake behaviour, film of breeding birds at the nest site was exposed at the shortest possible lapse interval. The whole film was then analysed as though it was film using the longer time-lapses as shown in Table 1. Each period of nest attendance could thus be described by several alternative estimates, all taken from the same film. These were: one based on 10 second time-lapses, two alternatives based on 20 second time-lapses, four on 40 second time-lapses, 8 on 80 second-lapses, 16 on 160 second-lapses and 32 on 320 second-lapses. As all of these estimates were measuring the same period of nest attendance then estimates based on longer time-lapses could be directly compared for accuracy with the 10 seconds per lapse standard. In order to indicate if a single time-lapse interval could accurately measure the varying nest site events occurring through the breeding cycle two different periods were analysed in this way. One was early in the brood care of the chicks and the other was later on when the chicks could fly.

TABLE 1. METHOD OF OBTAINING 20,40,80,160 and 320 SECONDS PER LAPSE ESTIMATES FROM ORIGINAL 10 SECOND PER LAPSE FILM

For a sequence of 32 frames exposed at 10 second intervals and identified by number from 1 to 32 the frames making up each estimate are as follows

a <u>10 sec/frame</u>

1	All frames from 1 to 32	) 1 possible estimate

b <u>20 sec/frame</u>

1	frame 1 and every second subsequent frame	) 2 possible
2	frame 2 " " " " "	) estimates

c <u>40 sec/frame</u>

1	frame 1 and every fourth subsequent frame	)
2	frame 2 " " " " "	) 4 possible
3	frame 3 " " " " "	) estimates
4	frame 4 " " " " "	)

d <u>80 sec/frame</u>

1	frame 1 and every eighth subsequent frame	)
2	frame 2 " " " " "	)
3	frame 3 " " " " "	)
4	frame 4 " " " " "	) 8 possible estimates
	etc.	
8	frame 8 " " " " "	)

e <u>160 sec/frame</u>

1	frame 1 and every sixteenth subsequent frame	)
2	frame 2 " " " " "	)
3	frame 3 " " " " "	) 16 possible estimates
	etc.	
16	frame 16 " " " " "	)

f <u>320 sec/frame</u>

1	frame 1 and every thirtysecond subsequent frame	)
2	frame 2 " " " " "	)
3	frame 3 " " " " "	) 32 possible estimates
	etc.	
32	frame 32 " " " " "	)

RESULTS

THE EFFECTS OF VARYING THE TIME-LAPSE INTERVAL ON THE ACCURACY OF THE METHOD

Clearly it is extremely important that the method employed in this study should provide an accurate timing of the start and ending of a particular category of behaviour. The average error of this type will be equal to the time-lapse interval, allowing for error at the start and end of a bout. If the time-lapse is short relative to the duration of a bout of a particular type of behaviour then the error will be unimportant.

MEASUREMENT OF ATTENDANCE BY PARENTS - The problem outlined above was first analysed using the partition of the nest attendance duties by the two parent birds. Attendance, has a definite duration which is variable. Fig. 2 illustrates estimates of the periodicity of the attendance types by the two parents using 10 and 80 seconds per lapse on the same information. This shows that the timing of the beginning and ending of all but the shortest behaviours, e.g. both adults present, is very accurate irrespective of which of the two time-lapses is used.

Table 2 shows the percentage of nest attendance undertaken by each parent for the two periods illustrated in Fig. 2 expressed as the average values of all estimates based on 10,20,40,80, 160 and 320 seconds time-lapse intervals. These average values were identical, allowing for the inaccuracy due to rounding up to one decimal place. Table 1 showed that the same total amount of information was used to produce the different numbers of estimates within each time-lapse category. The accuracy of a particular

Fig. 2. Comparison between estimates of the periodicity of nest site attendance based on 10 and 80 seconds per time-lapse film for two stages of chick attendance.

A = early chick attendance
B = late chick attendance
10 = 10 secs. per lapse time-lapse
80 = 80 secs. per lapse time-lapse
1 to 8 = number of estimates
▭ = male present
▨ = female present
■ = both adults present
⧍ = strange adult present
↴ = chick present

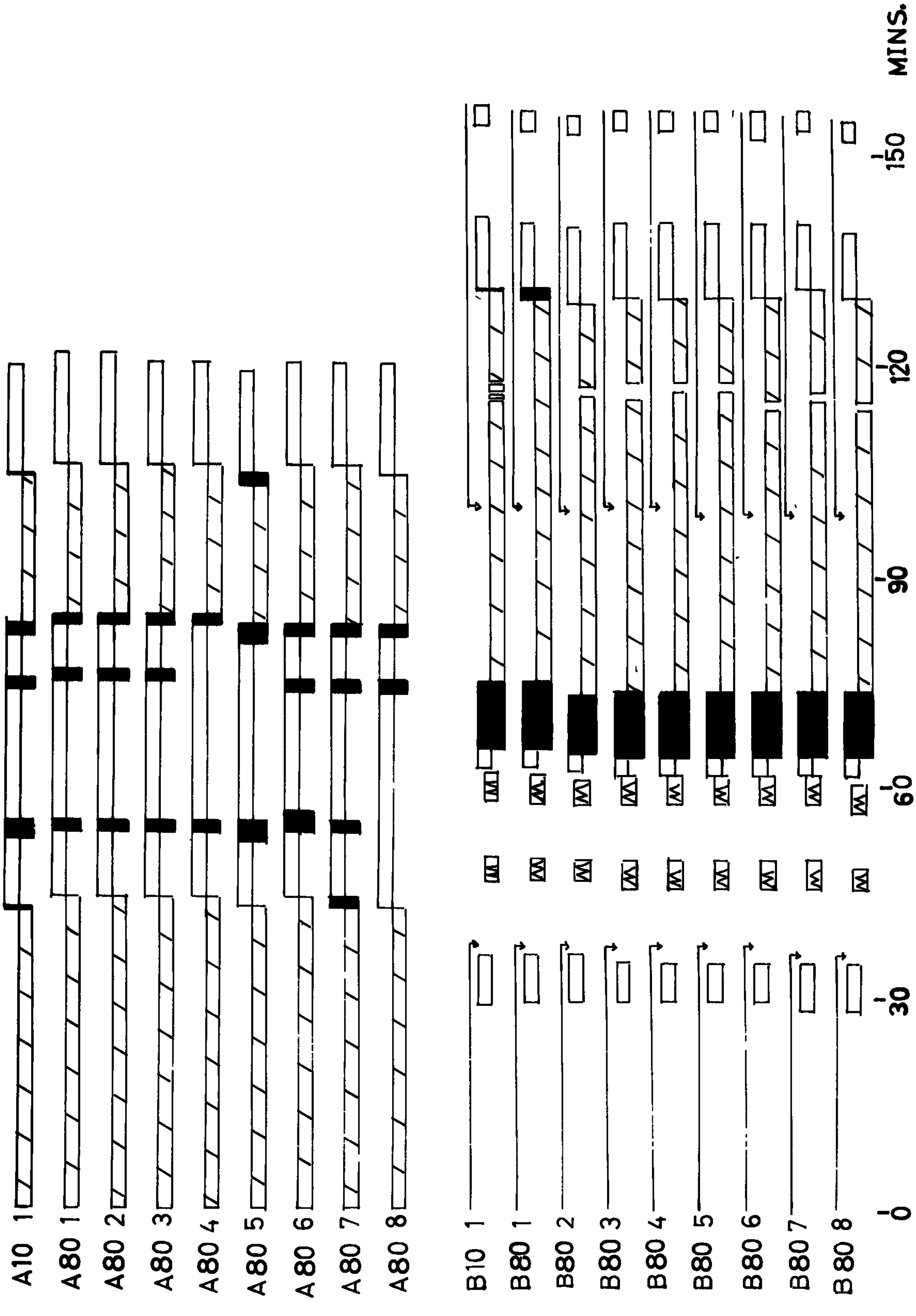

A10 1
A80 1
A80 2
A80 3
A80 4
A80 5
A80 6
A80 7
A80 8
B10 1
B80 1
B80 2
B80 3
B80 4
B80 5
B80 6
B80 7
B80 8
0
30
60
90
120
150
MINS.

TABLE 2. ESTIMATES OF THE PERCENTAGES OF NEST ATTENDANCE UNDERTAKEN BY EACH PARENT FOR THE SAME PERIOD USING DIFFERENT TIME LAPSE INTERVALS

Average values for the estimates of the percentage of nest attendance by each parent with standard deviation (Figures in parentheses are actual values of estimates)

<u>Early brood care</u>
Total duration 120 minutes

Lapse length	No of estimates	FEMALE	MALE	BOTH
10 sec/frame	1	(54.0	42.4	3.6)
20 sec/frame	2	(53.9	41.9	4.2)
		(54.0	42.9	3.1)
40 sec/frame	4	53.9	42.5	3.6
SD of estimates		0.46	0.99	0.96
80 sec/frame	8	53.9	42.4	3.6
SD of estimates		0.61	1.16	1.16
160 sec/frame	16	54.0	42.4	3.6
SD of estimates		1.08	3.24	2.79
320 sec/frame	32	54.0	42.4	3.6
SD of estimates		2.01	3.93	3.42

<u>Late brood care with chicks present</u>

Total duration 94 minutes

Lapse length	No of estimates	PARENTS PRESENT			PARENTS ABSENT *	
		FEMALE	MALE	BOTH	FEMALE	MALE
10 sec/frame	1	(30.8	20.3	0.2	1.4	47.2)
20 sec/frame	2	(31.0	19.9	0.4	1.4	47.3)
		(30.7	20.7	0.0	1.4	47.1)
40 sec/frame	4	30.8	20.3	0.2	1.4	47.2
SD of estimates		0.30	0.65	0.35	0.57	0.34
80 sec/frame	8	30.9	20.3	0.2	1.4	47.2
SD of estimates		1.32	0.60	0.49	0.78	1.06
160 sec/frame	16	30.8	20.3	0.2	1.4	47.2
SD of estimates		2.27	1.83	0.72	1.49	1.81
320 sec/frame	32	30.8	20.3	0.2	1.4	47.3
SD of estimates		3.49	3.28	1.04	2.51	4.01

* Representing a measure of the failure of an adult to remain at the nest site until relieved by the mate (See Fig. 2)

(TABLE 2 CONT.)

Late brood care without chicks present

Total duration 62 minutes

Lapse length	No of estimates	PARENTS PRESENT			PARENTS ABSENT
		FEMALE	MALE	BOTH	EMPTY SITE
10 sec/frame	1	(41.4	4.3	14.7	39.6)
20 sec/frame	2	(41.2 (41.7	4.3 4.3	15.0 14.4	39.6) 39.6)
40 sec/frame	4	41.5	4.3	14.7	39.6
SD of estimates		0.41	0.0	0.49	0.23
80 sec/frame	8	41.5	4.3	14.7	39.6
SD of estimates		1.02	0.04	0.78	0.96
160 sec/frame	16	41.5	4.3	14.7	39.6
SD of estimates		1.81	0.10	2.28	1.39
320 sec/frame	32	41.5	4.4	14.7	39.5
SD of estimates		2.61	4.48	3.83	2.95

time-lapse can be gauged by the variability of the estimates around this average and is represented by the standard deviations given in Table 2. Fig. 3 illustrates the relationship between standard deviations and the time-lapse intervals and indicates that over the range studied the variability of estimates increases as the time-lapse increases, but the slope of the graph indicates that doubling the time-lapse does not necessarily double the variability of estimates.

As previously mentioned, when the length of the time-lapse approaches that of the attendance bout only some of the estimates based on that time-lapse will record such attendance. The probability that an estimate will measure a short attendance bout is shown for different time-lapse intervals in Table 3. Short attendance bouts are defined as those accounting for less than five percent of the total nest attendance. This Table indicates that there is little difference in the probability of measuring short attendance bouts for estimates based on 10, 20 or 40 seconds per lapse but with 160 and 320 seconds per lapse the probability is greatly reduced.

It was concluded that the records with 80 second time-lapses showed little variation between estimates (indicated by small standard deviations) and a high probability of detecting short attendance bouts, and for these reasons was the longest lapse considered in the rest of this analysis.

MEASUREMENT OF THE BEHAVIOUR OF THE PARENTS AND CHICKS. Table 4 shows the percentages of time spent on different behaviours by the parents, during different conditions at the nest site,

Fig. 3. Variation of the standard deviations of the estimates of nest attendance with the time-lapse interval on which they were based. (Information from Table 2)

▲———▲ = male present

●———● = female present

×———× = both adults present

◬-----◬ = male absent

⊗-----⊗ = female absent

+-----+ = empty site

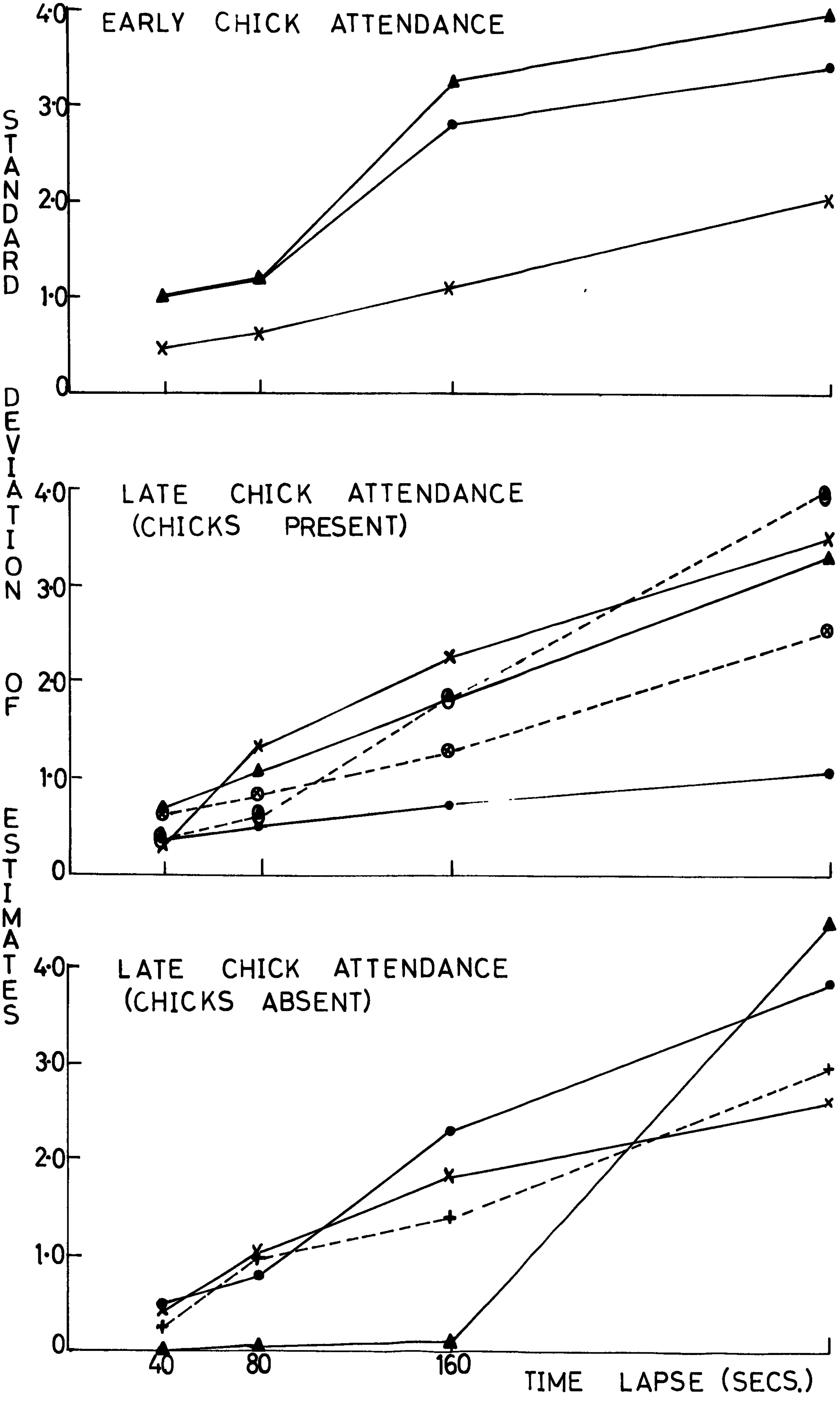

EARLY CHICK ATTENDANCE
LATE CHICK ATTENDANCE (CHICKS PRESENT)
LATE CHICK ATTENDANCE (CHICKS ABSENT)
STANDARD DEVIATION OF ESTIMATES
4·0
3·0
2·0
1·0
0
40
80
160
TIME LAPSE (SECS.)

TABLE 3. PROBABILITIES OF ESTIMATES USING DIFFERENT TIME-LAPSE MEASURING SHORT ATTENDANCE CATEGORIES (Those of < 5% of total nest attendance)

Lapse Length	No. of estimates	No. of estimates measuring short attendance	% of estimates measuring short attendance
1 <u>Early brood care, attendance by both parents together</u>			
10 sec/frame	1	1	100
20 sec/frame	2	2	100
40 sec/frame	4	4	100
80 sec/frame	8	8	100
160 sec/frame	16	11	69
320 sec/frame	32	19	60
2 <u>Late brood care, attendance by both parents together</u>			
10 sec/frame	1	1	100
20 sec/frame	2	1	50
40 sec/frame	4	1	25
80 sec/frame	8	1	13
160 sec/frame	16	1	6
320 sec/frame	32	1	3
3 <u>Late brood care with chicks present female absent</u>			
10 sec/frame	1	1	100
20 sec/frame	2	2	100
40 sec/frame	4	4	100
80 sec/frame	8	7	88
160 sec/frame	16	8	50
320 sec/frame	32	8	25
4 <u>Late brood care with chicks absent, male present</u>			
10 sec/frame	1	1	100
20 sec/frame	2	2	100
40 sec/frame	4	4	100
80 sec/frame	8	8	100
160 sec/frame	16	16	100
320 sec/frame	32	16	50

TABLE 4. ESTIMATES OF THE PERCENTAGES OF TIME DURING SINGLE ADULT ATTENDANCE SPENT ON EACH BEHAVIOUR FOR THE SAME PERIOD USING DIFFERENT TIME-LAPSE INTERVALS

Average galues for the estimates of the percentage of nest attendance spent on each behaviour with standard deviation (Figures in parentheses are actual values of estimates)

MALE ATTENDANCE

Early Brood care

Total duration 51 minutes

Lapse length	No. of estimates	STAND	PREEN	MOVE CHICKS	TURN HEAD	THREAT	CALL
10 sec/frame	1	(87.3	9.5	0.7	2.0	0.3	0.3)
20 sec/frame	2	(87.7	9.0	0.7	1.9	0.0	0.7)
		(86.8	9.9	0.7	2.0	0.7	0.0)
40 sec/frame	4	87.3	9.5	0.7	2.0	0.3	0.3
SD of estimates		1.23	2.13	0.75	1.72	0.65	0.65
80 sec/frame	8	87.3	9.5	0.7	2.0	0.3	0.3
SD of estimates		2.10	2.31	1.23	2.33	0.95	0.95

Late brood care with chicks present

Total duration 20 minutes

Lapse length	no. of estimates	STAND	SQUAT	TURN HEAD	CALL
10 sec/frame	1	(67.5	2.6	29.0	0.9)
20 sec/frame	2	(66.1	1.8	32.1	0.0)
		(69.0	3.5	25.9	1.7)
40 sec/frame	4	67.6	2.6	28.9	0.8
SD of estimates		11.41	1.76	12.71	1.65
80 sec/frame	8	67.6	2.6	28.9	0.8
SD of estimates		11.06	3.61	12.79	2.37

FEMALE ATTENDANCE

Early brood care

Total duration 65 minutes

Lapse length	No. of estimates	STAND	PREEN	MOVE CHICKS	THREAT	CALL
10 sec/frame	1	(80.2	18.3	0.5	0.8	0.3)
20 sec/frame	2	(81.5	17.4	0.0	1.0	0.0)
		78.9	19.1	1.0	0.5	0.5)
40 sec/frame	4	80.2	18.3	0.5	0.8	0.3
SD of estimates		3·04	1·72	0·58	1·0	0·50
80 sec/frame	8	80.2	18.3	0.5	0.8	0.3
SD of estimates		3.69	1.77	0.95	1.55	0.71

Late brood care with chicks present

Total duration 29 minutes

Lapse length	No. of estimates	STAND	PREEN	SQUAT	TURN HEAD	THREAT	CALL
10 sec/frame	1	(60.7	2.3	9.8	26.0	0.6	0.6)
20 sec/frame	2	(62.1	2.3	8.1	26.4	1.2	0.0)
		(59.3	2.3	11.6	25.6	0.0	1.2)
40 sec/frame	4	60.7	2.3	9.9	26.0	0.6	0.6
SD of estimates		2.25	0.0	2.96	3.63	1.15	1.15
80 sec/frame	8	60.6	2.3	9.9	26.1	0.6	0.6
SD of estimates		4.69	2.46	4.55	4.89	1.63	1.63

Late brood care with chicks absent

Total duration 26 minutes

Lapse length	No. of estimates	STAND	PREEN	SIT	THREAT	CALL
10 sec/frame	1	(63.9	31.0	1.3	2.6	1.3)
20 sec/frame	2	(63.6	29.9	1.3	2.6	2.6)
		(64.1	32.1	1.3	2.6	0.0)
40 sec/frame	4	63.9	30.9	1.3	2.6	1.3
SD of estimates		4.39	6.03	1.50	2.16	2.55
80 sec/frame	8	63.9	31.0	1.3	2.6	1.3
SD of estimates		7.20	6.87	2.39	2.79	3.54

expressed as the average values for all estimates based on 10 to 80 second time-lapse intervals. Complementary information for chick behaviour is given in Table 5.

Estimates of the percentages of time spent on different behaviours (Tables 4 and 5) are less uniforn than the corresponding estimates of attendance (Table 2) as is shown by the larger standard deviations. The reason for this is that the behaviour within an attendance category is of the same form as Fig. 2 but tends to be for shorter total time intervals, so that the errors at the beginning and end of a behaviour bout have a more disruptive effect on the estimates. Like Fig. 3, a comparison of the standard deviations ~~of~~ from 40 and 80 second per lapse estimates, given in Tables 4 and 5 for the partition of behaviour, in general indicates that doubling the time-lapse interval does not double the variability of the estimates. The size of the standard deviations indicates that the variation between estimates is in most cases small so that only with rare behaviours or very short attendance types will errors due to using 80 seconds per lapse be an important consideration.

A working criterion for the usefulness of estimates based on time-lapses greater than 10 seconds was that they should partition behaviour in the same rank order of importance as the standard. As the information for these estimates were derived from the 10 seconds standard, then if all of the estimates within a time-lapse showed significant agreement in their ranking this must thus be the same as the standard ranking. As the different estimates were not based on independent information they could not be compared by parametric methods but the degree of agreement between

TABLE 5. ESTIMATES OF THE PERCENTAGES OF TIME DURING THE DIFFERENT ADULT ATTENDANCE TYPES SPENT BY CHICKS ON EACH BEHAVIOUR FOR THE SAME PERIOD USING DIFFERENT TIME-LAPSE INTERVALS

Average values for the estimates of the percentage of nest attendance spent on each behaviour with standard deviation (Figures in parentheses are actual values of estimates)

MALE ATTENDANCE

Early brood care

Total duration 51 minutes

Lapse length	No. of estimates	STAND	SIT	PREEN	FLY	UNSUC. BEG	SUC. BEG	PECK
10 sec/frame	1	(9.4	57.6	3.9	0.3	21.0	5.3	2.6)
20 sec/frame	2	(9.9	57.4	3.2	0.6	21.5	5.1	2.2)
		(8.8	57.8	4.6	0.0	20.5	5.5	2.9)
40 sec/frame	4	9.3	57.6	3.9	0.3	21.0	5.4	2.6
SD of estimates		1.42	0.90	1.10	0.38	0.64	0.81	0.53
80 sec/frame	8	9.4	57.6	3.9	0.3	21.0	5.4	2.6
SD of estimates		2.35	2.35	2.36	~~1.74~~ 0·60	~~1.99~~ 2·36	1·74	1·99

Late brood care

Total duration 20 minutes

Lapse length	No. of estimates	SIT	PREEN	UNSUC. BEG	SUC. BEG	PECK
10 sec/frame	1	(21.8	0.6	69.2	5.8	2.6)
20 sec/frame	2	(21.8	1.3	66.7	7.7	2.6)
		(21.8	0.0	71.8	3.9	2.6)
40 sec/frame	4	21.8	0.7	69.2	5.8	2.6
SD of estimates		1.50	1.30	4.20	4.40	0.0
80 sec/frame	8	21.8	0.6	69.3	5.7	2.6
SD of estimates		2.03	1.77	6.82	5.02	2.75

FEMALE ATTENDANCE

Early brood care

Total duration 65 minutes

Lapse length	No. of estimates	STAND	SIT	PREEN	FLY	UNSUC BEG	SUC BEG	PECK
10 sec/frame	1	(12.3	70.8	2.3	0.1	7.2	2.1	5.1)
20 sec/frame	2	(11.8	69.7	2.1	0.0	8.7	1.8	5.9)
		(12.9	71.9	2.6	0.3	5.7	2.3	4.4)
40 sec/frame	4	12.4	70.8	2.3	0.1	7.2	2.1	5.1
SD of estimates		1.27	1.64	0.53	0.25	1.83	1.84	1.70
80 sec/frame	8	12.4	70.9	2.3	0.1	7.2	2.1	5.1
SD of estimates		1.70	2.16	1.70	0.35	1.73	1.74	1.95

Late brood care

Total duration 29 minutes

Lapse length	No. of estimates	STAND	SIT	PREEN	FLY	UNSUC BEG	SUC BEG	PECK
10 sec/frame	1	(1.8	14.1	0.6	0.6	72.4	5.9	4.7)
20 sec/frame	2	(2.3	14.0	0.0	1.2	72.1	4.7	5.8)
		(1.2	14.3	1.2	0.0	72.6	7.1	3.6)
40 sec/frame	4	1.8	14.2	0.6	0.6	72.4	5.9	4.7
SD of estimates		1.17	0.17	1.20	1.15	3.47	2.38	1.88
80 sec/frame	8	1.8	14.1	0.6	0.6	72.4	5.9	4.7
SD of estimates		2.45	3.57	1.70	1.63	7.14	3.39	3.52

ADULTS ABSENT

Late brood care

Total duration 40 minutes

Lapse length	No. of estimates	STAND	SIT	PREEN	PECK
10 sec/frame	1	(42.2	30.0	13.7	14.1
20 sec/frame	2	(38.8	30.6	15.7	14.9
		(45.6	29.4	11.8	13.2
40 sec/frame	4	42.2	30.0	13.7	14.1
SD of estimates		5.05	1.71	3.28	2.61
80 sec/frame	8	42.2	30.0	13.7	14.1
SD of estimates		7.39	4.47	5.03	3.75

the 8 estimates based on 80 seconds per lapse as ranked information, could be tested by the modification of Kendal's Coefficient of Concordance given by Moroney, (1962).

The results of such tests for both parent and chick behaviour, under all conditions of attendance using data derived from recordings made at 80 seconds per lapse are shown in Table 6. This table shows that even with the most variable set of 80 seconds per lapse estimates - male, late brood care with chicks, - there was a significant ($P < 0.01$) degree of agreement of the rank orders of the eight estimates.

Thus, as the sets of 80 seconds per lapse estimates of parent and chick behaviour tended to show rather small variation, indicated by the standard deviations in Tables 4 and 5, and sorted the behaviours into the same rank order as the 10 seconds per lapse standards, indicated by Table 6, all experimental results given in the rest of this study were based on information obtained from 80 seconds per frame time-lapse film.

TABLE 6. TESTS FOR THE DEGREE OF AGREEMENT IN THE RANKING OF ADULT AND CHICK BEHAVIOUR BY THE 8 POSSIBLE 80 SECONDS PER LAPSE ESTIMATES WITHIN EACH OF THE DIFFERENT ATTENDANCE CLASSES

	Attendance class	F - value *	Greater d.f.	Lesser d.f.
I	ADULT BEHAVIOUR			
a	Early brood care			
	(1) Male with chicks	20.1	4.75	33.25
	(2) Female with chicks	27.7	3.75	26.25
b	Late brood care			
	(1) Male with chicks	48.6	2.75	19.25
	(2) Female with chicks	39.9	4.75	33.25
	(3) Female alone	30.8	3.75	26.25
II	CHICK BEHAVIOUR			
a	Early brood care			
	(1) Male with chicks	57.2	5.75	40.25
	(2) Female with chicks	77.9	5.75	40.25
b	Late brood care			
	(1) Male with chicks	41.3	3.75	26.25
9	(2) Female with chicks	22.8	5.75	40.25
	(3) Chicks alone	41.0	2.75	19.25

* All F-values were significant ($P < 0.01$)

Test used was the modification of Kendall's Coefficient of Concordance, p.337, M.J. Moroney (1962).

THE ORIENTATION OF THE PARENT BIRDS AT THE NEST SITE

As shown in Fig. 4, during the pre-laying period the adult birds stand on all parts of the nest structure but after the eggs are laid they stand only on the nest cup. With young chicks present the outside edge of the nest is also used and later still the nest cup is vacated for the growing brood. During chick attendance the adults may even stand on the nest ledge at the side of the nest, which is classified as SIDE nest attendance as opposed to ON nest attendance when the parents stand on the nest structure itself. Only when the chicks vacate the nest site do the parents again stand on all parts of the nest structure.

The actual direction that parents faced was classified as inside, parallel or outside by reference to the hypothetical orientation circle shown in Fig. 4 whose centre was placed at the feet of the attending adult. The direction of facing was that segment of the circle that contained the birds head.

The direction f~~ound~~aced by 4 pairs of adults in all of the attendance at the nest site was classified into the categories, described above, using 80 seconds per frame time-lapse film and subdividing the results according to the stage of breeding, sex of parent, type of attendance and presence or absence of chicks. The nest sites of pairs 1 and 2 were in the exposed centres of window ledges whereas those of pairs 3 and 4 were in the more protected corners of adjacent window ledges.

THE RANDOMNESS OF THE PARENTAL FACING.

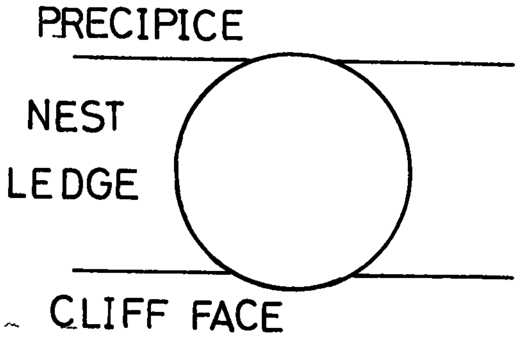
In a first analysis the orientation of each adult, on each day, was classified according to the direction in which the majority

Fig. 4. Details of the positions occupied by adults when attending the nest through the breeding season.

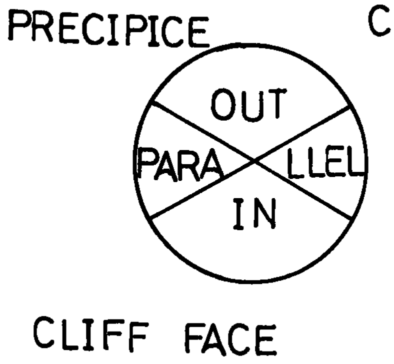
▥ = area of nest occupied by adult ON attending

▦ = area of nest occupied by adult SIDE attending

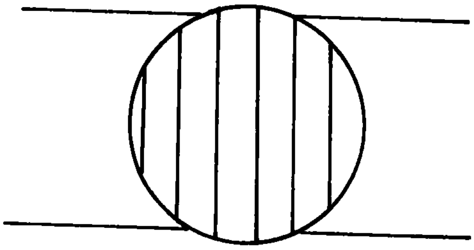
PLAN OF NEST SITE



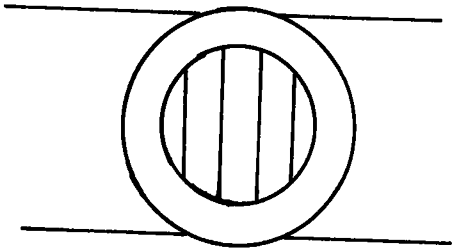
HYPOTHETICAL ORIENTATION CIRCLE



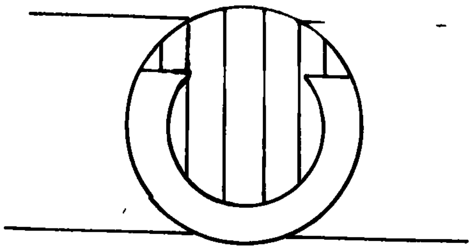
ACTUAL POSITION OCCUPIED BY ADULTS DURING DIFFERENT STAGES OF BREEDING



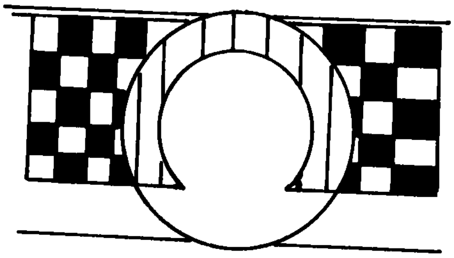
1. PRE-LAYING



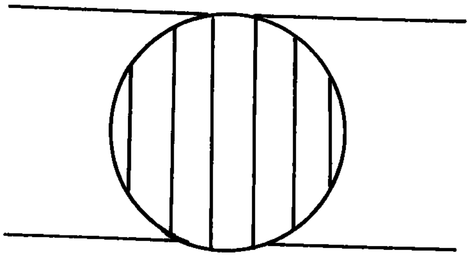
2. INCUBATION



3. BROODING



4. CHICK ATTENDANCE



5. POST FLEDGING

of the facing was observed. Random orientation would have given equal numbers of days on which a preference was shown for each of the 3 directions for each adult thus providing expected values to compare with the observed values by Chi-squared tests. Table 7 showed that the direction of facing deviated significantly from random, ($P < 0.001$), with the preferred facing directions in order, inside > parallel > outside. The results for pair 1 indicated that the preference for inside facing was not as strong as in the other three pairs but this was the only pair observed for the whole breeding cycle.

CHANGES IN THE FACING BEHAVIOUR THROUGH THE BREEDING SEASON.

In order to compare the orientation of the parents from day to day the raw results were converted to proportions of the total attendance spent on inside, parallel and outside facing. Because percentages follow a binomial rather than a normal distribution all percentage values based on sample sizes greater than 50 frames were transformed by means of the Arcsine square root transformation (Snedecor and Cochran 1969). Percentages based on attendance of less than 50 frames per day were transformed using the Table given in Mosteller and Youtz (1961). Unless otherwise stated all following graphs and calculations are based on arcsin transformed percentages. (see Appendix)

Figs. 5 to 8 show the different percentages of attendance spent facing inside, parallel or outside during the breeding cycles of the four pairs of kittiwakes. All graphs are timed from the date of hatching of the chicks so that observations from different pairs may be compared. Each point on the graphs is the

TABLE 7. DIRECTION OF ADULT FACING OF FOUR PAIRS OF BREEDING KITTIWAKES

OBSERVED DAILY ADULT ORIENTATION - (See text for details)

	INSIDE	PARALLEL	OUTSIDE	χ^2_1
Pair 1				
Male	69	33	9	49.3
Female	66	27	10	48.1
Pair 2				
Male	46	4	0	77.8
Female	41	8	1	54.7
Pair 3				
Male	50	3	0	88.9
Female	56	14	2	67.0
Pair 4				
Male	60	6	2	92.5
Female	49	15	4	48.5

All χ^2 values are significant ($P < 0.001$)

Fig. 5. Changes in the percentages of attendance spent facing IN, PARALLEL and OUT during the breeding cycle of pair 1.

●——● chicks present, parents ON attending

×——× chicks absent, parents ON attending

▲- - -▲ chicks present, parents SIDE attending

limits = 1 x S.E.

(Each point is the mean of 8 consecutive daily measures)

e = egg laying

h = hatching

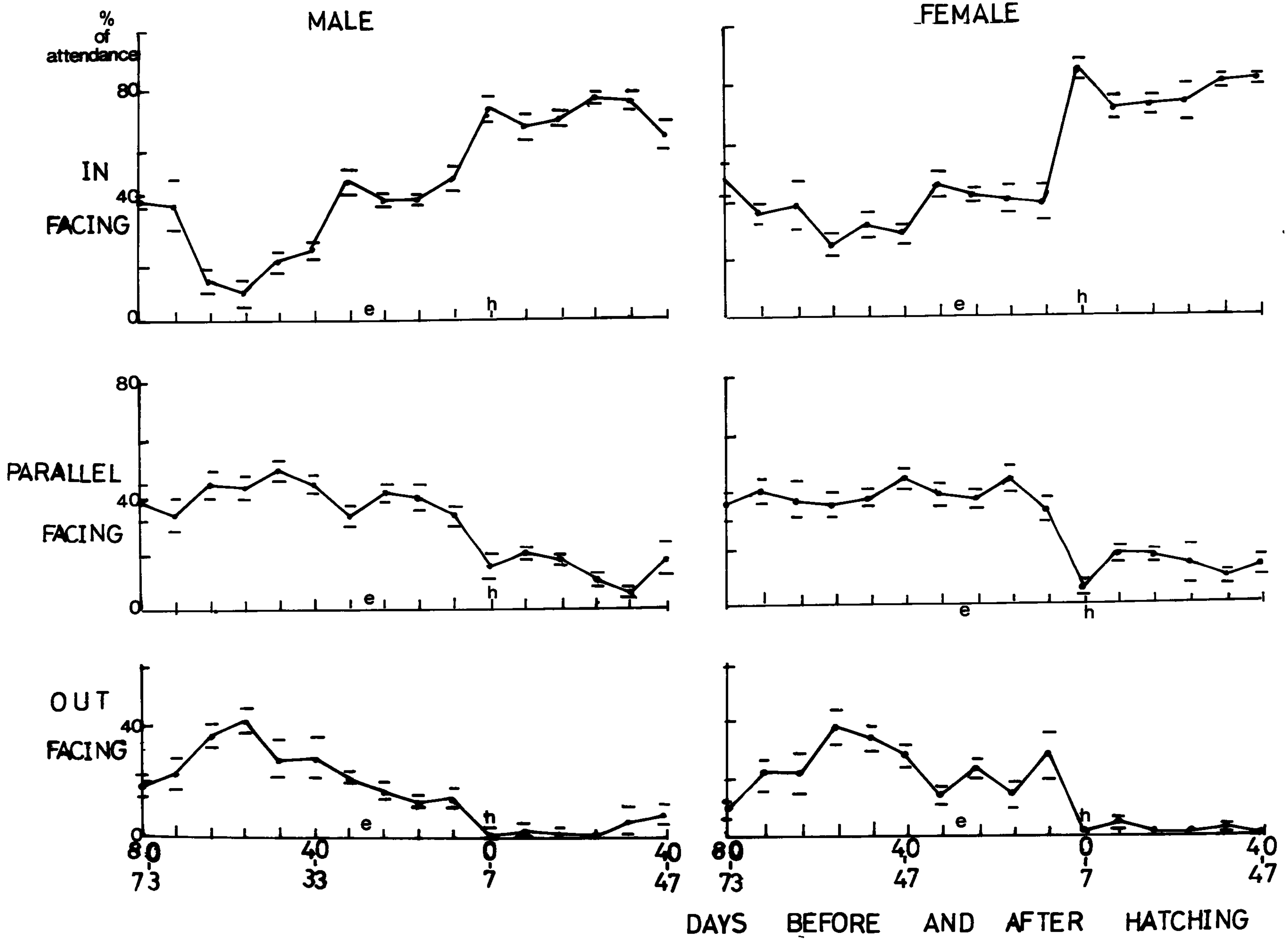

MALE
FEMALE
% of attendance
IN FACING
PARALLEL FACING
OUT FACING
80
40
0
e
h
80 73
40 33
0 7
40 47
80 73
40 47
0 7
40 47
DAYS BEFORE AND AFTER HATCHING

Fig. 6. Changes in the percentages of attendance spent facing IN, PARALLEL and OUT during the breeding cycle of pair 2.

●——● chicks present, parents ON attending

×——× chicks absent, parents ON attending

▲- - - -▲ chicks present, parents SIDE attending

limits = 1 x S.E.

(Each point is the mean of 8 consecutive daily measures)

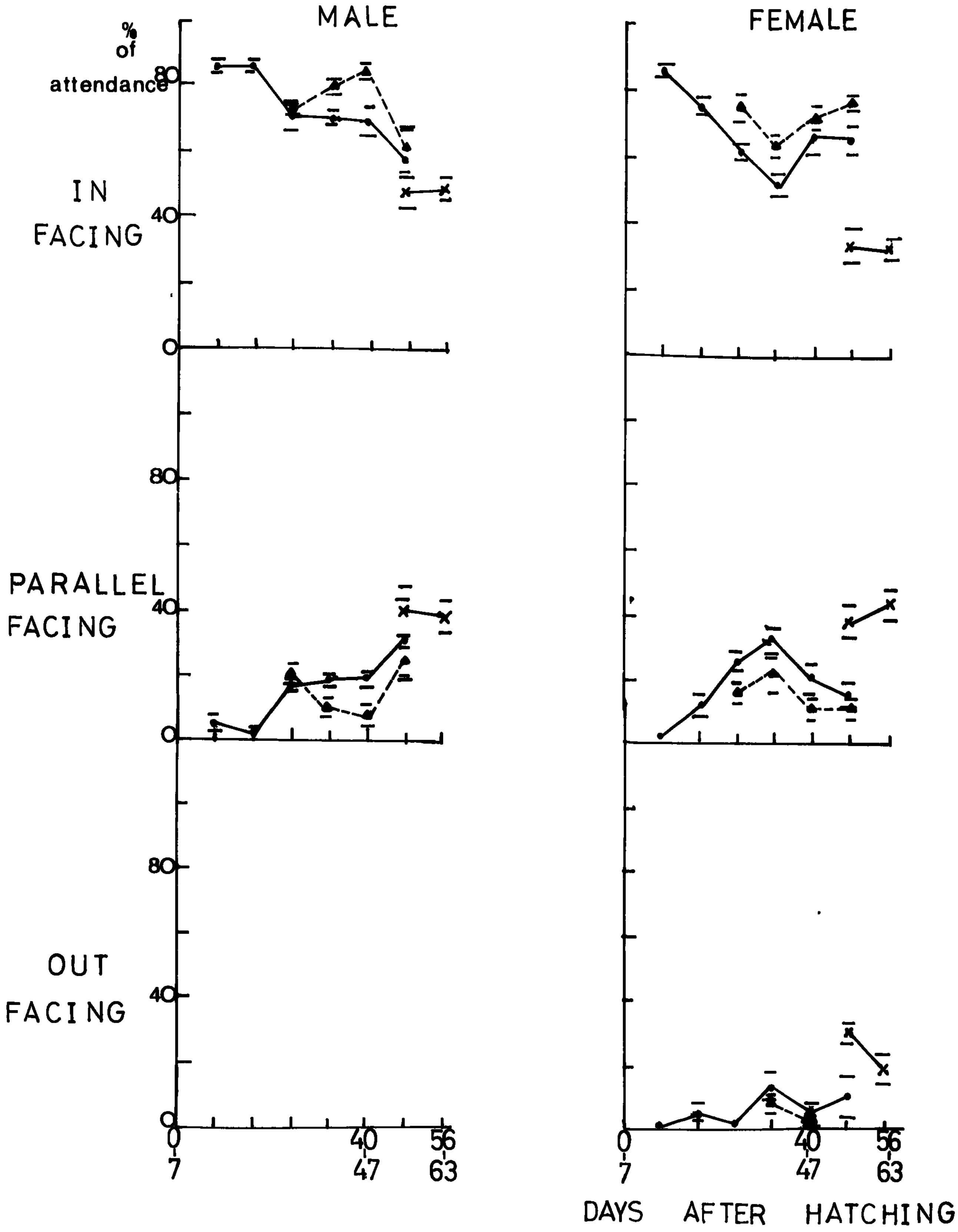

MALE
FEMALE
% of attendance
80
40
0
IN FACING
PARALLEL FACING
OUT FACING
0-7
40-47
56-63
DAYS AFTER HATCHING

Fig. 7. Changes in the percentages of attendance spent facing IN, PARALLEL and OUT during the breeding cycle of pair 3.

●——● chicks present, parents ON attending

×——× chicks absent, parents ON attending

▲------▲ chicks present, parents SIDE attending

limits = 1 x S.E.

(Each point is the mean of 8 consecutive daily measures)

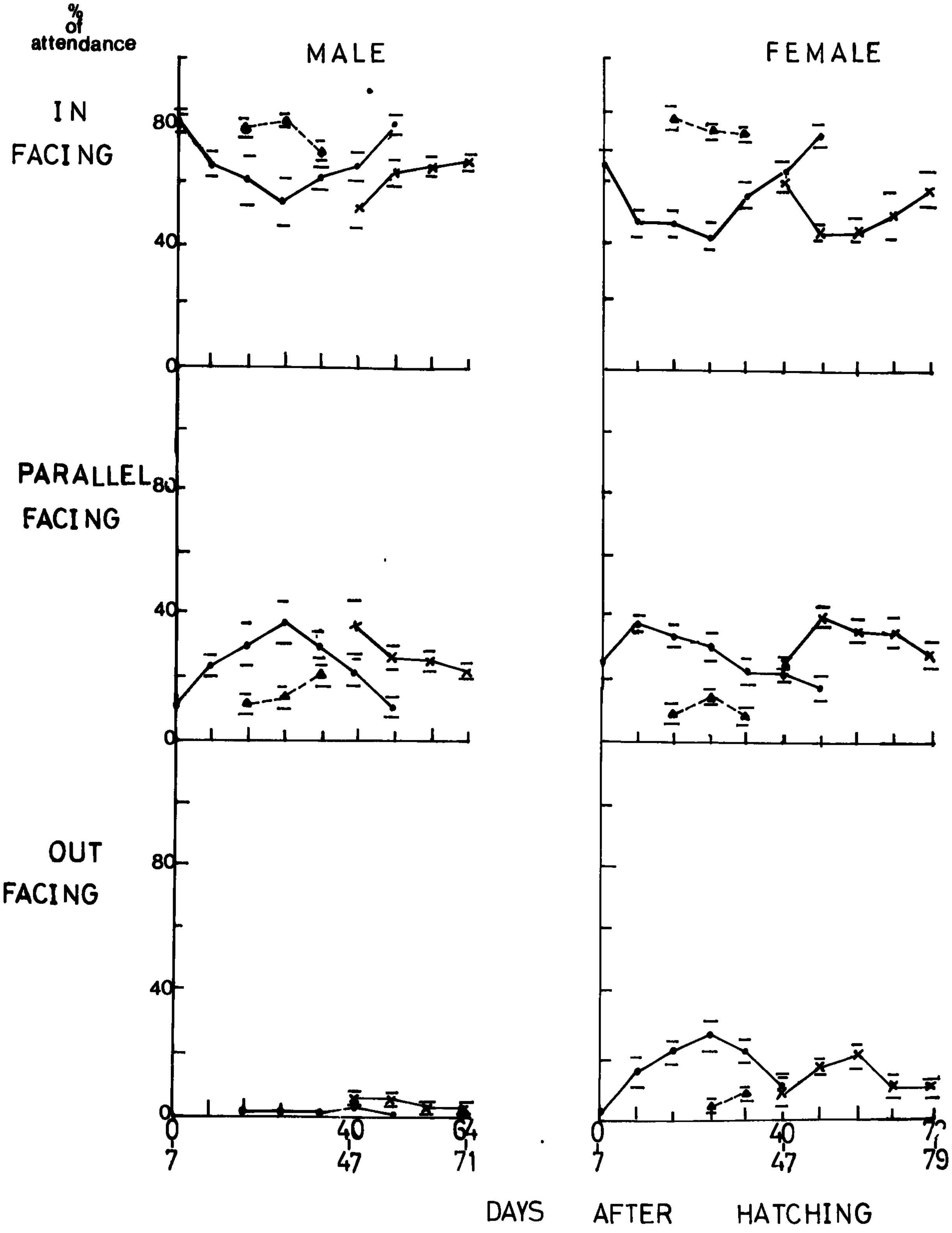

% of attendance
MALE
FEMALE
IN FACING
PARALLEL FACING
OUT FACING
80
40
0
0
7
40
47
64
71
0
7
40
47
72
79
DAYS AFTER HATCHING

Fig. 8. Changes in the percentages of attendance spent facing IN, PARALLEL and OUT during the breeding cycle of pair 4.

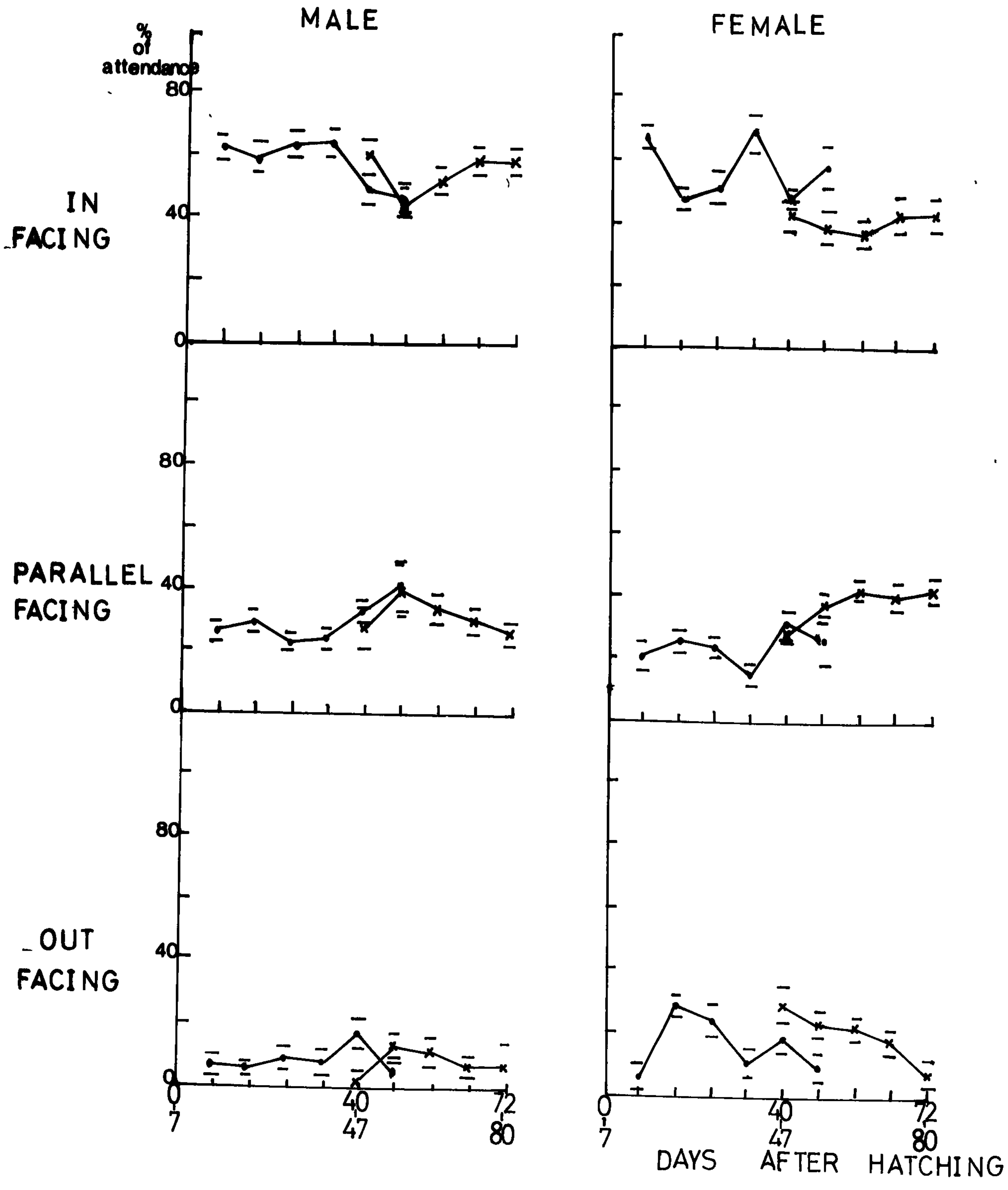
●——● chicks present, parents ON attending

×——× chicks absent, parents ON attending

▲- - - -▲ chicks present, parents SIDE attending

limits = 1 x S.E.

(Each point is the mean of 8 consecutive daily measures)


MALE
FEMALE
%
of
attendance
80
40
0
IN
FACING
PARALLEL
FACING
OUT
FACING
0
7
40
47
72
80
DAYS AFTER HATCHING

mean of a group of 8 consecutive daily measurements of the transformed percentages of attendance spent facing in a particular direction. The limit~~e~~s shown are one standard error from those means.

Fig. 5 shows the results from pair 1 from 80 days before batching of the chicks until their final abandonment of the nest site. Fig. 6, 7 and 8 show the results from pairs 2, 3 and 4 respectively from shortly after hatching until the final abandonment of the nest site. The information in these graphs has been split to show the effects on the percentages of the different facings of the presence or absence of chicks and whether the parents are ON or SIDE nest attending.

The most complete record, for pair 1, showed that the facing behaviour changed as the breeding cycle progressed. Fig. 5 illustrates that during the earliest stages of nest site occupation the orientation of the adults was mainly towards the nest ledge, i.e. inside and parallel facing, which was interpreted as a short period of familiarisation with the new site. This was followed by a longer period, where more attention was focussed on outside facing where other adults prospecting for nest sites would have created a diverting disturbance. When the adults were nest building at high intensity, egg laying and incubating, during the 32 days before the chicks hatched, outside facing changed to inside facing which may have been an adaption to minimise spillage of the eggs, particularly during egg turning. At the time of hatching adult facing became almost exclusively inside. Unlike the earlier changes the levels of both outside and parallel facing dropped dramatically, particularly the former. This was seen as a further measure to minimise the risk of losing the mobile yet uncordinated chicks and afford them protection from falling debris on the cliff-face habitat as the adults stood between the brood and the precipice. This behaviour makes observations of young chicks difficult on a normal cliff-face colony but by filming as here from behind the nest site, from inside the warehouse, no such difficulty arose. Fig. 5 indicated that throughout the period of attendance of the chicks the level of inside facing was always high and this situation was confirmed for pairs 2, 3 and 4 as is seen in Figs. 6, 7 and 8. These graphs also showed that when the chicks had left the nest site then the adult orientation tended to become more random than when chicks were present.

The existence of a major pattern of facing behaviour that varied between different breeding stages suggested that stimuli connected with the nest and its contents had an important effect on this behaviour.

The changes in facing behaviour could thus be interpreted as yet another adaptation of kittiwakes to the cliff-face nesting habitat (Cullen, 1957) that is not seen in the normal ground-nesting gulls e.g. (Beer, 1961, for black-headed gulls) where eggs and broods are not at risk from falling. McLannahan (1973) found that isolated, young kittiwake chicks (day 1 to 5) did not depress their activity to the same extent as older chicks either when close to a 'cliff' wall or when in darkness. This suggests that the effects of the most marked change in facing behaviour, seen at the time of hatching, could be an important factor in the reduction of young chick mortality.

INDIVIDUAL VARIATION IN FACING BEHAVIOUR

Although during chick care, inside facing was always the most favoured direction, a close examination of Fig. 5 to 8 indicated that the facing behaviour of the members of a particular pair was more similar to one another than to that of members of other pairs. The daily transformed percentages of inside facing were assumed to be independent estimates of the inside facing preference of individual adults. Hence, it was possible to test for differences between adults of the same sex on different nest sites by one-way analyses of variance and the differences between adults of a pair by d tests (Bailey 1959): These tests were made over the period from day 10 after hatching until the abandonment of the nest site by the chicks. This was the longest period for which inter-pair comparisons were possible. The results for these tests (Table 8) showed that the members of a pair tended not to differ in their percentage inside facing (only pair 3 showed a significant difference $P < 0.05$) yet adults of the same sex on different nest sites did differ significantly in their percentage inside facing ($P < 0.001$). The tendency for the members of a pair not to differ was taken to indicate that individual variation was not an important factor governing this behaviour and the tendency for individuals to differ from site to site was taken to indicate that the physical characteristics of the site, i.e. the amount of protection afforded by the 'cliff' face did affect this behaviour. The more exposed sites of pairs 1 and 2 gave higher values for inside facing than the more sheltered sites of pairs 3 and 4.

TABLE 8. COMPARISON BETWEEN THE PERCENTAGE INSIDE FACING OF FOUR PAIRS OF ADULT KITTIWAKES ATTENDING THE NEST SITES WITH CHICKS PRESENT - (DAY 10 AFTER HATCHING UNTIL CHICKS ABANDON SITE)

Sex of adult attending	MEAN DAILY PERCENTAGE OF ATTENDANCE FACING INSIDE (ARCSIN TRANSFORMED)				Significance level
	<u>Pair 1</u>	<u>Pair 2</u>	<u>Pair 3</u>	<u>Pair 4</u>	
Male	(36) 72.1	(35) 68.3	(35) 60.9	(40) 57.5	P<0.001
	n.s.	n.s.	P<0.05	n.s.	
Female	(32) 75.2	(35) 63.5	(42) 53.8	(38) 57.5	P<0.001

<u>Notes:</u> Numbers in parenthesis are numbers of days on which observations were made

Differences between adults of the same sex on different sites tested by one way analyses of variance

Differences between pairs on same site tested by d test (Bailey, 1959) n.s. = not significant

It is possible that the small scale serial fluctuations which were seen in the pairs of graphs for each site, for each orientation direction, may represent the effects of various changing environmental factors such as temperature, wind-speed and wind direction influencing in a similar way each of the two members of a pair.

FACING DIRECTION AND SIDE NEST ATTENDANCE

The analyses which are shown above refer to the facing orientation of adults attending on some part of the nest structure - namely ON nest attending. This is the normal position for adults to stand. In some pairs during late chick care, the nest ledge adjacent to the nest itself was utilized - SIDE nest attendance: see Fig. 4. During SIDE nest attendance the adults were out of close proximity to the chicks, whose movements were largely restricted to the nest structure itself.

Records were made of the facing direction in the SIDE position of only two of the pairs studied, as shown in Figs. 6 and 7. The occurrence of SIDE nest attendance varied widely between individuals. Thus, each day on which both types of attendance occurred was classified either as SIDE or ON, depending on where the larger percentage of inside facing was observed, for all 4 adults (Pairs 2 and 3). Similar facing orientation in the two attendance positions would have given equal numbers of days under the two conditions thus providing expected values to compare with the observed values in chi-squared tests. Table 9 showed that the number of days under the two conditions differed significantly, ($P < 0.05$), in all four cases so that adults that attended in both the SIDE and ON position on the same day tended to carry

TABLE 9. DIFFERENCES IN INSIDE FACING BEHAVIOUR WHEN PARENTS ARE 'ON' NEST ATTENDING OR 'SIDE' NEST ATTENDING

All days that included both ON and SIDE nest attendance were scored according to which type of nest attendance contained the greater proportion of inside facing

	No. of days when more inside facing with parents ON	No. of days when more inside facing with parents SIDE	χ^2_1	Significance level
PAIR 2				
MALE	6	17	5.26	$P < 0.05$
FEMALE	3	25	17.28	$P < 0.001$
PAIR 3				
MALE	1	14	11.26	$P < 0.001$
FEMALE	0	14	14.0	$P < 0.001$

out more inside facing in the former rather than the latter position.

Although the function of SIDE nest attendance did not emerge from this study, Fig. 4 and Table 9 showed that not only did the position occupied differ from normal but also that the facing orientation changed, so that adults tended to face away from their broods when nest attending in the SIDE position.

DISCUSSION

In an investigation of this type where relatively few individuals were examined closely rather than large numbers examined in lesser detail, the results obtained can not necessarily be regarded as representative of all kittiwakes. However, where replicate observations were available, there was close agreement between all of the individuals. The study did suggest that the direction of facing of adult kittiwakes at the nest site was adapted mainly to favour the safety of the eggs and chicks on the dangerous cliff-face habitat. SIDE nest attendance clearly differed from nest attendance in the ON position as adults did not face their brood in the former case. During chick attendance, there was tentative evidence to suggest that the physical characteristics of the nest site, rather than weather and individual variation was of greater relevance to this behaviour. Cullen (1957) concluded that the cliff-nesting habit of kittiwakes was probably an anti-predator device and that the mortality of chicks was at least as often caused by falling as by starvation. However Coulson and White (1958a) and Pearson (1968) could find no evidence to suggest that starvation was an important factor, so that death by falling appeared to be one of the main causes of chick mortality. This opinion was reinforced by my own observations of several North Sea colonies of kittiwake where chicks that were in good condition could often be found at the base of the cliffs. If this hypothesis were confirmed then vigorous selection in favour of an adaption of adult behaviour to minimise this source of danger, would be expected.

If the marked change noted above in facing direction, between incubation and chick attendance were general then this might provide a readily observable field measure of hatching date, and, by extrapolation, laying date, which could be used for inaccessible kittiwake colonies. These parameters have been shown by Coulson (1972) to be important in kittiwake population studies.

THE ATTENDANCE OF ADULT KITTIWAKES AT THE NEST SITE DURING THE BREEDING SEASON

Coulson & White (1958a) concluded that older, more experienced kittiwakes reacted to the breeding stimulus earlier, more intensely and with greater success than younger breeding birds. In a later study, Coulson (1972) illustrated the advantage for potentially good breeding birds in breeding together and concluded that this was achieved by the best birds returning to the colony first and hence pairing up with potentially good mates; segregation between the centre and edge of the colony enhanced this. In the earlier study it was demonstrated that before breeding started birds that had bred previously spent more of their time at the colony (and showed greater nest site tenacity in the following year) than those about to breed for the first time.

Not only was early occupation of the nest site important but also, as successful rearing of young involved a great deal of co-operation between the members of a pair (where both sexes assisted in incubation and care of the young Coulson & White 1958a) then the pattern of attendance of adults at the nest site throughout the breeding cycle was important.

METHODS

Kittiwakes differ from their ground-nesting relatives in their habit of breeding on very small cliff-ledges rather than in large territories on either flat ground or on large ledges where the actual nest site only occupies a fraction of the defended area. This restricted area of nest site made the recording of all adult attendance by time-lapse film much easier than would have been the case for a comparable ground-nesting species. Time-lapse records for Pair 1 extended from occupation of the nest site by the adults until abandonment by the chicks and for Pairs 2, 3 and 4 from soon after hatching until abandonment of the nest site by the adults sometime after the chicks had fledged.

During the filming of the breeding birds the colony was visited at intervals of not more than two days. Each visit consisted of recording, for all nest sites in the colony, the presence or absence of either adults, chicks or eggs. These records represented a series of independent spot observations of the attendance of individual kittiwakes at the nest site that could be compared with the results obtained from the four filmed pairs. During the later part of the 1969 and 1970 breeding seasons, when chicks were present in the nest, the visits were made daily and consisted of five consecutive hourly spot observations rather than the single observations carried out in the earlier part of the season.

PROCEDURE

The time-lapse records were analysed by splitting attendance into 6 categories.

1 Male alone, ON nest attending. * = MALE SINGLE ON
2 " " , SIDE " " = MALE SINGLE SIDE
3 Female alone, ON nest attending. = FEMALE SINGLE ON
4 " " SIDE nest attending = FEMALE SINGLE SIDE
5 Both parents together = BOTH
6 Neither parent present = LEAVE

* See Fig. 4 for definition of 'ON' + 'SIDE' nest attendance

Each frame of the time-lapse film was classified with respect to date, sex of adult, presence or absence of eggs or chicks and type of attendance. In order to compare the attendance of the parents on a day to day basis, the raw results were converted to percentages of the daylight hours spent on each of the six types of attendance. As percentage follows a binomial rather than a normal distribution all percentage values were transformed by means of the arcsine square root transformation. Unless otherwise stated all following graphs and calculations were based on arcsine transformed percentages.(see Appendix).

Each of the time-lapse records represented a particular example (accurately measured) of the pattern of nest site attendance shown by successful breeding pairs.

By utilizing the spot observation information, as shown below, it was possible to gain an indication of what form an 'average' pattern of attendance took in successful pairs. This was compared with the time-lapse records.

A minimum of 36 successful breeding sites were observed from 120 days before the hatching of the first egg until after the abandonment of the nest site by the adults after the breeding season. Each observation of a nest site was classified into the same 6 categories of attendance as the time-lapse data. In order to group the results from different nest sites all observations were converted to days before or after hatching of the chicks. So that all observations should be independent of one another, only the first observation, of a particular site, on a particular day, was used when more than one had been made.

CHANGES IN THE PATTERN OF ATTENDANCE BEHAVIOUR THROUGH THE BREEDING SEASON

Figs 9 to 12 show the different percentages of the total daylight hours spent on the six different categories of attendance during the breeding cycles of four pairs of kittiwakes. These are timed from the dates of hatching of the chicks. Each point on the graphs is the mean of a group of eight consecutive daily measurements of the transformed percentages of the different categories of attendance.

Fig. 9 shows the results for one pair of birds from 88 days before hatching of the chicks until the final abandonment of the nest site by the chicks. Figs 10 to 12 show the results for three further pairs from shortly after hatching until the final abandonment of the nest site by the adults. The spot observation information (Fig. 13) was grouped into the same eight day groups as Figs 9 to 12 and similarly shows the variation with the stage of breeding, timed from the hatching date, of the percentages of these groups of observations that fell into each of the six possible adult attendance categories. The observations used to construct each point of Fig 13 were obtained from at least 36 pairs of successful birds. The spot observation record was longer than any of the time-lapse records yet similarities between Figs 9 to 13 were evident.
These Figs. generally showed the same major pattern of adult attendance through the breeding season which can be summarised as follows.

(1) The Early Pre-breeding pattern was one of approximately equal amounts of male alone ON, female alone ON and BOTH

Fig. 9. Changes in the percentages of the total daylight hours spent on different categories of attendance during the breeding cycle of pair 1. (arcsin transformed)

●——●	male
▲- - -▲	female
×—·—·×	both
+·········+	neither

limits = 1 x S.E.

e = egg laying

h = hatching

|f| = chicks flying

(Each point is the mean of 8 consecutive daily measures)

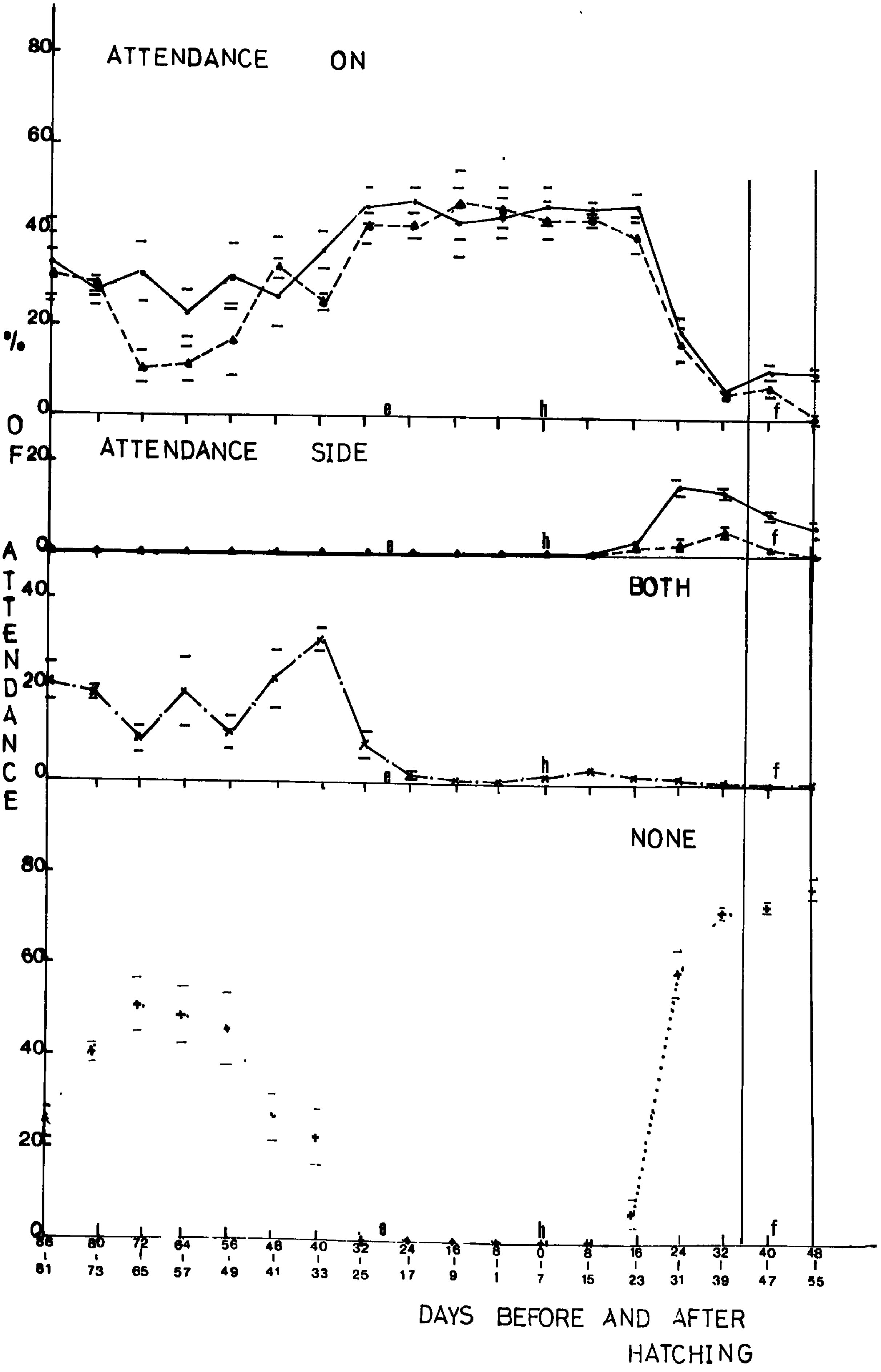

ATTENDANCE ON
ATTENDANCE SIDE
BOTH
NONE
% OF ATTENDANCE
80
60
40
20
0
e
h
f
88 81
80 73
72 65
64 57
56 49
48 41
40 33
32 25
24 17
16 9
8 1
0 7
8 15
16 23
24 31
32 39
40 47
48 55
DAYS BEFORE AND AFTER HATCHING

Fig. 10. Changes in the percentages of the total daylight hours spent on different categories of attendance during the breeding cycle of pair 2. (arcsin transformed)

●——●	male
▲-----▲	female
×—·—·×	both
+·········+	neither

limits = 1 x S.E.

~~e = egg laying~~

~~h = hatching~~

|f| = chicks flying

(Each point is the mean of 8 consecutive daily measures)

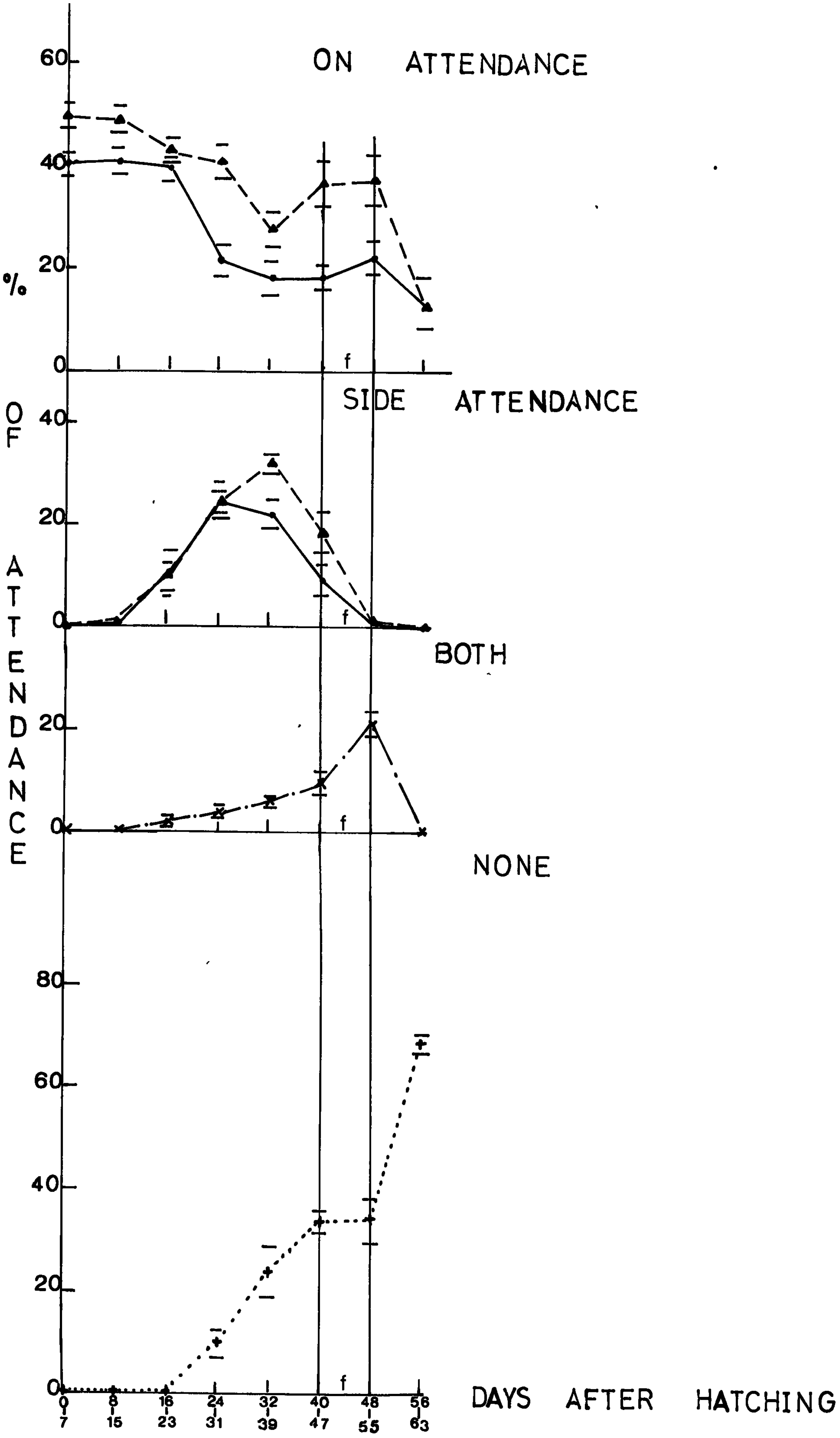

ON ATTENDANCE
SIDE ATTENDANCE
BOTH
NONE
% OF ATTENDANCE
60
40
20
0
40
20
0
20
0
80
60
40
20
0
f
DAYS AFTER HATCHING
0
7
8
15
16
23
24
31
32
39
40
47
48
55
56
63

Fig. 11. Changes in the percentages of the total daylight hours spent on different categories of attendance during the breeding cycle of pair 3. (arcsin transformed)

●——● male
▲- - -▲ female
x·-·-x both
+·······+ neither

limits = 1 x S.E.

~~e = egg laying~~
~~h = hatching~~
|f| = chicks flying

(Each point is the mean of 8 consecutive daily measures)

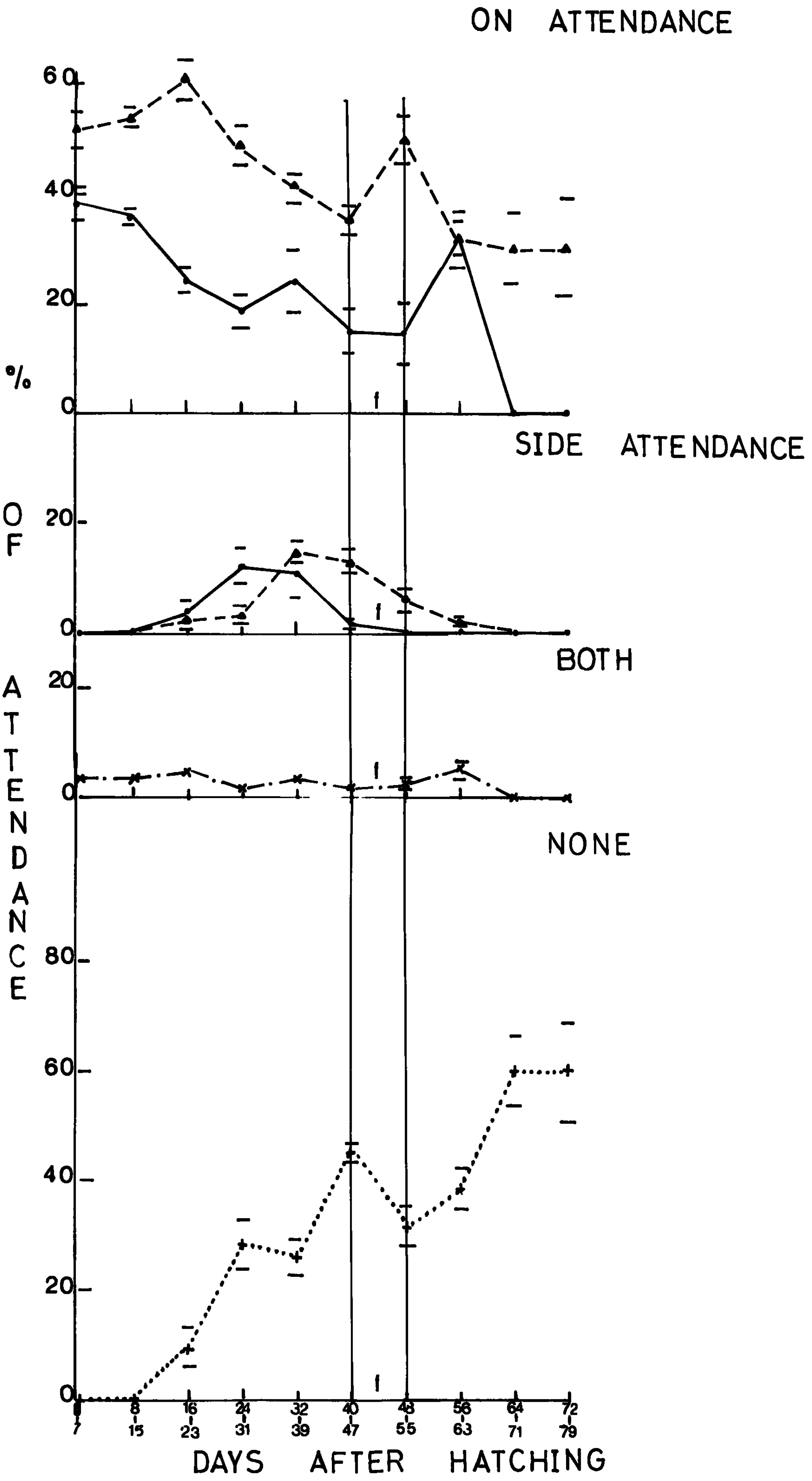
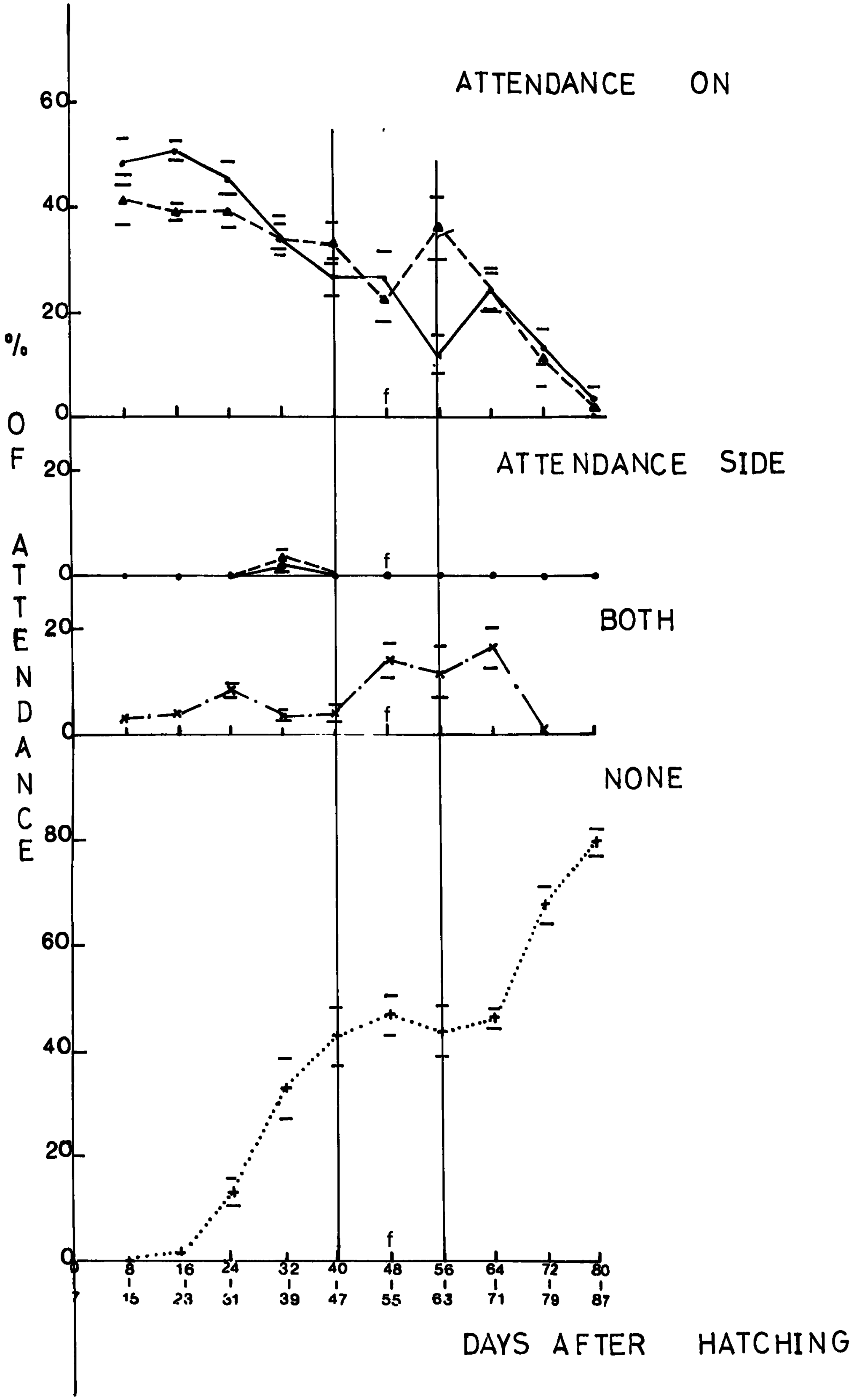

ON ATTENDANCE
SIDE ATTENDANCE
BOTH
NONE
% OF ATTENDANCE
60
40
20
0
20
0
20
0
80
60
40
20
0
0
7
8
15
16
23
24
31
32
39
40
47
48
55
56
63
64
71
72
79
DAYS AFTER HATCHING

Fig. 12. Changes in the percentages of the total daylight hours spent on different categories of attendance during the breeding cycle of pair 4. (arcsin transformed)

●——● male
▲----▲ female
×—·—·× both
+·······+ neither
limits = 1 x S.E.
~~·e —— = egg laying~~
~~·h —— = hatching~~
|f| = chicks flying

(Each point is the mean of 8 consecutive daily measures)



ATTENDANCE ON
ATTENDANCE SIDE
BOTH
NONE
% OF ATTENDANCE
60
40
20
0
20
0
20
0
80
60
40
20
0
f
0 - 7
8 - 15
16 - 23
24 - 31
32 - 39
40 - 47
48 - 55
56 - 63
64 - 71
72 - 79
80 - 87
DAYS AFTER HATCHING

Fig. 13. Changes in the percentages of the total spot observations made in consecutive 8 day periods spent on different categories of attendance during the breeding cycle of successful pairs. (arcsin transformed)

●——● male

▲- - - -▲ female

×——× both

+——+ neither

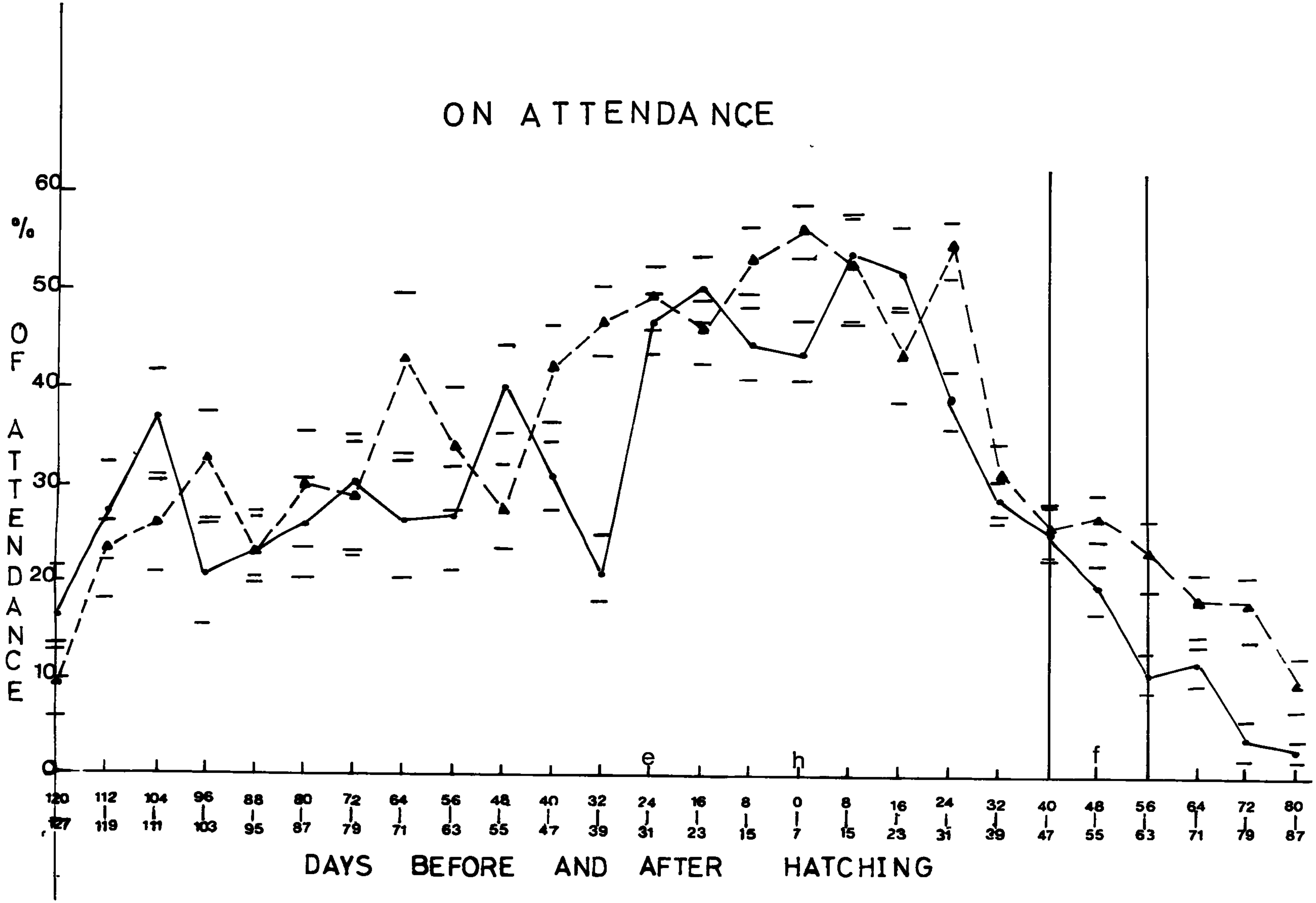
limits = 1 x S.E.

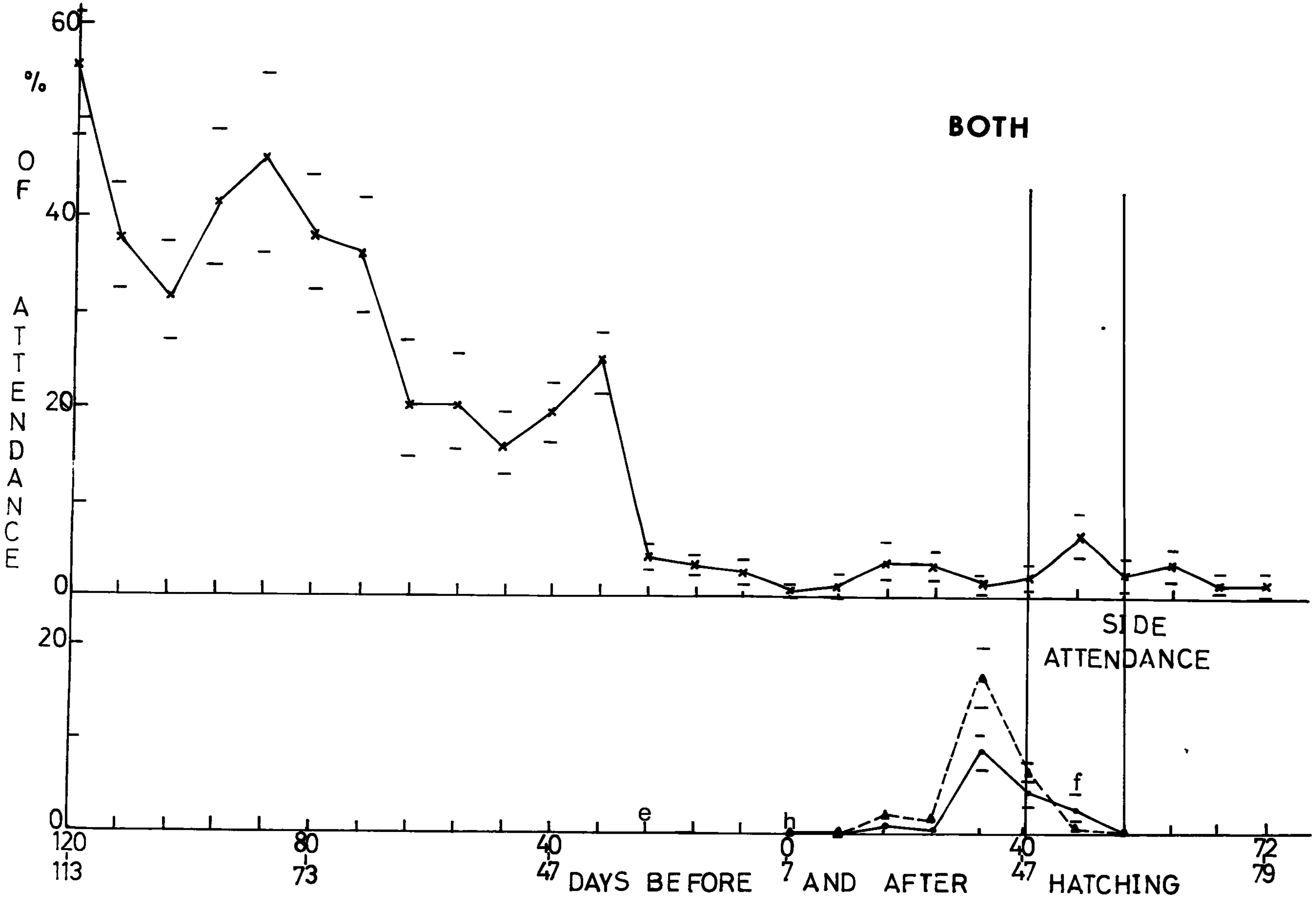
e = egg laying

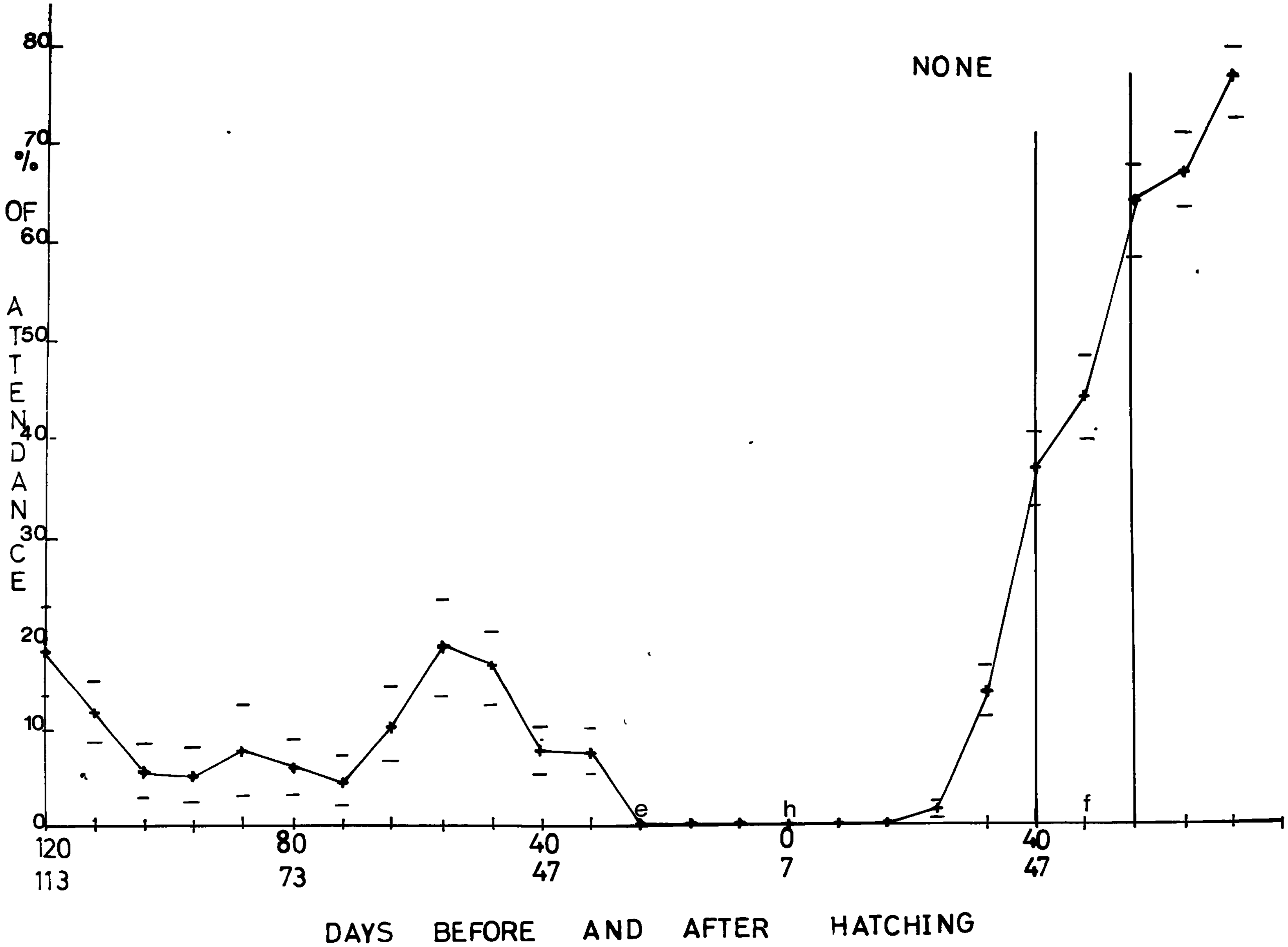
h = hatching

|f| = chicks flying

ON ATTENDANCE




BOTH
% OF ATTENDANCE
60
40
20
0
20
0
SIDE ATTENDANCE
e
h
f
120 113
80 73
40 47
0 7
40 47
72 79
DAYS BEFORE AND AFTER HATCHING


NONE
% OF ATTENDANCE
80
70
60
50
40
30
20
10
0
120
113
80
73
40
47
0
7
40
47
e
h
f
DAYS BEFORE AND AFTER HATCHING

attendance with the nest site left unattended for shorter periods., (Female attendance was somewhat variable).

(2) The period just prior to egg-laying marked a change in the attendance pattern such that the nest was never left unattended and BOTH attendance was reduced to very short changeovers which punctuated the constant adult attendance throughout Incubation and Early Chick-care. The two adults carried out approximately equal shares of the attendance in the ON position.

(3) Late Chick-care saw a reduction in the amount of attendance by each adult in the ON position that was partially compensated by each adult attending in the SIDE position. The nest site was also left unattended.

(4) The changes in the pattern of attendance prior to the first flight of the chicks were slowed down or reversed during the Fledging Period with a reduction of attendance in the SIDE position and a slight increase in BOTH attendance.

(5) After the abandonment of the nest site by the chicks, adult attendance was very variable but attendance in the SIDE position was never recorded. This stage was terminated by the abandonment of the nest site by the adults.

INDIVIDUAL VARIATION IN THE TIMING OF CHANGES IN ATTENDANCE PATTERNS THROUGH THE BREEDING SEASON.

The information contained in graphs 9 to 13 indicated that the attendance of adult kittiwakes at the nest site changed through the breeding season in an ordered way. However, the timing of these changes varied between pairs. As the results in Figs 9 to 13 were in the form of a sequence arranged in the order in which they were obtained, they were suitable for analysis using cumulative sum chart techniques (Woodworth and Goldsmith 1964). When each of a sequence of results, over time, is subtracted in turn from a constant 'reference' value, e.g. the mean of the whole sequence, and if each of the deviations (with regard to sign) is accumulated, then the serial accumulation can be plotted to form a 'cumulative sum chart'. On such charts a sequence of results of approximately equal value is represented by a straight section. The steepness of the slope of the section is proportional to the deviation of the average value of that section from the reference value. Downward slopes indicate values less than the reference value, upward slopes indicate values greater than the reference value. The point of onset of the changes in slope mark the changes in the average serial values.

Cumulative sum charts were constructed from the sequential values of the transformed daily percentages of the attendance in the ON position by each adult of Pair 1 - Fig. 14 and similarly for Pairs 2, 3 and 4 - Fig. 15 A chart, Fig 16 was also constructed from the spot-observation information of Fig. 13.

As ~~a~~ spot-observations represented the 'average' pattern then Fig. 16 was considered first.

On this Figure the two charts, for males and females, diverge. This shows that the two sexes did not carry out identical attendance behaviour.

The positions of the changes in the slope of the two charts indicated the timing of the changes in the amounts of single ON attendance and thus the changes in the attendance pattern. In this way the whole record could be split into the distinct stages

Fig. 14. Cumulative sum charts of the sequential daily values of the transformed percentages of SINGLE ON attendance during the breeding cycle of pair 1. (See text for details)

x x x x male

● ● ● ● female

reference value = 30

e = egg laying

h = hatching

|f| = chicks flying

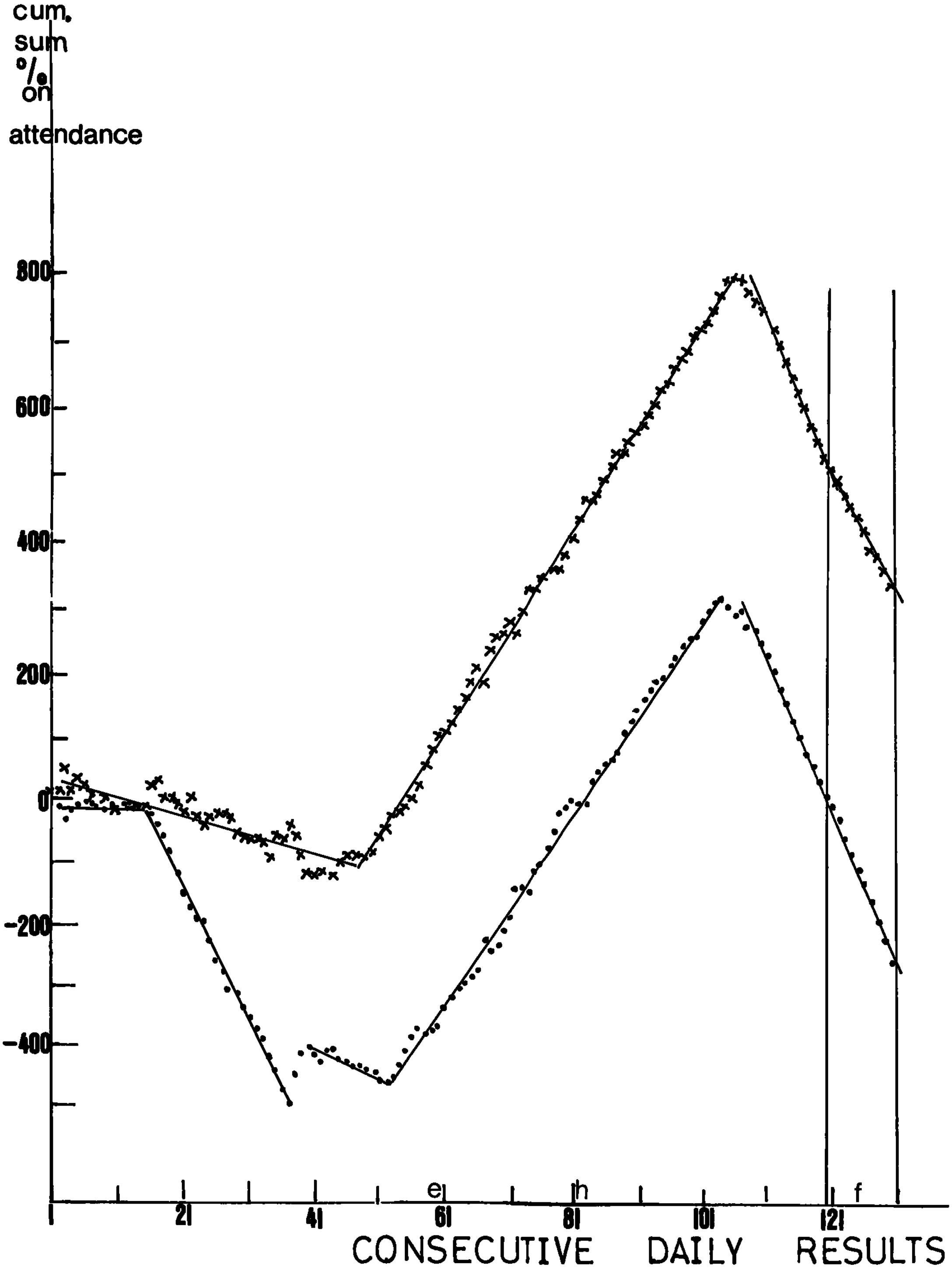

cum. sum
%
on
attendance
800
600
400
200
0
-200
-400
1
21
41
61
81
101
121
e
h
f
CONSECUTIVE DAILY RESULTS

Fig. 15. Cumulative sum charts of the sequential daily values of the transformed percentages of <u>SINGLE</u> <u>ON</u> attendance during the breeding cycle of pairs 2, 3, and 4. (See text for details)

reference value = 40

~~e = egg laying~~

~~h = hatching~~

|f| = chicks flying

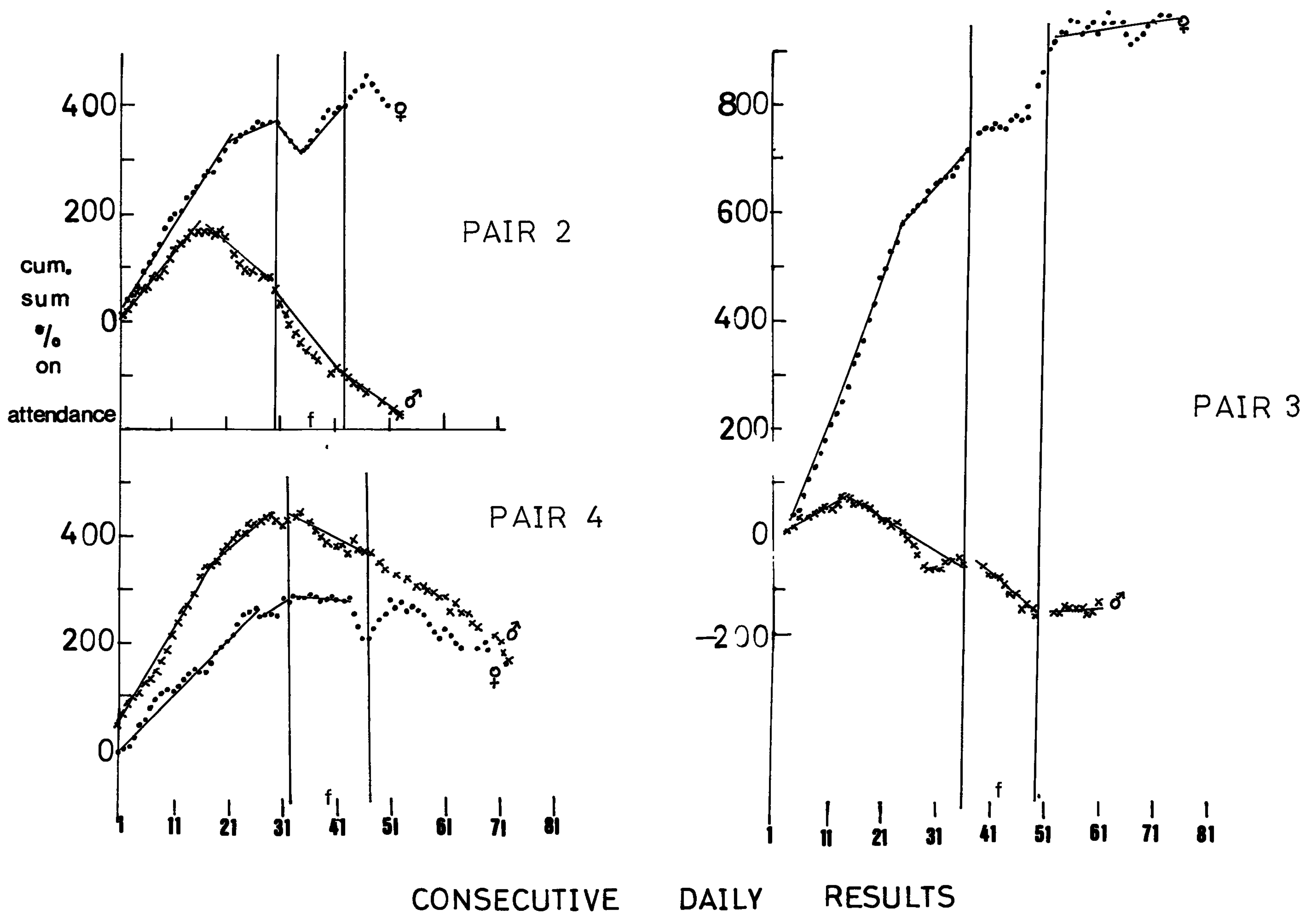

cum. sum % on attendance
400
200
0
PAIR 2
♀
♂
f
400
200
0
PAIR 4
♀
♂
f
800
600
400
200
0
−200
PAIR 3
♀
♂
f
1
11
21
31
41
51
61
71
81
CONSECUTIVE DAILY RESULTS

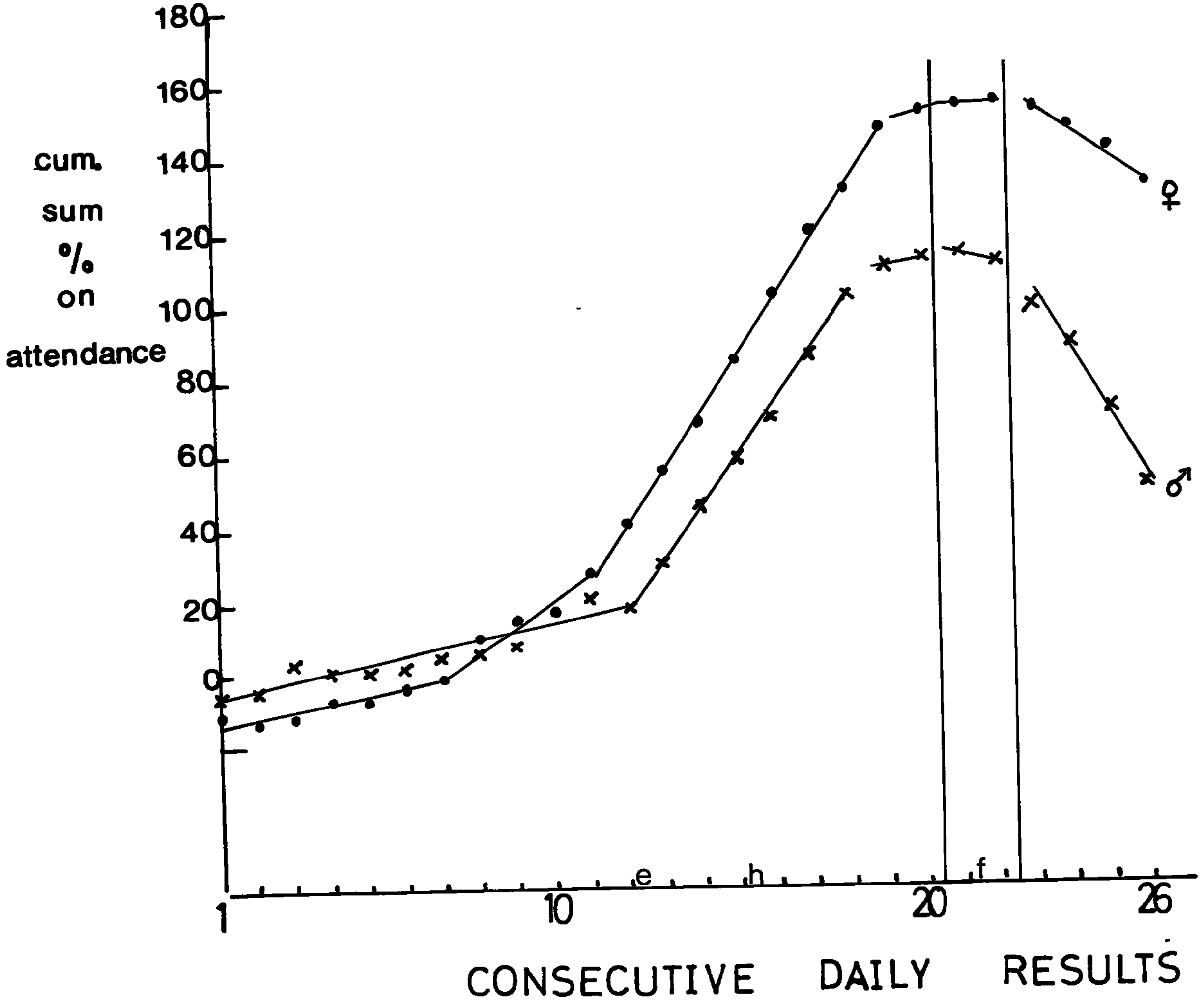
Fig. 16. Cumulative sum charts of the sequential values of the transformed percentage of the total spot observations made in consecutive 8 day periods spent on SINGLE ON attendance during the breeding cycle of successful pairs. (See text for details)

reference value = 40

e = egg laying

h = hatching

|f| = chicks flying


cum. sum % on attendance
180
160
140
120
100
80
60
40
20
0
1
10
20
26
e
h
f
♀
♂
CONSECUTIVE DAILY RESULTS

that were recognised in the original graphs 9 to 13. The high resolution of the cumulative sum chart method was shown in Fig. 16 where during the late pre-breeding stage the females were seen to exhibit an extra attendance stage, not shown by the males, that was difficult to pick out in Fig. 13. After this the two sexes showed parallel attendance stages for the rest of the breeding cycle although the precise timing of the beginning and ending of these stages differed in the two sexes. The change from late Pre-breeding to the Main Breeding stages (Nest building, Incubation and Early Chick-care) in the females, occurred during the 8 day period prior to that of the males and the change in the females from this stage to Late Chick-care occurred during the 8 day period after the males change.

The cumulative sum charts of pairs 1 to 4, derived from the time-lapse film, represented the diversity of patterns of attendance among successful breeding pairs.

The changes in slope of the cumulative sum charts precisely timed the start and finish of the different attendance stages for both the time-lapse and spot observation information and these, together with the lengths of the comparable attendance stages, are given in Table 10. This table shows that only the record from Pair 1 was available for comparison with the spot-observation information during the Pre-breeding stage. Although the length of this stage was shorter for Pair 1 than for the spot-observation information there were similarities between the 2 records. The male displayed a constant attendance pattern and the female a variable one with 3 rather than 2

TABLE 10 LENGTH AND TIMING OF PARALLEL ATTENDANCE STAGES THROUGH THE BREEDING SEASON TAKEN FROM FIGS. 9 TO 16 - SEE TEXT FOR DETAILS

Timing given as days before (-) or days after (+) hatching

Spot observation results given as ranges in parentheses

PRE-BREEDING STAGE (DAYS)

		START	FINISH	LENGTH
SPOT OBSERVATION				
Male		-(120-113)	-(32-25)	(95-81)
Female	early	-(120-113)	-(72-65)	(55-41)
	late	-(64-57)	-(40-33)	(31-17)
TIME-LAPSE				
Pair 1				
Male		-81	-33	49
Female	early	-81	-67	15
	middle	-66	-45	22
	late	-44	-30	15

II MAIN-BREEDING STAGE (DAYS)

	START	FINISH	LENGTH
SPOT OBSERVATION			
Male	-(24-17)	+(16-23)	(34-48)
Female	-(32-25)	+(24-31)	(50-64)
TIME-LAPSE			
Pair 1			
Male	-32	+26	59
Female	-29	+25	55
Pair 2			
Male	no record	+21	-
Female	"	+28	-
Pair 3			
Male	"	+17	-
Female	"	+28	-
Pair 4			
Male	"	+27	-
Female	"	+36	-
MEAN OF TIME-LAPSE			
Male	no record	+22.8	-
Female	"	+29.3	-

III LATE CHICK-CARE STAGE (DAYS)

	START	FINISH	LENGTH
SPOT OBSERVATION			
Male	+(24-31)	+(32-39)	2-16
Female	+(32-39)	+(32-39)	1-8
TIME-LAPSE			
Pair 1			
Male	+27	+38	12
Female	+26	+38	13
Pair 2			
Male	+22	+37	16
Female	+29	+37	9
Pair 3			
Male	+18	+39	22
Female	+29	+39	11
Pair 4			
Male	+28	+42	15
Female	+37	+42	6
MEAN OF TIME-LAPSE			
Male	+23.8	+39.0	16.3
Female	+30.3	+39.0	9.8

IV

FLEDGING STAGE (DAYS)

	START	FINISH	LENGTH
SPOT OBSERVATION			
Male	+(40-47)	+(48-55)	2-16
Female	"	"	"
TIME-LAPSE			
Pair 1			
Male	+39	+48	10
Female	"	"	"
Pair 2			
Male	+38	+49	12
Female	"	"	"
Pair 3			
Male	+40	+54	15
Female	"	"	"
Pair 4			
Male	+43	+57	15
Female	"	"	"
MEAN OF TIME-LAPSE			
Male	+40	+52	13
Female	"	"	"

V POST FLEDGING STAGE (DAYS)

	START	FINISH	LENGTH
SPOT OBSERVATION			
Male	+(56-63)	+(80-87)	18-32
Female	"	"	"
TIME-LAPSE			
Pair 1			
Male	no record	no record	-
Female	"	"	-
Pair 2			
Male	+50	+58	9
Female	"	"	"
Pair 3			
Male	+55	+68	14
Female	"	"	"
Pair 4			
Male	+58	+82	25
Female	"	"	"
MEAN OF TIME-LAPSE			
Male	+53	+69.3	16
Female	"	"	"

sub-patterns of attendance during Pre-breeding. Coulson & White (1958b) gave the mean incubation period of Kittiwakes as 27.3 days so that Table 10 showed the start of the Main Breeding stage just prior to the laying of the eggs.

All four pairs of filmed birds furnished information about the ending of the Main Breeding stage. The four males gave a mean of 22.8 days (range 17-27) and the females a mean of 29.3 days (range 25-36) after hatching for the termination of this stage. This result was in agreement with the spot-observation information, where males finished before females, but showed that individuals were variable in the timing of this change. The variability in the termination of the Late Chick-care stage, by the first flight of the chicks was much less; an average 39 days after hatching, (range 37-42). The net effect of this was that the length of the late Chick-care stage for individual adults was highly variable: males averaged 16.3 days (range 12-22) and females 9.8 days (range 6-13). In contrast to Late Chick-care, the fledging period was much less variable in length with a mean of 13 days and a range of 10-15 days, whereas the individual records for the post-fledging stage again showed wide variation with a mean of 16 days but a range of 9 to 25 days, a result in agreement with the spot observation information.

Thus Table 10 indicated that the female attendance before egg-laying, the timing of the changes in attendance by individual adults during chick care (♂♂ before ♀♀) and the final abandonment of the nest site by the pair were highly variable whereas the timing of changes at egg laying and the first flight of the chicks were not.

INDIVIDUAL VARIATION IN THE FORM OF ATTENDANCE WITHIN ATTENDANCE STAGES

The pairs of charts in Figs. 14, 15 and 16 all diverged indicating intra-pair differences. A comparison between the slopes of all charts showed a wide variation that denoted highly individual patterns of single attendance in the ON position during breeding. As the amount of attendance in the ON position was measured as the percentage of the day spent on this attendance category then any changes must have been compensated by changes in the amounts of the other forms of attendance.

As shown in Table 10 the two adults of a pair changed their attendance stages at different times. Thus, attendance within a stage was only considered during that period when both adults of a pair showed comparable attendance stages (the results where only one adult had changed stage were dropped from the analysis). During these parts of the time-lapse records the straight portions of the cumulative sum charts indicated periods of relative stability. Within these periods, the consecutive daily arcsine transformed percentages were considered to be a normally distributed populations of estimates of the amounts of each attendance category.

Inter-pair differences in attendance behaviour within the same attendance stages were investigated by one way analysis of variance tests and intra-pair differences by t-tests.

A similar procedure could not be carried out on the spot observation information, to investigate differences between the two sexes attendance behaviour, as the numbers of eight day grouped observations during the stable parts of each attendance stage were too few for t-test comparisons. Instead, as each individual spot observation was independent of every other, male and female attendance was compared by a 1:1 goodness-of-fit Chi-squared test.

The results of these tests, together with the information on which they were based, are given in Table 11 with the time-lapse average percentages retransformed for a more direct comparison with the spot observation information.

The 'average' spot-observation record indicated that there was no pronounced tendency for either sex to carry out significantly more attendance alone in the ON position than the other except during the Post Fledging stage where females were over-represented significantly ($P < 0.001$). There was also an indication during the Late Chick-care stage that females carried out significantly more attendance alone in the SIDE position than males ($P < 0.05$). This was not in agreement with Coulson & White (1958a) whose spot-observation study indicated that a significantly greater percentage of females were present during incubation, although at all other stages of breeding the sexes were equally represented. The number of observations used here was much larger than in the study by Coulson & White (674 of single adult attendance during the whole incubation period compared with 95). The discrepancy may have arisen due to concentration of Coulson's observations around the laying day. Fig. 13 indicates a female bias at about this time.

TABLE 11. INTER- AND INTRA-PAIR DIFFERENCES IN THE FORM OF ATTENDANCE WITHIN THE SAME ATTENDANCE STAGE

I PRE-BREEDING STAGE

SPOT OBSERVATIONS

	EARLY	LATE
TOTAL OBSERVATIONS	425	409

% of total observations in each category

	MALE		FEMALE	MALE		FEMALE
Single ON	26.4	ns	24.5	32.8	ns	36.4
Single SIDE	0		0	0		0
BOTH		40.5			18.6	
LEAVE		8.7			12.2	

TIME-LAPSE

Average % of daylight hours in each category (retransformed)

	EARLY	MIDDLE	LATE
Pair 1			
No. of days	15	22	12

	MALE		FEMALE	MALE		FEMALE	MALE		FEMALE
Single ON	20.5	ns	20.5	23.4	xxx	12.8	25.8	ns	33.9
Single SIDE	0		0	0		0	0		0
BOTH		11.2			5.5			16.5	
LEAVE		32.8			58.7			20.4	

No records for Pairs 2, 3 and 4.

STATISTICAL TESTS

Spot observation - Chi-squared 1:1 Goodness of fit tests between sexes

Time - Lapse - t tests intra-pair

" - One way anovar tests inter-pair

ns = not sig., x = $P < 0.05$, xx = $P < 0.01$ xxx = $P < 0.001$

II MAIN BREEDING STAGE

SPOT OBSERVATIONS

TOTAL OBSERVATIONS 1182

% of total observations in each category

	MALE		FEMALE
Single ON	47.0	ns	50.0
Single SIDE	0.1	-	0.1
BOTH		2.7	
LEAVE		0	

TIME-LAPSE

Average % of daylight hours in each category (retransformed)

	MALE		FEMALE	INTER-PAIR DIFFERENCE
Pair 1				
No. of days		52		
Single ON	50.9	ns	48.4	
Single SIDE	0	-	0	
BOTH		0.1		
LEAVE		0.01		Male single ON - xx
Pair 2				Female single ON - xx
No. of days		15		Male single SIDE - no test
Single ON	44.5	ns	52.9	Female " " - " "
Single SIDE	0.2	ns	0.5	BOTH - " "
BOTH		0.01		LEAVE - " "
LEAVE		0		
Pair 3				
No. of days		12		
Single ON	35.1	xxx	64.4	
Single SIDE	0	-	0	
BOTH		0.4		
LEAVE		0		
Pair 4				
No. of days		17		
Single ON	59.2	xxx	38.5	
Single SIDE	0	-	0	
BOTH		0.7		
LEAVE		0.3		

III LATE CHICK-CARE STAGE

SPOT OBSERVATIONS

TOTAL OBSERVATIONS 217

% of total observations in each category

	MALE		FEMALE
Single ON	28.6	ns	31.3
Single SIDE	8.8	x	16.6
BOTH		1.4	
LEAVE		13.4	

TIME-LAPSE

Average % of daylight hours in each category
(retransformed)

	MALE		FEMALE	INTER-PAIR DIFFERENCE
Pair 1				
No. of days		12		
Single ON	2.8	ns	2.1	
Single SIDE	5.2	xxx	0.6	
BOTH		0		
LEAVE		88.1		
Pair 2				Male single ON - xx
No. of days		9		Female " " - xx
Single ON	11.5	xxx	30.5	Male single SIDE -xx
Single SIDE	16.7	x	27.6	Female " " -xxx
BOTH		1.1		BOTH -no test
LEAVE		8.2		LEAVE - xxx
Pair 3				
No. of days		10		
Single ON	18.6	xx	41.9	
Single SIDE	7.0	ns	3.2	
BOTH		0.3		
LEAVE		22.0		
Pair 4				
No. of days		6		
Single ON	26.8	ns	28.3	
Single SIDE	0.2	ns	1.0	
BOTH		0.6		
LEAVE		39.4		

IV FLEDGING STAGE

SPOT OBSERVATIONS

TOTAL OBSERVATIONS 338

% of total observations in each category

	MALE		FEMALE
Single ON	22.5	ns	26.0
Single SIDE	3.6	ns	3.9
BOTH		4.1	
LEAVE		39.9	

TIME-LAPSE

Average % of daylight hours in each category
(retransformed)

	MALE		FEMALE
Pair 1			
No. of days		8	
Single ON	3.3	ns	1.6
Single SIDE	2.0	xx	0.1
BOTH		0	
LEAVE		92.1	
Pair 2			
No. of days		12	
Single ON	9.2	xx	29.0
Single SIDE	3.0	ns	10.5
BOTH		3.1	
LEAVE		33.0	
Pair 3			
No. of days		10	
Single ON	13.2	xx	38.7
Single SIDE	0.1	xxx	2.5
BOTH		0.3	
LEAVE		40.4	
Pair 4			
No. of days		14	
Single ON	19.0	ns	18.9
Single SIDE	0	-	0
BOTH		2.6	
LEAVE		53.6	

INTER-PAIR DIFFERENCE	
Male single ON	- xx
Female " "	- xx
Male single SIDE	- x
Female " "	- xx
BOTH	- ns
LEAVE	- xxx

V POST FLEDGING STAGE

SPOT OBSERVATIONS

TOTAL OBSERVATIONS 633

% of total observations in each category

	MALE		FEMALE
Single ON	7.6	xxx	17.4
Single SIDE	0	-	0
BOTH		2.2	
LEAVE		72.8	

TIME-LAPSE

Average % of daylight in each category (retransformed)

	MALE		FEMALE	INTER-PAIR DIFFERENCE
Pair 1				
		no record		
Pair 2				
No. of days		7		
Single ON	10.2	ns	29.1	
Single SIDE	0	-	0	
BOTH		7.2		Male single ON - xx
LEAVE		47.2		Female " " - ns
Pair 3				Male single SIDE - no test
No. of days		9		Female " " - no test
Single ON	26.5	ns	30.9	BOTH - ns
Single SIDE	0	-	0	LEAVE - ns
BOTH		0.6		
LEAVE		37.6		
Pair 4				
No. of days		15		
Single ON	13.2	ns	16.9	
Single SIDE	0	-	0	
BOTH		6.6		
LEAVE		56.2		

Only Pair 1 furnished time-lapse information during the Pre-breeding stage. This differed from the 'average' spot-observation record by the inclusion of a sub-period of low female attendance alone in the ON position and the fact that the amount of adults attendance was generally not as great. This may well have indicated a lower than average reproductive drive in the adults of Pair 1, particularly the female. Cullen (1957) noted that after the birds returned from their winter quarters females were attracted to the nest sites by the males advertising their status by the 'choking' display. She also noted how kittiwakes had to stake a claim to a nest site early, as the number of suitable ledges were often restricted and therefore the competition for nest sites severe (This must account for the small amounts of LEAVE attendance during Early Pre-breeding). Pair 1 occupied a site classified by Coulson (1968) as an 'edge' rather than a 'centre' site where the competition was less severe than for the central sites occupied by pairs 2, 3 and 4 (and by the majority of the pairs in the spot observation information). This difference may account for the success of Pair 1 in retaining their site even though their Pre-Breeding stage was shorter, and their attendance less complete, than in most breeding pairs.

Table 11 shows that the attendance pattern of Pair 1 was most similar to the 'average' pattern during the period just prior to egg laying (Late Pre-Breeding). At this time the necessity for co-operation of behaviour during nest building and copulation must be greater than at any previous part of the cycle.

Results from all four time-lapse pairs were available for comparison during the early chick-care portion of the Main Breeding stage, as is shown in Table 11. The information from spot observations indicated that there was no overall tendency for either of the sexes to carry out more attendance than ~~in~~ the other in the ON position but two of the time-lapse intra-pair comparisons indicated a highly significant difference (P< 0.001). As the vast majority of attendance was carried out in the ON position during this stage these differences were largely responsible for the significant inter-pair difference. (P<0.01), seen in Table 11.

Thus, during the Main Breeding stage the attendance by individuals during daylight hours (essentially all in the ON position) was not necessarily shared equally.

The Main Breeding Stage represented the simplest attendance pattern in the breeding cycle with single ON attendance bouts only interrupted by short changeovers, (BOTH attendance). This co-ordination of attendance behaviour, lasting for the whole of the early chick stage ensured that successful breeding adults did not leave their young brood or eggs unattended except for the rare occasions when they were disturbed at the nest site. (Beer (1969a), however, working with black-headed gulls, found a significant negative correlation between the amount of time spent by adults on the territory and the age of the chicks from hatching. This difference may well relate to the danger from falling in the cliff-face nesting situation of kittiwakes, which does not influence ground-nesting gulls. This danger is allayed by the position and facing direction of the attending adults (See ~~Chapter~~ Section III).

However, Beer's study showed that the amount of time spent together by the adults of a pair. (BOTH attendance) was not correlated with the age of the brood. Although his value 5% for percentage of observation periods when adult Black-headed gulls attended together is somewhat larger than the values given for kittiwakes in Table 11, the difference is small. This meant that the requirements for the co-ordination of attendance during this stage (that were assumed to take place during BOTH attendance) were similar in the two species despite the different nest site habitats.

The adult nest attendance pattern during the Late Chick-care stage was characterised by a reduction in attendance alone in the ON position compensated for by the appearance of attendance alone in the SIDE position and periods when the nest site was left unattended (as in black-headed gulls).

This was noticed by Cullen (1957) who reported that in the first weeks after hatching the parents guarded the nest site so well that strange birds were seldom able to land there but later the young were more often left alone so that adults searching for territory could land on the nest site.

Whereas adults which were SINGLE SIDE attending could readily be identified from the time-lapse film, it was more difficult to decide which adult was responsible for the brood being left unattended. Beer (1961) suggested that during incubation in the black-headed gull an attendance bout by one adult was terminated by the return of the other but when on the time-lapse film of kittiwakes an adult was seen to leave during Late Chick-care this may have been caused by the early leaving of this attending bird or the late arrival of the other returning bird. Often the chicks were alone at daybreak leaving no clue as to the identity of the last adult to attend the chicks. For these reasons the appearance of LEAVE attendance (when the nest site was unattended) was related to particular pairs not to individuals.

The spot observation information indicated that neither sex carried out more of the single ON attendance, but that there was an indication that females were more often observed in single SIDE attendance than males.

Inter-pair comparisons during the Late Chick-care stage showed that the percentage of the day devoted to all of the attendance categories, except for BOTH attendance, differed significantly from site to site ($P < 0.01$). The most interesting of these was LEAVE attendance as this meant that chicks on different sites were left unattended for significantly different percentages of the daylight hours and thus were differentially open to disturbance from prospecting, strange adults. Two of the intra-pair comparisons of single ON attendance showed a significant difference ($P < 0.01$) and two of the single SIDE comparisons also showed a significant difference ($P < 0.05$).

Thus during the Late Chick-care stage, the individuals of a pair did not necessarily show similar amounts of attendance alone in the ON position or in the SIDE position. This variation was reflected in the fact that the attendance patterns of pairs also differed considerably.

Although there were inter-pair differences in the amounts of the single ON attendance, during the Main Breeding stage, this was co-ordinated in all pairs so that the chicks were not left unguarded yet adults hardly overlapped in their attendance. During the Late Chick-care stage, however, this did not happen, as there were highly significant differences between the pairs, ($P < 0.001$), in the amount of LEAVE attendance. Firstly, this showed that the introduction of attendance in the SIDE position did not fully replace the reduction of attendance time in the ON position, and secondly that different pairs achieved different, success in replacing this reduction.

Table 11 showed that in the change from the Main Breeding stage to the Late Chick-care stage the individuals of a pair did not decrease their attendance in the ON position to the same extent. For example, Pair 2 showed no intra-pair difference in single ON attendance during the former stage but a highly significant differance ($P < 0.001$) during the latter stage. Conversely, Pair 4 showed a highly significant intra-pair difference during the former stage ($P < 0.001$) and a non-significant difference during the latter stage. The Late Chick-care section of Table 11 also showed that during this stage the individuals of a pair did not replace the reduction in single ON attendance by single SIDE attendance (to the same extent). Pair 1 showed a non-significant intra-pair difference in single ON attendance but a highly significant difference in single SIDE attendance ($P < 0.001$) the converse was shown by Pair 3.

The discussion of the time-lapse results above, indicated that attendance during the Late Chick-care stage was highly individual. The total attendance pattern of a pair arose from the sum of two individual patterns that did not succeed in guarding the chicks throughout the daylight hours as in the Main Breeding stage.

The start of the fledging stage was marked by the first flight of the chicks and was terminated by the abandonment of the nest site by the chicks. Table 11 showed that the same categories of adult attendance were seen as in Late Chick-care and that the results of inter and intra-pair comparisons were similar, although the absolute magnitude of the categories changed between stages. For this reason similar conclusions were drawn concerning the individuality of the patterns of attendance, as in the previous stage. The spot observation data showed that females carried out significantly more single ON attendance than males during the Post-Fledging stage ($P < 0.001$). All three time-lapse pairs showed the same tendency, but non-significantly ($P > .05$). This discrepancy may well have arisen due to the fact that the time-lapse information was based only on those days when both adults of a pair attended the nest site whereas the spot observation information also included those days when only one adult was present at the nest site.

During the Post-Fledging stage inter-and intra-pair comparisons indicated no significant differences between the attendance patterns of individuals (with the exception of the inter-pair male single ON comparison $P < 0.01$). This dramatic change from the previous two stages indicated that the presence of chicks had a profound effect on the attendance pattern of the adults (particularly as single SIDE attendance was never seen during the Post-Fledging period when chicks were never present).

Table 11 summarises information that illustrates the patterns of attendance during the stable portions of successive attendance stages at the nest sites of breeding kittiwakes during daylight hours. The spot observation data in this Table indicates in general that males and females fulfil similar attendance roles during breeding (although afterwards females attend more than males).

The time-lapse records of 4 pairs showed a great deal of variation in attendance patterns both between and within pairs. Although the information was limited during the early stages, Pre-breeding was a non-stable period (female attendance being particularly variable). In general adults attended alone or together much of the time but the nest site was frequently left empty. From just prior to the time of incubation until after early chick-care, the pattern of attendance remained relatively stable. Essentially in all pairs, adults only attend alone in the ON position so that the site was never left unguarded yet this was achieved without the adults of a pair overlapping their attendance. During the later stages of chick-care and fledging the pattern of attendance became more complex with adults attending in the SIDE as well as the ON position and also leaving the nest site unguarded. Again overlapping of attendance was rarely seen but the change in the patterns of attendance from the earlier stage was not of a similar extent in the 2 adults of a pair. This indicated that the individual changes were independant of each other. After the chicks had left the nest site, the individual variation was greatly reduced and single SIDE attendance was never recorded although attendance together was. This indicated the importance of the presence of chicks on the organisation of attendance patterns.

DISCUSSION

The information contained in Tables 10 and 11, illustrated in Figs. 9 to 13, showed that the interval between the arrival of the adults at the nest sites and the laying of the first egg was up to 2½ months (which agreed with the estimate of Coulson, 1958a) and that this period was split into two parts.

The earliest part, where Cullen (1957) noted intense competition for nest sites amongst pairs, was characterised by low levels of LEAVE attendance and high levels of attendance together. This presumably allowed the two adults of a pair to synchronise their reproductive physiologies and develop their pair-bond while it simultaneously prevented competing adults from usurping the nest site. At the later stage attendance together decreased, which allowed individual adults more time for seeking nest material and for feeding (in preparation for egg-laying). Increased food demands affected both sexes, females directly, males by courtship feeding.

Fig. 13 showed that during the 16 days prior to egg laying significantly more females than males were observed single ON attending, ($P < 0.05$). This disparity might have arisen due to the clustering of observations around the period just prior to egg laying but it also may have represented males showing increasing courtship feeding. Kittiwakes lay rather large eggs whose production must place a burden on the resources of the females. As the sharing of nest attendance duties by the two sexes was equal after egglaying then any strategy to reduce the difference in the demands on the two sexes might be expected to function prior to egg laying.

Table 11 showed that the total amount of attendance by an adult at the nest site was male, 66.8%; female, 64.9% during the early stage, and male 51.3%; female, 55.0% during the late stage, figures that agreed with Coulson's, (1958a), of 60% obtained by a similar spot observation method.

It was concluded from the pattern of attendance shown by Pair 1 during pre-breeding (which was more variable, shorter in duration and contained much less actual attendance at the nest site than the 'average' pattern) that the reproductive drive of this pair was lower than average. Unlike the majority of the spot observation sites, which were 'centre' sites (Coulson 1968) and keenly sought after pair 1 occupied an 'edge' site which was retained even when the pair left it unattended for much of the day. The pattern of attendance shown by Pair 1 was most similar to the spot observation pattern just prior to breeding when there must have been the greatest premium on co-ordination of attendance to ensure successful egg-laying.

Thus, perhaps there are two more essential features of the pre-breeding stage. Firstly there is then the necessity for high levels of attendance at the nest site to prevent other pairs taking the site, (although this would vary depending upon the position of the nest site in the colony). Secondly the pairs need to spend about 20% of the day together at the site for the month prior to egg laying, in order to synchronise their behaviour and physiology. Although the record for Pair 1 was the only time-lapse information that covered the incubation period, records from all four pairs were available for comparison during the early chick care portion of the Main Breeding stage.

Throughout the daylight hours of this stage the nest site was attended by each adult of a pair, turn and turn about with very short interruptions of attendance when both were present together at the changeover. Table 11 showed that the adults of Pairs 1 and 2 shared the attendance equally but the results from Pairs 3 and 4 showed that this was not always the case; male less than female (Pair 3), male more than female (Pair 4). This disagreement, responsible for the inter-pair differences shown in Table 11, may have arisen as a consequence of the film record covering the daylight hours only and thus not accounting for the possibility that one adult might carry out the majority of the night-time attendance, which could redress the balance.

These results, which suggested that the Main Breeding stage was a time of co-ordinated attendance at the nest site, were in accordance with those of Coulson (1972). They show that the eggs and young chicks were never left unattended, and were thus never at risk from chilling in the former case, or falling in the latter case. Coulson's record of the incubation patterns of two pairs, one successful and one unsuccessful, (obtained by a completely different technique in which the birds were radio-actively labelled) showed how, in successful incubation, a pair soon established a clear rhythm of attendance where both birds took an equal share with little attendance together. The unsuccessful pair also initiated a rhythm but the male failed to return and relieve the mate who finally left the eggs unattended after several successful attempts to fill the gap.

This pattern of attendance in the cliff-nesting kittiwake was continued during early chick-care in contrast to that ~~was not~~ seen in the ground-nesting black-headed gull (Beer, 1965a) where the time spent by the adults on the territory was negatively carrelated with the age of the chicks from hatching. This was understood to reflect the differences in the danger from falling between the two types of nest site, which, coupled with the position and orientation towards the brood of attending kittiwakes (shown earlier) ensured the greatest degree of protection and represented another adaption of the 'typical' gull behaviour to the cliff nest habitat (Cullen 1957). The co-ordination of the chicks improved as they grew (McLannahan, 1973) yet the presence of the adults at the nest site was still required. Unguarded nest sites were attended by non-breeding adults whose direct attacks on young chicks could be dangerous. Also, if the resident adult returned to an occupied site and vigorously engaged in a 'bill-twisting' fight (Cullen 1957) with the stranger, then there could have been a serious risk of young chicks accidentally falling.

The information from all four time-lapse pairs in Table 11 showed that during the Late Chick-care stage of breeding, individual adults and pairs differed greatly in their attendance patterns. Some individuals partially compensated for a decrease in their single ON attendance by attending in the SIDE position but all pairs were seen at times to leave their broods unattended. Inter and intra-pair comparisons in Table 11 indicated that there was wide variation between individuals in the size of the reduction in single ON attendance and the amount of single SIDE attendance which was carried out.

Despite these modifications of attendance, the pairs differed significantly in the amount of time that the broods were left unattended ($P < 0.001$). Thus the change from the Main Breeding stage to the Late Chick-care stage was a change from a simple pattern of constant attendance to a complex pattern of sporadic attendance that arose from the addition of two individual attendance patterns. The time-lapse and spot observation data of Table 10 showed that the males tended to make this change before the females.

Cullen (1957) noted that after the first few weeks post-hatching, the nest sites that were previously under continuous attendance by the adults were more often left unattended. This allowed strange adults searching for territory to land on them. The results given above suggest that during Late Chick-care different sites were open to different degrees of disturbance by strange adults.

The attendance patterns of adults during the Fledging stage (which extended from the day of the first flight of the chicks until their final departure from the site) was shown, by the time-lapse results, to be similar to that during the Late Chick-care stage. Although sites were more commonly left unattended during the later stage the individual differences in attendance, seen either inter or intra-pair, were generally maintained throughout. This indicated that during both stages the total pattern of daily attendance arose basically from the addition of two individual patterns.

The attendance pattern of adults during the Post-Fledging stage was simpler than it was previously as no SINGLE SIDE attendance was recorded, although there was a small increase in attendance together. In contrast to all previous breeding stages, however, both adults of a pair did not attend on all days. The spot observation information showed that significantly more females than males were present during this stage ($P < 0.001$). The time-lapse information (based only on those days when both individuals of a pair attended) showed that most of the former inter and intra-pair differences in attendance were no longer apparent (only male SINGLE ON attendance varied significantly between pairs, $P < 0.01$).

Thus adults only attended in complex individual attendance patterns when chicks were present and females attended the nest site more regularly than males during the Post-Fledging stage.

These observations can be considered with regard to the notion of co-ordination of attendance. For a pair of kittiwakes, that are very similar in appearance and size, attendance at the nest site (that was occupied by strange adults if unguarded) could only be considered fully co-ordinated if the following criteria were fulfilled.

(1) Nest attendance must be complete (i.e. nest site never unguarded).

(2) Nest attendance by the pair should be identical at the same stage of breeding (unless a particular sex-based difference was required, for example egg-laying).

(3) Nest attendance should be by one adult at a time (no duplication of effort).

At no part of the Pre-breeding stage were all of these criteria met. Attendance was never complete but as individuals spent long periods together at the nest site, as well as periods alone, then this could be the time of the greatest amount of daily attendance in the whole breeding cycle, for most individuals. This strain on adults, that were required to build up their body reserves for breeding, may be reflected in the short periods when the nest site was unguarded (Fig. 13). As previously suggested similar nest attendance was not expected when females prepared to lay eggs and males courtship fed. For the early part of the stage attendance was similar in the pair. Attendance together was required at this time to synchronise the pair's breeding cycles and for adults to learn to recognise and tolerate each others presence on the confined nest ledge.

Thus, during Pre-breeding, pairs were generally co-ordinated considering the special problems of this stage, but the degree of co-ordination probably varied between pairs (compare Fig. 9 with Fig. 13).

During the Main Breeding stage attendance was most perfectly co-ordinated with all criteria met in all pairs.

During Late Chick-care and fledging this position deteriorated so that (1) and (2) were rarely seen although there was little indication that (3) did not occur. These two periods could not be thought of as well co-ordinated.

During the post-fledging stage the attendance changed to become somewhat similar to the Pre-breeding stage although at a lower intensity. Criterion (2) was met and a resurgence of courtship took place requiring attendance together. This indicated a generally more co-ordinated pattern taking into consideration the requirements of this stage.

CHANGES IN THE ORGANISATION OF ADULT ATTENDANCE AFTER EARLY CHICK-CARE

The information in the previous section indicated that the timing of the change from the Main Breeding stage to the Late Chick-care stage was highly variable, both between and within pairs, but that females tended to change after males (Table 10). It was also found that during the former stage, attendance was simple and co-ordinated but that the pattern during the latter stage became more complex and individualistic, with less indication of co-ordination.

The pairs of cumulative sum charts of Fig. 14, 15 and 16 in no way indicated that at the time when the first member of a pair decreased its single ON attendance, (the change from the Main Breeding stage to Late chick-care) the other member of the pair increased its ON attendance, as one chart decreased in slope while the other remained unchanged. This was in contrast to the findings of Coulson (1972) where in a continuous record of kittiwake incubation attendance by a radioactive tagging technique, the shortcomings of one adults' single ON attendance was made up by that of the other member of the pair.

The increase in complexity was due to the inclusion of periods where the adults attended their broods in the SIDE position or left them unattended. In order to examine the development of these two forms of attendance more closely the information about the pairs for which time-lapse records were made was carefully re-examined.

In previous sections all attendance was expressed as the percentage of the total daylight hours spent by adults on a particular category, but after the change from the Main Breeding stage to the Late Chick-care stage there was a tendency for the nest site to remain unoccupied by adults for the whole day. So that this effect should not obscure the measure of the relative amounts of attendance in the SIDE position by individuals the daily time-lapse results were expressed as the percentage of an individual's total attendance alone spent in the SIDE position. Fig. 17 shows, for each adult of Pairs 1, 2 and 3 (which showed this attendance) the changes in the relative amount of attendance in the SIDE position, from initiation of the phenomenon to the start of the Fledging stage. Fig. 18 shows the change in the daily percentage of the daylight hours that all four pairs spent away from their nest sites (LEAVE attendance) from initiation to the start of the Fledging stage.

These graphs indicated that all the pairs which were studied sometimes left their chicks unattended and that most individuals (6 out of 8) showed some attendance alone in the SIDE position during the Late Chick-care stage. The timing of the initiation of these attendance categories was highly variable. A close examination of Figs. 17 and 18 shows that, at the time of the individual changes from attendance characteristic of the Main Breeding stage to that of Late Chick-care (marked by arrows) there was [illegible] compensation for the decrease in attendance in the ON position by [both or either of] attendance alone in the SIDE position, and LEAVE attendance]. The form of this compensation varied individually. At the time of this change, the female of Pair 1 LEAVE attended,

Fig. 17. Changes in the percentage of the total daily individual attendance spent in the <u>SIDE</u> position of each adult of pairs 1, 2 and 3 from initiation to the first flight of the chicks.

●——● male

×- - - - -× female

M↓ = decrease in male ON attendance (See text for details)

F↓ = decrease in female ON attendance (See text for details)

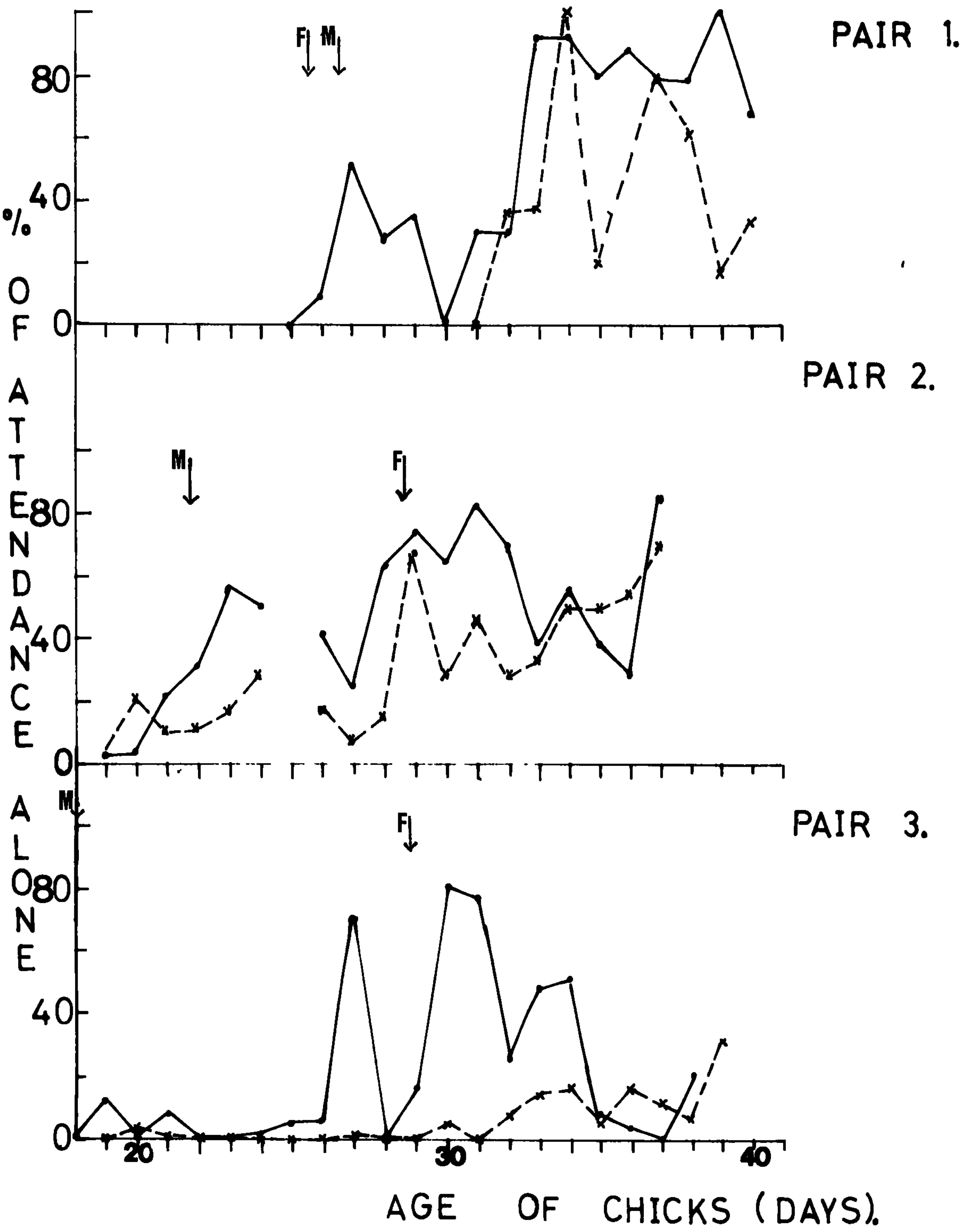
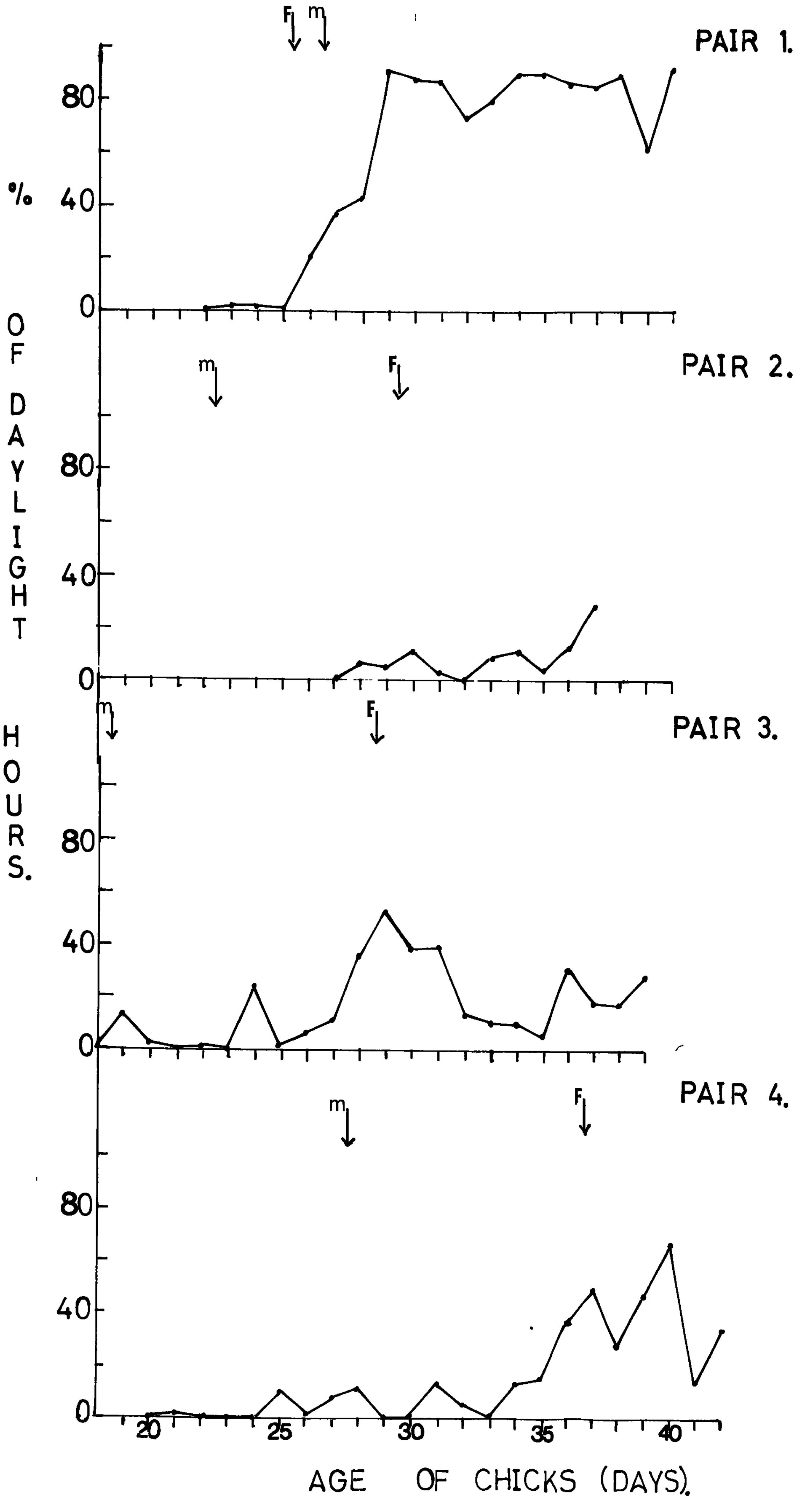

PAIR 1.
PAIR 2.
PAIR 3.
% OF ATTENDANCE ALONE
80
40
0
F
M
F
M
F
M
20
30
40
AGE OF CHICKS (DAYS).

Fig. 18. Changes in the percentage of the daylight hours, up to the first flight of the chicks, that adults left sites unattended.

M ↓ = decrease in male ON attendance (See text for details)

F ↓ = decrease in female ON attendance (See text for details)

PAIR 1.
F
m
PAIR 2.
m
F
PAIR 3.
m
F
PAIR 4.
m
F
% OF DAYLIGHT HOURS.
0
40
80
20
25
30
35
40
AGE OF CHICKS (DAYS).

the male of Pair 1 attended in the SIDE position and possibly LEAVE attended whereas the male of Pair 2 attended only in the SIDE position.

The shape of the two sets of graphs in Figs. 17 and 18 suggest that attendance in the SIDE position becomes increasingly important to the individual adults and also that broods are left unattended for increasing portions of the day. In order to test these suggestions, linear regression analyses were carried out on the arcsin transformed values of Fig 17 and 18 (Snedecor & Cochran 1957, P 148). The resulting regression coefficients for LEAVE attendance were then compared between pairs and those for single SIDE attendance between and within pairs (Bailey 1959). The results of these comparisons are given in Table 12 and show that, after the initiation of LEAVE attendance, up to the end of the Late Chick-care stage there was in all four pairs a significant ($P < 0.05$) positive association between the percentage of the daylight hours spent on this attendance type and the increasing age of the brood. The position was not quite so clear with single SIDE attendance over the same period (Table 12 II). After the initiation of this category of behaviour five out of six individuals showed a positive association between the percentage of the total attendance alone spent in the SIDE position, and the age of the brood - four of these relationships were significant ($P < 0.01$). The inter-pair comparisons of the regression coefficients for LEAVE attendance indicated that the rate of increase in this type of attendance with time was significantly greater ($P < 0.01$) in Pair 1 than in Pairs 2, 3 and 4. None of the other differences were significant. With SINGLE SIDE attendance, none of the intra-pair differences were significant and only one

TABLE 12 COMPARISON BETWEEN AND WITHIN PAIRS OF THE REGRESSION COEFFICIENTS FOR THE PERCENTAGE OF THE DAYLIGHT HOURS SPENT LEAVE ATTENDING AND FOR THE PERCENTAGE OF THE TOTAL ATTENDANCE ALONE IN THE SIDE POSITION, WITH AGE OF THE BROOD

(Pairs 1, 2, 3 and 4 - Information from Figs. ~~8~~ 17 & ~~9~~ 18 arcsin transformed)

* d.f. refers to degrees of freedom associated with deviations from regression

\- degree of freedom associated with regression is 1, in all cases (Snedecor & Cochran 1957 p. 148)

I <u>LEAVE ATTENDANCE</u> (% of total daylight hours brood attended)

	No. of days	Variance	Regression coefficient-	F-ratio	d.f.*	Significance level
Pair 1	19	180.91	+ 4.23	56.40	17	0.001
Pair 2	12	41.15	+ 1.60	8.93	10	0.05
Pair 3	21	130.29	+ 0.92	5.05	19	0.05
Pair 4	18	121.00	+ 2.01	16.14	16	0.001

<u>Comparison between pairs</u> (Bailey 1959)

	Pair 1	Pair 2	Pair 3	Pair 4
Pair 1	-	0.01	0.001	0.01
Pair 2		-	ns	ns
Pair 3			-	ns

II SIDE ATTENDANCE (% of total individual attendance in SIDE position)

	No. of days	Variance	Regression Coefficient	F-ratio	d.f.	Significance level
Pair 1						
Male	15	251.17	+ 3.66	14.90	13	0.01
Female	9	283.38	- 0.97	0.20	7	ns
Pair 2						
Male	18	183.47	+ 1.85	9.00	16	0.01
Female	18	67.66	+ 2.05	30.00	16	0.001
Pair 3						
Male	20	429.25	+ 1.03	1.64	18	ns
Female	20	46.72	+ 1.28	23.27	18	0.001

Comparison within pairs (male and female)

Pair 1	Pair 2	Pair 3
ns	ns	ns

Comparison between pairs (Individuals of same sex)

	Pair 1	Pair 2	Pair 3
MALES			
Pair 1	-	ns	ns
Pair 2		-	ns
FEMALES			
Pair 1	-	ns	ns
Pair 2		-	0.05

inter-pair difference between the female of Pair 3 and the female of Pair 2 was significant ($P < 0.05$).

Fig. 18 shows that after the initiation of LEAVE attendance by the adults of Pair 1, the increase in this form of attendance was particularly pronounced so that within 4 days chicks were being left unattended for approximately 80% of the daylight hours. This degree of abandonment was much higher than any of the other pairs (as shown by the anomalous result in the comparison between Pairs in Table 13) and may reflect a lower than average reproductive drive. In the previous section where the Pre-Breeding attendance stage of this pair was shown to be more variable in pattern, shorter and where the nest site was left unattended more frequently than in average pairs, a reduced drive was also postulated.

The regression coefficients of Table 12 indicated a more pronounced positive relationship between the incidence of LEAVE attendance and the age of the brood, than between attendance in the SIDE position and age of the brood. This may suggest that the organisation of the two attendance types were open to disturbance by different external variables. Thus, although there was a great deal of daily variation (as indicated by the size of the variances of the regression coefficients in Table 12) the results showed that after the initiation of LEAVE attendance, broods were left unattended for increasing percentages of the daylight hours. After the initiation of SINGLE SIDE attendance, individual adults tended to spend an increasing percentage of their attendance alone in the SIDE position, as the brood aged.

The inter and intra-pair comparisons between regression coefficients showed generally that the rates of increase in the two forms of attendance were independent of individual or pair variation among successful breeding pairs, although Pair 1 was an exception to this generalisation.

It was previously stated that with time-lapse information it was often impossible to identify which adult of the pair was responsible for leaving the chicks unattended. This meant that it was difficult to decide if the two members of a pair initiated LEAVE attendance on the same day or independently (as is the case with SIDE attendance). The records for Pairs 3 and 4 in Fig. 18 however, showed that LEAVE attendance was initiated (i.e. the chicks were left unattended) before both members of the pair had changed from the Main Breeding stage to the Late Chick-care stage, marked by arrows. As adults maintained daily levels of attendance in the ON position during the Main Breeding stage, it appears that the earliest abandonment of the broods of Pairs 3 and 4 was due to the males. In both cases, those males had changed by this time to the Late Chick-care stage, with a concomitant reduction in attendance in the ON position. These results indicated that, as with the initiation of attendance in the SIDE position, individual adults initiated their periodic abandonments of the brood independent upon the activity of their mate.

The picture that emerges of the organisation of attendance patterns at the nest site during chick care, is one of complexity, as shown below.

(1) During early chick-care attendance is essentially all in

the ON position and may or may not be equally shared during the daylight hours.

(2) At a later stage each adult, independent of its mate, decreases its daily share of attendance in the ON position. At this point there are two possible attendance categories that can be initiated which may replace it.

A. attendance in the SIDE position,

B. temporary absences from the nest site.

The strategies seen were:-

initiation of,

i A, that was probably followed at a later stage by B e.g. male Pair 2.

ii B only, e.g. male (?) and female (?) Pair 4

iii A and B, e.g. male (?) Pair 1.

The influence of these strategies on the total pattern of adult attendance at a particular nest site was modified by the extent to which there had been sharing of attendance in (1). Fig. 17 showed an unusual case where the female of Pair 2 initiated attendance in the SIDE position before any marked decrease in attendance in the ON position. This may have represented an atypical attempt at compensation by the female for the male's shortcomings, usually seen only during earlier stages (see Coulson 1972).

(3) After the initiation of these attendance types the regression analyses showed:-

i that the amounts of time an adult left the brood tended to increase,

ii that adults tended to spend an increasing percentage of their attendance alone in the SIDE position,

and iii that the rates of these increases tended to be similar in all individuals.

In the previous section it was concluded that the total pattern of attendance at a particular site during Late Chick-care arose from the addition of two individual patterns. The results above accord with that conclusion by showing that the adults tended to initiate the two new forms of ~~an~~ attendance in an individual way, independent of their mates. Once initiated, whilst the chicks developed, each of the two new categories of attendance became increasingly important components of the total individual attendance pattern. These individual differences were responsible for the wide inter - and intra-pair variations shown in Table 11 during Late Chick-care.

TIMING OF THE CHANGES IN THE PATTERN OF ATTENDANCE DURING CHICK-CARE (Spot observation information)

The timing of the initiation of SINGLE SIDE and LEAVE attendance was investigated in a larger population by taking five consecutive spot observations per day at hourly intervals of all successful nest sites. In this way the age of the chicks at the time a particular adult was first seen in SINGLE SIDE nest attendance and the age when a brood was first left unattended, could be determined. In all 53 nests were observed in 1969 and 52 in 1970, and it was found that although all 105 broods were left unattended at some stage before fledging, 71 (34%) of the 210 adults on whom observations were made, never carried out SINGLE SIDE attendance at any stage. (Compare Pair 4 with Pairs 1, 2 and 3).

THE EFFECTOF THE AGE OF THE BROOD - The table below (from spot observation data) gives the age of the broods when they were first left unattended and when individual adults first initiated SINGLE SIDE attendance.

TABLE 13

Age of the brood in days

Initiation of SINGLE SIDE attendance by individuals

	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45+	Total	Mean
1969	0	1	12	14	14	20	6	1	60	31.6
1970	1	4	11	16	12	20	5	2	71	30.6
Total	1	5	23	30	26	40	11	3	139	31.1

Initiation of LEAVE attendance by pairs

	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45+	Total	Mean
1969	0	1	3	14	18	11	6	0	53	32.2
1970	0	1	4	10	15	13	5	4	52	34.0
Total	0	2	7	24	33	24	11	4	105	33.1

This table shows that the mean age of chicks at the initiation of SINGLE SIDE attendance by individuals was very similar to the mean age of chicks at the initiation of LEAVE attendance by pairs (irrespective of the season). It also showed that there was an increasing probability that adults would initiate both forms of attendance as the chicks developed.

THE EFFECTS OF BROOD SIZE AND SEX OF ADULT - Of the 194 adults that were sexed, it was found that 65 started SINGLE SIDE attendance before their broods were 32 days old, 65 after this time and 64 never showed this type of attendance. Using this division of the chick-care period as a measure of the tendency of adults to SINGLE SIDE attend it was possible to draw up contingency tables to show the effects of the sex of the adults and the brood size on this behaviour, as shown in Table 14. The results of the chi-squared tests on these tables showed that there was no significant difference between the sexes in this behaviour but that adults with two chick broods showed a significantly greater tendency ($P < 0.01$), to SINGLE SIDE attend than adults with single chick broods.

As the spot observation information could not reveal the sex of an adult that had left the brood unattended, differences between the sexes is the timing of the initiation of this behaviour could not be investigated directly. Observations of 100 broods over two breeding seasons showed that broods of two chicks were first left unattended when the chicks had a mean age of 32.3 ± 0.63(s.e) days and that the comparable value for one chick broods was 35.1 ± 1.25(s.e) days. This difference was just significant ($P < 0.05$).

These results thus showed that adults with two-chick broods tended to leave their broods unattended at a younger age than adults with single-chick broods. They also showed that, although the sexes did not differ, pairs with the larger brood size showed a greater tendency to attend in the SIDE position than pairs with the smaller brood size.

THE EFFECTS OF NEST SITE CONDITIONS - The occurrence of single SIDE attendance required space to one side of the nest structure and thus its appearance seemed likely to depend, to a large extent, on the particular conditions at individual nest sites. As there was little difference in size between male and female kittiwakes any factor of this type was likely to affect both

TABLE 14. THE EFFECT OF BROOD SIZE AND SEX OF ADULT ON THE TENDENCY FOR ADULTS TO ATTEND IN THE SIDE POSITION (SPOT OBSERVATIONS)

	TENDENCY TO SIDE ATTEND				
	EARLY SIDE ATTEND (Chicks 16-31 Days)	LATE SIDE ATTEND (Chicks 32-47 days)	NEVER SIDE ATTEND (None)	χ^2_1	SIGNIFICANCE LEVEL
2 CHICK BROOD					
MALES	25	18	11	0.84	ns
FEMALES	22	17	15		
1 CHICK BROOD					
MALES	10	15	18	0.33	ns
FEMALES	8	15	20		
	POOLED DATA				
2 CHICK BROOD	47	35	26	13.25	$P<0.01$
1 CHICK BROOD	18	30	38		
TOTALS	65	65	64		

N.B Day 1 = HATCHING DAY OF FIRST CHICK OF BROOD adults of a pair in a similar way. This would have been reflected in an association between the measures of the initiation (or lack of initiation) of SINGLE SIDE attendance in the two members of a pair. In order to test for such an association a Spearmans Rank Correlation Coefficient test (Siegel, 1956) was carried out on the pairs of scores for all nest sites, which took brood size into consideration. (Correlation coefficients were not suitable as the scores, including no SIDE attendance, formed an ordinal scale). The Spearman r for 54 two-chick broods was 0.5782 ($P<0.001$) and for 43 one-chick broods r was 0.7194 ($P< 0.001$) indicating a highly significant degree of association between the tendencies of the two adults of a pair to show SINGLE SIDE attendance. Thus, the particular conditions at the individual nest sites had a very important effect on the tendency for adults to attend in the SIDE position. The conditions that varied inter-pair but not intra-pair were weather, space at the nest site and chick numbers and the interactions of these. There was no reason to expect that weather conditions (wind speed, direction, rainfall, sunlight) were similar in the two seasons 1969 and 1970.

Coulson & White (1956) reported that winds of over 7.8 knots markedly depressed the number of kittiwakes at the colony during the pre-breeding stage. The mean wind speed in knots for the months June, July and August were respectively 6.5, 8.3 and 5.5 in 1969 and 7.2, 7.7, and 6.5 in 1970 (data from South Shields Weather Centre). This showed that wind conditions during the 1969 breeding season were more variable than those of the 1970 season. As Table 13 showed very little difference between breeding seasons in the mean age of chicks at the initiation of both SINGLE SIDE and LEAVE attendance it was concluded that wind speed had a relatively unimportant effect on these phenomena.

Coulson (1966) showed that about 64% of kittiwakes retained their mate from the previous breeding season and that many of these also retained the same nest sites. Included in the spot observation results were the two measures of (a) initiation or failure to initiate SINGLE SIDE attendance and (b) initiation of LEAVE attendance for the adults of 11 pairs that retained their mate and nest site and raised similar sized broods in both years of the study. Spearman rank correlation coefficient tests showed a significant association between the scores for the initiation of LEAVE attendance by the 11 pairs over the two years ($r= 0.7793$, $P< 0.01$) and of the scores for the initiation or failure to initiate SINGLE SIDE attendance by the 22 individual adults ($r= 0.3726$, $P< 0.05$). Thus it appears that conditions external to the nest site itself had rather a small effect on both the timing of the initiation of absences from the nest site by the pair or on the tendency for adults to attend in the SIDE position.

As all nests on the North Shields colony were on window ledges that were capable of holding two nests, each successful site that was observed could be classified either as Nest Alone, Nest with Non-breeding Pair or Nest with Breeding Pair. All of the data obtained by spot observation about the initiation of absences from the nest site by the pairs, and the initiation (or failure to initiate) attendance in the SIDE position by individuals, was split into these three nest site categories. When the distributions of these results were plotted as frequency histograms they were found not to be normally distributed therefore unsuitable for parametric methods of analyses. The effects of nest site conditions (taking brood size and sex of the adult, where appropriate, into consideration) on the measures of these two forms of attendance was investigated using non-parametric Mann-Whitney U tests (Siegel, 1956), as shown in Table 15 and 16.

Table 15 showed that neither the nest site conditions or brood size had a marked effect on the timing of the initiation of absences from the nest site. Only on isolated nest sites were broods of one left unattended at a later stage than broods of two ($P < 0.02$). In contrast, Table 16 showed that both brood size and nest site conditions had an effect on the tendency for adults to SINGLE SIDE attend. The following conclusions are possible.

1. The sexes did not differ in their tendency to SINGLE SIDE attend.
2. On nest sites with broods of two the tendency for adults to show SINGLE SIDE attendance significantly decreased from nest alone to nest + non-breed ($P < 0.008$), and from nest + non-breed to nest and breed ($P < 0.046$).
3. On nest sites with broods of one those adults occupying sites with adjacent breeding pairs showed a significantly reduced tendency ($P < 0.004$) to attend in the SIDE position compared with the other categories of sites.
4. On isolated nests and nests with adjacent breeding pairs, individuals showed a significantly greater tendency to attend in the SIDE position ($P < 0.006$) with broods of two rather than broods of one.

These data not only indicated that an increased brood size was associated with an increase in the tendency for individuals

TABLE 15. THE EFFECTS OF ADJACENT NEST SITE CONDITIONS AND SIZE OF THE BROOD ON THE INITIATION OF ABSENCES FROM THE NEST SITE

Mean age of chicks at initiation of LEAVE attendance (with ranges)

	Nest Alone	Nest + Non-breed	Nest + Breed
2 CHICK BROOD			
Range	25-45	26-39	16-39
Mean age in days	33.69(16)	31.63(16)	32.63(27)

↑—— U=100 ns ——↑ ↑—— z=1.14 ns ——↑

↑—————— z=0.39 ns ——————↑

	Nest Alone	Nest + Non-breed	Nest + Breed
1 CHICK BROOD			
Range	33-44	21-43	16-54
Mean age in days	38.89(9)	32.50(12)	34.83(23)

↑—— U=27 ns ——↑ ↑—— z=0.52 ns ——↑

↑—————— z=1.64 ns ——————↑

	Nest Alone	Nest + Non-breed	Nest + Breed
EFFECT OF BROOD SIZE	U=31 P=0.02	U=92.5 ns	z=0.28 ns

All comparisons tested by Mann-Whitney U tests (Siegel 1959)

Numbers in parenthesis are sizes of samples

TABLE 16. THE EFFECTS OF ADJACENT NEST SITE CONDITIONS AND SIZE OF THE BROOD ON THE TENDENCY FOR ADULTS TO ATTEND IN THE SIDE POSITION

The table shows the Mean age of those broods where adults initiated SIDE attendance and the number of instances where this type of attendance was not observed

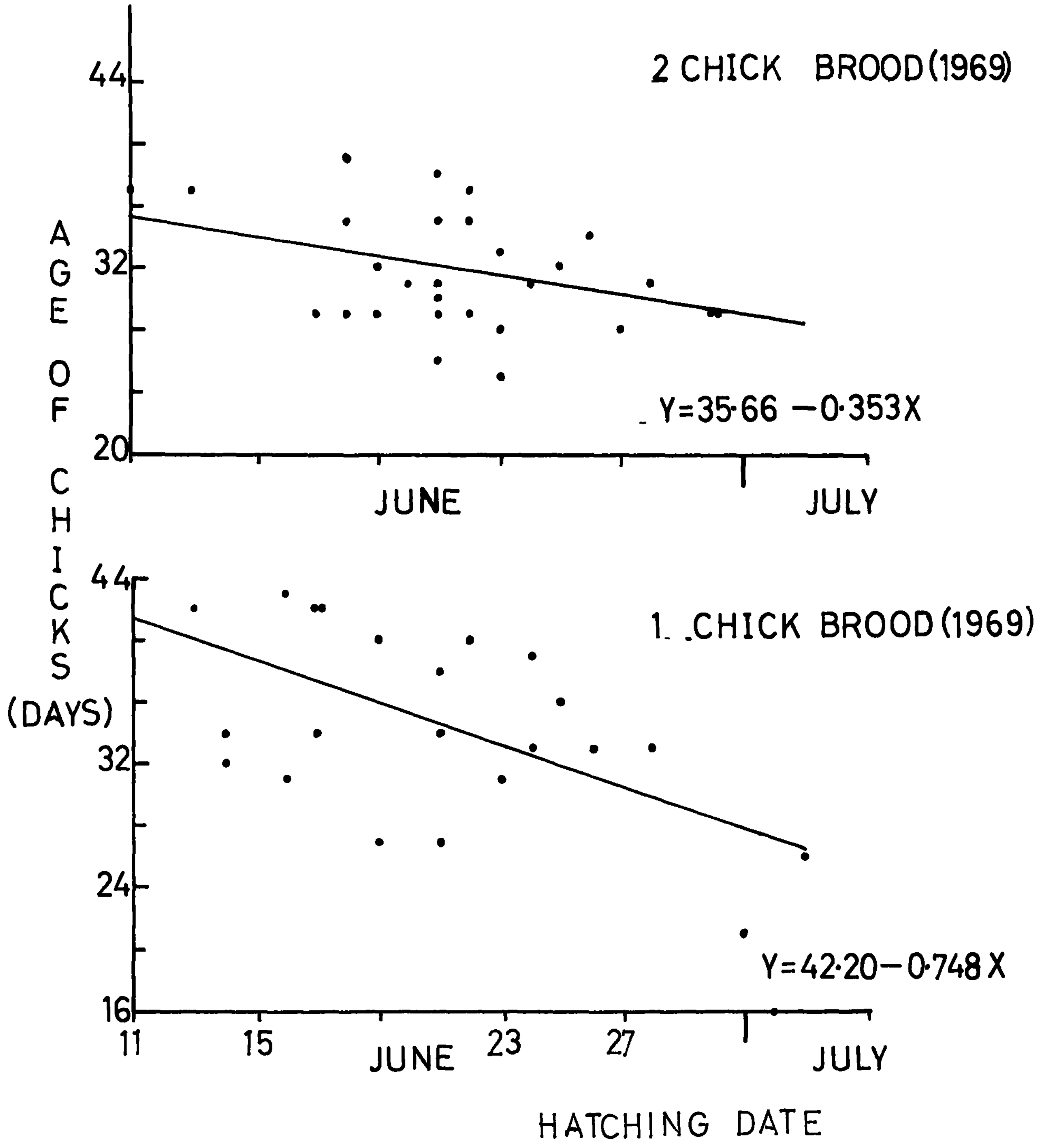
	Nest Alone		Nest + Non-breed		Nest + Breed	
	Male	Female	Male	Female	Male	Female
2 Chick Brood						
Range	17-39	18-36	24-42	22-40	20-41	20-44
Mean age in days	27.63(16)	27.36(18)	31.36(18)	31.08(19)	31.78(36)	32.00(36)
None shown	0	2	2	3	9	9
	U=114 ns		U=122.5 ns		z=0.02 ns	
	z=2.42 P=0.008					
			z=1.69 P=0.046			
	z=3.80 P=0.0001					
1 Chick Brood						
Range	23-38	22-36	14-41	24-38	24-46	29-46
Mean age in days	29.33(12)	31.17(12)	30.10(14)	29.88(16)	35.50(36)	39.11(37)
None shown	3	3	2	4	13	14
	U=36 ns		U=62 ns		z=0.73 ns	
	z=0.40 ns					
			z=3.57 P= 0.0003			
	z=2.89 P =0.004					

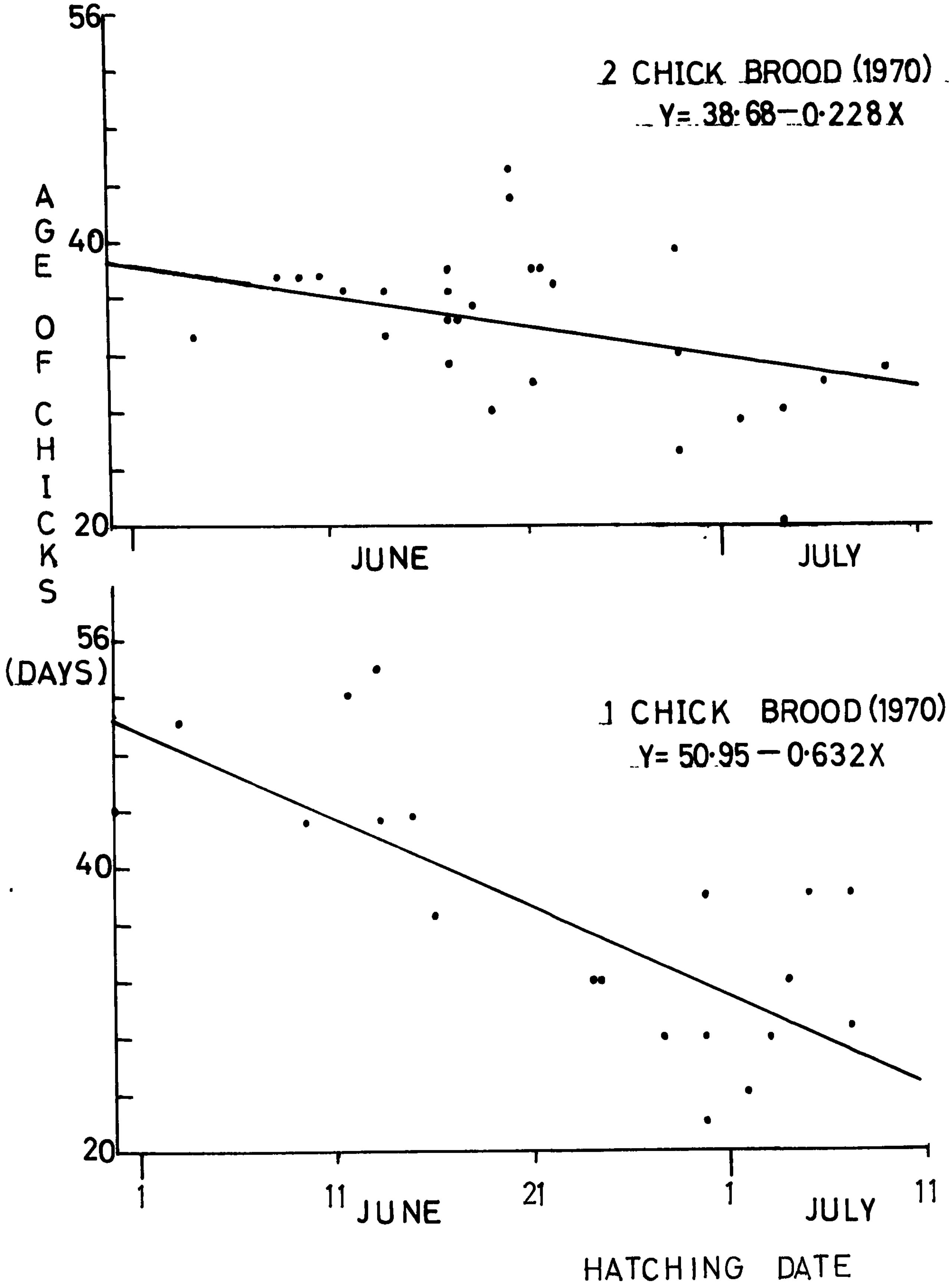
Effect of brood size	2C	1C	2C	1C	2C	1C
Range	17-39	22-38	22-42	14-41	20-44	24-47
Mean age in days	27.50(34)	30.25(24)	31.22(37)	30.00(30)	31.89(72)	37.21(73)
None shown	2	6	5	6	18	27
	z=2.49 P =0.006		z=0.35 ns		z=3.44 P =0.0003	

Key as for Table 15

Numbers in parentheses are the sizes of the samples.

Fig. 19. Regression of date of hatching and age of brood when first left unattended.


2 CHICK BROOD (1969)
44
32
20
Y=35·66 −0·353X
JUNE
JULY
AGE OF CHICKS (DAYS)
1 CHICK BROOD (1969)
44
32
24
16
Y=42·20−0·748 X
11
15
23
27
JUNE
JULY
HATCHING DATE


2 CHICK BROOD (1970)
Y= 38·68 − 0·228 X
1 CHICK BROOD (1970)
Y= 50·95 − 0·632 X
AGE OF CHICKS (DAYS)
56
40
20
56
40
20
JUNE
JULY
1
11
21
1
11
JUNE
JULY
HATCHING DATE

result of a smaller than average spread of hatching date during 1969 that was caused by the nesting attempts of a pair of kestrels (Falco tinnunculus) during the early part of the season.

An idea of the biological significance of these coefficients can be gained by taking average values over the two years of study. On average adults with two chick broods initiated LEAVE attendance 1 day earlier for every 3.5 days delay in breeding through the season. For one chick broods the initiation was 1 day earlier for every 1.5 days delay in breeding.

Thus Coulson showed pairs that bred early in the season tended to be birds of high quality. ~~Table~~ Fig. 19 showed that these pairs left their broods for the first time when they were at a more advanced stage of development than those of lower quality that bred later in the season.

The difference between the regression coefficients in Fig. 19 suggested that either adults reacted to the two brood sizes differently and/or that the effects of quality were more clearly demonstrated with broods of 1 rather than broods of 2 chicks. Table 15 indicated that although it was not generally possible to demonstrate a brood size effect on the initiation of LEAVE attendance when pairs occupied isolated nest sites, this was shown earlier in 2 chick rather than 1 thick broods. Also it has already been reported that breeding success is related to the quality of adults. This implies that the graphs for 2 chick broods were based on the behaviour of mainly high quality pairs. In contrast the graphs for 1 chick brood would have been based on the behaviour of (a) a few high quality birds that had accidentally lost an egg or chick, that bred early (b) mainly lower quality pairs that bred later and (c) a few of the lowest quality of pair capable of rearing a chick, that bred latest of all. Thus it is suggested that the larger regression coefficients for 1 rather than 2 chick broods in Fig. 19 arose due to (a) adults showing a tendency to initiate LEAVE attendance earlier with 2 rather than 1 chick broods which restricted the possible range of expression in the former case, and (b) the biased sampling of pairs of adults with hetereogeneous quality, with 1 chick broods.

The association between the age of the brood at the initiation of SINGLE SIDE attendance (or the lack of any SIDE attendance) by each adult of a pair, and the date of hatching of the brood (expressed as days after the first chicks of the colony hatched for that year) was assessed by a Spearman Rank test on the ordinal scores, taking into account brood size and breeding season.

The results of these calculations are given in Table 17 which shows that seven of the eight correlations were negative, two of them significantly so ($P < 0.05$). Thus, pairs that bred late in the season tended to be low quality birds that left their broods unattended at a less advanced stage of development than the higher quality birds that retained their mates and bred earlier. A similar relationship was seen to a lesser extent for the tendancy to SINGLE SIDE attend by the individuals of a pair.

INTER-RELATIONSHIP BETWEEN THE INITIATION OF SINGLE SIDE AND LEAVE ATTENDANCE

The factors affecting the tendency for individuals to attend in the SIDE position and the timing of the initiation of absences from the nest site by the pair have been shown to differ, in the previous sections. These differences made any association between the organisation of the two forms of attendance very difficult to demonstrate. However, when the information from only those pairs

TABLE 17. THE ASSOCIATION BETWEEN THE TENDENCY OF ADULTS TO ATTEND IN THE SIDE POSITION AND THE DATE OF HATCHING OF THE BROOD (EXPRESSED AS DAYS AFTER THE FIRST CHICKS OF THE COLONY HATCHED FOR THAT YEAR) AS MEASURED BY SPEARMANS RANK CORRELATION COEFFICIENT (SIEGEL, 1956)

SPEARMAN 'r' FOR ASSOCIATION BETWEEN INITIATION OR LACK OF INITIATION OF ADULTS' SINGLE SIDE ATTENDANCE AND DATE OF BREEDING

<u>1969</u>	2 CHICK BROOD	(P)	1 CHICK BROOD	(P)
MALE	(28) - 0.2240	ns	(23) - 0.1953	ns
FEMALES	(28) - 0.1997	ns	(23) - 0.3039	ns
<u>1970</u>				
MALE	(25) - 0.0572	ns	(20) - 0.4966	0.05
FEMALES	(25) + 0.2404	ns	(20) - 0.4966	0.05

Numbers in Parenthesis = Sample Size

~~Significance Levels, (P) as Table~~

that carried out both forms of attendance was considered, and when the initiation of SINGLE SIDE attendance was assumed to have occurred on the first day that it was observed at a particular site (like LEAVE attendance), then the ages of the chicks at the initiation of these attendance categories could be compared. Table 18 shows the results of these comparisons (analysed by Mann-Whitney U tests). This analysis takes adjacent nest conditions and brood size into consideration.

The Table showed that only when the adjacent nest site was not occupied did pairs start attending in the SIDE position significantly before starting to LEAVE the chicks unattended ($P < 0.02$ for both brood sizes).

Of the three conditions 'nest alone' was the simplest as disturbance of a pair's attendance pattern by other adults was then minimal. Tables 15, 16 and 18 indicate that, in this simple situation, individual adults initiated SINGLE SIDE attendance during late chick-care. This was followed, at a later stage by the initiation of temporary abandonments of the brood. Further, this pattern was seen earlier in pairs with two chicks rather than in those with one-chick broods. Fig. 19 and Table 17 indicate that the actual timing of these changes in attendance by individuals was related to the date of breeding, and thus to the quality of the adults. This meant that, in general, broods of high quality birds were attended in the ON position for longer than broods of low quality birds.

As the tendency for adults to SINGLE SIDE attend their sites appeared to be reduced by the presence of adults on adjacent sites, and as these adjacent sites themselves would have been occupied with some pattern of attendance, then the lack of similarity between the

TABLE 18. THE RELATIONSHIP BETWEEN THE TIMING OF THE INITIATION OF SINGLE SIDE AND OF LEAVE ATTENDANCE BY THE SAME PAIRS (TAKING ACCOUNT OF BROOD SIZE AND ADJACENT NEST SITE CONDITIONS)

Mean age of chicks at initiation of attendance types (with ranges)

	Nest alone		Nest + Non-breed		Nest + Breed	
	SIDE	LEAVE	SIDE	LEAVE	SIDE	LEAVE
2 Chick Brood						
Range	17-39	25-45	22-42	26-39	20-40	21-39
Mean age in days	26.06(16)	33.69(16)	30.13(15)	31.80(15)	30.33(21)	32.86(21)
	U= 51 P=0.02		U= 87 ns		z=1.38 ns	
1 Chick Brood						
Range	22-38	33-42	14-39	21-43	24-46	27-52
Mean age in days	29.86(7)	38.29(7)	28.40(10)	32.50(10)	35.62(13)	34.00(13)
	U= 4.5 P=0.006		U=36.5 ns		U=59.5 ns	

All comparisons tested by Mann-Whitney U tests (Siegel 1956)

Numbers in parentheses are sizes of samples timing of changes in adult attendance on different categories of nest site was only to be expected. A further complication, indicated by Table 18, is that there is the possibility that pairs on sites occupied also by adjacent pairs may compensate for decreased tendencies to SINGLE SIDE attend by initiating their temporary absences from the nest site earlier than if no adjacent pair were present.

THE TIMING OF THE INITIATION OF LEAVE ATTENDANCE BY THE TWO SEXES. - In Section 3, Table 10 and Fig. 16 indicated that males generally changed from the Main Breeding to the Late Chick-care attendance patterns before females. As Table 16 showed that this could not be attributed to a tendency on the part of the males to initiate attendance in the SIDE position before females, then this implies that there exists a difference between the sexes in their respective initiations of LEAVE attendance. Although this could not be measured directly it could be investigated by an indirect method using data derived from spot observations.

The day when the chicks were first abandoned was identified from the spot observation record for each pair. Using information from all pairs, the ratio of the sexes attending on the day before this event was compared with the ratio of the sexes attending on the day after this event. A chi-squared significance test was used as is shown in Table 19. From the table, it appears that the ratios changed, there being a significant excess of females present during the later stage ($P<0.05$). These results could only be adequately explained by supposing that the initiation of LEAVE attendance at nest sites was generally attributable to males rather than to females, so that the latter sex tended to be over represented after this event.

TABLE 19 COMPARISON OF THE SEX RATIO OF ADULTS ATTENDING THE NEST SITE ON THE DAY BEFORE INITIATION OF LEAVE ATTENDANCE WITH THE RATIO ON THE DAY AFTERWARDS (SPOT OBSERVATION INFORMATION)

	ADULT	PRESENT
	MALE	FEMALE
Day before initiation of LEAVE attendance	48	46
Day after initiation of LEAVE attendance	32	62

$$\chi^2_1 = 4.90 \quad (P < 0.05)$$

DISCUSSION

Successful adults showed simple, co-ordinated and stable attendance patterns at the nest site throughout incubation and early chick-care. During late chick-care, however, these features were absent (as is shown in Table 11).

In the previous section, cumulative sum charts based on the consecutive daily percentages of the day spent on SIngle ON attendance by particular individual birds (Figs. 14 and 15) allowed the chick-care part of the breeding cycle to be split into 2 stages (see Table 10). The change from the early to the late stage was seen as a decrease in the slope in the charts denoting a decrease in the daily amounts of this form of attendance. The charts from breeding pairs showed changes in slope at this time that were independent of one another (a decrease in one followed later by a decrease in the other) rather than co-ordinated (a decrease in one with an increase in the other) or synchronised (a decrease in both at the same time). Thus the two adults of a pair decreased their daily attendance in the ON position at different stages of chick development. In contrast, Coulson (1972) showed that during incubation when one adult of the pair did not relieve its mate at the nest site then the attendance of the sitting bird was prolonged, i.e. that co-ordination of attendance took place.

There was replacement corresponding to the decrease in SINGLE ON attendance during Late Chick-care by the individuals attending in the SIDE position or by the adults leaving the chicks unattended - see Figs. 9 - 13. A consideration of the precise timing of (a) the individual decrease in SINGLE ON attendance (b) the individual initiation of SINGLE SIDE attendance and (c) the initiation of LEAVE attendance by the pair indicated that the timing of the initiation of the 2 new forms of attendance varied according to the individual and were independant of the mates' attendance pattern. After the initiation of chicks left unattended until the first flight, broods were left for an increasing percentage of the daylight hours ($P< 0.05$). After the initiation of attendances in the SIDE position by individual adults there was a tendency for them to spend an increasing percentage of their attendance at the nest site in this position. In general the rates of these increases were independent of individual or pair variation. The time-lapse records (Figs. 17 and 18) showed that the pronounced changes in adult attendances patterns between early and late chick-care (See Table 11) arose from the highly individual variation in the timing and form of attendance by the individual of a pair. During chick-care, independent of the attendance pattern of the mate, an individual was found to decrease its daily amount of attendance in the ON position. This decrease was replaced by attendance in the SIDE position or by leaving the brood unattended or by both. In some cases the latter attendance category was initiated some time after the former. The analysis suggested that, after the initiation of LEAVE attendance, broods were left for an increasing portion of an adults share of nest attendance. After initiation of SINGLE SIDE attendance, it tended to form an increasing portion of the total SINGLE attendance (and so ON attendance continued to decrease). The effect of these changes on the total adult attendance pattern at a nest site (as experienced by the brood) was modified by the sharing of the days' attendance between the two members of the pair.

During the Main Breeding stage the total daily attendance was shared between the adults of a pair (not necessarily equally) in a shift system with one adult relieving the other at intervals. During Late Chick-care there was no indication that compensation for any shortcomings in attendance by one adult was made by the other or that adults 'overlapped' their attendance i.e. BOTH attended. For these reasons it was concluded that the former basic pattern of sharing was retained during the later stages but that each adult modified its own forms of attendance within this basic pattern.

The evidence given above indicates that the highly variable timing of the initiation of SINGLE SIDE and LEAVE attendance by individuals profoundly affected the total pattern of adult attendance experienced by individual broods. In an effort to discover why adults changed their attendance patterns, the timing of the initiation of the former category (by individuals) and the latter category (by pairs) was measured for 105 successful breeding pairs by spot observation methods. As with that for the time-lapse pairs, this information showed that although all nest sites were left unattended at some stage only some of the adults (66%) were seen to attend in the SIDE position. So that information should not be discarded, most of the analyses concerning SINGLE SIDE attendance were based on the tendency for adults to attend in this position.

The factors that were found to affect these two forms of attendance are summarised below.

	SINGLE SIDE attendance	LEAVE attendance
1	Probability of individual adults initiating increased with age of the brood.	Probability of pairs initiating increased with age of the brood.
2	Neither sex showed a greater tendency.	More females than males were present on the day following initiation ($P < 0.05$) indicated males initiated before females.
3	Greater tendency with 2 chick broods than 1 chick broods ($P < 0.01$)	Mean age of chicks in days at initiation. 2 chick broods = 32 ($P < 0.05$) 1 chick broods = 35
4	Significant association between tendencies of pairs ($P < 0.001$).	Not possible to measure.
5	In pairs that retained nest site mate and brood size over two year,	
	Significant association between tendencies of individuals ($P < 0.05$)	Significant association between timing of initiation by pairs ($P < 0.01$)
6	Presence of adjacent pairs decreased the tendency (breeders more so than non-breeders).	Little effect of adjacent pairs.
7	Some evidence for a greater tendency in late breeding, "low quality" birds compared with early breeding, "high quality" birds.	Significant association such that late breeding, "low quality" pairs leave chicks earlier than early breeding, "high quality" pairs ($P < 0.05$).

This list of factors may be broadly classified into 2 categories:-

a Those related to obvious external conditions (1,3,4,5 and 6)

b Those with a strong individual component (2 and 7).

Of the first type conclusions 1, 3 and 5(?) imply that the presence of the chicks has an important influence on the initiation of both attendance types. Brood size and age of the chicks both affected these measures. Factor 5 implied that food or weather stimuli, variable from year to year, did not significantly affect the time at which adults first changed their attendance pattern. Factors 4 and 6 highlighted a difference in that SINGLE SIDE attendance required sufficient room, free from interference, at the side of the nest structure, whereas LEAVE attendance was hardly affected by these constraints.

In the second category Factor 2 reveals that related to the sex of the adults there is a difference in the timing of the initiation of LEAVE attendance but not of SINGLE SIDE attendance. It is suggested that any tendency for such a difference between sexes in the case of SINGLE SIDE attendance would be small and would probably be swamped by the crowding effect, Factor 6. (Of pairs nesting on isolated sites, 13 males initiated SINGLE SIDE attendance before their mates yet only 5 females initiated it before their mates. However, the difference was not significant). Factor 7 implies that the quality of adults affected when and how adults changed their attendance patterns.

From this review it would appear that the crucial factor differentially affecting the occurrence of the two forms of attendance was related to the presence of pairs on adjacent nest sites. When this variable was removed, by only considering pairs on isolated nest sites, it was found that pairs initiated attendance in the SIDE position significantly earlier than LEAVE attendance (Table 18, $P < 0.02$). It appeared that the actual stimuli which the adults reacted to (in both forms of attendance) were associated with the presence of the chicks. If it were assumed that the changes in the drive to attend in the ON position did not change with internal changes in the adult, then the stimuli from the chicks must have increased in intensity with the age of the brood and must have been to some extent related to the number of chicks that were present. When conditions at the nest site did not preclude attendance in the SIDE position, the threshold for evoking this attendance type was reached before that for LEAVE attendance. Assuming equal stimuli from all chicks, the thresholds for the former category of attendance was higher in early breeding high quality than in late breeding low quality birds. The thresholds for the latter category of attendance were also higher in high quality pairs (and possibly in these birds as individuals) than in low quality pairs (and, maybe, individuals). It is also probable that they were higher for females than for males.

THE EFFECTS OF THE FLEDGING OF THE CHICKS ON THE ATTENDANCE OF THE ADULTS

Table 20 shows that kittiwake chicks make their first flight a mean 40.8 (st. dev. 2.4) days after hatching. After this they return at intervals to the nest site, where they are fed, but spend much of the day away from the site. Chicks finally abandon the nest a mean 51.8 (st. dev. 3.7) days after hatching. The brood size has little effect on these measures.

Coulson and White (1958b) noted that any estimate of the period between hatching and first flight would involve many days of uninterrupted observation. In the present study all pairs were observed at least 5 times per day at hourly intervals during that period when chicks were fledging in the colony (see also Table 10 for time-lapse results). These authors further reported that the young kittiwake does not necessarily desert the nest site after its first flight but may return after an interval of as little as a few minutes and remain there for several days. Table 20 shows that in kittiwakes, there is typically a period of about 11 days between the first flight of chicks and their abandonment of the site.

The more detailed observations used in this study to construct Table 20 reveal a discrepancy between these results and those of Coulson and White (1958b) who gave a mean of 42.7(st. dev. 4.4) days between hatching and the final vacation of the nest site by the chicks. The value given was, however, close to that given in Maunder and Threlfall (1972) for the time of the first flight (41.6 days SD = 3.1 which was also based on many daily observations.

The fledging period was an appropriate time for an investigation to be made of the effects of chick presence on the attendance of adults,

TABLE 20 THE FLEDGING PERIOD OF THE KITTIWAKE

Hatching to first flight (days)

	32-34	35-37	38-40	41-43	44-46	47-49	Total	Mean
Broods of 2 chicks	0	5	23	32	3	0	63	40.6
Broods of 1 chick	1	4	13	19	8	1	46	41.1
					Grand Mean			40.8 (ST. DEV ± 2.4 days)

Hatching to abandonment of the site (days)

	41-43	44-46	47-49	50-52	53-55	56-58	59-61	Total	Mean
Broods of 2 chicks	0	2	7	23	17	9	1	59	52.3
Broods of 1 chick	1	6	9	16	6	8	1	47	51.2
					Grand Mean				51.8 (ST.DEV ± 3-7 days)

Hatching day of chicks is Day 1

Maximum error on each hatching date was ± 1 day

" " " " fledging " " ± 1 day(5HOURLY OBSERVATIONS PER DAY)

Total maximum error on each observation of the fledging period is ± 2 days which would not have been possible during earlier stages. This was carried out by re-examining the time-lapse and spot observation data, taking the number of chicks present into consideration. The latter information was based on observations of 59 two-chick and 48 one-chick broods where only one observation per day per site was considered so that all observations were independent of one another.

CHANGES IN THE PATTERN OF ATTENDANCE THROUGH THE FLEDGING STAGE

The first essential was to gain some indication of the stability of the pattern of adult attendance during the fledging period (taking brood size into consideration). Previously it was shown that during Late Chick-care, the chicks were left unattended for an increasing percentage of the daylight hours and that there was a tendency for adults to spend an increasing percentage of their attendance with chicks in the SIDE position (Figs ~~12~~ 17 & 18). In order to establish whether this process was maintained during the fledging stage, under all conditions of brood size, the daily changes in these two forms of attendance (of both time-lapse pairs and spot observation information) was subjected to regression analysis.

The results of these analyses are given in Tables 20 and 22. The spot observation results on LEAVE attendance showed that in all but one case (no chick present of a one chick brood) there was a significant positive association between the percentage of the observed nest sites that were left unattended, and the age of the brood ($P < 0.05$). With the time-lapse pairs, although 10 of the 11 regression coefficients were positive (and hence significant $P < 0.01$)

TABLE 21 CHANGES WITH THE AGE OF THE BROOD, DURING THE FLEDGING STAGE, IN THE PERCENTAGE OF THE TIME THAT PAIRS LEFT DIFFERENT CHICK NUMBERS UNATTENDED (ARCSIN TRANSFORMED)

* d.f. refers to degrees of freedom associated with 'deviations from regression'

\- degrees of freedom associated with regression is 1, in all cases (Snedecor and Cochran, 1957. p 148)

I LEAVE ATTENDANCE (% of total daylight hours brood unattended)

	No. of days	Variance	Regression Coefficient	F-ratio	d.f.	Significance level
(a) Two chicks present						
Spot observation (2 chick)	13	81.73	+1.68	7.63	11	$P<0.05$
Pair 1	9	7.26	+0.36	1.07	7	ns
Pair 2	6	74.00	+2.15	1.09	4	ns
Pair 4	9	66.07	+2.22	4.48	7	ns
(b) One chick present						
Spot observation						
(2 chick)	16	30.60	+1.18	15.55	14	$P<0.01$
(1 chick)	13	43.30	+1.40	8.21	11	$P<0.05$
Pair 1	10	52.65	+0.48	0.37	8	ns
Pair 2	12	133.36	+3.95	16.74	10	$P<0.01$
Pair 3	14	107.00	+1.18	2.98	12	ns
Pair 4	14	156.95	+3.42	16.98	12	$P<0.01$
(c) No chick present						
Spot observation						
(2 chick)	16	48.97	+1.23	10.53	14	$P<0.01$
(1 chick)	13	57.81	+0.14	0.06	11	ns
Pair 1	9	227.75	+2.16	1.23	7	ns
Pair 2	9	207.15	-1.35	0.53	7	ns
Pair 3	13	46.61	+0.57	1.55	11	ns
Pair 4	12	178.64	+0.99	0.92	10	ns

@ Spot observation information was based on either nests with two chick broods (2 chick) or one chick broods (1 chick).

TABLE 22 CHANGES WITH THE AGE OF THE BROOD DURING THE FLEDGING STAGE IN THE PERCENTAGE OF ADULT INDIVIDUAL ATTENDANCE SPENT IN THE SIDE POSITION TAKING CHICK NUMBER INTO CONSIDERATION (ARCSIN TRANSFORMED)

* d.f. refers to degrees of freedom associated with 'deviations from regression'

\- degrees of freedom associated with regression is 1 in all cases (Snedecor & Cochran, 1957. p 148)

II SIDE ATTENDANCE (% of total individual attendance in SIDE position)

	No. of days	Variance	Regression coefficient	F.ratio	d.f*	Significance level
(a) Two chicks present						
Pair 1						
Male	10	170.77	-2.31	2.58	8	ns
Female	6	381.97	+3.47	0.88	4	ns
Pair 2						
Male	6	313.29	-6.77	2.56	4	ns
Female	6	203.34	-4.62	1.84	4	ns
(b) One chick present						
Pair 1						
Male	10	423.27	-1.73	0.59	8	ns
Pair 2						
Male	12	361.71	-1.31	0.68	10	ns
Female	12	100.62	-2.68	10.22	10	$P < 0.01$
Pair 3						
Male	8	124.39	-0.72	0.17	6	ns
Female	13	211.64	+0.05	0.01	11	ns

only two of these were individually significant ($P < 0.01$). This shows that, irrespective of chick numbers present, there was a general tendency for pairs to leave their nest sites unattended for an increasing percentage of the available time through the fledging stage. In individual cases, however, this was masked by a great deal of day-to-day variation (shown by large variances in Table 21).

The time-lapse information about the changes in the percentage of the total individual attendance spent in the SIDE position during this time (with different chick numbers present) gave a rather different picture from the one above. Table 22 showed seven of the nine regression coefficients for individuals to be negative, of which one was individually significant ($P < 0.01$). Thus, in contrast to LEAVE attendance, there was a slight general tendency for adults to spend a decreasing amount of their total individual attendance in the SIDE position throughout the fledging stage (irrespective of whether 1 or 2 chicks were present). In a similar way to LEAVE attendance this tendency was masked by large day-to-day variation (shown by large variances).

Thus, as is seen in Tables 12 and 21, within these limits of variation, pairs generally tended to increase the amount of time for which they would leave the nest sites unattended as the brood increased in age. This tendency continued throughout Late-Chick-care and the fledging stage, and was not dependent upon the number of chicks that were present. In contrast Tables 12 and 22 also showed that individuals tended to increase the amounts of their attendance in the SIDE position with age of the brood during Late Chick-care, yet to halt or reverse this trend during the fledging stage (irrespective of numbers of chicks present). Adults did not attend in the SIDE position with chicks absent.

THE EFFECTS OF THE PRESENCE OF CHICKS UPON THE ATTENDANCE OF ADULTS. Each of the spot observations of chick and adult attendance at the nest site, during the fledging stage, could be categorised in a contingency table with respect to the number of chicks present (as all observations were independent). When this was carried out, for both two-and one-chick brood classes, (Table 23) then the distribution of categories of chick attendance could be compared by chi-squared tests with the distribution of adult attendance (under these different conditions of numbers of chicks present). If chick and adult attendance did not interact then these two distributions would have been expected to be similar but Table 23 showed that this was not the case with either brood class ($P < 0.05$). The distributions were even different when only considering 1 or 2 chicks present of a 2 chick brood ($P < 0.01$). As adults were considerably more proficient at flying to and from the site than the chicks it was concluded that this difference arose from the behaviour of the adults. It appeared that the presence of the chicks significantly discouraged the adults from attending the nest site and that two chicks provided a stronger stimulus than one ($P < 0.05$).

In an effort to investigate the development of the avoidance of the chicks by the adults through the fledging stage the timing of all of the spot observations was converted to days after the first flight of the chicks and, was displayed in Fig. 20 (which

TABLE 23 INTERACTION OF THE ATTENDANCE OF ADULTS AND CHICKS AT THE NEST SITE DURING THE FLEDGING STAGE (SPOT OBSERVATION INFORMATION)

I <u>TWO CHICK BROODS</u> (59 nests)

	Chick number present at site			Chi-squared	Significance level
	2 CHICKS	1 CHICK	0 CHICKS		
Chick attendance	116	248	162	20.54 (2d.f)	$P < 0.001$
Adult attendance	35	138	132		
	χ^2=7.29 $P < 0.01$				

II <u>ONE CHICK BROODS</u> (48 nests)

	Chick number present at site		Chi-squared	Significance level
	1 CHICK	0 CHICK		
Chick attendance	171	177	4.48 (1d.f)	$P < 0.05$
Adult attendance	95	141		

Fig. 20. Comparison between

(a) the percentage of daily spot observations different chick numbers occupied the nest through the fledging stage, ●———●

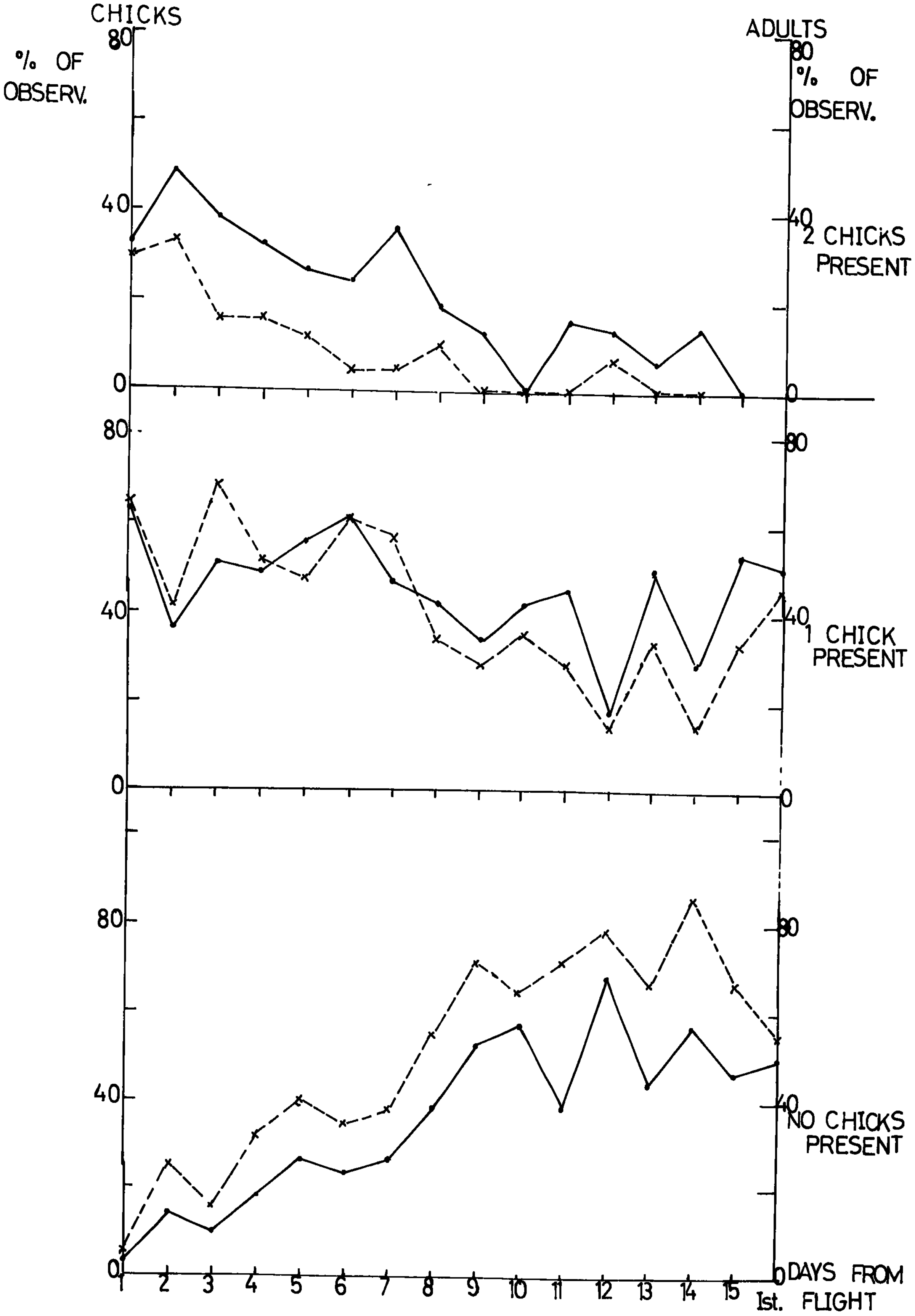
together with (b) the percentage of total daily spot observations of adult attendance that took place under these different brood conditions. ✕———✕ [illegible])

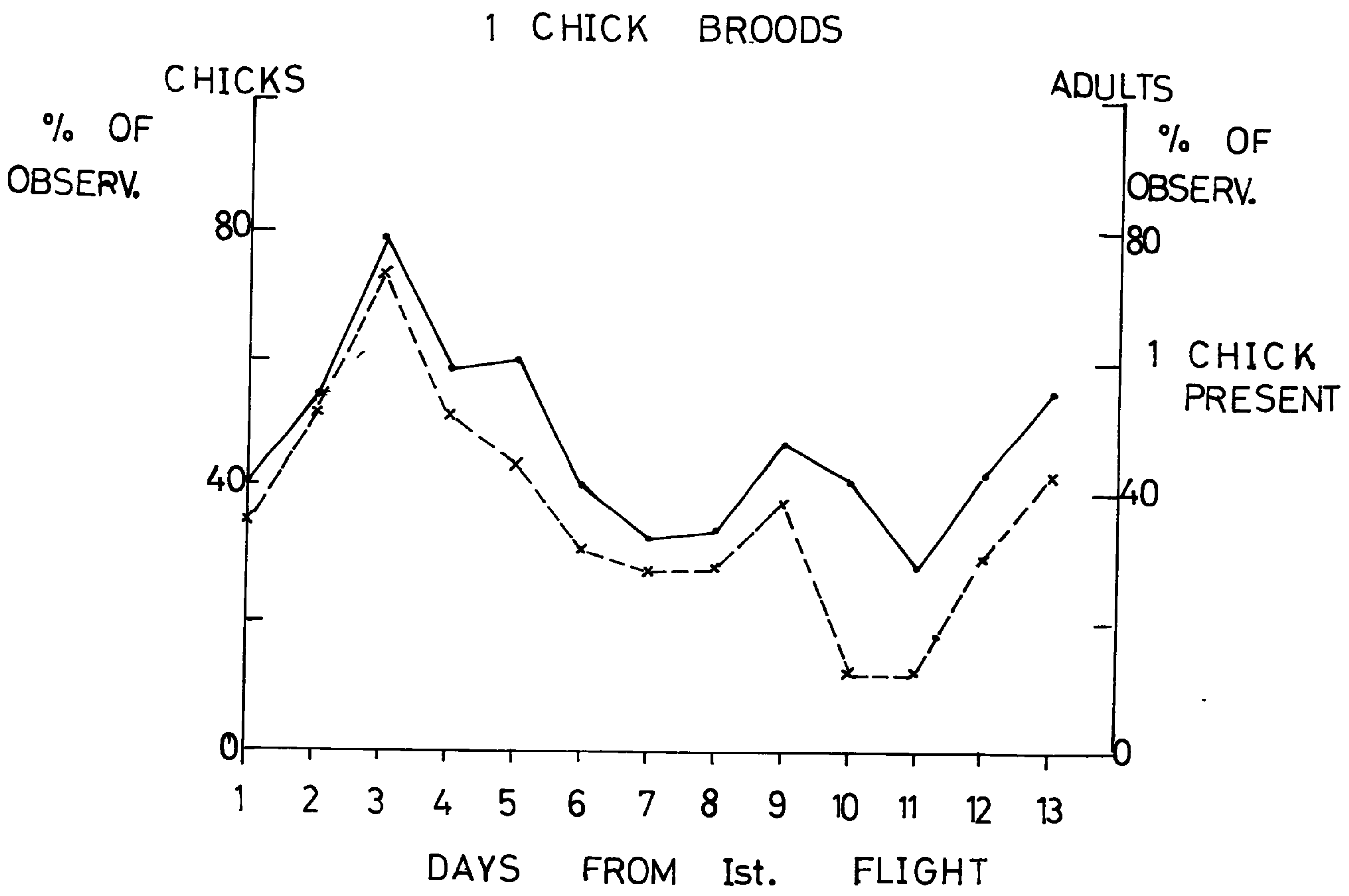
(See text for details)

●———●——— ~~chicks~~

✕———✕——— ~~adults~~

2 CHICK BROODS




1 CHICK BROODS
CHICKS
% OF OBSERV.
80
40
0
ADULTS
% OF OBSERV.
80
1 CHICK PRESENT
40
0
1
2
3
4
5
6
7
8
9
10
11
12
13
DAYS FROM Ist. FLIGHT

takes account of brood size). Chick attendance was measured as the percentage of the total observations on a particular day in the period, for which each chick number was present. Adult attendance was measured as the percentage of all nests with adults which were observed on a particular day in the period to be with two chicks, one chick or no chicks present. These two measures were plotted on the same axes for comparison.

Fig. 20 shows that for both brood 'classes', ~~that~~ as the fledging stage progressed so chick attendance decreased. In other words, there was a decrease in the percentage of the day for which the largest chick number was present and an increase in the percentage of the day for which no chicks were present. This seems to indicate progressive development of independence of the nest site in the chicks.

In Fig. 20, if chick and adult attendance at the nest site had not interacted then, on a particular day, if 80% of the nests had been occupied by two chicks it would have been expected that approximately 80% of the adults seen on that day would have accompanied two chicks. Allowing for random variation in these two measures, the pairs of graphs in Fig. 20 would have been expected to be generally superimposed. Evidence of significant deviation from this expectation indicated avoidance of chicks by adults.

The pairs of curves for the simplest case, that of one-chick broods clearly showed that, although they were very similar in shape, the adult attendance curve was always below the chick attendance curve with the chick present (the converse would have been true with the chick absent). This difference tended to increase as the fledging stage progressed. Thus, adults with one chick broods increasingly attended their chick less intensely than their empty sites through the fledging stage. This same process was also seen in the more complex situation of broods with two-chicks. When both chicks were absent the adult attendance curve was consistently higher than that for the chick and the position was reversed when both chicks were present. With one chick present, of a two-chick brood, the differences between the graphs were less extreme than either of the previous two conditions. For the first 7 days of this stage (when either one or two chicks occupied the site for the majority of the day), the pair of curves were approximately coincident, denoting no avoidance of single chicks. For the remaining 9 days, (when either one or no chicks occupied the site for the majority of the day), the adult attendance curve was consistantly below the chick attendance curve, denoting avoidance of single chicks.

Thus, (throughout the fledging stage), the adults consistently carried out relatively more of their daily attendance during those times for which the fewest chicks were present. There was also an indication that this avoidance of chicks increased with the age of the brood.

The fact that the pairs of curves were so similar in shape, throughout the fledging stage, could only have arisen if the adults had sampled the nest site and its brood-size status at fairly regular intervals during their periods of absence. If the chicks' presence had caused the attending adult to leave for long periods then the adults could not have reacted accurately to changes in the chick attendance.

If an adult makes regular visits to the nest site during its periods of abandonment (LEAVE attendance) then it would be difficult for it to travel far from the colony. As all breeding birds were individually colour-ringed then any appearing in the 'club' area could readily be identified through binoculars. The club area consisted of adjacent roofs of buildings, a little distance from the breeding ledges, where space was not contested in any territorial sense yet birds of all groups (including breeders, non-breeders and chicks) rested and preened without disturbance. During the fledging period 5 consecutive hourly observations were made per day on each nest site, noting, for each site with chicks, the presence or absence of adults. As soon as the circuit of the colony was finished (approximately 20 minutes) the presence of all breeding adults in the club area was also noted. These last observations were categorised with respect to the adults present (or absent) from the appropriate nest site e.g.

	ADULT PRESENT		
	NEST SITE (Time n)	CLUB (Time n+20mins)	CATEGORY (of club adult)
1			
Observation 1*	A present	None	
Observation 2	A present	B present	RELIEF
2			
Observation 1	A present	None	
Observation 2	B present	A present	RELIEVED
3			
Observation 1	A present	None	
Observation 2	none or A present	A present	LEAVE

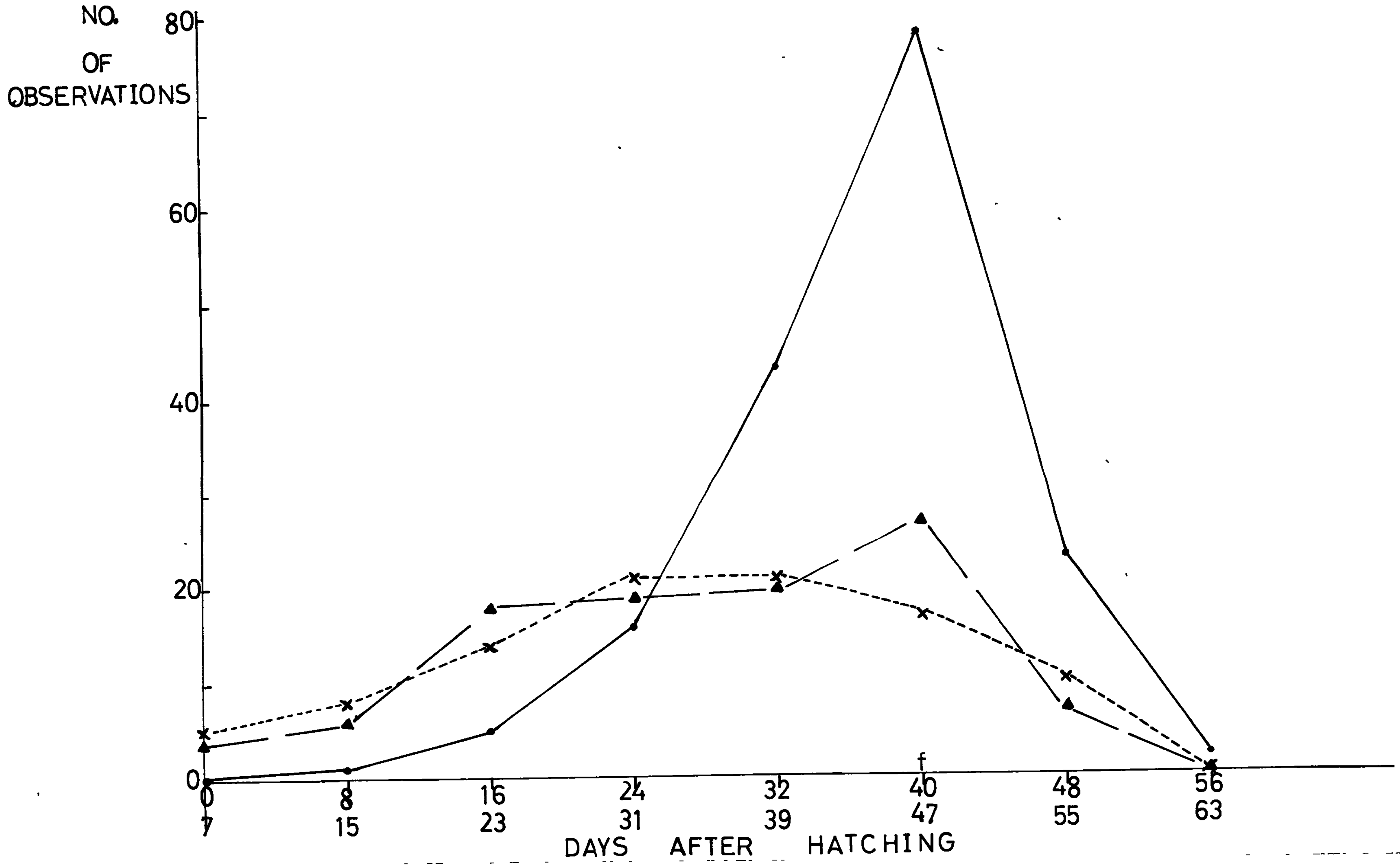
* 1 hour between observations 1 and 2.

Fig. 21 showed the change in the number of each of these categories of breeding adults seen on the 'club' area as a function of the age of their broods. RELIEF and RELIEVED birds were represented about

Fig. 21. 'Status' of breeding birds observed in the club area at different stages of chick development. (See text for details)

●———●	parents LEAVE
▲— —▲	relieved parents
×-------×	relief parents

f = first flight of chicks


NO.
OF
OBSERVATIONS
80
60
40
20
0
0
7
8
15
16
23
24
31
32
39
f
40
47
48
55
56
63
DAYS AFTER HATCHING

equally throughout the time that chicks were at the nest. The lowest numbers were seen during the early part of chick care (day 1 to 16) and just after fledging of the chicks (day 52 onward). The number of adults LEAVE attending showed very great changes, being negligible prior to day 24 (the early chick care stage) but building up to a maximum between days 40 to 47 (the early fledging stage) and then dropping steeply as the chicks left the breeding sites.

Thus, Fig. 21 showed that breeding adults could be present in the club area for the whole period that chicks were present at the nest. This suggested that the task of obtaining sufficient food for the growing brood presented no great problem to the pair (Coulson and White 1958b, Pearson, 1968). The shape of the LEAVE attendance graph mirrored the results from the observations on nest sites (Figs. 9-13 and 18) in that, as more adults were known to LEAVE attend their broods, so more were observed in the club area. From this evidence it was concluded that adults observed in the club were representative of LEAVE attending adults which therefore had the opportunity to pay short visits to their nest sites to sample the brood size and modify their attendance appropriately, as shown in Fig. 20.

The range in pair variation, for the effects of brood size on adult attendance, was indicated by the time-lapse records of Pairs 1 to 4 in Fig. 22. These were organised in a comparable way to Fig. 21. All records showed how the average number of chicks which were present at the nest site decreased through the fledging periods but that there was considerable variation in the way that this occurred. The nest site was rarely free of chicks

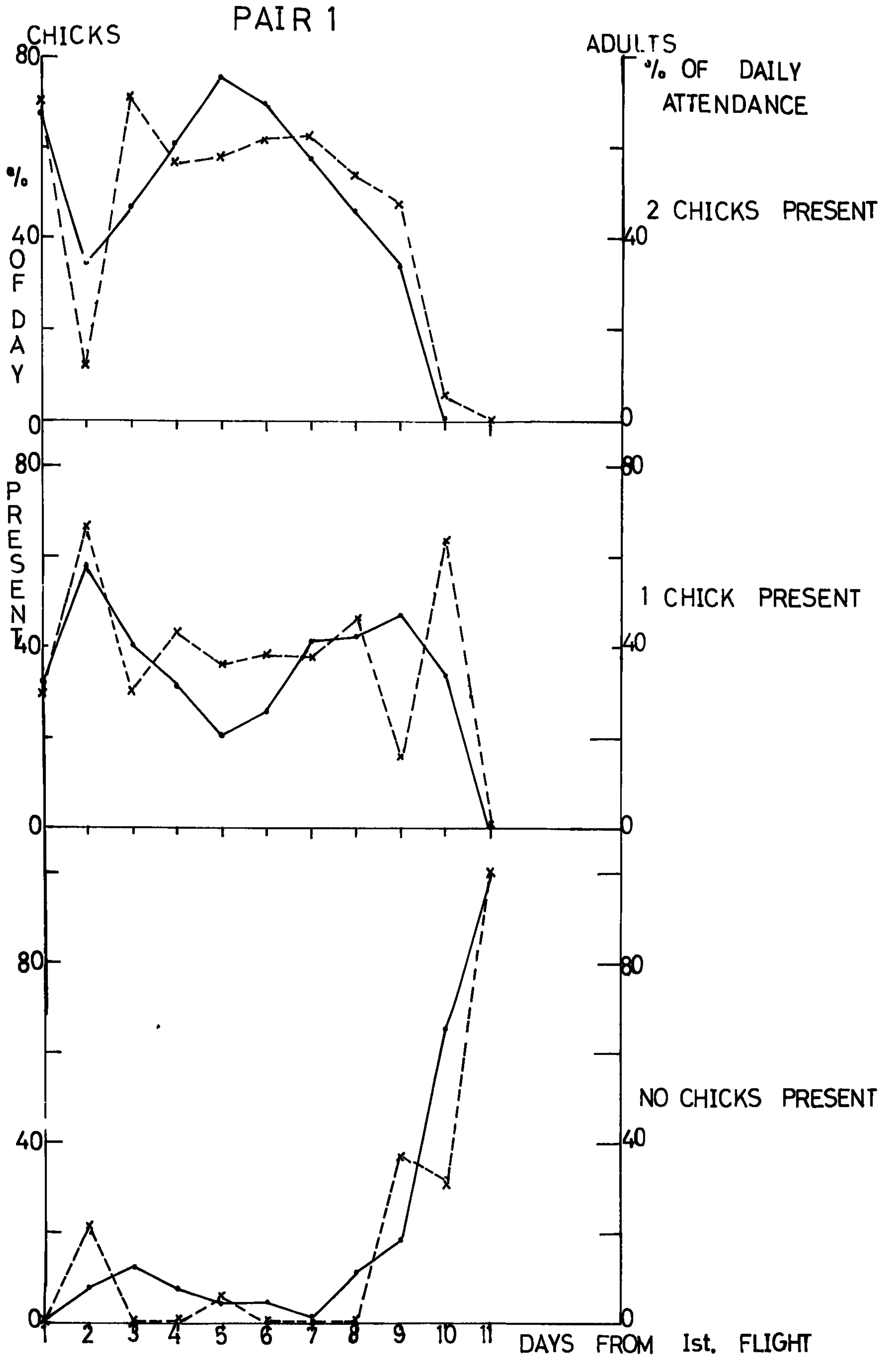
Fig. 22. Comparison between

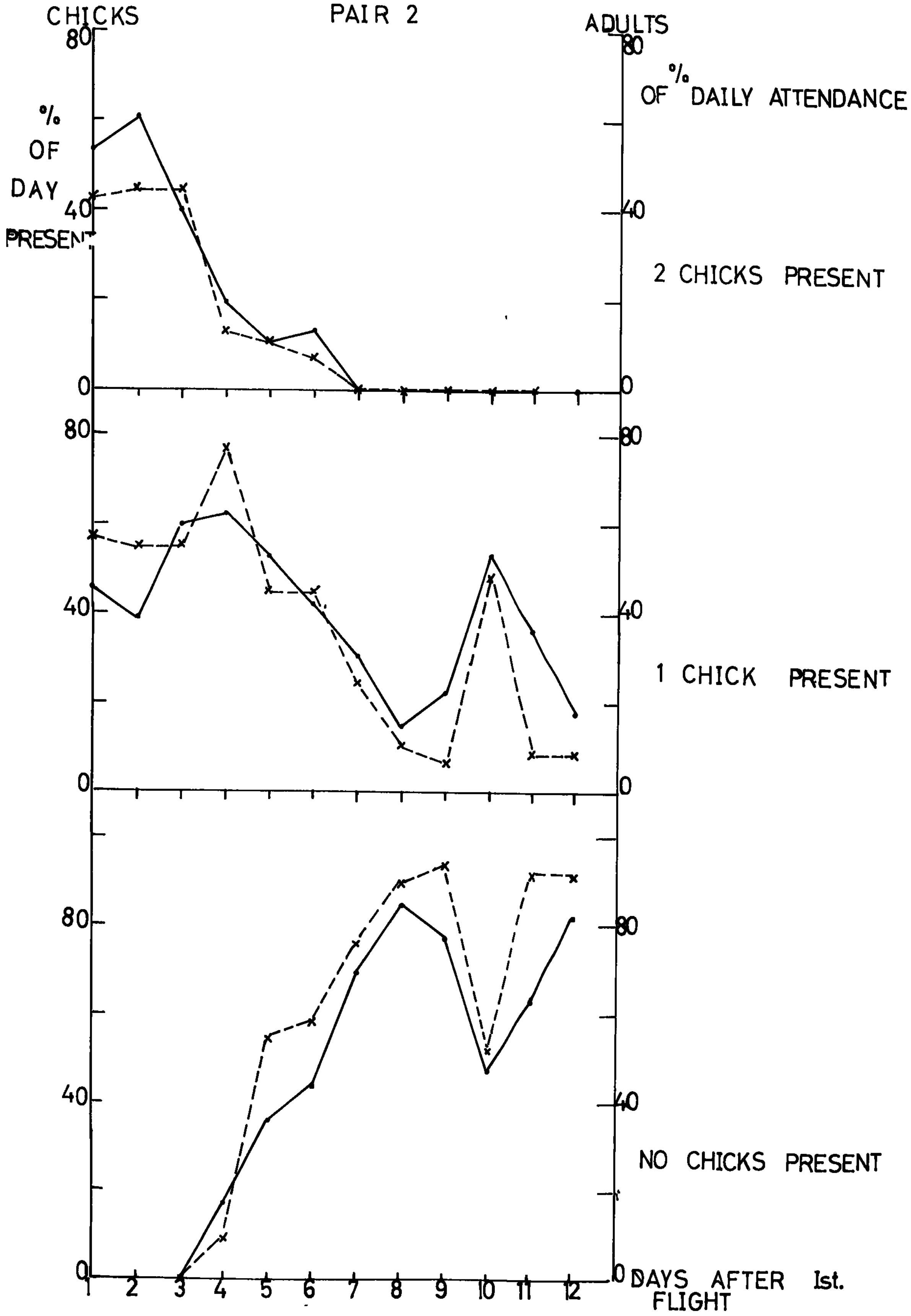
(a) the percentage of the day that different chick numbers occupied the nest site through the fledging stage,

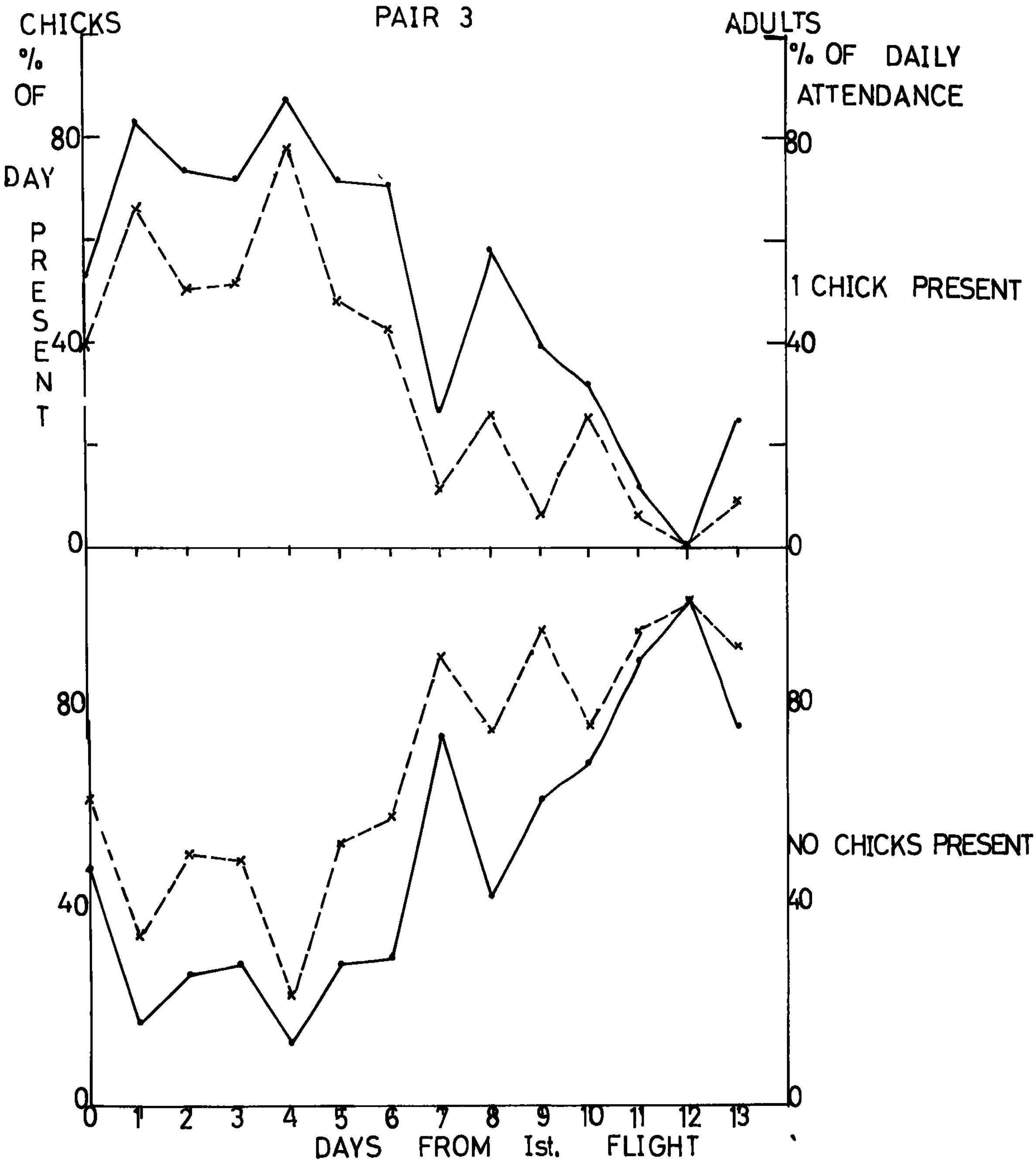
together with (b) the percentage of the total adult attendance that took place under these different brood conditions, for pairs 1 - 4.

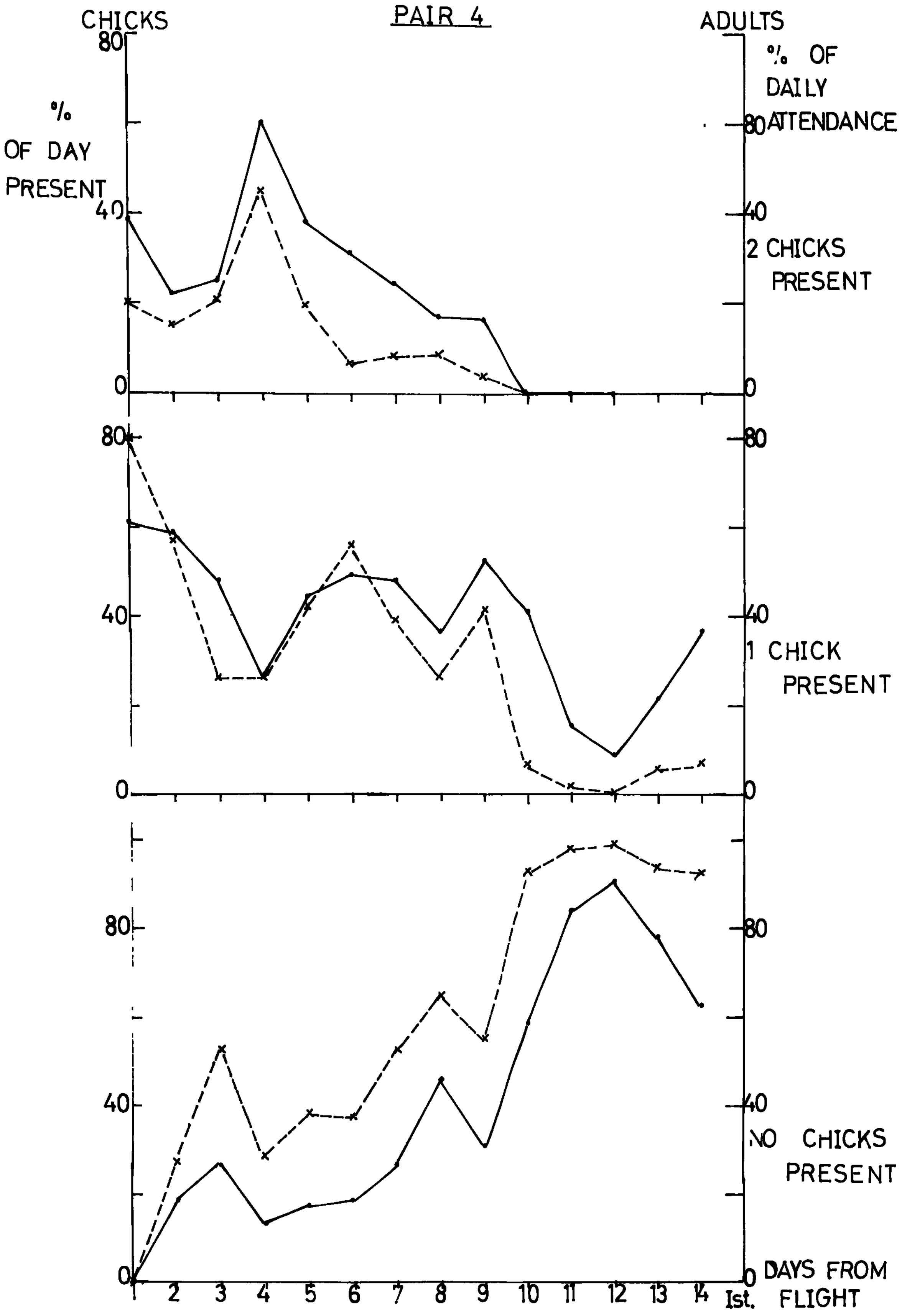
●——● chicks

x- - - - -x adults


PAIR 1
CHICKS
ADULTS
% OF DAILY ATTENDANCE
% OF DAY PRESENT
80
40
0
2 CHICKS PRESENT
1 CHICK PRESENT
NO CHICKS PRESENT
1
2
3
4
5
6
7
8
9
10
11
DAYS FROM Ist. FLIGHT


PAIR 2
CHICKS
ADULTS
% OF DAY PRESENT
% OF DAILY ATTENDANCE
80
40
0
2 CHICKS PRESENT
1 CHICK PRESENT
NO CHICKS PRESENT
1
2
3
4
5
6
7
8
9
10
11
12
DAYS AFTER Ist. FLIGHT


CHICKS
% OF DAY PRESENT
PAIR 3
ADULTS
% OF DAILY ATTENDANCE
80
40
0
1 CHICK PRESENT
NO CHICKS PRESENT
0 1 2 3 4 5 6 7 8 9 10 11 12 13
DAYS FROM Ist. FLIGHT



PAIR 4
CHICKS
ADULTS
% OF DAY PRESENT
% OF DAILY ATTENDANCE
80
40
0
2 CHICKS PRESENT
1 CHICK PRESENT
NO CHICKS PRESENT
DAYS FROM Ist. FLIGHT
1
2
3
4
5
6
7
8
9
10
11
12
13
14

during the fledging stage of Pair 1 and two chicks were commonly together. In contrast, the nest site of Pair 2 was often free of chicks and two young were rarely recorded together.

The graphs of Pair 3 were very similar ~~to~~ in form to the generalised brood situation with a single-chick (as is shown in Fig. 20), as were the graphs relating to Pair 4 form the two-chick brood situation. Of the other ~~brood~~ pairs with two chicks the record for Pair 2 showed a less extreme reaction of the adults to the presence of the chicks, but was of the same form as Pair 4, whereas Pair 1 showed no discernable reaction. The time-lapse information showed that the size of the effect of chicks on adult attendance varied widely from pair to pair. The curves for Pairs 2 and 4, where one chick was present of a two-chick brood, showed as in the spot observation information how it was possible to split the fledging period into two parts. There was an early part (where the adult and chick curves often coincided) and a late part (where the adult curve was always below that of the chick). This change in the relationship accounted for the significant positive associations shown in Table 21 for one chick present. In the conditions of presence of two, or no chicks, the time-lapse graphs did not show such an obvious change in the relationship with time and so the associations in Table 21 ~~were~~ tended not to be significant.

With the exception of Pair 1, the time-lapse information produced pairs of adult and chick graphs (under the different conditions of chick number) which were quite similar in shape. This was in agreement with the spot observation information. It thus appeared that the members of a pair, in general visited their sites at intervals during LEAVE attendance to sample chick numbers.

The relationships between the adult attendance and brood number, (for a particular brood condition) appeared in Figs 20 and 22 to be largely independant of the fluctuating brood size status encountered by the adults of a pair during successive days of the fledging period. This meant that the variation in chick attendance from nest site to nest site did not preclude comparisons between the pairs in their reaction to the different brood sizes. The arcsin transformed percentage of each successive day for which pairs left the brood unattended (under the different conditions of brood size) gave a measure of the individual pairs' reaction to brood size that could be used for inter-pair comparisons. As there was an indication in Table 21 of a positive association between this measure of LEAVE attendance and the age of the brood then comparisons were only carried out between serial records of the same length. Also as the daily values were unlikely to be normally distributed then non-parametric Mann Whitney U, and Kruskal Wallis one way analysis of variance (Siegel 1956) were used for the tests between pairs Table 24. The relevant spot observation values are also included in Table 24 for comparison. These showed that, irrespective of whether single chicks at a nest site originated from single or double chick broods, on average, adults left them unattended for similar percentages of the available time. This meant that the results from the 1 chick brood (Pair 3) could be included with the single chick present of a double chick brood results, as shown in Table 24.

A striking feature of this Table was the anomolous record for Pair 1 which showed very high values for LEAVE attendance

TABLE 24 INTER-PAIR COMPARISONS OF THE REACTION TO DIFFERENT BROOD SIZES OVER THE SAME PART OF THE FLEDGING PERIOD AS MEASURED BY THE DAILY ARCSIN TRANSFORMED PERCENTAGE OF SUCCESSIVE DAYS THAT PAIRS LEFT THE BROOD UNATTENDED UNDER THE DIFFERENT CONDITIONS OF BROOD SIZE. (SPOT OBSERVATION INFORMATION,AS TRANSFORMED% INCLUDED FOR COMPARISON)

AVERAGE DAILY ARCSIN TRANSFORMED % LEAVE ATTEND

1. TWO CHICKS PRESENT

No. of days	Spot observation	Pair 1	Pair 2	Pair 4
6	53.45	74.15	42.23	59.17

$U=3$
$P < 0.008$

$\chi^2=12.012$
$P < 0.01$

2. ONE CHICK PRESENT

No. of days	Spot Obs. (w chick brood)	Spot Obs. (1 chick brood)	PAIR 1	Pair 2	Pair 4	Pair 3 (1 chick brood)
10	39.61	42.27	72.56	35.48	49.82	56.55

$U=39.5$
ns

$U=21$
$P < 0.05$

$\chi^2=9.306$
$P < 0.01$

$\chi^2=21.60$
$P < 0.001$

3. NO CHICK PRESENT

No. of days	Spot Obs. (2 chick brood)	Spot Obs. (1 chick brood)	Pair 1	Pair 2	Pair 4	Pair 3 (1 chick brood)
9	20.26	27.04	77.09	23.62	24.37	21.51

$U=22$
ns

$U=38$
ns

$\chi^2=0.08$
ns

$\chi^2=19.11$
$P < 0.001$

N.B U = Mann-Whitney U Value
χ^2 = Kruskal Wallis One-way Analysis of Variance Value
ns = not significant
P = Probability

that were unaffected by the number of chicks present. It was concluded that the attendance at the nest site by the adults of this pair was so infrequent that they did not sample the brood size often enough to react to the changed brood sise caused by chick attendance, and so this record was dropped from part of the analysis.

The most rigorous comparison of the LEAVE attendance of pairs was between the records of Pairs 2 and 4 as both these reared broods of two. With two chicks present there was a significant difference, such that Pair 4 tended to LEAVE their chicks unattended for a greater percentage of the available time than Pair 2 ($P < 0.008$). With one chick present the difference was again significant. ($P < 0.05$) and in the same direction, but with no chick present the difference was not significant. When the results from Pair 3, (that reared a brood of 1) were included, the difference was significant between the three pairs in the amounts of available time that the chick was left unattended ($P < 0.01$) but not significant when chicks were absent. The inclusion of the anomolous Pair 1 record made the differences significant ($P < 0.01$) between all pairs under all conditions of brood size (including the no chick present condition). The differences in the extent of the avoidance reaction seen between pairs in Fig. 22 was not caused by differences in the attractiveness of the empty nest site, as all pairs attended empty sites in a similar way, but rather by differences in the strength of the inhibition of nest attendance caused by similar sized broods, as is seen from Table 24. Larger broods caused greater aversion.

The lack of inter-pair difference in the attendance of empty sites during the Fledging stage was in accordance with the information in Table 11 on all forms of attendance during the Post Fledging stage, where inter-pair differences were at a minimum for the first time in the breeding sequence.

THE SHARING OF NEST SITE ATTENDANCE BY THE PAIR

In the previous section there was a lack of evidence that one adult increased its attendance to compensate for the shortcomings of the mate during Late chick-care, or that adults overlapped their attendance by BOTH attending. This was taken to indicate that the basic pattern of attendance sharing (seen during the Main Breeding stage) was retained during Late chick-care but that individuals modified their own forms of attendance within this basic pattern. If the fledging attendance of the chicks did not affect this basic pattern and if chicks did not react to the two adults of a pair with different attendance then the difference in the sharing of adult attendance during fledging (taking brood size into account) would be expected to reflect the differences shown in the preceeding Late Chick-care stages (as shown in Table 11). Table 25 gives the intra-pair comparisons, for the time-lapse pairs, of the sharing of adult attendance during the same parts of the Fledging stage with different brood sizes. This was measured by using the successive daily arcsin transformed percentages of the total single attendance undertaken by each adult. The table showed that this sharing reflected the situation in the Late Chick care stage when chicks were present (see Table 11) i.e. male > female ($P < 0.007$) Pair 1; female > male ($P < 0.002$) Pairs 2 and 3; male = female, Pair 4. With no

TABLE 25 INTRA-PAIR COMPARISONS OF THE SHARING OF ADULT ATTENDANCE DURING THE SAME PART OF THE FLEDGING PERIODS OF PAIRS 1 TO 4 WITH DIFFERENT BROOD SIZES, AS MEASURED BY THE SUCCESSIVE DAILY ARCSIN TRANSFORMED PERCENTAGES OF THE TOTAL SINGLE ATTENDANCE UNDERTAKEN BY EACH ADULT

AVERAGE DAILY ARCSIN TRANSFORMED % OF TOTAL SINGLE ATTENDANCE

	2 CHICKS PRESENT		ONE CHICK PRESENT		NO CHICKS PRESENT	
PAIR 1	Male	Female	Male	Female	Male	Female
	62.32(8)	27.68	61.52 (8)	28.48	59.31(3)	30.69
	U=9 P< 0.007		U=0 P <0.0001		U=2 ns	
PAIR 2	23.61 (6)	66.39	29.8 (12)	60.20	35.32 (9)	54.68
	U=0 P <0.001		U=6 P <0.002		U=21 ns	
PAIR 3			26.38 (8)	63.62	34.26 (10)	55.74
			U=7 P < 0.003		U=32.5 ns	
PAIR 4	57.76 (9)	32.24	48.29 (14)	41.71	35.42 (13)	54.58
	U=19.5 ns		U=75 ns		U=47 ns	

U = Mann Whitney U Value

ns = Not significant

P = Probability

( )= No. of days

chicks present, however, no intra-pair differences were significant. This is in accordance with the information for the Post Fledging stage of Table 11, where pairs of adults did not differ in the sharing of single attendance after the chicks had abandoned the nest site. Thus, it appeared that for each pair there was an individual basic pattern of attendance sharing which was initiated just prior to egg laying and was continued throughout incubation and all of chick care. During at least the later stages the maintenance of this pattern depended on the presence of the chicks.

CHANGES IN THE FORM OF ATTENDANCE BY ADULTS WHEN BROOD SIZE VARIED - As brood size affected the pattern of presence and absence at the nest site by adults, it was important to discover if this variable also affected the form of that attendance.

The weighting of SINGLE SIDE attendance in each individual studied by the time-lapse method, during the successive days of the fledging stage (taking chick number present into consideration) was estimated from the arcsin transformed percentage of the total attendance by that individual, in the SIDE position. As Table 22 showed a slight negative association between this measure and the age of the brood then records from the same days only could be compared by Mann-Whitney U tests. Using this information, comparisons were carried out to investigate the effects of brood size on individuals' reliance on SINGLE SIDE attendance. It was also possible to analyse the spot observation information with respect to the effect of brood size on the frequency of adults attending in the SIDE position. The incidence of adults attending in the SIDE position was compared, under the various conditions of the numbers of chicks that were present, in a contingency table, using Chi-squared tests. The results of both of these analyses are given in Table 26.

The spot observation information in this table showed that the incidence of attendance in the SIDE position was significantly related to the chick number present (2 chicks > 1 chick > no chick = 0, $P < 0.01$). The information from all individuals of the time-lapse pairs also showed that adults did not SINGLE SIDE attend when chicks were absent. Although the females of Pairs 1 and 2 tended to spend significantly less of their single attendance in the SIDE position when 1 rather than 2 chicks were present ($P < 0.03$) this relationship was not seen in the males. This could not necessarily be taken to indicate a sex based difference. Using time-lapse information in the same form as Table 26 it was possible to make intra-pair comparisons of the importance of SINGLE SIDE attendance to individual adults (taking brood size into consideration). These comparisons, tested by Mann-Whitney U tests, are given in Table 27. The intra-pair differences were not significant when two chicks were present but 2 of the 3 differences were significant when one chick was present ($P < 0.03$). These results indicate that intra-pair differences in the importance of SINGLE SIDE attendance to individuals (seen also in Fig. 17 during the Late Chick-care stage) did not necessarily cease during the fledging stage.

Thus, during the fledging stage adults attend in the SIDE position, in response to the presence of chicks. Although this attendance was more commonly seen in the presence of two rather than one chick, individual adults varied in the amounts of their single

TABLE 26 THE EFFECTS OF CHICK NUMBER PRESENT ON ADULT ATTENDANCE IN THE SIDE POSITION (FLEDGING STAGE)

SPOT OBSERVATION

NUMBER OF CHICKS AT NEST

a 2 chick broods

	2 chick	1 chick	0 chick
Adult not SINGLE SIDE attending	19	105	132
Adult SINGLE SIDE attending	16	29	0

2 chick – 1 chick: $\chi^2_1 = 7.61$ $(P < 0.01)$

2 chick – 0 chick: $\chi^2_2 = 53.85$ $(P < 0.001)$

b 1 chick brood

	1 chick	0 chick
Adults not SINGLE SIDE attending	70	141
Adults SINGLE SIDE attending	25	0

$\chi^2_1 = 37.19$ $(P < 0.001)$

TIME-LAPSE

Mean daily arcsin-transformed % of single attendance in SIDE position on successive days

	2 chicks		1 chick	No. of days
PAIR 1				
Male	32.39	U = 31 ns	48.80	10
Female	26.11	U = 1 P <=0.03	9.38	4
PAIR 2				
Male	46.79	U = 15 ns	38.80	6
Female	66.56	U = 3 P <=0.008	46.55	6

N.B. No SINGLE SIDE attendance when chicks absent (record for Pair 3 with single chick brood not included)

U = Mann-Whitney P = probability ns = not significant

TABLE 27 INTRA-PAIR COMPARISONS OF THE IMPORTANCE OF SINGLE SIDE ATTENDANCE TO INDIVIDUALS DURING THE SAME PART OF THE FLEDGING STAGE (TAKING BROOD SIZE INTO CONSIDERATION)

Mean daily arcsin transformed % of single attendance in SIDE position on successive days

	PAIR 1		PAIR 2		PAIR 3	
	male	female	male	female	male	female
2 CHICKS PRESENT	31.93 (6)	31.98	46.79 (6)	66.56	-	-
	U=16.5		U = 8			
	ns		ns			
1 CHICK PRESENT	52.09 (6)	11.85	35.91 (12)	38.60	14.63 (8)	28.68
	U = 1		U = 67		U = 13	
	P = 0.002		ns		P = 0.03	

N.B No SINGLE SIDE attendance when chicks absent.

NB In parenthesis = number of successive days

U = Mann-Whitney U

P = Probability

ns = not significant

attendance spent in the SIDE position under the same conditions of brood size (as was the case for the Late chick-care period). Attendance at the nest site by both adults together was the rarest category seen during the fledging stage. Because of this rarity daily measures were not calculated for the time-lapse pairs. Instead it was expressed as a percentage of the total overall attendance under each condition of brood size (as shown in Table 20).

The information from spot observations, for both brood 'classes', was cast into contingency tables of chicks present or absent against adults attending alone or together (as seen in Table 28). The chi-squared tests on these tables showed that adults attended together significantly more often with chicks absent than with chicks present ($P < 0.01$). This same tendency was seen in each of the time-lapse pairs where the percentage of the total attendance spent together was greater when chicks were absent than when chicks were present.

Thus the presence of chicks at the nest site did deter the adults from attending together.

ATTENDANCE AFTER THE DEPARTURE OF THE CHICKS

After the abandonment of the nest site by the chicks, attendance by the adults was somewhat similar to that during the Fledging stage with no chicks present. No SINGLE SIDE attendance was recorded and, at least during the first part of this period (as shown in Table 11) both adults of a pair attended together for appreciable amounts of time. The cumulative sum charts of Pairs 2, 3 and 4 (Fig 15) for this period showed by their fluctuations a great deal of day to day variation in the amounts of single attendance by individuals as well as days on which individuals did not attend at all (which had only previously been recorded during

TABLE 28 THE EFFECT OF THE PRESENCE OF CHICKS ON THE INCIDENCE OF ATTENDANCE BY BOTH ADULTS OF THE PAIR TOGETHER DURING THE TOTAL FLEDGING PERIOD

SPOT OBSERVATION

	Number of chicks at nest			
a 2 chick brood	2 or 1 chick present	No chick present	Chi-squared 1 d.f.	Probability
Adult alone	173	120	12.36	0.001
Adults together	0	12		
b 1 chick brood				
Adult alone	93	120	9.15	0.01
Adults together	2	21		

TIME-LAPSE

	Overall % of adult attendance pair together		
	2 chicks	1 chick	0 chick
PAIR 2	0.71	2.4	11.6
PAIR 3	-	0.1	1.2
PAIR 4	0.6	0.5	15.1

the Pre-Breeding stage). To test for any progressive change in adult attendance during this period the serial arcsin transformed percentage of the day taken up by each of the categories of attendance were subjected to regression analyses, as shown in Table 28. Only the results from Pairs 2, 3 and 4 were included as the adults of Pair 1 did not attend the nest site after the chicks had left. The table showed that there was a significant positive association between the amounts of the day that the nest site was left unattended and the length of time since the chicks were last seen, for all pairs ($P < 0.01$). Thus, pairs of successful birds tended progressively to abandon their breeding sites after the chicks had left. Table 28 showed that the length of the post-chick period varied from pair to pair, (range 0 to 27 days). Also attendance by both adults together was only recorded during the first half of each of these periods and the amounts seen were not associated with the length of time since the chicks left. However, the amounts of SINGLE ON attendance by all females was significantly and negatively correlated with this measure, ($P < 0.05$), whereas that of the males was not, (the male of pair 3 gave a significant positive correlation, $P < 0.02$ as this adult did not attend for the first 2 days of the period). The spot observation information for this period shown in Table 11 revealed that significantly more female than males were present in SINGLE ON attendance, which must have reflected the difference in the organisation of this attendance category between the sexes.

After the chicks left the nest site, adults were seen progressively less often. Adults were only observed attending together during the first half of the period, which between pairs varied widely in length. Female SINGLE ON attendance decreased through the period but male attendance remained relatively constant and then ceased abruptly.

TABLE 28 CHANGES WITH THE AGE OF THE BROOD DURING THE POST-CHICK STAGE IN THE PERCENTAGE OF TIME SPENT ON ALL CATEGORIES OF ATTENDANCE BY PAIRS 2, 3 and 4

(ARCSIN TRANSFORMED)

*d.f refers to degrees of freedom associated with 'deviations from regression'
degrees of freedom associated with regression is 1, in all cases (Snedecor & Cochran, 1957. P. 148)

I LEAVE ATTENDANCE (% of total daylight hours brood unattended)

	No. of days	Variance	Regression Coefficient	F-ratio	d.f.*	Significance level
Pair 2	11	111.49	+4.97	24.16	7	$P < 0.01$
Pair 3	24	208.32	+1.71	16.12	22	$P < 0.001$
Pair 4	27	105.63	+1.62	40.60	25	$P < 0.001$

II MALE SINGLE ON ATTENDANCE (% of total daylight hours male alone)

Pair 2	11	53.82	-0.96	1.87	7	ns
Pair 3	11	120.65	+3.10	8.76	9	$P < 0.05$
Pair 4	27	123.65	-0.14	0.25	25	ns

III FEMALE SINGLE ON ATTENDANCE (% of total daylight hours female alone)

Pair 2	11	105.66	-4.08	17.18	7	$P < 0.01$
Pair 3	24	258.10	-1.00	4.44	22	$P < 0.05$
Pair 4	27	176.53	-1.50	20.86	25	$P < 0.001$

IV ATTENDANCE TOGETHER (% of total daylight hours pair together)

Pair 2	5	54.54	+0.31	0.02	3	ns
Pair 3	11	19.07	+0.64	2.33	9	ns
Pair 4	16	174.99	+0.22	0.09	14	ns

DISCUSSION

Kittiwake chicks make their maiden flight an average 40.8 days after hatching. There then follows a period, when they return at intervals to the nest site for feeding, which is terminated an average 51.8 days after hatching by their final abandonment of the nest site. The periodic absence during this stage allowed an investigation of the effects of this variable on adult attendance.

During the fledging stage, allowing for different chick numbers there were slight general tendencies for adults both to decrease the time they spent in SINGLE SIDE attendance, and to increase the amount of time for which they left the site unattended (Table 21 and 22) as their brood aged.

Although there were differences between nest sites all chicks became more and more independent of the nest site during the fledging period. Throughout this time the adults of a pair typically carried out consistently less of their daily attendance with the largest number of chicks present and consistently more when the nest site was empty. This consistency demanded a frequent sampling of the nest site conditions, by an adult away from the nest site, so that there could be a reaction to changed chick numbers (caused by the chicks periodic absences) by changed adult attendance. Field observations indicated that breeding birds were present in the club areas during the whole of the breeding sequence but that the greatest numbers were seen LEAVE attending at the time when their broods were in the Late Chick-care and Fledging stages. This indiaated that typically, adults LEAVE attending remained in the vicinity of the breeding colony, where frequent returns to the nest could be made, and did not embark on prolonged trips to the distant fishing grounds, (Pearson 1968). Thus, the presence of chicks at the nest site inhibited the attendance of the adults. A close examination of the time-lapse pairs showed further that intra and inter-pair differences in the pattern of attendance and leaving arose from individual differences in the reactions of adults to the chicks' presence, as differences were not found when the chicks were absent. With chicks present it appeared that the basic pattern of attendance-sharing by individuals of a pair (initiated before the eggs were laid) was maintained during the fledging period. The presence and absence of chicks modified individual patterns of attendance within this basic framework. When chicks were absent there was much less evidence for the existence of this basic framework of attendance sharing which indicated that its existence depended on the presence of chicks.

The actual categories of attendance shown by individuals at the nest site were also affected by the chicks' presence. Unlike the Late Chick-care stage, with chicks present, the amounts of single attendance spent in the SIDE position did not increase significantly with the age of the chicks but rather showed a slight decrease. SINGLE SIDE attendance was only seen when chicks were present and although there was considerable intra and inter-pair variation in the amounts, adults generally carried out more when two rather than one chick was present. In a similar way attendance by both adults of a pair together was only observed when chicks were absent.

After the chicks finally had abandoned the nest site, ~~a~~ inter- and intra-pair differences in attendance by adults diminished. This indicated that the presence of chicks is important for maintenance of the former diversity of behaviour. As SINGLE SIDE attendance was never recorded during this stage, then the remaining attendance categories (SINGLE ON by each adult and attendance together) formed a pattern that was reminiscent of the pre-breeding stage, although less extensive. Throughout this late stage the nest-site was progressively abandoned by the pair although there was an indication that males abandoned the sites more abruptly than females.

As the post-chick stage represented the first opportunity for pairs extensively to attend the nest site together since the pre-breeding stage then this period might be expected to represent a time of resurgence of sexual activity that could act to 'cement' the pair bond for the following years' breeding season. The wide variation in the length of this period may well reflect the success in the co-ordination of effort over the present breeding season. (Pair 1 appeared to be least well-adjusted pair of those studied by time-lapse and this pair showed no post-chick attendance). A resurgence of territorial activity after breeding was noted by Nelson (1966a) in the gannet (Sula bassana). Coombs (1960) working with rooks (Corvus frugilegus) found that sexual activity was as intense and frequent in the Autumn as in the Spring.

In the previous section it was concluded that certain stimuli from the chicks increased with age and were related to the number present. Adults reacted to these stimuli, in the simplest instances, by first initiating SINGLE SIDE attendance and later LEAVE attendance. Both of these attendance categories removed adults from the close proximity of the chicks. After initiation these two forms of attendance became increasingly important fractions of an individuals' attendance pattern. The threshold for reaction was higher in birds of high 'quality' (the pairs with the greatest potential breeding capacity) than with birds of low 'quality' and may have been higher in females than males.

The present section showed that during the fledging stage the individual and pair organisation of attendance patterns also depended on the presence of the chicks. Individual pairs of adults avoided the chicks to a greater or lesser extent (2 chicks more than 1 chick) yet showed similar amounts of attendance at sites devoid of chicks. This latter point indicated that even during the latest part of the chick care cycle the levels of motivation to attend the nest site did not vary substantially between pairs.

Over the whole fledging period adults tended increasingly to avoid chicks, ~~and~~ as is shown in Figs. 20 & 22, which may indicate increased stimulation from the chicks. However, SINGLE SIDE attendance was observed with decreasing frequency over the same period. This may have been due to a difference in stimuli for the two behaviours or that the SINGLE SIDE ATTENDANCE become less effective in allowing the adults to avoid the chicks as they developed.

Three possible changes in chick behaviour with age could be transmitted to the attending adults on the restricted nest ledges, which were also related to chick number.

1. Increased food requirements of the growing brood.
2. Increased space necessary for successful development.
3. Increased strength and frequency of interactions with the adults.

Field observations showed that adults LEAVE attending were in fact 'attending' the colony in the club area and were not away from the site and engaged in fishing (Fig. 21). Thus, like SINGLE SIDE attendance, this strategy did not increase the amount of food available to the growing chicks.

As adults which were SINGLE SIDE attending removed themselves from the nest structure completely and stood on the adjacent nest ledge (Fig. 4) then this form of attendance, like LEAVE attendance, increased the amount of space available to the developing brood. Unlike LEAVE attendance, SINGLE SIDE attendance reached a peak at about the start of the Fledging stage and then decreased. There was no reason to suppose that adults attending on the nest ledge in any way restricted the activity of older chicks any more than they did when the chicks were younger. (Chicks on sites with adjacent breeding pairs rarely strayed from the nest structure itself as they could be attacked by neighbouring adults). Also the chicks reached an asymptotic maximum weight at day 28 (Coulson & White 1958b) before 58% of individuals had initiated SINGLE SIDE attendance + 69% of pairs had initiated LEAVE attendance (data from Table 13).

One feature that did change at the start of the fledging period was that chicks, which had largely been restricted in their movements to the nest structure itself prior to this event were now freely mobile over the nest ledge. This meant that the capacity for chicks to interact with adults changed after fledging. The increased frequency and strength of interactions between adults and chicks as the brood aged was considered to be the most important stimulus set potentially able to cause adults to LEAVE and SINGLE SIDE attend well-grown chicks. In the situation where pairs of birds occupied sites that were unrestricted by the presence of adjacent pairs SINGLE SIDE attendance was initiated before LEAVE attendance and so appeared to be the less extreme form of chick-avoidance behaviour.

Thus, as the chicks developed on the restricted nest sites it was supposed that adults became less able to withstand their close attention. Where space was available adults first avoided close contact by removing themselves to the side of the nest structure but later at all sites eventually adults avoided contact by removing themselves completely. The success of the former strategy decreased with the increasing mobility of the chicks on the nest site.

THE ATTENDANCE BY NON-BREEDING ADULTS AT THE NEST SITES OF BREEDING PAIRS

Cullen (1957) noted that strange birds rarely landed on the occupied ledges from the time that the eggs were laid until the adults first left the nest site unattended (the Main Breeding stage) as they could easily be repulsed by the resident adults. At a later stage when the young were more often left alone (the Late Chick-care stage) adults searching for territory could land on the ledges which already carried chicks. Over the three years of study it was found that the majority of broods were left unattended during July and August. These months coincided with the influx of non-breeders arriving at the colony for the first time (Coulson & White, 1958a).

The attendance of strange adults at unattended breeding sites was investigated, using both the time-lapse and spot-observation information. Particular attention was given to the interaction of these adults with resident chicks.

As the attendance by strange adults was sporadic, daily values for the amounts of time these adults and resident chicks spent together (called interference) were not used for time-lapse broods. Instead, for each time-lapse site, the percentage was calculated of the total time that the nest site was unguarded for which strange adults were present. Due allowance was made for brood size during the fledging period (as shown in Table 30), the comparable spot observations for the two stages are also given in Table 30 in the form of contingency tables of number of chicks present against presence or absence of strange adults.

As the time-lapse data in Table 30 was based on percentage measurements this showed that the relative degree of interference

TABLE 30. THE RELATIONSHIP BETWEEN CHICK NUMBERS AND THE INCIDENCE OF STRANGE ADULTS ATTENDING NEST SITES UNGUARDED BY RESIDENT ADULTS

(a) SPOT OBSERVATION

I LATE CHICK CARE

Number of Chicks at Nest

	2 Chick Brood	1 Chick Brood	χ^2_1	P
No adult present	104	54	0.18	n.s
Strange adult present	14	5		

II FLEDGING PERIOD

	2 Chicks	1 Chick	No chick	$\chi^2_{\cancel{1}}$	P
(a) 2 Chick Brood					
No adult present	72	86	17	13.92	0.001
Strange adult present	9	24	13		
(b) 1 Chick Brood					
No adult present		70	22	12.46	0.001
Stranger present		6	13		

(b) TIME-LAPSE INFORMATION

Overall % of Total Time Nest Site unguarded Strange adults present

	I LATE CHICK CARE	II FLEDGING PERIOD			III TOTAL TIME UNGUARDED SITE OCCUPIED
	FULL BROOD PRESENT	2 CHICKS	1CHICK	0CHICK	
Pair 1	5.5	4.4	3.69	1.6	3·5
Pair 2	1.3	3.0	3.0	13.5	5·3
Pair 3	3.0	/	5.0	29.8	10·2
Pair 4	6.8	6.8	10.3	31.9	14·3

varied from site to site, during their Late Chick-care stages, irrespective of the different total amounts of time for which nest sites were left unguarded (as indicated by Table 11 & Fig.18). However, sites differed in a number of ways that might affect this interference.

(1) The calendar dates for Late Chick-care by different pairs varied so that the number of strange adults searching for nest sites might also have varied with the date. This was not considered to be an important variable, especially bearing in mind the results of Coulson & White (1958a) who indicated that large numbers of non-breeding adults were present throughout the later part of the breeding season.

(2) Interference might generally be expected to be greatest on those sites with adjacent breeding pairs (for example Pairs 3 and 4) where a strange adult was generally nearby when a site was left unguarded, 11.4% (32/281) of all instances of strange adults attending chicks on the nest site involved adults from adjacent nest sites.

(3) Individual adults may well have differed in the periodicity of their visits to sites when LEAVE attending (see previous section on the sampling of chicks numbers by adults). The length of a strange adults' stay must to some extent have depended on the periodicity of attendance by the resident adult.

(4) Some sites may well have been inherently more attractive to strange adults than others. Coulson (1968) showed that 'centre' sites in the colony were strongly contested by potential breeding birds at the beginning of the season at which time completely empty 'edge' sites were ignored. In a 4 day period (18-21st August 1969)

just after the majority of chicks in the colony had deserted their nest sites, spot observations showed that strange adults were present in 13.7% (128/935) of the cases of unguarded breeding sites yet only 1.7% (14/832) of the cases of empty non-breeding sites.

The variation in the relative degree of interference at each of the time-lapse sites (Table 30) could be interpreted in the light of these variables. Pair 1 differed from the other 3 pairs in occupying an 'edge' site which had probably been less keenly sought after than the 'central' sites - see (4) above. This pair was also atypical (see Fig. 22) in that there was little indication that adult attendance was sufficiently frequent to be affected by brood size. The infrequent attendance by the resident adults would have had little effect on the length of the occasional visits of strange adults on this site (See (3) above). The combination of these two factors would have produced an atypically variable record of interference through Late Chick-care and Fledging - as shown in Table 30. There was no reason to suppose that the nest sites of Pairs 2, 3 and 4 differed with respect to (3) and (4) above. However, Pair 2 occupied an isolated nest site while Pairs 3 and 4 occupied sites with adjacent breeding pairs. Whenever adults LEAVE attended the latter type of site the adjacent adult could move over (from the close attention of its own brood) and attend a site where the chicks elaborately hid from the 'strange' adult (see below). In the former case prospecting adults had to 'find' the unguarded site. Table 30 shows that throughout Late Chick-care and fledging the broods of Pairs 3 and 4 received similar high intensities of interference compared with the brood of Pair 2.

The spot observation data showed that during Late-Chick-care (when chicks were always present at unguarded nest sites) there was no difference in the attraction of strange adults to unguarded sites with either 1 or 2 chicks present.

During the fledging stage Table 30 showed that the percentage of the total time for which unguarded individual nest sites were attended by strange adults, was generally associated with the number of chicks present. (The strange adult attendance at the nest site of Pair 1 was thought to be atypical, for the reasons given above). The smaller the number of chicks that were present the greater the occupation of the site by strange adults. The spot observation data on both2 and 1 chick broods showed a similar relationship. The frequency of attendance at unguarded nest sites differed significantly according to the different chick numbers present ($P < 0.001$). This may have arisen from strange adults selecting those nest sites where fewest chicks were present, but this seems unlikely for the following reasons.

1 The spot observation results of the Late Chick-care, when chicks could not fly, indicated that there was no difference in the attraction of strange adults to unguarded nest sites where two or one chicks were present.

2 Chicks did not behave aggressively towards strange adults. Cullen (1957) noted that when a strange adult landed on an unguarded site it was likely to attack the chick, whose reaction was elaborately to 'head-turn' and 'beak-hide'. The chicks remained immobile until the strange adult left. The time-lapse film showed that chicks reacted in this way very soon after the arrival of a strange adult.

An alternative hypothesis to explain the spot observation results shown in Table 30 was that during the fledging period, when chicks and strange adults met on unguarded nest sites, some of the chicks reacted by leaving the site. Chicks were mobile during the fledging period but not during the Late Chick-care stage. Of the few occasions (6) when strange adults were seen to arrive at a nest site with chicks, or when chicks arrived at their nest site to find strange adult present, on as many as four of them the consequence was that the chick left.

In order to test the hypothesis mentioned in the previous paragraph certain assumptions had to be made.
These were that:

1 Strange adults did not 'choose' nest sites on the basis of chick numbers present - (as during the Late Chick-care stage)
2 The possible departure of a chick was a discrete event that occurred at the meeting of a strange adult and chick at the nest site; all of these interactions had occurred before the observations recorded in Table 30 were made, (arrivals of strangers or chicks were not included in the results).
3 The probability of a chick leaving or staying at the nest site upon meeting a strange adult was independent of the presence or behaviour of a sibling.

If the probability of a chick leaving the nest site upon meeting a strange adult was z and the probability of staying was y;

$$z + y = 1$$

There were three types of meetings between adults and chicks for which the possible outcomes, and their probabilities can be expressed as:

A Two chicks and strange adult.

	Outcome		
	(1) Both chicks stay	(2) One chick stay	(3) Neither chick stay
Probability	y^2	$2zy$	z^2

B One chick and strange adult.

	outcome	
	(1) Chick stay	(2) Chick leave
probability	y	z

C Strange adult alone

outcome

(1) No change

In the two chick brood situation:-

If the relevant part of Table 30 were rewritten,

	2 chicks	1 chick	No chick
No adults	NA(2)	NA(1)	NA(0)
Adults	D(2)	D(1)	D(0)

Then the hypothesis supposes that,

D(2) arose from meetings between adults and chicks with outcome A(1) - see above

D(1) arose from meetings between adults and chicks with outcome A(2)+B(1)

D(0) arose from meetings between adults and chicks with outcome A(3)+B(2)+C(1)

Let A(1), A(2), B(2) etc. = the number of instances that arose from the relevant outcomes.

so that: D(2) = A(1)

D(1) = A(2) + B(1)

D(0) = A(3) + B(2) +C(1)

Assuming that the probability p of an adult landing on <u>any</u> unguarded site was constant throughout the observation period the best estimate was:

$$P = \frac{\text{Total number of instances with strange adult present}}{\text{Total number of instances of nest sites at risk}}$$

$$\text{Thus } P = \frac{D(2) + D(1) + D(0)}{D(2) + D(1) + D(0) + NA(2) + NA(1) + NA(0)}$$

substituting in the values from Table 30

$$P = 46/221 = \underline{0.208}$$

With the same assumptions for the probability Q of a strange adult not landing on any unguarded site the best estimate was:

$$Q = 1 - P \quad \text{(Since adults either land or do not land).}$$

$$Q = \underline{0.792}$$

The probability of not finding strange adults with two chicks

$$= \frac{\text{Total number of instances with 2 chicks alone}}{\text{" " " " " " " "} + \text{Total numbers of instances where adults and 2 chicks met}}$$

in symbols:

$$Q = \frac{NA(2)}{NA(2) + A(1) + A(2) + A(3)}$$

Substituting in the values known:

$$Q.792 = 72/(72 + A(1) + A(2) + A(3))$$

$$\text{Thus } A(1) + A(2) + A(3) = \underline{18.92}$$

Similarly the probability of not finding strange adults with one chick

$$Q = NA(1) \,/\, NA(1) + B(1) + B(2)$$

By substituting in the values known: it can be shown that:

$$B(1) + B(2) = \underline{22.61}$$

And again:

$$C(1) = \underline{4.47}$$

As shown earlier, in a meeting of 2 chicks and a strange adult the probability of both chicks staying = Y2

$$\text{Now } Y2 = \frac{\text{Total number of instances with two chcks staying with strange adult}}{\text{Total number of instances where two chicks and strange adult met}}$$

in symbols $Y2 = A(1) / \big(A(1) + A(2) + A(3)\big)$

Substituting in the values known:

$$Y2 = 9 / 18.93 = 0.476$$

$$Y = \underline{0.690}$$

Since probability Y + probability Z = 1

$$Z = 1 - 0.690 = \underline{0.310}$$

Then probability $2ZY = 2 \times 0.690 \times 0.310 = \underline{0.428}$

As shown earlier, in a meeting of 2 chicks and a strange adult the

probability of one chick leaving = 2ZY

$$\text{But the probability } 2ZY = \frac{\text{Number of instances 1 chick left a meeting of 2 chicks + strange adult}}{\text{Total no. of instances 2 chicks + strange adult met}}$$

In symbols $2ZY = A(2) / \big(A(1) + A(2) + A(3)\big)$

By substituting in the values known $A(2) = \underline{8.10}$

In a similar way it can be shown that $A(3) = \underline{1.82}$

As shown earlier in a meeting of one chick and a strange adult the

probability of a chick staying was = Y

$$\text{But probability } Y = \frac{\text{Number of instances of 1 chick staying with strange adult}}{\text{Number of instances where 1 chick and strange adult met}}$$

In symbols $Y = B(1) / \big(B(1) + B(2)\big)$

It has already been shown that $D(1) = A(2) + B(1)$

Thus substituting in the values known:

$$Y = (24 - 8.10) / 22.61 = 0.703$$

Since probability Y + probability Z = 1

$Z = 1 - 0.703 \qquad = \underline{0.297}$

As ~~(~~$B(1) = B(1) - A(2) = 24 - 8.10 \qquad = \underline{15.90}$

and $B(1) + B(2) = 22.61$ (as previously shown) $\neq 22.61$

$B(2) = 22.61 - 15.90 = \underline{6.71}$

As a check

$D(0) = A(3) + B(2) + C(1)$

Substituting in the calculated values

$D(0) = 1.82 + 6.71 + 4.47 = \underline{13.00}$

The observed D(0) from Table 30 = 13

\+ + +

In the one chick brood situation

Similar calculations to the above carried out on the information in Table 30 on one chick broods gave:

$P = 19 / 111 = \underline{0.171}$

$Q = 1 - 0.171 = \underline{0.829}$

$B(1) + B(2) = 14.46$

$C(1) = 4.54$

$Y = 6/14.46 = \underline{0.415}$

$Z = 1 - 0.415 = \underline{0.585}$

$B(2) = 14.46 - 6 = \underline{8.46}$

As a check

$D(0) = B(2) + C(1)$

Substituting in the calculated values

$D(0) = 8.46 + 4.54 = \underline{13.00}$

The observed D(0) from Table 30 = 13

The calculations above indicated that during the fledging period the probabilities were equal that strange adults would land on sites where two chick or one chick broods had been reared (2 chick broods, P = 46/221; 1 chick broods, P = 19/111; Chi-squared = 0.428, not significant).

In the two chick brood situation, the calculations indicated that the significant differences noted in Table 30 could be explained in terms of a constant probability of strange adults landing on any unguarded site and constant probabilities that chicks would react to meeting a strange adult by either leaving or staying at the nest site, (probability of staying, two chicks + strange adult meeting = 0.690 probability of staying Y, one chick + strange adult meeting = 0.703).

In the one chick brood situation the calculated value for probability Y, (= 0.415) was lower than the previous values. In order to compare these 3 estimates of probability Y then they had to be in the form of whole numbers. From the previous calculations taken to the nearest whole number.

Two chick broods

A(1) = 9, A(2) = 8, A(3) = 2

Thus total chicks staying = (9 x 2) + (8 x 1) = 26

total chicks leaving = (2x2) + (8x1) = 12 Probability Y=26/38-0.684

B(1) = 16, B(2) = 7

Thus total chicks staying = 16

total chicks leaving = 7 Probability Y=16/23 =0.696

One chick brood

B(1) = 6, B(2) = 8

Thus total chicks staying = 6

total chicks leaving = 8 Probability Y=6/14 =0.429

The difference between these three estimates of probability Y were not significant, (Chi-squared 2 df. = 3.35). As stated earlier of the six occasions when chicks + strange adults were observed meeting at the nest site four resulted in the chicks' departure (Probability Y = 0.33).

Thus the model in which strange adults were landing randomly on unguarded nest sites and where the chicks on those sites were reacting independently by staying or leaving each act with constant probabilities, provided a simple explanation of the spot observation information of Table 30.

As previously stated, when strange adults landed on the unguarded sites of broods which were too young to fly, the chick reaction was to turn ~~their~~ its head away from the adult and hide the bill in the breast feathers. The chicks also crouched very low to the nest surface and erected the 'collar' of black feathers (as described by Cullen, (1957). The orientation of the chicks was away from the precipice rather than towards the 'cliff-face', seeFig. 4.

The chicks of the pairs that were time-lapse filmed had no cliff face, but only a dark 'cave', yet they all faced in the typical direction under these circumstances. This behaviour was indistinguishable from that seen when chicks of similar age were disturbed at the nest site for ringing or weighing. When they were actually removed the nest surface was gripped so tightly by the sharp-clawed feet that it was often removed also. Strange adults were seen to attack chicks at the nest site by pecking them vigorously at the nape of the neck(where the characteristic neck-band of black feathers ~~were~~ was erected). These attacks occurred 11.4% (32/281) of all instances of strange adults and chicks together and were never observed to draw blood. Although the behaviour, body orientation position and grip on the nest surface were all interpreted as adaptions of the chick against damage or removal by strangers, it was possible that the attention of a particularly vigorous stranger on the restricted nest ledge could result in the removal of a chick before it was able to fly. In ground-nesting gulls the chicks could simply run away.

The individual colour ringing of chicks during the 1970 breeding season made it possible to investigate the mortality of chicks after they had reached their asymptotic maximum weight (day 28 Coulson and White 1958b) as shown in the Table below.

TABLE 31

Mortality of full-grown chicks (1970)

Nest site	Brood size	Age when first unattended (days)	Age at first flight (days)	Age when last seen (days)	Comments
W3Ba	1	27	35	35	Taken from river waterlogged *
S3C top	2	23	39	39	"
S2Cb	1	31	41	41	"
W1Aa	2	36	41	41	"
S4Cb	2	20	39	41	not found
W2Ab	1	30	41	41	"
N1Aa	2	18	41	41	"
S1Cb	1	27	42	42	"
S1Aa	2	23	39	39	"
S1Bb	1	18	-	30	Missing from nest
MEANS		25.3	39.8		

TOTAL CHICKS IN COLONY = 90

* not died, but could not have extricated themselves or survived

The colony of kittiwakes nested on a four-sided building on the bank of the river Tyne. The initial letter of the nest site code corresponds to the nearest compass direction of the particular side of the building concerned (N = north etc.). The colony is split into 4 levels corresponding to 4 floors of the building which is indicated by the first number in the code (the highest floor = 1). The row of windows on a particular floor, facing in a particular direction, are coded A,B,C etc. which forms the third element of the code. The last element indicates which side of the sill the nest occupies (a or b) or if the nest is on an artificial ledge placed half way up the window frame (top).

Table 31 shows that of the 9 chicks in the colony during 1970 that were known to have abandoned their nest sites within 2 days of their first flight, 4 were rescued from the river in a water-logged state. This meant that they could not have extricated themselves from the water or be expected to survive. Of these 2 subsequently died and 2 were eventually released after several weeks of intensive care (data from M. McConnell, pers. comm.) It seemed reasonable, therefore, to assume that the 5 remaining chicks, not accounted for, had suffered a similar fate.

In only one of the cases in Table 31 was there any strong likelihood that a chick might have been removed by the actions of a strange adult. The chick on site S1Bb disappeared from the site at an age of 30 days when Table 20 showed that the mean age of the first flight of chicks was 40.8 days after hatching.

Table 30 indicated that 10.7% (19/177) of unguarded nest sites with chicks were occupied by strange adults during their Late Chick-care stages. The same table indicates an increase in this measure to 14.6% (39/267) of nest sites with chicks during the fledging stages. (The comparable measures from time-lapse pairs give an indication of inter-pair variation). This information might appear to indicate that the major disadvantage of strange adult attendance to chicks was the immobilisation which was self imposed, as in the behaviour described above. There was the possibility of this being of particular importance during the Late Chick-care stage where restrictions on movement and perception could possibly affect the performance on the maiden flight.

Table 32, below, shows the distribution of lengths of visits by strange adults to the unguarded nest site of Pair 3. The information has been split so that the attendance before and after the first flight of the chicks can be compared.

TABLE 32

Frequency distribution of attendance bouts by strange adults at the site of Pair 3.

Length of attendance bout (in minutes)

DURATION	0	6.8	13.4	20.1	26.8	33.4	40.1	46.8	53.4
CLASSES	6.7	13.3	20.0	26.7	33.3	40.0	46.7	53.3	60.0
I Late Chick Care	13	7	2	1	1	0	0	1	0
II Fledging (with chicks)	27	17	6	3	1	0	0	0	0
(without chicks)	38	11	3	5	1	1	0	0	1

The intervals of duration classes represent 5 time-lapse periods of 80 seconds.

The table shows little difference between the distributions of attendance bouts by strangers at the two stages of chick development. In general it can be said that the vast majority of attendance bouts in this case are short duration, lasting up to 14 minutes. Thus, although strange adult attendance occupied appreciable amounts of the time that chicks were left unattended by their parents, the duration of each disturbance was probably short. This meant that the duration of immobilisation of chicks must also have been short and so its effects on any potential 'critical stage of development' might not have been important.

In the previous calculations on spot observation data from the Fledging stage, it was possible to make 3 estimates of the probability that a chick would remain at the site when a strange adult arrived (under the various conditions of different numbers of chicks present). These estimates were not significantly different among themselves. The combined estimate (probability $y = 48/75=0.64$) indicated that 36% of flying chicks left their nest sites at the arrival of a strange adult. As Table 32 indicated that visits by strange adults tended to be short, then the number of arrivals must have been relatively large. Interference by strange adults may thus have been an important variable affecting the periodicity of chick attendance at the nest site that would have affected nest sites differentially depending on how often they were left unattended (i.e. on the adults attendance pattern). Fig. 22 showed that there was a great deal of variation in the Fledging patterns of chicks from different sites. Part of this may well have reflected differential disturbance by strange adults. The earliest stage of the fledging period (when chicks had least expertise on the wing and when their capacity for independent foraging was at its poorest) must have been the time when such disturbance was potentially most harmful. Enforced absence from the natal nest site must have decreased the probability that chicks and adults would meet for feeding. Moreover, chicks that remained away from the nest site in the club area were exposed to the effects of bad weather. Observations on chicks of known age at the colony and in a bird rehabilitation centre showed them to have inadequate waterproofing of their plumage during the first 6 days after the first flight. Table 31 showed that 4 out of 9 chicks missing from their sites would certainly have drowned if they had not been recovered. The information in Table 31 indicated that those chicks which would not have survived the fledging stage had made their first flight at a perfectly normal age (39.8 compared with a mean of 40.8 for the colony - see Table 20). However, the mean age of these chicks at the initiation of LEAVE attendance was low compared with that of the colony (25.3 days against 33·1 days - Table 13). In 1970, half of the total successful pairs (those that reared chicks to their first flight) had not left their broods unattended before they were 34 days old. Of the 9 cases in Table 31 where chicks reached a fledging stage) 8 had been left unattended before reaching 34 days of age (Chi-squared = 6.4, $P < 0.01$). Thus chicks that died during fledging tended to have been left unattended earlier in their development than ~~for~~ the average chick that survived the fledging period. ~~As~~ In the previous sections, it has been shown that after its initiation the amount of LEAVE attendance by adults increases with age of the brood. Thus It seems reasonable to suppose that the broods shown in Table 31 had beenleft unattended rather more than average pairs. They would have been likely, therefore, to have experienced more interference by adults than average pairs. It is suggested that interference by strange adults with the fledging attendance patterns of chicks can decrease the chances of a chick surviving beyond the fledging period. Even if chicks survive the fledging stage then their weight at abandonment of the site may reflect the degree of success in co-ordinating their attendance with that of their parents. This could have been modified by strange adult attendance.

Coulson and White (1958~~a~~) gave an estimate of 21% for the mortality in the first year after fledging. For 1970 this would represent 18.9 of the 90 chicks that made their first flight in this season. 47.6% of this expected first year mortality was accounted for in Table 31 which indicates that the fledging period represents a major 'hurdle' to kittiwake chicks. Maunder and Threlfall (1972) gave estimates of chick mortality over 2 seasons in a study of canadian kittiwakes. They defined chick mortality as loss of individuals up to the 35th day after hatching (i.e. before the first flight). In 1969 mortality was 19% (sample of 58) in 1970 it was 26.3% (sample of 141). Of the 37 chicks that died during 1970; 10 were chilled, 2 fell, 1 was pecked to death and 24 were 'missing' presumed pushed or ~~fell~~ fallen from nest. Although no information concerning the age of these chicks is given (other than that they were up to 35 days old) up to 25 of these deaths could have been influenced by strange adult attendance (up to 10 could have resulted from inadequate brooding). Predation of chicks by other birds was reported to be rare. These authors stated that in 1970 chicks died on the nests aften the 38th day (i.e. during the fledging period) and also that premature attempts to fly, with the resulting chilling (and death?) - when chicks landed in the sea, ~~was~~ were common.

TABLE 33

Mortality of chicks in 1968 (All bodies recovered)

Age in days	1-10	11-20	21-30	31-40	41-50	Total	%
Dead at nest	9	2	0	0	0	11	28.2
Fell at colony	16	4	1	3	4	28	71.8
Total	25	6	1	3	4	39	
%	64.1	15.4	2.6	7.7	10.3		

Total Chicks hatched in 1968 = 160

Total Chicks died in 1968 = 39 (24.4%)

In the present study Table 33 shows comparable data on the mortality with age of chicks during the 1968 breeding season (all bodies were in good condition with food in the gut). Chick mortality was estimated as 24.4% over the total breeding season Of these 71.8% fell from the breeding ledges (compared with 70.3 presumed fallen in the canadian study). As can be seen from Table 33, ~~although~~ the majority of chick mortality (79.5%) occurred before chicks reached 21 days of age, although a second peak of mortality was seen after day 31. As individual fledging of chicks was not studied during 1968 this second peak was probably underestimated; 7 dead of the 128 chicks surviving after day 28 in 1968 represents 5.5% mortality ~~in 1968~~ compared with 11.1% (10 of 90 survivings), during 1970. Of the 7 chicks that were known to have died after reaching at least 31 days of age, 6 were recovered away from the colony i.e. after their first flight. No details were available of their cause of death.

Thus both Table 32 and the information in Maunder & Threlfall (1972) provide similar estimates of chick mortality prior to the first flight. The majority of chicks disappear from the nest ledges during early chick care (Days 1-20) but there was evidence for a second peak after day 31, which was poorly estimated by both analyses. The information given above suggests that the main effect of attendance by strange adults at breeding sites (of which the duration and amount is controlled to a large extent by the attendance patterns of the resident pairs) is to modify the attendance patterns of chicks during their fledging stage. As chicks are not waterproofed at the time of their first flight and are only likely to have poorly developed hunting skills (see Dunn 1972, for the effects of age on the hunting success of terns) then they must be dependent on their parents for food. Interference with the attendance patterns of the chicks at the site can only serve to decrease the chances of chicks and adults meeting. Those sites where the attendance of parents is least frequent (which in itself is not conducive to chick feeding) are also the sites where strangers will most often land and where the attendance of the chicks will be most severely disrupted. The effects of poorly co-ordinated chick/adult attendance patterns could be seen in two consequences: (a) failure to survive the fledging stage - see Table 31. or (b) low body weight at the final abandonment of the nest site which could predispose a youngster to form part of the 21% of the fledglings that die in the first year of life, (adult mortality is about 7%, Coulson & White, ~~(~~1959~~c~~). Low body weight at final abandonment of the nest site may also predispose chicks to become 'low quality' adults if fledging weights are correlated with subsequent weights in adulthood. (It will be recalled that the high quality adult males were significantly heavier at recruitment than low quality males, ~~(~~Coulson, 1972).

ADULT BEHAVIOUR AT THE NEST SITE THROUGH THE BREEDING SEASON

In the previous sections it was shown that the adults of breeding pairs exhibited patterns of attendance through the breeding cycle that were related to the changing stimulus conditions at the nest site. Generally it was found that neither sex carried out more of the attendance than the other but that there was wide variation, both between and within pairs, in the actual sharing of attendance duties and in the timing of some of the changes in the attendance pattern. These variations might explain some of the differences in the breeding success of different pairs.

In order to investigate the adult behaviour that accompanied these attendance patterns, all of the filmed information of the four time-lapse pairs was classified into eleven behaviour categories that could be recognised readily from the discontinuous film record. The categories of behaviour used were as follows.

STAND Adults stood out of physical contact with the contents of the nest.

SIT Adults sitting on the nest surface.

SQUAT Adults crouching over chicks with wings drooped.

MOVEMENT OF EGGS Adults shifting eggs (or brood at a late stage) by using the underside of the bill or 'chin'.

PREEN Adults preening

HEAD TURN Adults turning head away from the chicks

THREAT Adults jabbing horizontally at intruders to the nest site, or adjacent birds as described by Cullen, (1957), Tinbergen, (1959).

CALL Adults carrying out the characteristic 'choking' call as described by Cullen (1957).

NEST BUILDING Adults carrying out all acts of nest building including arrival with nest material, depositing it on the nest surface, trampling and rearrangement of material, as described by Cullen (1957).

Fig. 23. Changes in the percentage of the total adult daily individual attendance alone spent on different categories of behaviour during the breeding cycle of pair 1. (arcsin transformed)

●——● male ON attending
▲——▲ female ON attending
○——○ male SIDE attending
△- - -△ female SIDE attending
e = egg laying
h = hatching
|f| = chicks flying
limits = 1 x S.E.

(Each point is the mean of up to 8 consecutive daily measures)

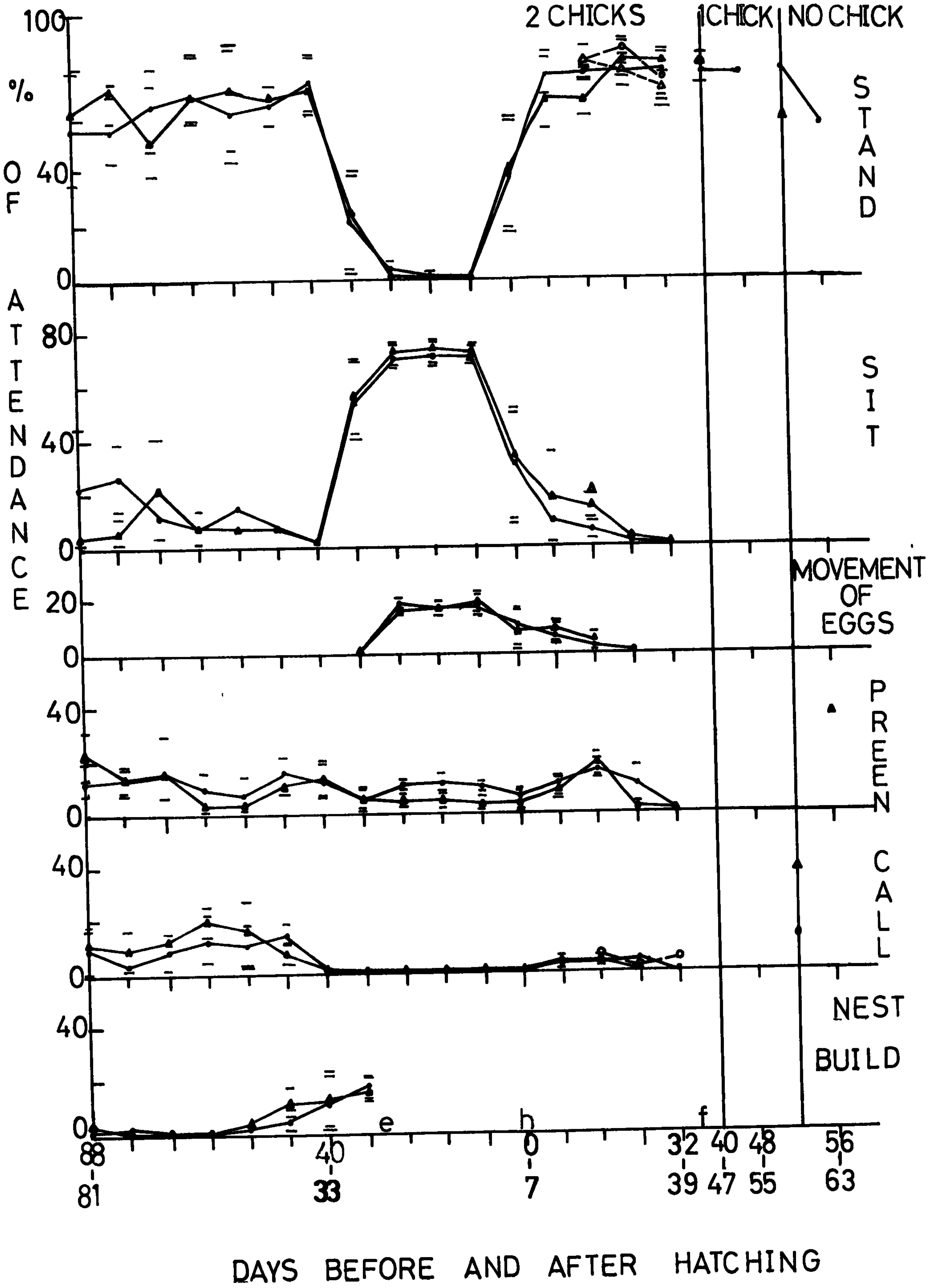

2 CHICKS
1 CHICK
NO CHICK
% OF ATTENDANCE
100
40
0
80
40
0
20
0
40
0
40
0
40
0
STAND
SIT
MOVEMENT OF EGGS
PREEN
CALL
NEST BUILD
e
h
f
88-81
40-33
0-7
32-39
40-47
48-55
56-63
DAYS BEFORE AND AFTER HATCHING

Fig. 24. Changes in the percentage of the total daily adult individual attendance as a pair spent on different categories of behaviour during the breeding cycle of pair 1. (arcsin transformed)

●——● male ON attending
▲——▲ female ON attending
○——○ male SIDE attending
△- - -△ female SIDE attending

e = egg laying
~~h = hatching~~
~~|f| = chicks flying~~
limits = 1 x S.E.

(Each point is the mean of up to 8 consecutive daily measures)

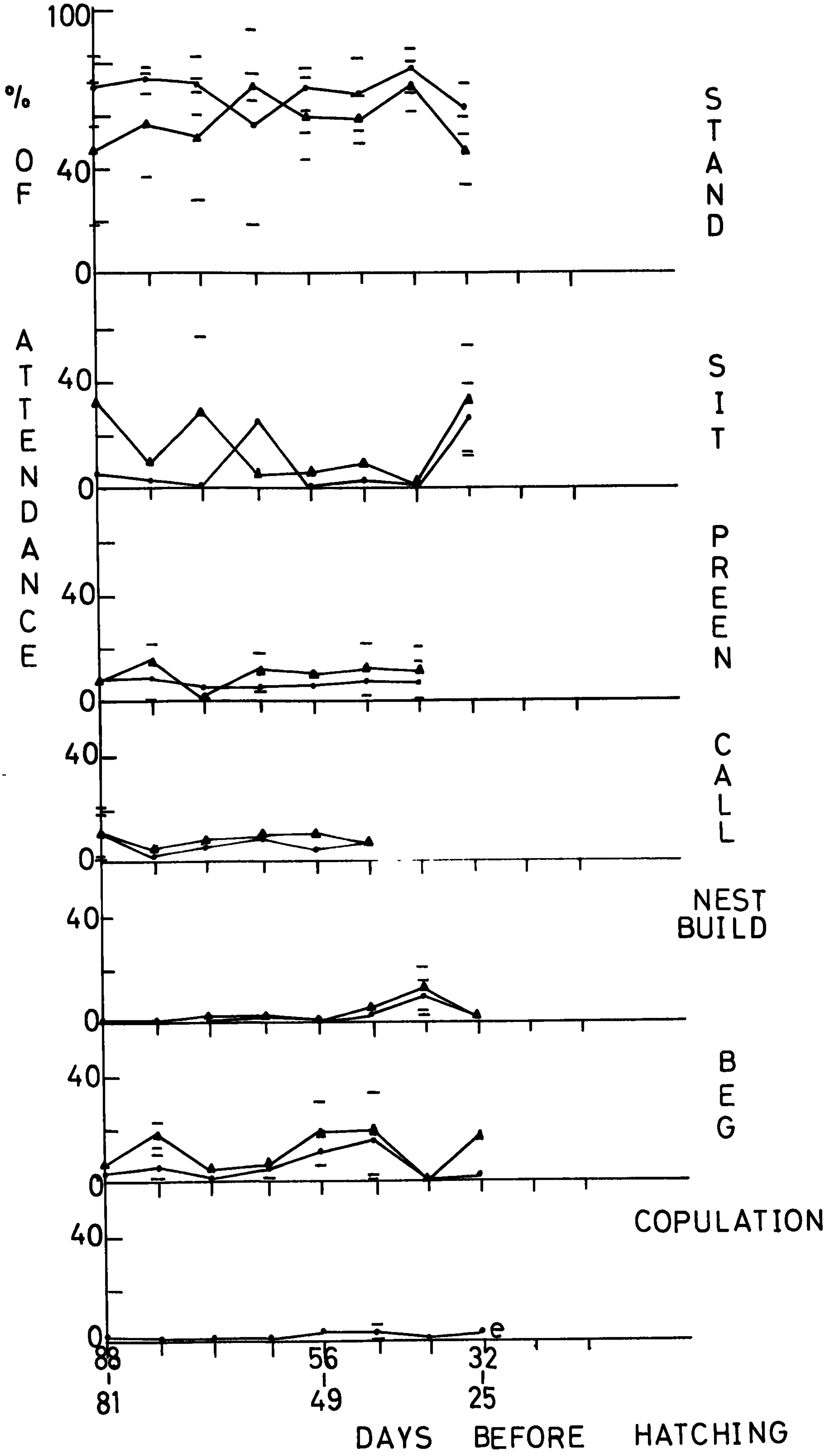

% OF ATTENDANCE
100
40
0
STAND
40
0
SIT
40
0
PREEN
40
0
CALL
40
0
NEST BUILD
40
0
BEG
40
0
COPULATION
40
0
e
88-81
56-49
32-25
DAYS BEFORE HATCHING

Fig. 25. Changes in the percentage of the total daily adult individual attendance alone spent on different categories of behaviour during the breeding cycle of pair 2. (arcsin transformed)

●——● male ON attending

▲——▲ female ON attending

○— —○ male SIDE attending

△- - - -△ female SIDE attending

~~e = egg laying~~

~~h = hatching~~

|f| = chicks flying

limits = 1 x S.E.

(Each point is the mean of up to 8 consecutive daily measures)

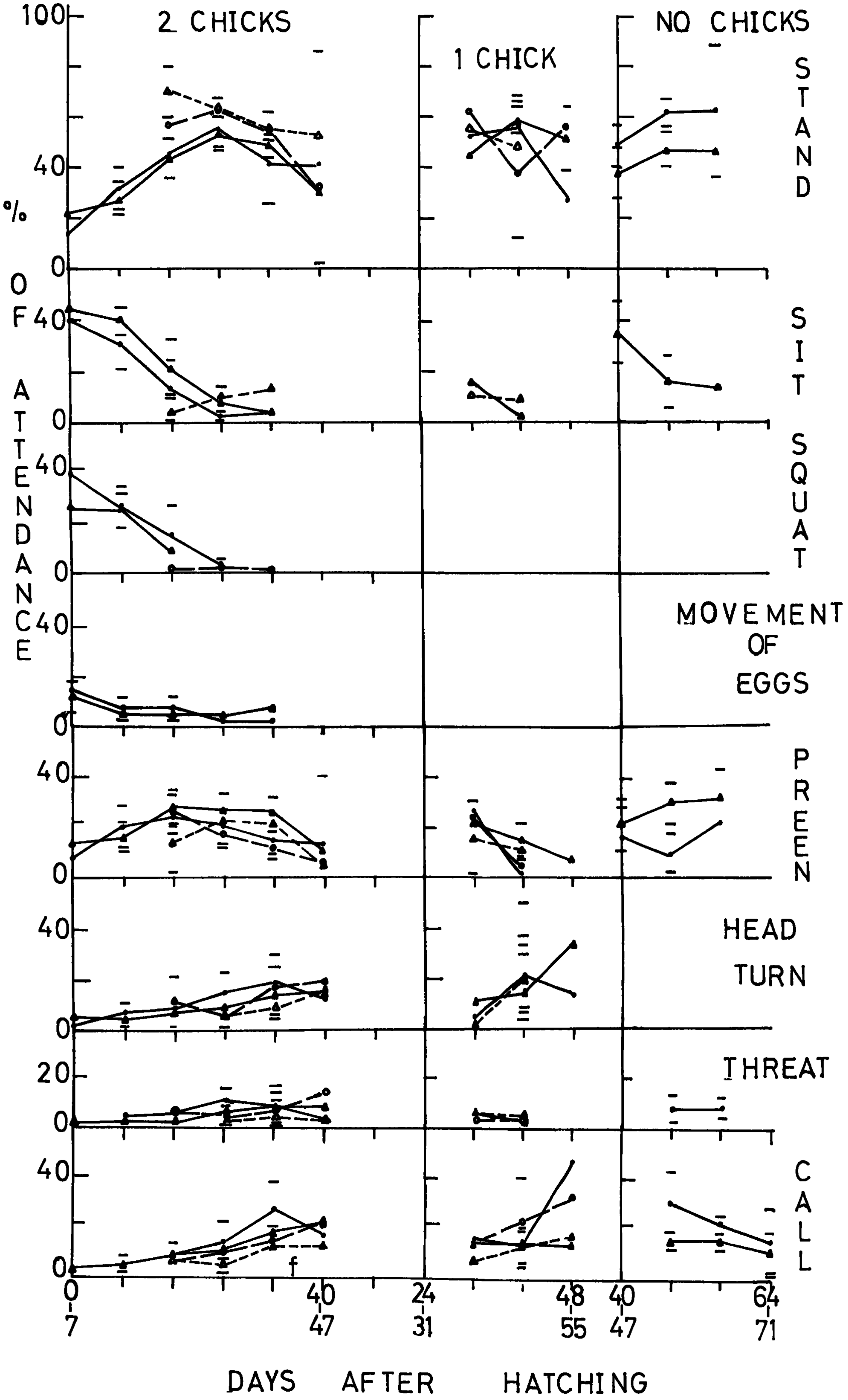
2 CHICKS
1 CHICK
NO CHICKS
100
40
0
% OF ATTENDANCE
STAND
SIT
SQUAT
MOVEMENT OF EGGS
PREEN
HEAD TURN
THREAT
CALL
40
20
f
0-7
40-47
24-31
48-55
40-47
64-71
DAYS AFTER HATCHING

Fig. 26. Changes in the percentage of the total daily adult individual attendance alone spent on different categories of behaviour during the breeding cycle of pair 3. (arcsin transformed)

●——● male ON attending

▲——▲ female ON attending

○——○ male SIDE attending

△---△ female SIDE attending

~~e = egg laying~~

~~h = hatching~~

|f| = chicks flying

limits = 1 x S.E.

(Each point is the mean of up to 8 consecutive daily measures)

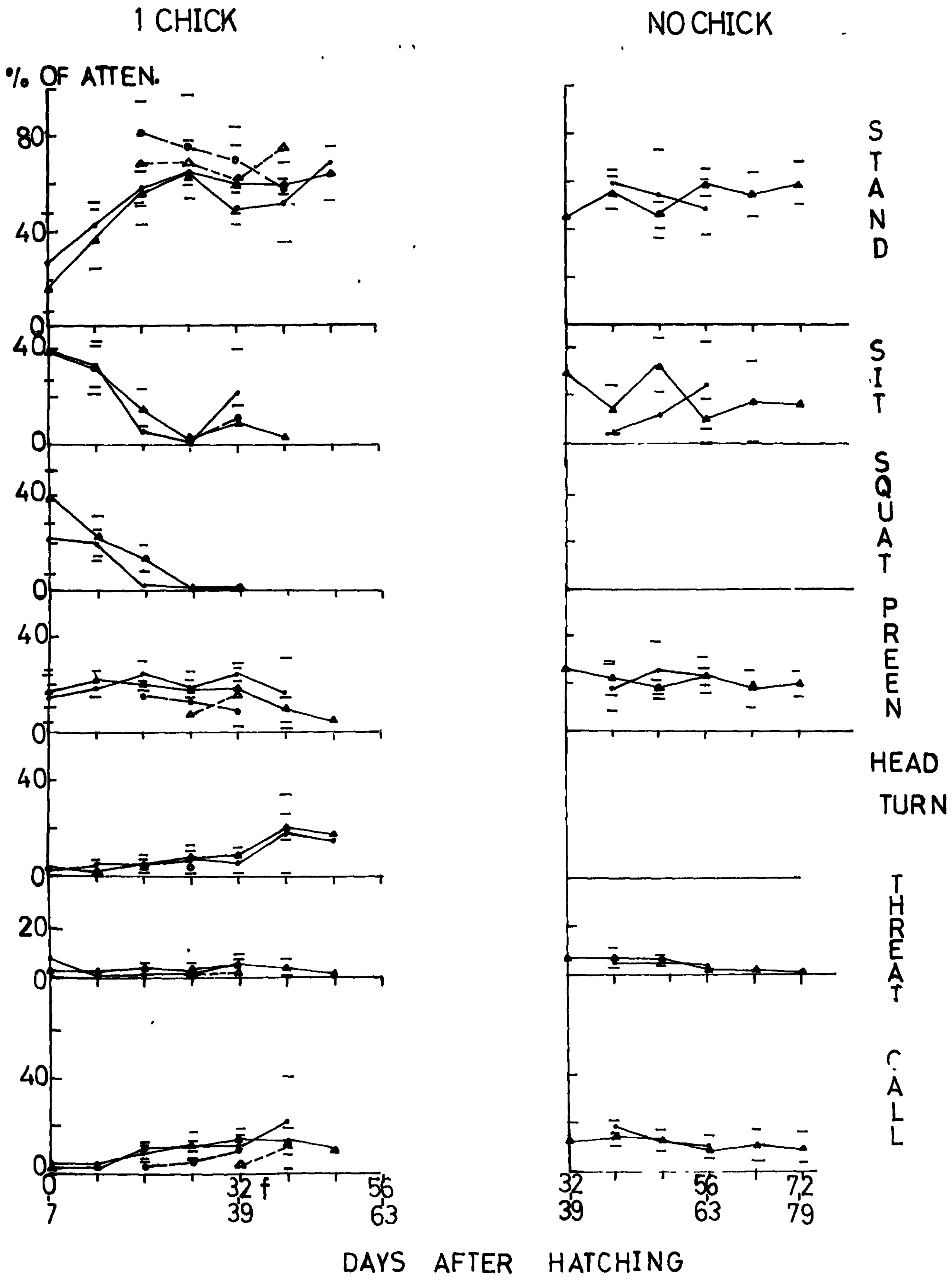

1 CHICK
NO CHICK
% OF ATTEN.
80
40
0
STAND
40
0
SIT
40
0
SQUAT
40
0
PREEN
40
0
HEAD TURN
20
0
THREAT
40
0
CALL
0
7
32 f
39
56
63
32
39
56
63
72
79
DAYS AFTER HATCHING

Fig. 27. Changes in the percentage of the total daily adult individual attendance alone spent on different categories of behaviour during the breeding cycle of pair 4. (arcsin transformed)

●——● male ON attending

▲——▲ female ON attending

○— —○ male SIDE attending

△- - - -△ female SIDE attending

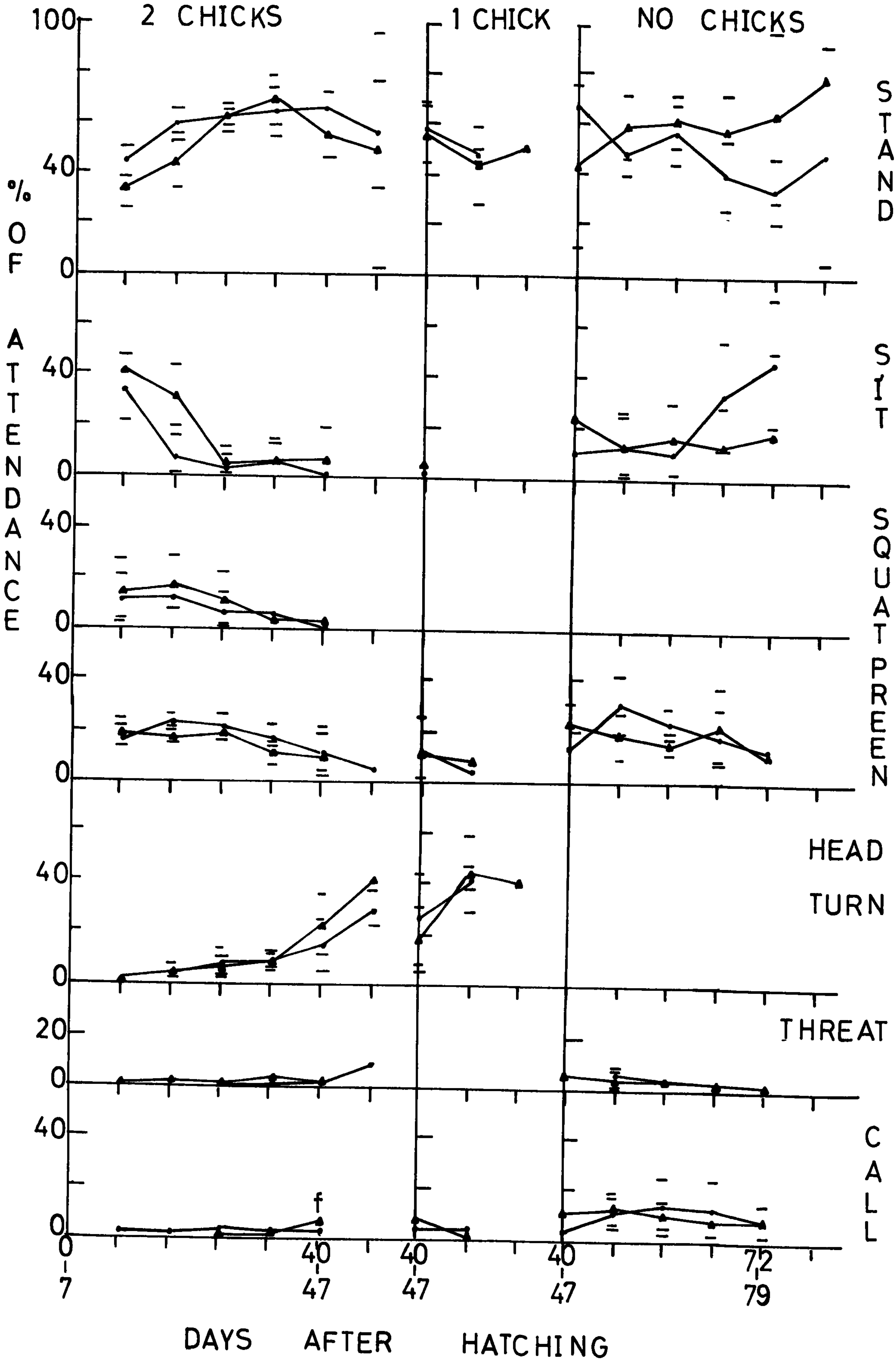
~~e ——— = egg laying~~

~~h ——— = hatching~~

|f| = chicks flying

limits = 1 x S.E.

(Each point is the mean of up to 8 consecutive daily measures)


2 CHICKS
1 CHICK
NO CHICKS
% OF ATTENDANCE
100
40
0
STAND
SIT
SQUAT
PREEN
HEAD TURN
THREAT
20
CALL
f
0-7
40-47
40-47
40-47
72-79
DAYS AFTER HATCHING

to the restricted room for other behaviours at the nest side.

In Section 2, it was shown that the direction in which the adults' faced was subject to change through the breeding season. The most striking modification of this behaviour occurred during early chick-care where young, mobile yet unco-ordinated chicks (McLannahan 1973) were seen to be protected from the precipice by the adults presence. Except for this specialised function of STANDING at one particular part of the breeding cycle there was little direct evidence that this behaviour represented anything more than the mere presence of the adults at the nest site. However, the commonness of the behaviour throughout the breeding cycle indicated that this presence probably had important biological significance to the species (see final DISCUSSION).

2 SIT

SITTING occurred at all stages of the breeding cycle but increased dramatically during the 8 day period prior to egg laying in both sexes. The amounts of this behaviour did not decrease to their former levels until about 24 days after the hatching of the brood (see Figs. 23 to 29). Fig. 9 shows that the first of these changes in the amounts of SITTING occurred at the time when the attendance pattern typical of pre-breeding changed to the attendance pattern typical of incubation and early chick-care. The second of these changes was not parallelled by a change in attendance pattern. The incubation and brooding requirements of eggs and young chicks were clearly catered for by the very large amounts of SITTING during the parts of the main breeding stage when they were present. Maunder and Threlfall (1972) working with kittiwakes, showed that although incubation over the first few days did not succeed in maintaining the high egg temperature of the later incubation period, yet the embryo started development from the first day. Drent (1970) supposed that the steady rise in temperature of herring gulls eggs after the first day was probably due to the increased attentiveness of the adults. Fig. 23 shows that the quantity of incubation remained constant throughout the period when eggs were in the nest so that in kittiwakes the lower temperature of eggs during the early stages must have arisen from a qualitative change in incubation with time from laying. The former study showed that full homoiothermy was probably not achieved by chicks until day 12 and that chicks did not have a full covering of feathers until day 25 (although these were not fully developed even then). Figs. 23 to 27, in broad agreement with the results of McLannahan (1973) who gave a value of about 20 days, showed that the brooding of chicks by adults decreased in quantity during that time when chicks developed their means of thermoregulation after hatching.

The requirements of chicks and eggs were not served by the fairly consistant small amounts of SITTING throughout the rest of the breeding cycle or by the increase in this behaviour by both sexes prior to egg laying. Beer (1961, 1966a) working with black-headed gulls, distinguished two forms of sitting at the nest site: roost sitting and incubation sitting. These differed in the methods used by adults to settle on the nest surface. As the time-lapse film rarely recorded this settling then this criterion could not be used but, as in Beer's results, Fig. 23 showed that the amounts of SITTING by both sexes increased from an initial low level with the approach of the laying date and decreased during early chick care to the same low level. This indicated that the constant low level of SITTING represented roost sitting and that the increase by both sexes represented incubation sitting (as in black-headed gulls). Thus, kittiwakes of both sexes (like black-headed gulls) did not require the changed external stimulus of the presence of eggs to initiate incubation SITTING.

3 SQUAT

After carrying out the analysis of the behaviour of Pair 1 it was noticed that 2 forms of brooding could be recognised during early chick-care (as shown in Figs. 25-27 for Pairs 2, 3 and 4). Adults brooding young chicks were sometimes seen to hold their bodies somewhat higher off the nest than during SITTING with the chicks visible under the breast of the adult or under the front edge of the drooped wings. The position of the chicks meant that they were out of contact with the brood patches (unlike SITTING). This suggested that the alternative form of brooding, called SQUATTING, was less efficient for heat transference than SITTING but carried with it a reduced change of smothering the chicks. Beer (1966a) described in detail the changes in brooding of eggs and chicks in black-headed gulls but noted the difficulty in separating what he termed 'roost sitting', incubation sitting' and 'brood sitting' (the latter called SQUATTING in the present study). His composite measure of 'time spent sitting on the nest' showed a sharp decrease in amount over the first 7 days of the post-htaching period. Evans (1970a) working with ground-nesting ring-billed gulls (*Larus delawarensis*) found a somewhat similar decrease in 'brooding' by adults from 92% of the first day after hatching to only 13% of the 7th day of life. For the black-billed gull (*Larus* bulleri) that nests on river beds subject to flooding, Beer (1966b) showed that brooding was highly reduced as chicks and adults abandoned their nest sites often within 2/3 days. After this they became nomadic and for the 'early days' of this phase chicks were only brooded during temporary halts.

Figs. 25 to 27 showed that although SQUATTING in kittiwakes (like SITTING) decreased in amount during early chick-care, these two forms of brooding behaviour persisted for over twice the length of the brooding periods of ground-nesting gulls. As there was no evidence to indicate that kittiwake chicks were unusually intolerant of low temperature at this time then the difference in lengths of brooding periods (also noted by McLannahan 1973) were seen as an adaption to cliff-nesting. The large amounts of brooding coupled with the adult facing strategy (shown in Section 2) will ensure a decreased likelihood of chicks wandering from the safety of the nest ledge.

4 MOVEMENT OF EGGS

In order that the embryo within the egg should efficiently develop and hatch, the eggs have to be turned periodically by incubating adults, (New 1957). This MOVEMENT OF THE EGGS in kittiwakes was achieved by adults rising and turning the eggs with the underside of the bill as described for black-headed gulls by Beer (1961). Fig. 23 showed that kittiwakes of both sexes initiated this behaviour at the appearance of the eggs and that amounts remained fairly constant throughout the incubation period. After this time the behaviour did not necessarily stop abruptly (as shown for Pairs 1 and 2)in Figs 23 and 25, but could continue at a low frequency throughout the brooding period.

Beer (1966a) found that black-headed gulls behaved similarly after the hatching of their chicks but, like brooding, this behaviour waned quickly.

5 PREENING

This is a behaviour that as well as being recognisable due to the juxtaposition of bill and feathers also usually involved a change in body position which made it posturally distinct from the more common STANDING and SITTING. For this reason adult PREENING was assigned to a separate behaviour category, as shown in Figs. 23 to 27. There was no indication that this was other than a maintenance behaviour, as amounts were fairly constant under all conditions of adult attendance throughout the breeding cycle. Only towards the end of chick-care with chicks present, did the amounts decrease when the length of attendance bouts were very short (see Fig. 9 to 13) and other behaviour categories received higher 'priorities'.

Cullen and Ashmole (1963) reported that 'toilet' allopreening (i.e. mutual preening for feather maintenance) occurred in the cliff-nesting kittiwake and black noddy (*Anous tenuirostris*). They suggested that 'display' allopreening might also occur as a form of appeasement in the restricted nest habitat (as did Hailman, 1965, for the cliff-nesting swallow tailed gull *Larus furcatus*). Allopreening was rarely distinguished on the time-lapse film and so was included in the PREENING category. Figs. 23-24 do not show~~n~~ an obvious difference in the amount of PREENING when the adults of Pair 1 were alone or together during the pre-breeding stage. Thus for this pair of kittiwakes there was no indication that 'display' allopreening played an important role at that time when appeasement would have been expected to be most necessary.

6 HEAD TURNING (measured in Pairs 2, 3 and 4 only)

The response of adults to the behaviour of the chicks in the feeding situation was difficult to assess from time-lapse film. In the next section it will be shown that although chicks show prolonged orientation and pecking towards the bill of the adult only a small fraction of this time is taken up by the actual transfer of food from adult to chicks. At this part of the interaction the adults assume a characteristic posture with the head bent low and the bill wide open, where regurgitated food is present in the throat for the chicks to take. Only at this time is there a positive indication of an adult's readiness to feed chicks. As this behaviour was so rare and as the information also appeared in the chick behaviour results as SUCCESSFUL BEGGING (see next section) then it was included in the STANDING behaviour category.

It was possible to identify only one other type of response by adults to begging chicks. This occurred when an adult abruptly turned its head through 90° and thus came to face away from the chicks, and was called HEAD TURNING.

As was shown in Section 2 adults with chicks normally orientate away from the precipice facing the brood. This position ensures that the greenish-yellow bill of an adult ON attending is closest to them. Cullen & Cullen (1962) showed that the bill provided an important stimulus releasing and directing begging in the chicks. However, Cullen (1957) and Tinbergen (1959) showed that the bill also directed and released attacks by adult kittiwakes disputing ownership of a site and that an intruder could only remain unmolested when it head-turned and hid the bill in the breast feathers. These authors reported the homologous action in ground-nesting gulls of 'head-flagging' which like the low intensity 'facing away' rather than full bill hiding of kittiwakes, removed the stimulus from the opponent. Hailman (1965) cites 2 instances where the adult cliff-nesting swallow-tailed gull may also have employed bill-hiding in nest site disputes.

The pecking of the bill by chicks during begging (particularly in well-grown chicks) contained many elements of an aggressive encounter. When this chick behaviour became particularly frequent or violent then it did not seem unreasonable to suppose that HEAD TURNING would be utlilized by adults to reduce stimulation so that they could remain on the restricted nest site. The incidence of the adult tactic would be expected to vary with the chicks' motivation to beg and with their increasing agility and strength as they became older. Figs 25 to 27 showed that HEAD TURNING became an increasingly important fraction of adult attendance as the chicks developed (although during late chick-care the actual daily amount of adult attendance decreased as was shown in Section 4). There was an indication in the records of Pairs 2 and 3 (Figs 25 to 26) that adults HEAD TURNED less when SIDE attending than when ON attending particularly with young chicks whose movements were restricted to the nest structure. When the chicks became more mobile (after their first flight) they could follow an adult onto the SIDE position where it would have to HEAD TURN to the same extent as when ON attending.

7 THREAT

High intensity aggression in kittiwakes has been described by Cullen (1957) and Tinbergen (1960) as 'jabbing', a specialised fighting method adapted to the cliff-nesting habitat consisting of low horizontal lunges at the opponents bill. Since these studies Bateson and Plowright (1959), for the ivory gull (Pagophila eburnea), Nelson (1967) for the gannet and Nelson (1968) for the swallow-tailed gull have all described similar fighting methods in these cliff-nesting species.

In the present study all low lunges at conspecifics by resident adults have been called THREAT. The incidence of this behaviour appeared to be largely determined by the proximity of conspecifics. At the 'edge' site of Pair 1, where strange adults never landed when the resident adults were present, none was recorded. In the other 3 'centre' sites THREAT was seen at consistently low levels throughout the breeding cycle. This behaviour may well have been important in spacing out the nests in the most densely populated parts of the colony as the minimum distance between nests must have been such that 2 adjacent birds just could not reach one another when THREAT behaving.

8 CALL

As time-lapse film does not record sound then only a very coarse measure of the species' vocalisation through the breeding season could be obtained by the recognition of CALLING postures. In the kittiwake the majority of CALLING takes the form of 'choking' (the call from which the species gets its name) as has been described by Cullen (1957). Fortunately this call is accompanied by a very characteristic posture but no information can be gained of the completeness of the call from the film. Figs. 23-27 showed that CALLING was an important part of adult attendance during 2 parts of the breeding cycle: (a) during the Pre-breeding stage and (b) during the latest stages of the breeding cycle, particularly after the chicks had abandoned the nest site. Although there was no clear difference between the rates of CALLING in the 2 periods, the maximum daily amounts of CALLING were greater during (a) than (b) due to the more complete daily attendance of the former period.

Coulson & White (1958a) showed that when the majority of successful pairs were in their pre-breeding periods (March-April) many birds were returning to the colony to breed for the first time. Additionally when most of the successful pairs were in their late chick-care periods (July & August) many birds were still arriving at the colony for the first time. Thus, at the two times during the breeding cycle of successful pairs when competition for nest sites was most fierce, relatively large amounts of CALLING by both adults of the pair took place. Adults (during pre-breeding) also CALLED when attending the nest site together (Fig. 24) but the amounts were similar to those when birds attended alone (Fig. 23) so that it seemed likely that the main function of CALLING was to establish ownership of the nest site although it may also function to cement pair-bond relationships. Nelson (1968b) noted that in the swallow-tailed gull the pair carried out a typical form of CALLING repeatedly during the period between pair formation until a week or so before egg laying.

9 NEST BUILDING

Cullen (1957) and Maunder and Threlfall (1972) gives accounts of the behaviour involved in the construction of nests in the kittiwake. These studies stressed the unfamiliarity of the sites used for the collection of building material and the use of mud in the nests. The former study stresses the complex behaviours of 'head jerking' when depositing nest material and prolonged trampling on nest material (irrespective of whether it was wet or dry). Both of these behaviours, together with an exaggerated lowering and pushing of the breast into the fibrous top layers of the nest to form the deep cup (see 'bracing' in the black noddy, Cullen and Ashmole, 1963) were all included in the category of NEST BUILDING.

Figs. 23 and 24 showed that NEST BUILDING was shared fairly equally between the adults of Pair 1 regardless of whether they attended singly or together. These graphs also showed that this behaviour became an increasingly greater fraction of adult attendance over the 24 days prior to egg-laying (a feature that was further enhanced by the increase in the daily amounts of adult attendance over the last few days of this period as seen in Figs 9 and 13). The behaviour ceased abruptly at egg-laying. Maunder and Threlfall (1972) however, reported that material was regularly (?) inserted under the eggs without making clear where this material originated from. The accurate estimates of the time taken for construction of nests in this study (2-9 days) were for rebuilding after a natural catastrophe and so could not be taken as normal NEST BUILDING.

Beer found that in the black-headed gull (1966a) and in the black-billed gull (<u>Larus bulleri</u>), (1966b) both of which are ground-nesting birds, small quantities of nest material were taken to the nest site throughout incubation and chick-care. Male black-headed gulls carried out more NEST BUILDING than females. However, in the cliff-nesting black noddy, Cullen and Ashmole (1963) found that spasmodic building was normal for several weeks before laying and that the collection of nest material was of rare occurrence during incubation. Males again collected more nest material than females.

It is suggested that the prolonged and complicated nest construction of kittiwakes serves the important biological need of extending the area and safety of the cliff ledges used for breeding (as in the black noddy). The lack of obvious NEST BUILDING after egg-laying appeared to reflect the dropping out of a typical ground-nesting habit that became inappropriate to the cliff-nesting habit of the kittiwake where nest material was not readily available and where this species showed a reluctance to land on the ground to collect material (Cullen 1957).

10 BEG and COPULATION

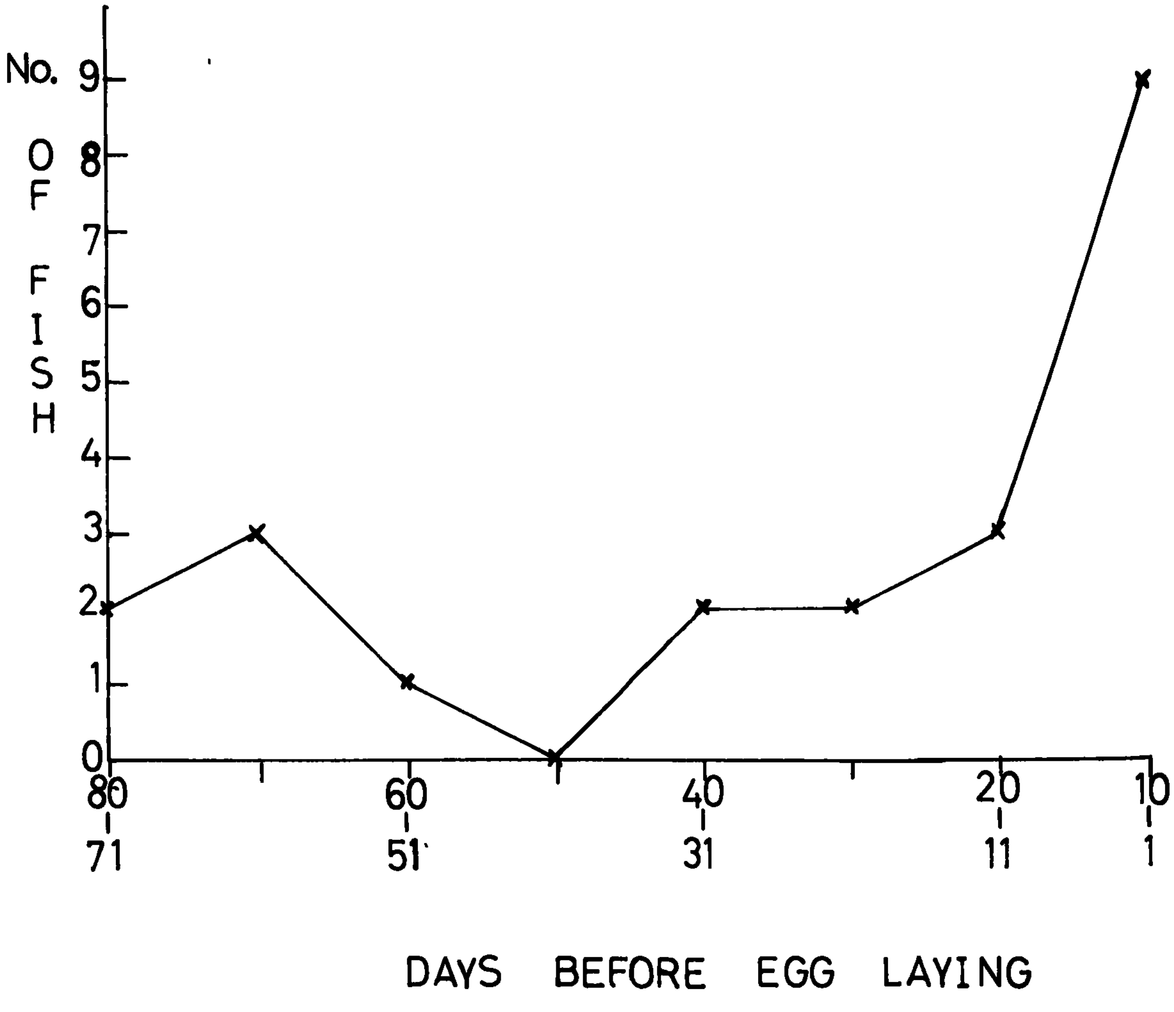
Unlike all the other categories of behaviour both of these could only take place when both members of a pair were present together. BEGGING included the behaviour of adults of both sexes crouching low on the nest surface tossing their bill tips rhythmically upwards. Females extended this behaviour by pecking at the corner of the males' bill where upon the male adopted a more erect posture and regurgitated food into the throat where it was taken by the females. The second type of BEGGING was sometimes seen without the males previously showing any of the first type. Cullen (1957) reported that COPULATION was only carried out on the nest site with the female sitting on the nest surface (rather than standing, as is the case in ground-nesting gulls). This category included instances when the male stood on the female as well as when there was actual cloacal contact of which there were usually several together (recognisable by the males' use of the wings for balance).

Fig. 24 of Pair 1 indicated that the incidence of these two forms of behaviour were related as both were seen throughout the pre-breeding period with an initial peak of low intensity soon after pairing and a second peak of greater intensity during the 32 days prior to egg laying.

While observing the occupation of nest sites in the colony before breeding the presence of whole fresh fish was occasionally noted at the nest site. Although the arrival of the fish was never observed (or any adult paying any attention to the fish) it was assumed that this was the residue of courtship feeding as this was the only time that adults were observed to feed at the nest site. A total of 28 fish were left at 24 nest sites. Early in the breeding season these were mainly clupeids, with a preponderance of gadoids later on. The timing of these events, relative to the laying of the first egg at the particular nest site was shown in Fig. 28. This graph indicated two peaks of courtship feeding, the largest within the 40 days before egg laying and the smaller soon after pairing which was in agreement with the data from Pair 1 (Fig. 24).

Following the interpretation of Tinbergen (1959), the initial pairing corresponded to the time of greatest conflict between individuals of a pair. Aggression and sexual attraction are aroused at the same time in both sexes when they are in close proximity (but particularly in the site 'owning' male). This conflict is resolved by the arousal of a behaviour pattern not directly related to the situation, a displacement activity of BEGGING. This juvenile behaviour serves to appease aggression in both sexes, but particularly the male, by arousing the parental

Fig. 28. Incidence of whole fresh fish on the nest sites of breeding pairs relative to the date of egg laying. (See text for details)


No. OF FISH
9
8
7
6
5
4
3
2
1
0
80
71
60
51
40
31
20
11
10
1
DAYS BEFORE EGG LAYING

behaviour (seen as regurgitation and feeding of the female by the male). The confined nest site of the kittiwake would be expected to encourage the development of conspicuous appeasement behaviours, particularly at pairing (see Fig. 24).

During the second peak of activity all acts of COPULATION were preceeded by acts of BEGGING although these may not have involved food transfer. The converse was not true. Evans (1970b) showed that in the black-billed gull the probability of copulation by a pair was not affected by the passage of food during previous food begging. As both food transfer and COPULATION involve intimate contact between the adults of a pair then the occurrence of similar appeasement behaviour as a *preliminary* to these two behaviours was not unexpected.

The difference in the BEGGING of the sexes was reflected in Fig. 24 which clearly showed that females BEGGED more than males at all stages of Pre-breeding. These figures showed that BEGGING was the second most common behaviour after STANDING during the aftendance of the pair together. This not only indicated that a relatively large part of this attendance was taken up by a mutual behaviour that may be important in cementing the pair-bond but that the male must have made a substantial contribution to the food reserves of the female. The importance of this latter role of courtship feeding was first stressed by Royama (1966). Cullen and Ashmole (1963) however, noted the occurrence of conspicuous courtship feeding in the black noddy during the 3 weeks prior to hatching. This was the length of time required to produce a replacement egg. They deduced from this that courtship feeding helped the female to produce the single large egg. In the kittiwake, where Figs. 9 and 13 indicated that attendance at the nest site after egg laying tended to be equally shared, it appeared reasonable that a strategy should have been evolved to ensure that the food demands of egg laying should be shared (via courtship feeding). It was interesting to note that both sexes carried out bouts of mutual BEGGING during pre-breeding yet only males responded by regurgitation and feeding. At the later chick-care stage both adults responded in this way to a similar behaviour by the chicks. This might indicate the existence of a different threshold for susceptibility to begging in the two sexes.

THE PATTERN OF ADULT BEHAVIOUR THROUGH THE BREEDING SEASON - A comparison of Figs. 9 to 13 with Figs. 23 to 27 show the changes in the pattern of adult behaviour that accompanied the changing pattern of adult attendance through the breeding season, as shown below.

I Pre-breeding (Pair 1)

Day 88 to 57 before egg laying

The early pattern of behaviour with adults SINGLE ON attending was one where adults STOOD for most of the time and spent the remainder equally on CALLING, ~~ROOST~~ roost SITTING and PREENING. When adults attended together the behaviour was very similar except for a very low incidence of COPULATION and a small early peak of BEGGING.

During the early part of the pre-breeding stage Fig. 9 showed that the female attendance was particularly variable. The small amounts of mutual behaviour may well have been important in appeasing aggression at pairing and CALLING might be used to communicate ownership of the site. In previous sections it was suggested that this pair showed a lower than average reproductive drive so that these latter behaviours (not concerned with body maintainance or occupation of the site) might have occurred at frequencies which were lower than average.

Day 56 to 27 before hatchings, i.e. egg laying.

Adults SINGLE ON attending maintained their former pattern of STANDING, ~~ROOST~~ roost SITTING and PREENING until the 6 day period prior to egg laying when the former behaviour decreased sharply in importance as incubation SITTING correspondingly increased (in both sexes). CALLING was at a maximum prior to this change, whereas NEST BUILDING became an increasingly important element throughout the whole period. When adults attended together the pattern of STANDING, PREENING, NEST BUILDING, roost SITTING and incubation SITTING showed fluctuations similar to those seen with adults alone, if less pronounced. However, a second, more important, period of BEGGING and COPULATION occurred during this period as a preliminary to the NEST BUILDING.

Figs 9 and 13 showed that throughout this period the daily amounts of SINGLE ON attendance increased and LEAVE attendance decreased. The peak of attendance together overlapped with the time that BEGGING, COPULATION and NEST BUILDING were at their highest levels in Figs. 23 and 24. This meant that these behaviours were important elements of the total adult attendance at this time. A close examination of the sequence of behaviours through the pre-breeding stage suggests that after pairing individual CALLING might serve as the initial experiential factor timing the start of the whole breeding cycle from a condition of physiological readiness induced by the photoperiodic regime of Spring daylength. This was followed by a great deal of [intimate and mutual] COPULATION and FOOD BEGGING (the latter behaviour bringing with it advantages of food sharing between the sexes) and at a later stage NEST BUILDING. All of these might serve to cement the pair-bond that was shown by Coulson (1972) to play a major part in successful breeding in kittiwakes. Maunder and Threlfall (1972) cited 3 examples of kittiwakes laying eggs on bare rocks and only later making nests, although they thought these may have been laid by young birds. This might have suggested that NEST BUILDING was not an important factor in the formation of the pair-bond but Coulson (1958a) showed that the urge to incubate and the ability to raise chicks was not neccessarily developed in birds (particularly young birds) capable of egg laying.

In other species of cliff-nesting sea birds several different behaviours have been implicated in the cementing of the pair-bond. These are, in the black noddy, display flights (Cullen and Ashmole, 1963) in the swallow-tailed gull the building of architecturally functionless nests (Nelson 1968) and in the gannet the 'ecstatic meeting ceremony' (Nelson, 1970). In this last reference it was noted that many species with particularly long breeding cycles had not evolved elaborate meeting ceremonies, e.g. some albatrosses, penguins and frigate birds, but that all had complex pair behaviour before egg laying. It appears from the limited evidence of Fig. 24 that this may be the strategy utilized by kittiwakes.

The presence at the site of the well-formed nest may well have triggered the initiation and increase of incubation SITTING in both sexes at the end of pre-breeding.

II Incubation (Pair 1, Fig 23)

At egg laying the amounts of incubation SITTING reached a maximum and a new category of MOVEMENT OF EGGS was seen. The initiation of this new behaviour and the termination of all other behaviours except PREENING was presumably in response to the presence of the eggs. The nett effect of these changes was that the 2 adults performed essentially identical behaviour patterns throughout incubation which must have reflected the simple physiological requirements of the eggs. The nest site was never left unguarded during this period.

III Early chick-care (Pairs 1 to 4, Figs. 23 and 25-27)

As mentioned previously over the 24 days post-hatching a new behaviour, SQUATTING, was added to the behaviours seen during the incubation period. In two cases no MOVEMENT OF BROOD was seen (Pairs 1 and 2). Brooding decreased in absolute amounts over this period and was replaced by adults STANDING. All of this parental attendance served a protective function for the brood that was never left unguarded. This period represented a change of frequency of behaviours at the hatching of the chicks rather than a switch of behaviours.

IV Late chick-care (Pairs 1 to 4, Figs. 23 and 25-27)

During Late chick-care, in the three pairs where the behaviour was measured, (Pairs 2, 3 and 4), the percentage of the adult attendance taken up by HEAD TURNING increased, with the age of the chicks, from the low levels of early chick-care. This indicated that as chicks became more mobile and stronger so the adults spent progressively more of their attendance in avoiding any begging interactions with their chicks Fig. ~~10-13~~ 25-27 indicated that the absolute amounts of HEAD TURNING did not increase however as adults left their broods unattended for increasing amounts of the day. CALLING, to communicate ownership of the site, was also seen to increase, probably as a result of the influx into the colony at this time, of many non-breeding adults seeking nest sites.

The increase in these two forms of behaviour was accompanied by a decrease in PREENING (which had been maintained at a constant low level throughout the whole breeding cycle) and a slight decrease in STANDING (which was otherwise maintained at a high level throughout late chick-care). This suggested that these latter 2 behaviour categories were of a lower priority, during the restricted attendance bouts of the adults, than the former two categories.

In pairs 1, 2 and 3, where the adults showed SIDE attendance during late chick-care, levels of STANDING tended to be higher and levels of all other behaviours lower than when adults were ON attending. This was probably due to the restricted space available to adults at the side of the nest, as well as to the restricted mobility of the pre-flying chicks.

The incidence of adults THREATENING conspecifics remained a rare but consistent event throughout the whole chick-care period.

V Fledging period (Pairs 1 to 4 Figs. 23 and 25-27)

These figs. showed that, during the fledging period, the pattern of adult behaviour was very similar to the former period irrespective of whether one or two chicks were present. Only with no chicks present was there any obvious difference in the behaviour pattern, as adults did not then HEAD TURN and all other behaviour categories increased in frequency to replace this behaviour.

DISCUSSION

The changes in the pattern of adult behaviour through the breeding cycle represented in part a response to the obviously changing external conditions at the nest site, e.g. SQUATTING, THREAT and HEAD TURNING, in part those changes with a strong endogenous component, e.g. BEGGING, COPULATION, NEST BUILDING and the initiation of incubation SITTING, and otherwise those with both components e.g. CALLING and MOVEMENT OF EGGS. Beer (1966a and 1963) showed that changes in parental behaviour in the black-headed gull were often not sudden switches from one behaviour pattern to another but rather gradual transitions that took several days. The behaviour of incubation built up over the pre-laying period and declined in completeness, frequency and duration after hatching. This was seen to be broadly the position in kittiwakes (as is shown in Figs. 23-27).

Lott and Comerford (1968) reviewed the literature of endocrinology and parental behaviour in ring doves. They concluded in their study that parental behaviour was substantially pre-organised. It normally appeared particularly as a result of changes in progesterone levels but also required important experiential factors. After initiation (requiring progesterone) the behaviours of brooding and feeding became independent after they were established. In the kittiwake this initiation may well be facilitated by individual pair and colonial calling, and then become dependent on the experiential factors of BEGGING, COPULATION and NEST BUILDING in order that the ~~breeds~~ adults should react appropriately to the stimuli provided by the eggs and brood.

The most striking feature to emerge from Figs. 23-27 was the degree of similarity between the behaviour patterns of all of the 8 individuals of 4 pairs. Only during the brooding of young chicks was there any real indication of individual differences in the exact amounts of SITTING, STANDING and SQUATTING employed by the two members of a pair. Generally, for so long as the adults were attending, the 'quality' of the attendance would be similar from pair to pair so that this would not be a factor that is likely to influence the breeding success of a pair.

The most striking effect on adult behaviour of the absence of the chicks was in the reduction of HEAD TURNING (which was a major adult behaviour with well-grown chicks). There was some evidence to indicate that during late chick-care this adult behaviour was reduced when adults SIDE attended compared with ON attendance although this difference could not be seen with flying chicks.

CHICK BEHAVIOUR AT THE NEST SITE

As a parallel study to the previous section, those patterns of chick behaviour which accompanied the changes in the attendance patterns of the adults through the full chick-care period were investigated.

Cullen (1957) and McLannahan (1973) both noted that kittiwake chicks were restricted in their movements to the nest structure itself. The second author showed that there was little increase in movement (that is in actions that changed the position of the chick in the nest) over the first 30 days after hatching. Such activity occurred for an average of 2% of the total time in kittiwakes whereas in the ground-nesting herring gull the figure was 7%. This study indicated that the lack of movement arose not from an inability to move but rather from a complex of behavioural factors that depended for their expression on experience of the cliff ledge habitat. These results were in agreement with those of Emlen (1963) who found that the mobility of herring gull chicks was largely governed by the experience at the nest site. Cliff ledge reared chicks showed less mobility than ground reared chicks.

The lack of mobility in the chicks of cliff-nesting species has been recognised as an adaption to the dangerous habitat by a number of authors: Nelson (1968), Hailman (1965), and Snow and Snow (1967) in the swallow-tailed gull, Cullen and Ashmole (1963) in the black noddy, and Nelson (1966a) in the gannet. Smith (1966) showed a range in the extent of this behaviour in cliff-nesting populations of glaucous, thayer's and iceland gulls. This was in contrast to the behaviour of chicks reared on the ground where the nest site was frequently abandoned by the mobile chicks a few days after hatching although movement was usually restricted to the relatively large territories, for example in the black-headed gull (Beer, 1966a) and in the ring-billed gull (Evans, 1970a). An extreme example of early developed mobility on land and water was reported by Beer (1966b) in the black-billed gull. This species nested close to rivers subject to flooding and the adults and chicks permanently abandoned the small nesting territories a few days after hatching to take up a nomadic chick-care existence.

The lack of mobility in kittiwake chicks made them ideal subjects for filming at the nest site as they did not wander over the nest ledge thus getting out of focus.

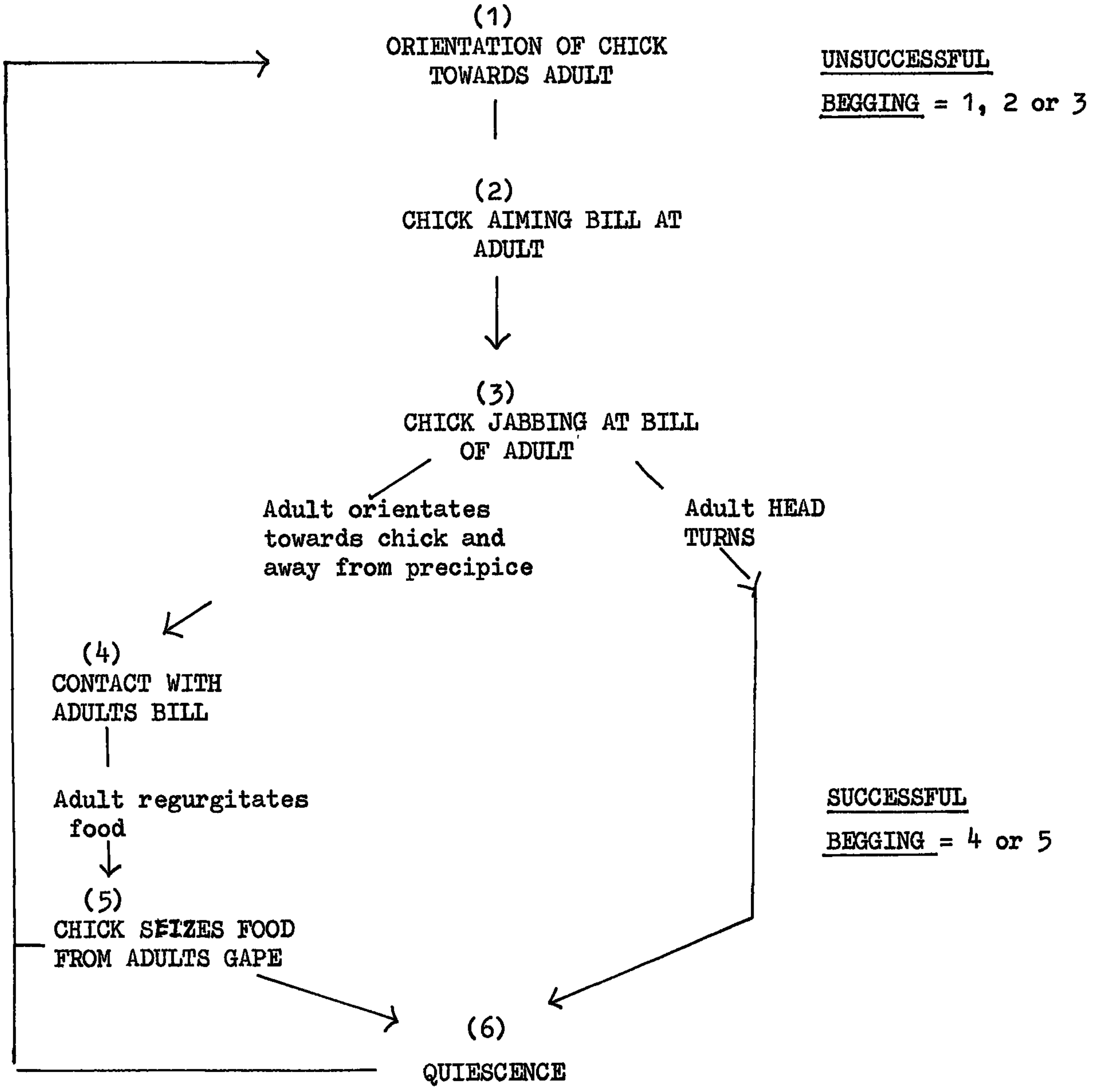
In order to investigate chick behaviour the film of the four time-lapse broods was classified into 7 behaviour categories that could be readily identified from the discontinuous film record (after prolonged observation at the nest sites). The categories used in this study were as follows.

STAND	Chicks standing, not obviously reacting to any part of the nest environment. (similar to STANDING in adults).
SIT	Chicks sitting, not obviously reacting to any part of the nest environment (similar to roost SITTING in adults although also including those instances where the adults brooded).
PREEN	Chicks preening (similar to the adults)
FLY	Chicks 'wing-flapping', as described by Cullen (1957).

The other three categories of behaviour were all concerned with the reaction of the chicks towards some feature of the nest site environment, as explained below.

After continuous observation of the feeding behaviour of the chicks at the nest site, certain characteristic elements were recognisable on the time-lapse film. These elements formed a chain of behaviour represented diagrammatically below.

CHICK FEEDING BEHAVIOUR



Elements (1) to (5) represent the complete chain necessary for the transfer of food from adult to chick. Except during the very earliest stages of chick care (see the later section on BEGGING) the appearance of the first 3 elements of this chain was largely independent of the behaviour of the adult, i.e. there was no indication of a reaction of adults to chicks. In contrast, the appearance (or not) of the last 2 elements of the chain was dependent on the readiness of the adult to feed the chick, i.e. adults did react to the chicks. For this reason (and because the discontinuous time-lapse film did not record all elements of the chain) (1) to (3) were grouped together and classified as UNSUCCESSFUL BEGGING and (4) and (5) were grouped together and classified as SUCCESSFUL BEGGING, for the purposes of this study. Chicks were also found to carry out behaviour identical to stages 3 and 4, in the diagram above, but orientated, not towards the bill of the adult, but to some other feature of the nest site environment. These included the nest bottom and walls of the nest site, the head, wings and legs (particularly with leg rings on) of the adult, or to similar parts of the anatomy of the brood mate. All of this behaviour was classified as PECKING.

In a previous section it was reported that when the resident adult left the nest site unattended there was a high risk of strange adults landing there. Prior to the fledging period, the reaction of chicks to these stranges was for them to turn the head away and hide the bill in the breast feathers while adopting a low crouched posture with the neck band erect. After the first flight, however, chicks tended to leave the nest site. Whether this behaviour was in response to an attack by the stranger (as was seen in 11.4% of all spot observations of strangers and resident chicks together) or whether it implied 'recognition' of the stranger by the chicks was not clear. Time-lapse chicks were never seen to beg to a stranger (the normal situation at the arrival of a parent) although this was reported to occur rarely in the black noddy, but no feeding took place, as adults drove the chicks away (Cullen and Ashmole 1963). Similarly this was never recorded when making spot observations of the undisturbed kittiwake colony.

Adults arriving at a site usually 'choke' and at nest relief this call is usually 'answered' by the resident mate during the brief time before the newcomer actually lands. This suggests that it is possible to pick out an individual arrival call out of the background noise. It may well be that chicks are effectively conditioned to recognise the parents' arrival call by the opportunity to beg and receive food reward and that attack acts as a reinforcing stimulus to discriminate against the arrival calls of strange adults. Evans (1970)[b] demonstrated individual recognition of adult calls by chicks in the ground-nesting black-billed gull. Here, the particular call of a parent became increasingly effective at eliciting approach by chicks as they developed.

Cullen (1957) showed that it was possible to foster out chicks onto different nest sites and that these would be accepted up to 4/5 weeks of age. This implied a lack of recognition on the part of both chicks and adults at the resident adult's site. These findings were in agreement with my own observations of 6 cases where chicks of up to 3 weeks of age swapped sites on large nest ledges and were successfully fostered. Presumably in these cases adults did not recognise, and thus attack the young chicks on their own nest site and the chicks had little experience of strange adults and thus had no way to recognise an adult as 'strange'. In another fairly common situation, which throws light onto this problem, chicks that could fly were seen to land on the 'wrong' nest site containing resident chicks. When the resident adult was present then my observations agreed with those of Cullen (1957) as in 9 out of 10 such cases ($P < 0.025$) the newcomer was instantly attacked and eventually driven off. All of these chicks bill-hid and head-turned immediately after their arrival. When the resident adult was absent then the behaviour of all chicks depended on their relative ages. Younger broods treated strange chicks like strange adults, although these were never observed to attack resident chicks but rather to behave like normal fledging chicks on their own site. When the chicks were of equal age then the stranger was attacked by the resident chicks. A similar behaviour was reported for the cliff-nesting black noddy with strange chicks present by Cullen and Ashmole (1963) and also in the ground-nesting blue-footed booby (Sula nebouxii) by Nelson (1970). In kittiwakes, nest mates were rarely observed to attack each other. The strange chick responded by adopting the typical appeasement postures found in kittiwakes. If a resident adult returned to its site to find a strange chick present then this chick (irrespective of others present) would show bill-hiding and head-turning and appeared to be tolerated to a greater extent than when strange chicks arrived at sites with resident adults. Although no accurate measures were made, of 12 instances where resident adults arrived at sites with single strange chicks present (incompany with 14 resident chicks capable of flight) 8 of the strange chicks and 1 of the resident chicks were absent 1 hour later ($P < 0.005$, Fisher exact probability test, Siegel (1956)). This indicated that recognition of chick by adult, or adult by chick, or both had taken place.

The observations above generally agreed with those of Cullen (1957) who concluded that there was little evidence of individual recognition between parents and chicks when they were young (up to about 30 days) but that speedy and accurate mutual recognition developed later on.

As the behaviour seen in chick/stranger interactions was unique to the situation and thus depended for its timing on the irregular arrivals of strangers, its occurrence was not included in the following analyses of resident chick behaviour accompanying the attendance pattern of the parents.

Two further difficulties remain.

1. Adult birds were individually recognisable from the time-lapse film by their unique leg ring combinations. Other differences that were useful in separating the individuals when their rings were hidden (for example when SITTING) were: wing tip markings, position of wings when folded (most birds habitually folded left over right or the opposite) and small differences in apparent head shape (males appeared to have more 'angular' heads than females). Thus there was no problem in allocating behaviour to individual adult birds (in the previous section). However, the identification of individuals of a 2 chick brood was more difficult. During the early chick-care stage the legs of chicks were too small for leg rings and the whole chick was often totally invisible under the brooding adult. At a later stage, although they were more often

visible, most of their activity was restricted to the deep nest cup (as mentioned earlier) where it was impossible to see their legs. Changes in size, shape and plumage with age made these characteristics useless for speedy identification. Only at fledging, when the nest cup was flattened and movements were less restricted was it relatively easy to identify individuals by ring combinations. For these reasons chick behaviour could not be allocated to individual chicks so that for each of the 7 behaviour categories given previously chick behaviour was measured as:-

$$\frac{\text{Total instances of a behaviour by chicks (x 100)}}{\text{Total instances of all behaviours by chicks}}$$

Thus, for each frame of the time-lapse film of a two chick brood there were 2 instances of chick behaviour.

2. Hailman (1967) in his monograph of the pecking response in chicks of the laughing gull (*Larus atricilla*), demonstrated one of the major problems in the study of ontogeny. Even when considering a behaviour that would have been classified by the early ethologists as a 'fixed action pattern' (Lorenz, 1950, and Tinbergen, 1951) he shows that the ontogeny of this response is neither stereotyped within the species or independent of experience. Thus, as Kruijt (1964) illustrated, in a study of development of behaviour one is faced with the problem of identifying units for analyses when those units themselves continuously change during the course of development. This problem was also present in the earlier section of the present study on the behaviour of adults but it seemed reasonable to suppose that, particularly during breeding, the behaviour of mature animals should (a) be well

buffered against environmental fluctuation and (b) have shown decreased spontaneous variation with increased breeding experience. That mature breeding adults showed a high degree of stereotypy in their behaviour was indicated by Coulson (1971) who reported that typically a good breeding male kittiwake that retains its mate is successful at rearing young all its life whereas others are consistently poor at breeding.

In the present study no attempt was made to measure the change in the form of the units of behaviour selected. Discontinuous time-lapse film did not lend itself to the assessment of this kind of subtle change. In a preliminary investigation of this type it did not appear appropriate to attempt to select units of analysis that were so detailed as to confuse the comparisons between the major changes in chick behaviour and the major changes in adult attendance and behaviour. Seven gross categories of behaviour were selected that were posturally discrete from one another and therefore easy to identify yet retained throughout development a fairly consistent relationship to some recognisable feature of the nest site environment.

Some recognisable behaviours e.g. defaecation and allopreening (as in the study of adult behaviour) occurred so infrequently that their measurement by 80 second time-lapse film (see Section I) was considered to be too inaccurate for inclusion. The occurrence of other behaviours e.g. sleeping (again like the study of adult behaviour) could not be recognised from the time-lapse film.

THE BEHAVIOUR OF CHICKS

Figs. 29-32 show the changes, through the chick-care period, in the (arcsin square root transformed) measure (see above) of each chick behaviour category under the different conditions of adult

Fig. 29. Changes with age in the percentage* of chick attendance (Pair 1) spent on each category of behaviour under the different conditions of adult attendance (arcsin transformed).

WITH ADULTS PRESENT

●——● chick behaviour with male ON attending

▲——▲ chick behaviour with female ON attending

○— —○ chick behaviour with male SIDE attending

△----△ chick behaviour with female SIDE attending

unsuc beg = unsuccessful begging

suc beg = successful begging

|†| = chicks flying

limits = 1 x S.E.

(Each point is the mean of up to 8 consecutive daily measures)

$$* \ \text{\% of attendance} = \frac{\text{total instances of a behaviour by chicks}}{\text{total instances of all behaviours by chicks}} \times 100$$

(See text for details)

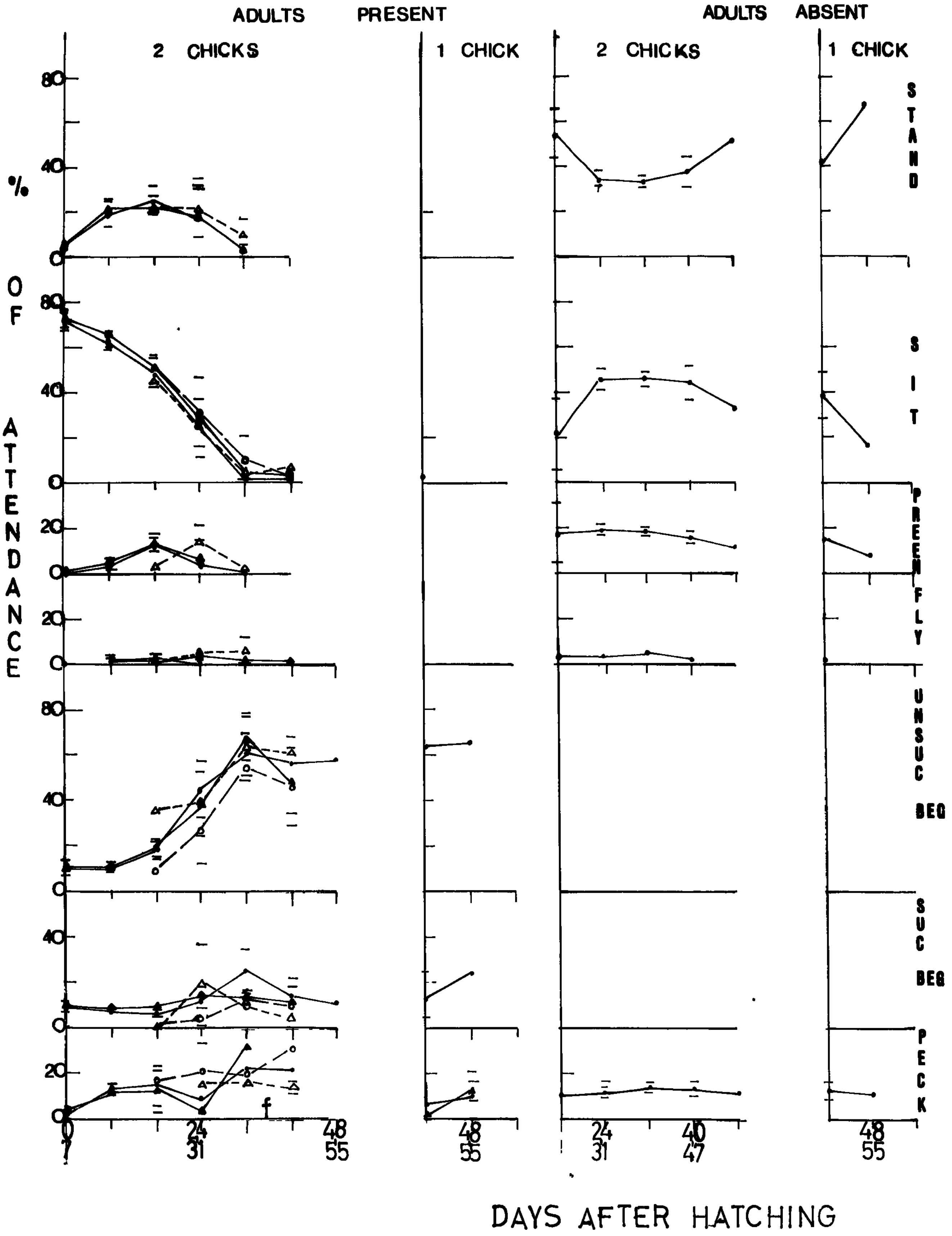

ADULTS PRESENT
ADULTS ABSENT
2 CHICKS
1 CHICK
2 CHICKS
1 CHICK
% OF ATTENDANCE
80
40
0
20
STAND
SIT
PREEN
FLY
UNSUC BEG
SUC BEG
PECK
0
7
24
31
48
55
48
55
24
31
40
47
48
55
DAYS AFTER HATCHING

Fig. 30. Changes with age in the percentage* of chick attendance (Pair 2) spent on each category of behaviour under the different conditions of adult attendance (arcsin transformed).

WITH ADULTS PRESENT

●——● chick behaviour with male ON attending

▲——▲ chick behaviour with female ON attending

○— —○ chick behaviour with male SIDE attending

△- - - -△ chick behaviour with female SIDE attending

unsuc beg = unsuccessful begging

suc beg = successful begging

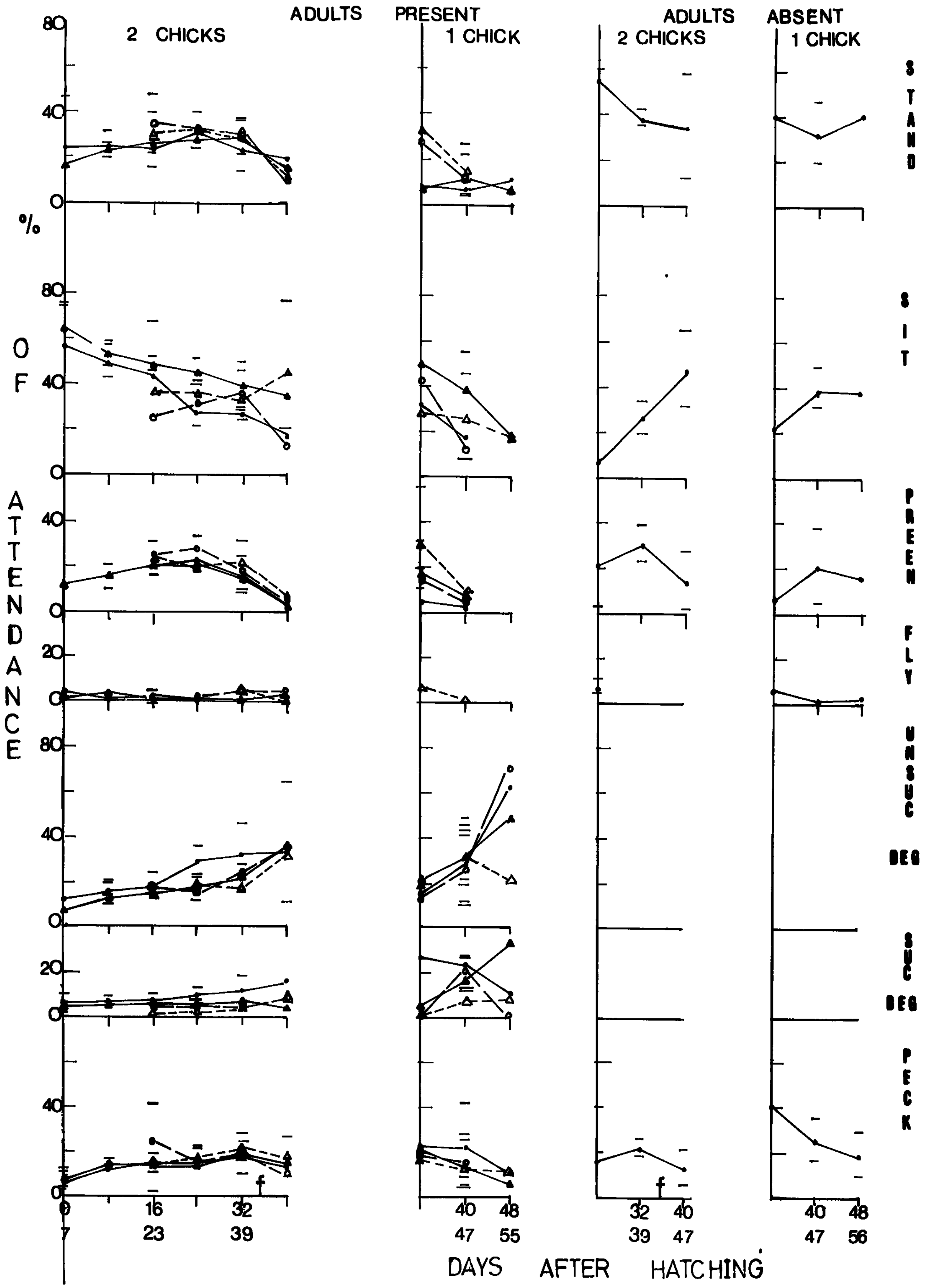
|f| = chicks flying

limits = 1 x S.E.

(Each point is the mean of up to 8 consecutive daily measures)

$$\text{* \% of attendance} = \frac{\text{total instances of a behaviour by chicks}}{\text{total instances of all behaviours by chicks}} \times 100$$

(See text for details)



ADULTS PRESENT
2 CHICKS
1 CHICK
ADULTS ABSENT
2 CHICKS
1 CHICK
% OF ATTENDANCE
STAND
SIT
PREEN
FLY
UNSUC BEG
SUC BEG
PECK
80
40
0
80
40
0
40
0
20
0
80
40
0
20
0
40
0
f
f
0
7
16
23
32
39
40
47
48
55
32
39
40
47
40
47
48
56
DAYS AFTER HATCHING

Fig. 31. Changes with age in the percentage* of chick attendance (Pair 3) spent on each category of behaviour under the different conditions of adult attendance (arcsin transformed).

WITH ADULTS PRESENT

●——● chick behaviour with male ON attending

▲——▲ chick behaviour with female ON attending

○— —○ chick behaviour with male SIDE attending

△– – –△ chick behaviour with female SIDE attending

unsuc beg = unsuccessful begging

suc beg = successful begging

|f| = chicks flying

limits = 1 x S.E.

(Each point is the mean of up to 8 consecutive daily measures)

$$* \ \text{\% of attendance} = \frac{\text{total instances of a behaviour by chicks}}{\text{total instances of all behaviours by chicks}} \times 100$$

(See text for details)

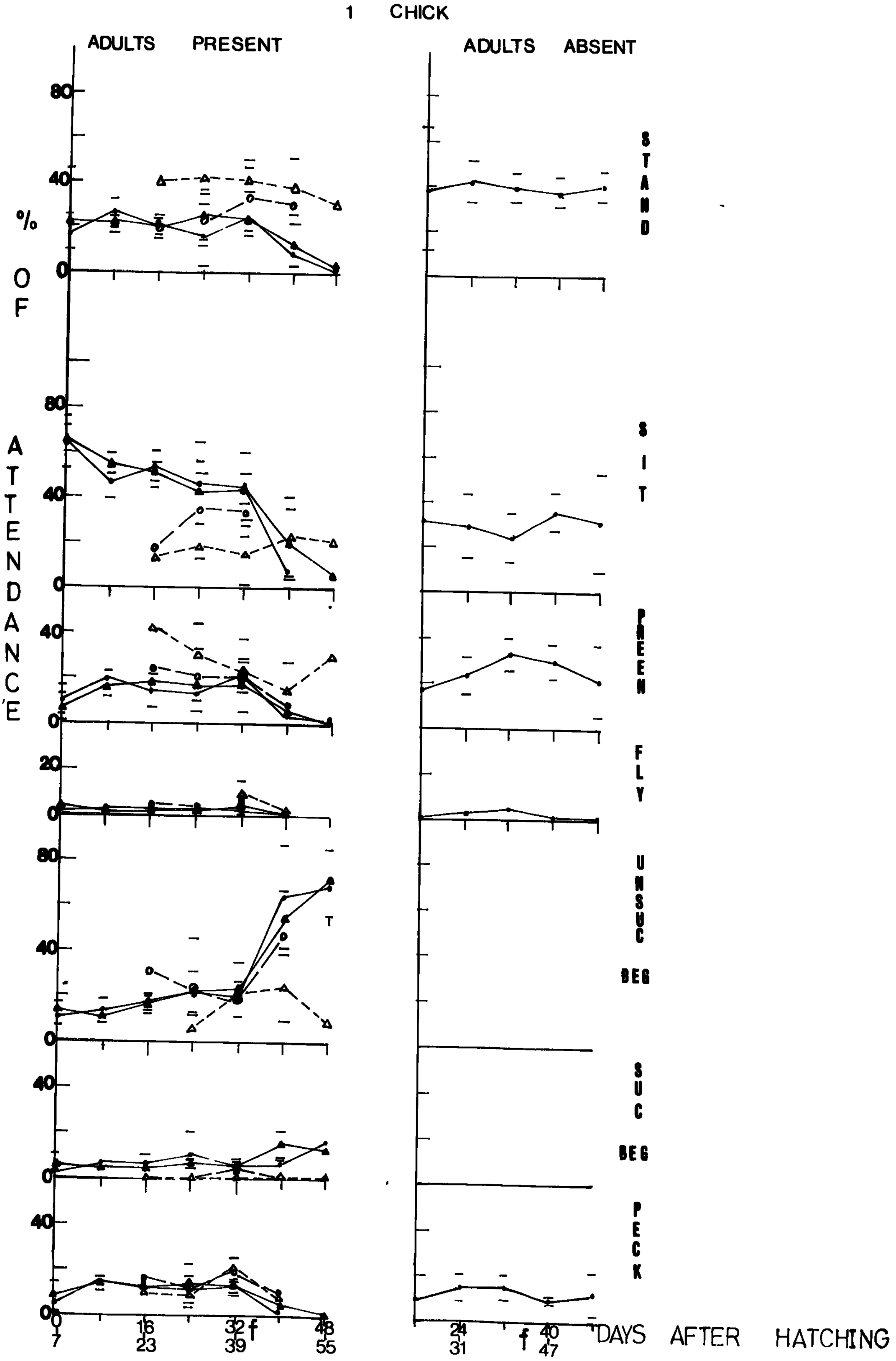

1 CHICK
ADULTS PRESENT
ADULTS ABSENT
% OF ATTENDANCE
80
40
0
STAND
80
40
0
SIT
40
0
PREEN
20
0
FLY
80
40
0
UNSUC BEG
40
0
SUC BEG
40
0
PECK
0 7
16 23
32 39
48 55
24 31
40 47
DAYS AFTER HATCHING

Fig. 32. Changes with age in the percentage* of chick attendance (Pair 4) spent on each category of behaviour under the different conditions of adult attendance (arcsin transformed).

WITH ADULTS PRESENT

●——● chick behaviour with male ON attending

▲——▲ chick behaviour with female ON attending

○——○ chick behaviour with male SIDE attending

△– – –△ chick behaviour with female SIDE attending

unsuc beg = unsuccessful begging

suc beg = successful begging

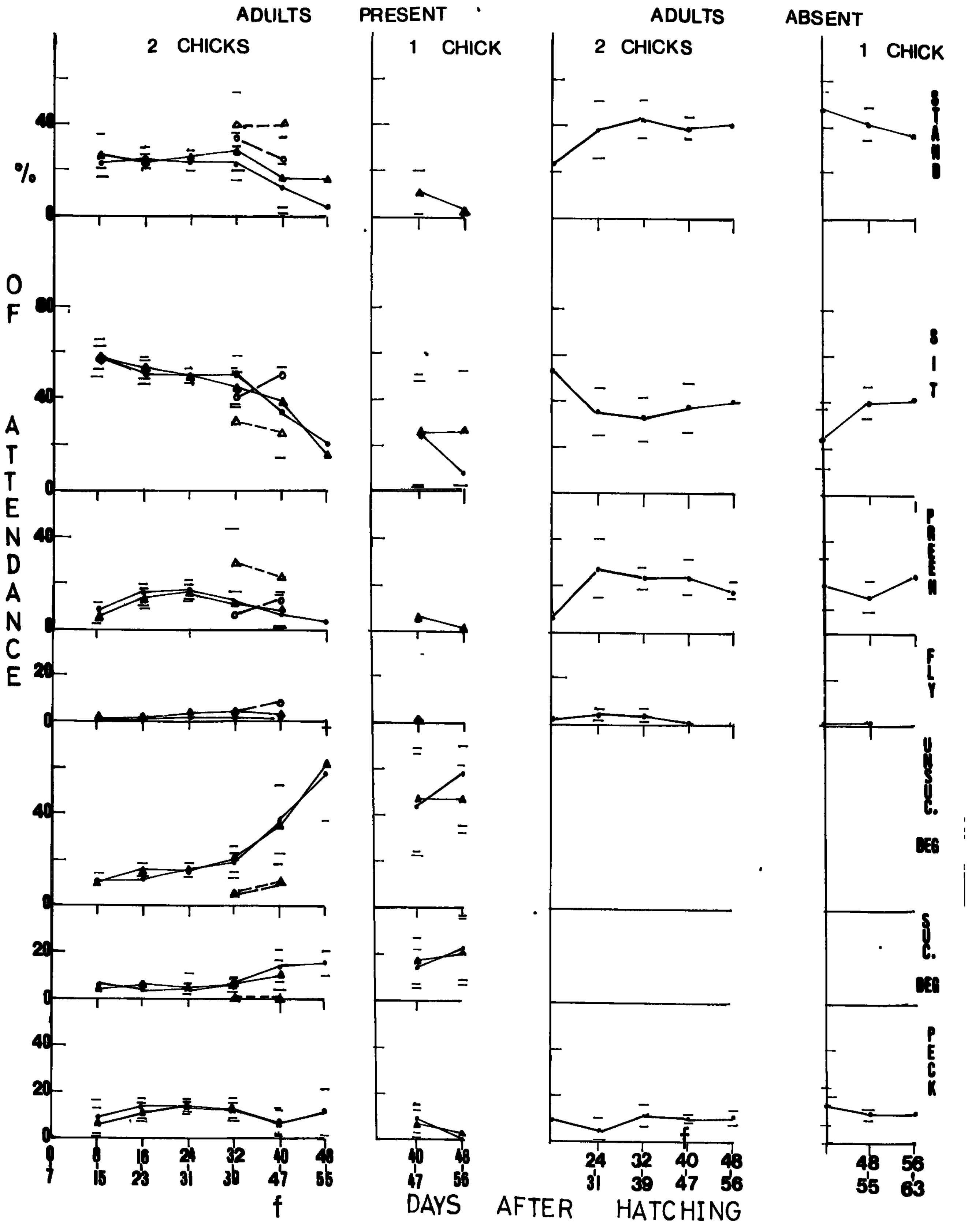
|f| = chicks flying

limits = 1 x S.E.

(Each point is the mean of up to 8 consecutive daily measures)

$$* \ \% \text{ of attendance} = \frac{\text{total instances of a behaviour by chicks}}{\text{total instances of all behaviours by chicks}} \times 100$$

(See text for details)


ADULTS PRESENT
ADULTS ABSENT
2 CHICKS
1 CHICK
2 CHICKS
1 CHICK
% OF ATTENDANCE
STAND
SIT
PREEN
FLY
UNSUC. BEG
SUC. BEG
PECK
40
0
80
40
0
40
0
20
0
40
0
20
0
40
20
0
0 7
8 15
16 23
24 31
32 39
40 47
48 55
f
40 47
48 56
24 31
32 39
40 47
48 56
f
48 55
56 63
DAYS AFTER HATCHING

attendance i.e. ON, SIDE and LEAVE. All graphs were timed from the date of hatching, for case of comparison, and each point on the graphs was the mean of 8 successive daily results. After the first flight of the chicks the information was split to show the effects of different chick numbers on their behaviour. Graphs for the behaviour with ~~control~~ each of the adults of a pair were included on the same axis for ease of comparison.

As formerly, the records for all four time-lapse pairs (Pairs 1 to 4) covered essentially the same period from soon after hatching until the abandonment of the nest site by the chicks.

These graphs (Figs. 29-32) showed that chicks carried out each of the behaviour categories throughout the whole chick-care period. By considering the graphs of these categories individually, as follows, the evidence for a total pattern of chick behaviour throuthout development could be evaluated. Comparisons could then be made between these patterns and those of adult attendance.

1 STAND

Like adult STANDING, this behaviour was recognised more by a lack of characteristic features than by their presence and represented non-specialised attendance at the nest site by the chicks. This was, however, a significant chick behaviour since chicks STANDING, with adults attending in the ON position, were not being brooded and were therefore potentially free to carry out the other behaviour categories, e.g. PREENING, FOOD BEGGING etc. Thus, particularly during the stage of early chick-care, when other behaviours were relatively infrequent, this behaviour was then a measure of the degree of independence of the chicks from the influence of the adults, (together with the attendant risk of accidental falling).

Figs. 29-32 show that the amounts of chicks' STANDING stayed at a fairly high constant level, from soon after hatching (within the first 8 days) until the late chick-care period, when levels fell. Maunder and Threlfall (1972) gave a galue of 6 days from hatching and McLannahan (1973) 5 days from hatching for the development of the ability of kittiwake chicks to stand firm. When adults were attending in the SIDE position there was a suggestion, from the graphs, that chicks STOOD more than when adults attended in the ON position. However, the highest levels of chicks' STANDING took place, in all broods, when adults were absent from the nest site, i.e. LEAVE attending. The presence of one or two chicks did not affect these differences.

2. SIT

This category included a mixture of two forms of behaviour that were distinguishable only with reference to the adults behaviour; chicks SAT when adults brooded them and chicks sometimes SAT when adults STOOD. The information in the previous chapter (Figs. 23 and 25-29) showed that adults brooded chicks mainly during the first 24 days after hatching so that after this time most SITTING by the chicks was of the second type, i.e. chicks resting in the nest.

Figs. 29-32 showed that this was the most commonly observed behaviour category. However, when adults attended in the ON position, there was an obvious decrease with the age of the chicks. Except, perhaps, for the chicks of Pair 1 (Fig. 29), the decrease in the amount of SITTING by chicks over the first 24 days after hatching (shown by the slope of the graphs in Figs. 30-32) was not sufficiently pronounced to indicate that chicks only SAT when adults brooded them. However, these same graphs indicated that at a later stage SITTING was a less common chick behaviour with adults SIDE attending (out of close contact with the brood) than when they were ON attending (inclose contact with the brood). Except for the chicks of Pair 1, the amounts of SITTING when adults were absent tended to remain fairly constant at a similar level to that seen during mid chick-care with adults SIDE attending neither of these differences were affected by chick number present. Thus, at least during the first 30 days after hatching the chicks of Pairs 2, 3 and 4 tended to spend relatively more of their time SITTING when adults ON attended than when adults SIDE or LEAVE attended. This difference was not due to adults brooding the chicks.

After the earliest stages of chick-care the amounts of SITTING represented a measure of the 'safety' of the brood as all other behaviour categories occurred with chicks standing up and so at greater risk of falling. McLannahan (1973) showed that over the first 30 days of life the amount of time spent by chicks in STANDING (i.e. not SITTING) increased from 0 to 45% of the available time. Figs. 30-32 (and the first 24 days of Fig. 29) showed similar results to these but was illustrated as a decrease in SITTING. McLannahan found that the chicks of cliff-nesting herring gulls behaved similarly whereas the increase in standing of ground nesting individuals of this species was more pronounced (up to 60% of the available time at 30 days). This indicated that the cliff nest habitat inhibited young chicks from STANDING. This author went on to assume that the relatively small amount of standing was an adaption to cliff dwelling. In support of this assumption she quoted an example of an adult being blown off a ledge by the wind when the 2 chicks remained safely sat in their nest. Interpreted in this way Figs. 30-32 indicate that, for at least the first 30 days, chicks tended to be safest (particularly as adults stood between the brood and the abyss) when the adults ON attended.

3 PREEN

The chicks hatched with a dense covering of grey down that was gradually replaced by feathers as the chicks aged. The time taken for the body and wings to become feathered, (although not the head where the process took much longer), was 17-18 days, (personal observation on 44 chicks). A full account of feather development is given in Maunder and Threlfall (1972). The waxy sheathing of the emerging feathers was removed by friction and PREENING and the new feathers were maintained by PREENING behaviour identical to that of the adults.

Figs. 29-32 showed that when adults attended in the ON position, PREENING behaviour by the chicks increased to a maximum over the first 24 days of life (during the period of feather growth), but thereafter tended to decrease. A similar situation was seen when adults attended in the SIDE position, but here there was a tendency for the amounts to be a little larger. The largest relative amounts of PREENING occurred when adults left the broods unattended, and these were maintained at consistantly high levels. The presence of one or two chicks did not affect these differences.

After the period of feather growth (during early chick care), the main function of PREENING behaviour by chicks would have been expected to be the same as in adults, i.e. regular maintainence of the feathers. Thus it would have been expected that the frequency of PREENING would remain at a constant level, irrespective of any changes in the pattern of attendance by either adults or siblings.

The only exception to this would be where other behaviours attained a greater priority when time was limited. Figs. 29-32 indicated that, during late chick-care, other behaviours became more predominant than PREENING when adults attended in the ON or SIDE position, but that these priorities were not present when adults were absent. The difference in priority of behaviours when ON attendance was rare probably accounted for the unusually small amounts of chicks SITTING in the brood of Pair 1 whose adults showed smaller amounts of ON attendance from a time early in chick-care.

4 FLY

Cullen, (1957), noted that incipient flying movements in kittiwake chicks were shown at about the same early stage as ground-nesters, i.e. within the first few days of life, but that the movements were less vigorous and that jumping into the air with wing-flapping was of rarer occurrence. The orientation of chicks during this behaviour was always towards the wall. The observations of McLannahan (1973) were basically in agreement with this but she maintained that kittiwake chicks did not jump into the air during this behaviour. She also proposed that kittiwakes differed from herring gulls in emitting a call during wing-flapping that ensured that the sibling remained still. Although a slight increase in wingflapping with age was demonstrated, even at 30 days this behaviour was only shown to occupy 0.9% of the available time.

In the present study, chicks carrying out this behaviour, called FLYING, were never observed to release the nest surface or to FLY when a sibling was FLYING. The eventual maiden flight of the chicks was seen to be much more of a hurdle in kittiwakes than in ground nesting species as the particular cliff-nest site had to be relocated and landed on in difficult wind conditions after this initial flight.

Figs. 29-32 showed that FLYING movements were very rare at the nest site, under all conditions of adult attendance and brood size, and only showed a very slight increase in frequency, just before the first flight. From this it would appear that flight in kittiwake chicks was likely to be a maturation rather than a learnt phenomen as the practice effects appeared to be negligible.

5 UNSUCCESSFUL AND SUCCESSFUL BEGGING

BEGGING was a clear example of motivated behaviour on the part of the chicks, as their response on a particular day to the relatively constant stimuli from the adults was highly variable. Sometimes the response was undetectable whilst at others it takes the form of a complex chain of behaviour, as shown in the previous diagram. The response of the parents to the chicks was also variable; after UNSUCCESSFUL BEGGING by the chicks the parents either orientated towards the chicks, where the SUCCESSFUL BEGGING stimulated the adults to regurgitate food or alternatively adults HEAD TURNED, which usually stopped the feeding cycle. The persistence of the chicks and the motivation of the adults probably dictated which of these responses was activated.

The early development of food begging in chicks is probably similar in most gull species. Hailman (1967), working with the laughing gull, reported that the description by Beer (see Beer, 1966a) of the earliest begging in the black-headed gull was very similar to his own observations of laughing gulls. (The description also agrees with my own observations of the kittiwake). "Stretching movements of the chick, like those made when chicks leave the shell, stimulate the adults to rise slightly and look down; this presents the chicks with the visual stimulus of the underside of the bill which the chick responds to by pecking". (Hailman, 1967 and Weidmann and Weidmann, 1958 showed that the stimuli present in this situation were highly likely to evoke pecking by the chicks). "This pecking stimulates the parent to regurgitate food and further pecking results in getting food to the mouth". Both Hailman and Beer observed that pecking was not a necessary condition for regurgitation as this was seen when chicks had not pecked. With experience, the accuracy and co-ordination of chick pecking improved.

At a later stage (6-7 days) when kittiwake chicks were strong enough to STAND, they developed a typical hunched posture when facing the parents and tossed their bills rhythmically while emitting a 'piping' call. Using the scheme in the earlier diagram of chick feeding behaviour, this was interpreted as primarily a development of (1) - the orientation of chicks towards adults, but with older chicks bouts of 'piping' tended to be interspersed with bouts of attempting to jab at the adults bill (3). This description is very similar to that given in Cullen and Ashmole (1963) of the begging in chicks of the cliff-nesting black noddy. Hailman (1967) also described a similar development in the ground-nesting laughing gull over the first few days of life. In this species, however, (in common with many ground-nesters, Cullen 1957) Hailman found that at about 5/7 days of age a larger pumping movement of the head develops which seems to serve a food begging function that replaces pecking. My own observations agreed with those of Cullen (1957) in that this movement was lacking in the kittiwake. Smith (1966) found that, in cliff-nesting individuals of glaucous and thayer's gull, head pumping was absent yet the chicks of ground-nesting glaucous gulls showed it as did the chicks of both ground and cliff nesting Iceland gulls. Another difference was that adult ground-nesting gulls gave a feeding call when arriving at the territory to attract chicks. McLannahan (1973) Cullen (1957) and my own observations showed no feeding call by adult kittiwakes. Smith (1966) and McLannahan (1973) report that the adults of cliff-nesting glaucous and thayer's gulls did not give a feeding call whereas cliff-nesting herring and iceland gulls did, but that of the ground-nesting individuals of these species only thayer's gulls did not give a feeding call.

To summarise this information, ground-nesting gulls tended to show a greater development of communication and differentiation of behaviour in the chick feeding situation, where distances were greater than is seen in cliff-nesting gulls. Only during the earliest stages of chick development ~~continued~~ could kittiwake adults be described as 'soliciting' begging by the chicks whereas typical ground-nesting gulls (due to their feeding call) could be described as soliciting begging throughout chick-care.

Coulson and White (1958b) and Maunder and Threlfall (1972) showed that kittiwake chicks reached a peak weight at about 28-29 days after hatching which then decreased. Tha latter study also showed that the size of the chicks' bill increased throughout the time chicks were present at the nest. These observations provided indirect evidence to support the conclusion that was arrived at from unquantified observation at the nest sites, that the vigour of chick

BEGGING tended to increase with age. The effect on an adult of a BEGGING chick of 10 days of age (40% of the adult weight) was unlikely to be similar to the effect of a 29 day old chick (96% of the adult weight) whose own bill had effectively doubled in length over this period (the information from previous references).

In the present study only quantitative measures of the frequency of the elements of BEGGING were made.

Begging by chicks could obviously only take place when adults attended the chicks either in the ON or SIDE position. Figs. 29-32 clearly showed that under either of these conditions of adult attendance the relationship between age and UNSUCCESSFUL BEGGING increased in an exponential way from an initial fairly low level during early chick-care to a high level during late chick-care with the greatest rate of increase during the latter period. Essentially similar curves were obtained when one or two chicks were present but there was an indication that the amount ~~intensity~~ of UNSUCCESSFUL BEGGING by chicks was less when adults attended in the SIDE position. This situation was not paralleled by the SUCCESSFUL BEGGING information where the increase in this behaviour with time could be seen to be very slight, although again less SUCCESSFUL BEGGING occurred with adults in the SIDE position.

A simple illustration of these trends is shown by a consideration of chick BEGGING when adults attend in the ON position. Two periods of chick development were selected from Figs. 29-32; one in early chick care (days 8-15) and one during the fledging stage (days 49-47). The measures of chick SUCCESSFUL and UNSUCCESSFUL BEGGING (see above) were obtained from the Figs. for each of the 8 time-lapse adults when ON attending at these two stages. The retransformed means of these measures were: 1.0 for SUCCESSFUL BEGGING and 4.7 for UNSUCCESSFUL BEGGING during early chick-care and correspondingly 4.0 and 60.4 during the fledging stage. Thus SUCCESSFUL BEGGING increased over this period by a factor of about 4 while UNSUCCESSFUL BEGGING increased by a factor of about 13. In addition whereas UNSUCCESSFUL BEGGING was about 4.7 times more frequent than SUCCESSFUL BEGGING during early chick-care this had risen to about 15 times more common during fledging.

When adults attended in the ON and SIDE position on the same day during the chick-care period, then it was possible to score which of these positions attracted the greatest relative number of SUCCESSFUL and UNSUCCESSFUL BEGGING elements by the chicks.

These results are presented in Table 34 which shows that the effects of the position of the attending adult on the intensity of BEGGING by the chicks was similar in all individual broods irrespective of where the nest site was or the sex of the adult attending. This Table also showed that there was a significant tendency, $(P < 0.01)$, for chicks to BEG at a higher intensity when adults attended in the ON position than whey they attended in the SIDE position and also that this tendency was significantly greater, $(P < 0.02)$, with SUCCESSFUL BEGGING than with UNSUCCESSFUL BEGGING.

Thus the general conclusions to be drawn from the Figs. 29-32 and Table 34 were that, particularly during late chick-care, the periods of attendance by the adults were dominated by the UNSUCCESSFUL BEGGING of the chicks yet the intensity of this form of begging was only very loosely connected with the intensity of SUCCESSFUL BEGGING, (and therefore feeding of the chicks). The position that adults occupied on the nest site had a significant effect on the intensity of chicks' BEGGING in that chicks tended to BEG

TABLE 34 EFFECT OF POSITION OF ADULTS ON THE INTENSITY OF BEGGING BY THE CHICKS (AS MEASURED BY RELATIVE NUMBER OF BEGGING ELEMENTS).

	UNSUCCESSFUL BEGGING			SUCCESSFUL BEGGING		
	No. of days when intensity highest with adults 'ON'	No. of days when intensity highest with adults 'SIDE'		No. of days when intensity highest with adults 'ON'	No. of days when intensity highest with adults 'SIDE'	
MALE						
Pair 1	12	4		14	2	
Pair 2	13	6	n.s	14	5	n.s
Pair 3	9	7		11	2	
TOTAL	34	17		39	9	
FEMALE						
Pair 1	6	5		8	2	
Pair 2	10	8	n.s	13	6	n.s
Pair 3	10	3		13	0	
TOTAL	26	16		34	8	

POOLED DATA

MALE	34	17	n.s	39	9	n.s
FEMALE	26	16		34	8	
TOTAL	60	33		73	17	
	$\chi^2 = 7.84$ (P < 0.01)			$\chi^2 = 34.84$ (P < 0.001)		

POOLED DATA

	No. of days when intensity highest with adults 'ON'	No. of days when intensity highest with adults 'SIDE'	
UNSUCCESSFUL BEGGING	60	33	$\chi^2 = 5.54$ (P < 0.02)
SUCCESSFUL BEGGING	73	17	

both SUCCESSFULLY and UNSUCCESSFULLY at a higher intensity with adults in the ON rather than SIDE position, the tendency being particularly marked in the former behaviour.

6 PECKING

Pecking contained elements of both types of begging but was directed towards various parts of the nest site rather than the bill of the adult. The parts of the nest environment that the chicks of Pair 2 directed their PECKING towards are given below (as measured by numbers of time-lapse frames).

Adults body									
LEG	RINGS	NECK	HEAD	BODY	SIBLING CHICK	NEST CUP	NEST SITE	TOTAL	
11	55	5	116	4	49	3166	286	3692	No.
0.3	1.5	0.1	3.1	0.1	1.3	85.8	7.8	100	%

The Table shows that all but a fraction of PECKING was directed towards the nest or nest site. Hailman (1967) and Beer (1966a) both observed that very young chicks will peck at various parts of the parent, sibling or nest environment, where no food reward was involved, but n~~ieht~~either study furnished any information on such pecking in older chicks. Belopolskii (1961) found a higher incidence of insect remains in the stomachs of kittiwake chicks than in adults and he maintained that these were obtained from the nest surface. Although insects were rarely seen on the nests at the North Shields colony 5 chick stomachs were examined (all about 25-30 days old) and none of these were found to contain any recognisable insect remains. Traces of material, clearly derived from the nest itself were found in 3 of these stomachs.

Figs. 29-32 show that PECKING increased in a short time from an initial low level, during the earliest chick care period, to a higher stable level that was maintained until late chick-care. At this time there was an indication that PECKING decreased when adults were present. However, for much of the breeding cycle the presence or absence of adults or brood mates did not appear to alter the frequency of this behaviour.

THE PATTERN OF CHICK BEHAVIOUR AT THE NEST SITE

Figs. 29-32 showed that chicks carried out 7 behaviours after hatching that could be recognised from the records of all four broods. These behaviours were initiated at, or soon after hatching so that the behaviour pattern of the developing chicks arose from changes in the frequencies rather than changes in the major types of behaviour utliized. Some behaviours showed fairly predictable changes in frequency throughout the chick-care period whereas others changed less predictably. With adults attending in the ON position the best examples of the former type of chick behaviour were chicks SITTING and UNSUCCESSFUL BEGGING. SITTING decreased in a regular way with the age of the chicks and UNSUCCESSFUL BEGGING increased exponentially over the same period. Less striking, but still regular changes in frequency occurred with FLYING and SUCCESSFUL BEGGING. The former behaviour was always the rarest one measured but did show a slight increase before the timing of the first flight. It appeared unrealistic, however, to explain the acquisition of the skills of flying by a learning process based on this amount of practice. It appeared more likely that flying in chicks was based on a maturation phenomenon. The frequency of SUCCESSFUL BEGGING increased slowly but at a fairly constant rate over the whole period in a way that was in obvious contrast with the changes in UNSUCCESSFUL BEGGING.

This difference indicated that the amounts of SUCCESSFUL BEGGING (and thus feeding) were not related in any simple way to the amounts of UNSUCCESSFUL BEGGING carried out.

The remaining behaviours of STANDING, PREENING and PECKING showed less regular changes in frequencies as they were all seen at maximum levels at other than the beginning or ending of the chick-care period. PREENING increased over the first 23 days of chick life, (during the time that the chicks grow their feathers), and thereafter showed a tendency to decrease in frequency. STANDING became more common over the very earliest period of chick-care but remained at a fairly high constant level until late chick-care when frequencies decreased. A rather similar pattern was followed by PECKING but this was a much less common behaviour. At no stage was there any indication that the pattern of chick behaviour was to any extent affected differently by the presence of either of the 2 adults of a pair.

When adults attended in the ON position, the changes in the pattern of chick behaviour with the age of the brood was from one dominated by chicks SITTING and STANDING, with small amounts of more active behaviour, to a pattern dominated by chicks both SUCCESSFULLY and UNSUCCESSFULLY BEGGING and PECKING.

The total pattern of chick behaviour was also similar to that described above when adults attended in the SIDE position, except that the relative importance of some behaviours changed. Chicks carried out less SITTING, UNSUCCESSFUL and SUCCESSFUL BEGGING and more STANDING, PREENING, FLYING AND PECKING than when adults attended in the ON position. Table 34 showed that the decrease in UNSUCCESSFUL BEGGING was relatively ~~more~~ less pronounced than that of SUCCESS BEGGING.

With no adults present chick behaviour was not only very stable, (there were no trends of changing frequencies of behaviour as in former cases) but also as neither UNSUCCESSFUL or SUCCESSFUL BEGGING could take place then the pattern of behaviour was simpler than formerly. Chicks were more frequently observed STANDING and PREENING and less frequently observed SITTING than when adults were present.

There was no indication from the Figures that during the fledging period single chicks behaved any differently from chicks with a peer present.

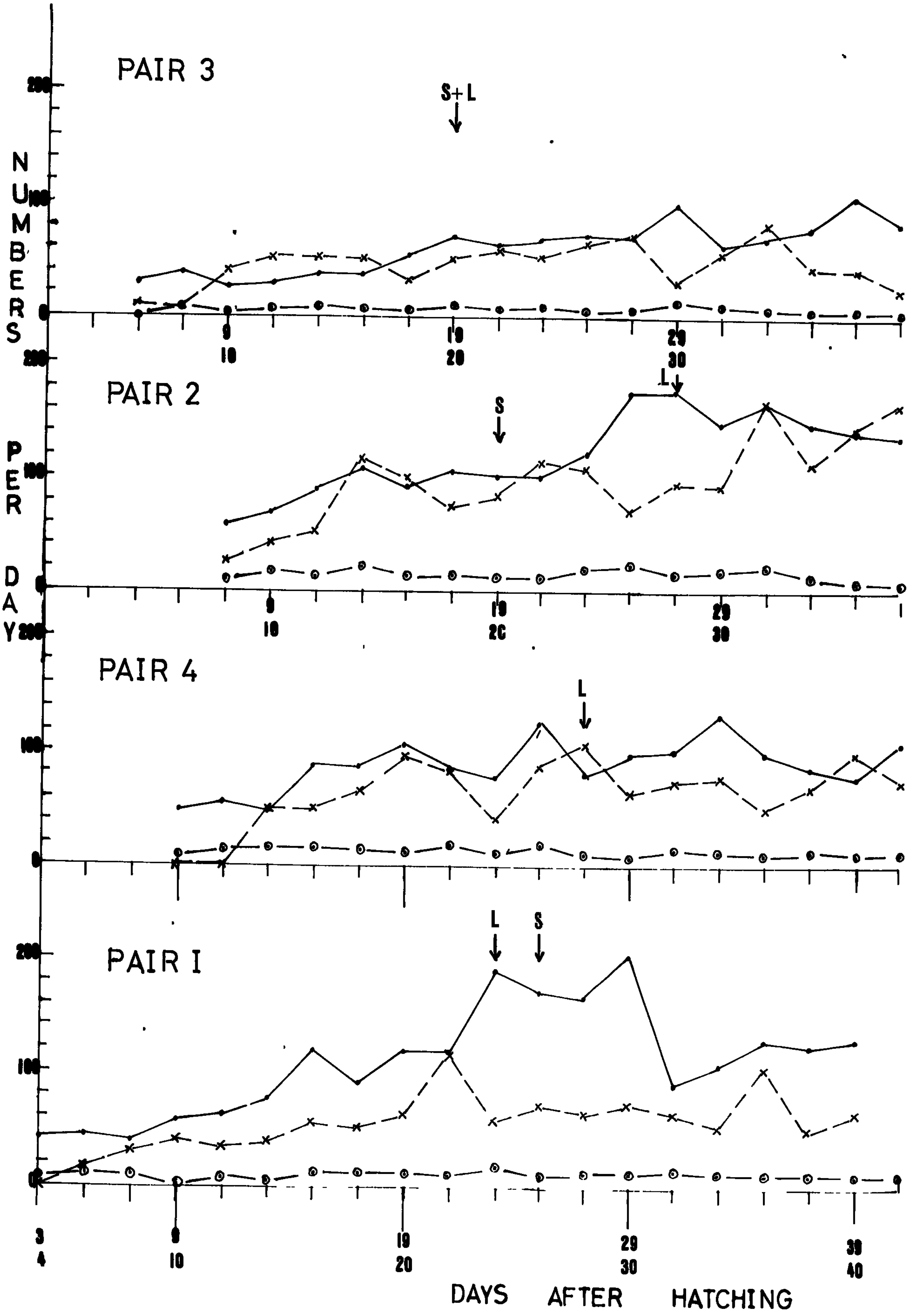
At least during the early stages of chick-care (up to day 30) the higher frequency of SITTING by chicks that were associated with the presence of the adult in the ON position must have added to the safety of the chicks on the dangerous nest site.

The most obvious difference between the behaviour of chicks alone and chicks with adults, particularly during late chick-care, was that chicks alone carried out no BEGGING and a very stable pattern of other behaviours and that chicks with adults carried out behaviour pattern dominated by BEGGING behaviour so that other categories of behaviour changed in frequency with age of the chicks. Chicks with adults present in the SIDE position showed behaviour patterns that were not so completely dominated by UNSUCCESSFUL and SUCCESSFUL BEGGING as those of chicks with adults in the ON position. Thus, the incidence of chicks' BEGGING was the most variable of chicks behaviours depending, more than any other, on the age of the chicks and the type of adult attendance. In contrast, the incidence of PECKING, which contained elements of BEGGING, did not vary greatly with the type of adult attendance. So as to illustrate this difference Fig. 33 shows the change with the age of the chicks up to the time of

Fig. 33. Changes in the total number of time-lapse frames per day spent on UNSUCCESSFUL BEGGING, SUCCESSFUL BEGGING and PECKING by the chicks of pairs 1,2,3 and 4 from hatching until their first flight.

●——● unsuccessful begging
⊙——⊙ successful begging
x----x pecking
↓S = adult SIDE attendance initiated
↓L = adults LEAVE attendance initiated

(Each point is the mean of 2 consecutive daily measures)


PAIR 3
S+L
PAIR 2
S
L
PAIR 4
L
PAIR I
L
S
NUMBERS PER DAY
200
100
0
3
4
9
10
19
20
29
30
39
40
DAYS AFTER HATCHING

of the first flight in the total daily amounts of these three categories of behaviour for the four broods. After the first flight this measure was confused by the attendance pattern of chicks. In each case the initiation of SIDE and LEAVE attendance was marked on the graphs.

Four major points emerged from these graphs:-

1 Daily amounts of SUCCESSFUL BEGGING remained remarkably stable throughout the chick-care period and were not depressed by changes in adult attendance patterns.

2 Daily amounts of PECKING increased steadily throughout the chick-care period and were unaffected by changes in adult attendance patterns.

3 UNSUCCESSFUL BEGGING occurred in two phases:-

(a) An initial early chick-care phase, when daily amounts increased with the age of the chicks.

(b) A late chick-care phase (after the initiation of SIDE and LEAVE attendance by the adults) when daily amounts either remained constant, (Pairs 3 and 4), or decreased, (Pairs 1 and 2).

4 Allowing for the fact that Pair 3 only raised a single chick brood, the inter-pair differences in the daily amounts of SUCCESSFUL BEGGING and PECKING were less than those of UNSUCCESSFUL BEGGING. Evidence from the study of adult attendance (Section 5) suggested that the patterns of attendance arose from the avoidance reactions of adults to interactions with the chicks. It is suggested that the function of adult attendance patterns was to control the amounts of UNSUCCESSFUL BEGGING, received by individual adults, in the following way.

1 The overall rate of UNSUCCESSFUL BEGGING at the nest site increased throughout the chick-care period with the age of the brood (Figs. 29-32).

This was reflected in an increase of the daily amounts of UNSUCCESSFUL BEGGING during early chick-care, Fig. 33, as the chicks got older.

2 If all attendance during chick-care had been in the ON position then it was assumed that this process would have continued so that both the rate at the nest site and thus the daily amount of UNSUCCESSFUL BEGGING would have increased with the age of the brood.

3 During mid and late-chick care, increasing amounts of adult attendance were spent either SIDE or LEAVE attending (Figs. 17, 18). Both of these forms of attendance reduced the overall rates of UNSUCCESSFUL BEGGING to the individual adult so that the major effect of this altered attendance was to decrease the daily amounts of this behaviour below that expected if attendance had remained in the ON position. This reduction was seen to result in fairly constant daily amounts of UNSUCCESSFUL BEGGING through this period (Fig. 33). This meant that the overall daily rates of UNSUCCESSFUL BEGGING received by adults, irrespective of attendance type, also remained constant (although daily rates at the nest sites increased as shown in (Figs 29-32).

4 It was not clear from the information available which function of UNSUCCESSFUL BEGGING was responsible for the reduction in adult ON attendance. Features such as vigour, short term rates or lengths of BEGGING bouts may all be important. Differences in adult attendance patterns, and thus the characteristic daily constant levels of UNSUCCESSFUL BEGGING for each pair, shown in Fig. 33, could have resulted from differences in some critical thresholds for receiving UNSUCCESSFUL BEGGING above which adults respond by altering the pattern of attendance.

The graphs of UNSUCCESSFUL BEGGING in Figs. 29-32 were in fact a measure of overall daily rates of BEGGING. Observations at the nest site showed that BEGGING actually occurred in bouts (as seen in the gannet, Nelson 1964, although here only bouts that included the equivalent of SUCCESSFUL BEGGING were measured). As the absolute amount of time available for chicks to BEG decreased with the decrease in ON attendance (as the chicks developed) so less and less of the time between bouts of BEGGING were included in these estimates. They then became more and more close to estimates of the short term rate of BEGGING during a BEGGING bout as the chicks developed. If adults were reacting to short term high rates of BEGGING then these graphs would be expected to reach a plateau of BEGGING rate above which they would never remain ON attending (the threshold mentioned above). Fig. 29 and 30 indicated that a plateau might have been reached in Pairs 1 and 3. In all cases the very high rates of UNSUCCESSFUL BEGGING seen towards the end of the period chicks were present,indicated that short term BEGGING (within a BEGGING bout), was probably the critical stimulus for adults to change their attendance. (It seemed highly likely that vigour of BEGGING, although not measured, would also be extremely important).

As SIDE attendance was less effective than LEAVE attendance at reducing rates of chicks UNSUCCESSFUL BEGGING (Table 34) then it was to be expected from the model above that the former behaviour would have been used earlier in chick care than the latter (chicks were less mobile early on and the rates of UNSUCCESSFUL BEGGING at the nest were likely to be closest to the critical threshold below which no action was taken by adults).

In cases where adults could freely SIDE attend at the nest site without interference from adjacent pairs this strategy was adopted, see Section 4.

That adults increasingly avoided UNSUCCESSFUL BEGGING by the chicks as they developed (as stated in the model) was indicated in Figs. 25-27 where in the six records where the behaviour was measured, HEAD TURNING by the adults increased with the age of the chicks.

The analyses carried out so far raise an important question: why should the daily rates of UNSUCCESSFUL BEGGING by chicks at the nest site increase throughout the chick-care period, as assumed in the model?

This problem was particularly important as the evidence above indicated that the greater the rate of UNSUCCESSFUL BEGGING at the nest site, the greater the reduction of attendance by adults in the ON position.

As stated earlier, UNSUCCESSFUL BEGGING was concerned with feeding and was an essential prelude to SUCCESSFUL BEGGING, thus the simplest explanation for this increase was that it functioned to increase the amount of SUCCESSFUL BEGGING and thus feeding for the growing brood. Several observations cast doubt on this hypothesis.

1 Figs. 29-33 showed an obvious lack of correlation between the amounts of the two forms of BEGGING so that they appeared not to be related in any simple way (also see following discussion).

2 As the increased amounts of UNSUCCESSFUL BEGGING by the chicks during late chick-care appeared to encourage adults to either attend in the SIDE position or LEAVE the nest site so, in order to increase

feeding of the chicks, these attendance types would have been expected to increase the amount of food reaching the chicks. Attendance in the SIDE position obviously did not increase feeding and adults observed LEAVE attending were commonly observed 'loafing' in the club area not away from the colony fishing (see Section 6).

3 When the nest site was temporarily abandoned by the chicks during the fledging period, when food demands were high, then evidence from Section 6 showed that adult attendance at the nest site increased, indicating the inhibiting effect of the presence of chicks rather than any stress to provide food.

Pearson (1968) in agreement with the results of Coulson and White (1958b) found that there was no difference in the growth rates of 1 or 2 chick broods of kittiwakes whether they were reared early or late in the season. This indicated that kittiwakes found little problem in supplying chicks with sufficient food (except perhaps in inexperienced pairs whose chicks were shown by Coulson and White (1958a) to suffer reduced growth rates compared with those of experienced pairs).

An interesting point concerning growth in kittiwakes, noted by Coulson and White (1958b) and Maunder and Threlfall (1972) was that chicks lose weight before fledging. The fact that they reach a maximum weight and then decrease (as mentioned earlier) implies that the parents have the capacity to provide sufficient food to maintain this weight in their brood. Thus either chicks require excess body tissue some time prior to final abandonment of the nest for some particular developmental function or it may be that the behaviour of the chick during BEGGING tends to inhibit the adult from maintaining the former high rates of feeding by 'driving' it from the nest ledge during the actual feeding process. A similar decrease in weight prior to fledging is clearly shown in the gannet and many other sulids as shown by Nelson (1970), so that this phenomenon is not restricted to kittiwakes.

It appears safe to assume that there is a strong selective pressure for small chicks to BEG lustily so that they might maintain a growth rate conducive to survival. A problem appears when chicks reach a similar size to their parents, when strong BEGGING may well have the effect of threat on adults. If this were so, then to be perfectly adapted chicks would be expected to BEG strongly during early and mix chick care and then to decrease the strength of BEGGING when they had reached their maximum body weight. This implies the loss of a facet of their behaviour that had been strongly reinforced during the whole of their early experience. Another answer to this problem would be that there is selection in favour of adults capable of withstanding the attention of the chicks (see Section 4).

If an adult left the site after intense UNSUCCESSFUL BEGGING but before SUCCESSFUL BEGGING could take place then when it returned the chick would still have to carry out UNSUCCESSFUL BEGGING before it could feed (i.e. SUCCESSRULLY BEG). By repeating the behaviour the chicks may well reduce its intensity (drive reduction). The effect of this process would be to make the apparent overall rate of UNSUCCESSFUL BEGGING at the nest site increase in a way that was not simply related to the increase in SUCCESSFUL BEGGING, as in Figs. 29-32. As adults had obtained the food but could not transfer it to the chicks, then there would be no need for them to obtain more food when SINGLE SIDE or LEAVE attending.

Another hypothesis was that the increase in UNSUCCESSFUL BEGGING behaviour was a developmental phenomenon that was independent of food reward and was important in the development of the co-ordinated eye and bill movements necessary to a predator of quick-moving prey, particularly one reared in an environment starved of stimuli, (unlike ground-nesting gulls, that lived in a stimulus rich environment). This hypothesis supposed that the excess UNSUCCESSFUL BEGGING was similar to PECKING in function and contained similar elements but were directed at other aspects of the nest environment. PECKING was never rewarded by food yet Fig. 33 indicated that the daily amounts increased as the chicks developed. Although experiments were not quantified, observations on 9 hand-reared kittiwakes showed that they would frequently peck at any contrasting mark on the white cage walls. Also observations on 30 large free-living chicks which were offered a variety of coloured pencils, or even a finger, through the back of the window-ledge nest site, showed that they would PECK strongly at all these objects.

If PECKING was so readily elicited by these diverse stimuli then it seemed reasonable to suppose that the adults bill would prove an even more powerful stimulus that would produce behaviour indistinguishable from UNSUCCESSFUL BEGGING, when adults attended in the ON position. Earlier it had been shown that cliff-nesting species of gulls tended to exhibit BEGGING behaviour that was less well differentiated than in ground nesting gulls hence the difficulty in identification. One problem remains. If generalised pecking (both PECKING and some UNSUCCESSFUL BEGGING) were taking place at the same time during adult ON attendance then it might reasonably be expected that when adults ~~LEAVE attended~~ left the site, the rates and amounts of PECKING would become greater. Figs. 29-33 do not show such an increase.

DISCUSSION

This study has shown that young chicks were brooded by adults for much of the day but as chick co-ordination improved and their size increased so their behaviour became more active with increased amounts of time spent on PREENING, PECKING and UNSUCCESSFUL BEGGING.

Adult attendance altered during mid to late chick-care and the chick behaviour patterns progressively changed so that UNSUCCESSFUL BEGGING dominated the attendance of adults in the ON position with a corresponding reduction in all other behaviours except SUCCESSFUL BEGGING. When adults attended in the SIDE position these changes tended to be less extreme and when adults left the nest sites unattended, patterns of chick behaviour remained more stable and simpler than formerly as chicks could not BEG. Chicks were not affected either by the individual identity of the adult of the pair which attended them or whether they were singletons or one of a pair.

The only chick behaviours that directly impinged on the adults were UNSUCCESSFUL and SUCCESSFUL BEGGING. These were the only ones that decreased when adults changed their attendance patterns. After initiation of SIDE and LEAVE attendance the amounts of attendance in the ON position decreased steadily at a time when rates of UNSUCCESSFUL BEGGING at the nest site increased rapidly; these two were assumed to be connected.

It was suggested that individual adult attendance patterns arose from situations where individual thresholds for rates of receiving UNSUCCESSFUL BEGGING (probably over short time periods) were being exceeded. This may have caused the adults to alter their attendance in such a way that the daily rates of receiving UNSUCCESSFUL BEGGING remained fairly constant. In the previous section the similarity between chick BEGGING and adult THREAT had been noted. Different pairs of adults were assumed to show different thresholds and thus different attendance patterns.

As, throughout the chick care period:-

(1) the amounts of UNSUCCESSFUL BEGGING did not appear to be associated in any simple way to the amounts of SUCCESSFUL BEGGING, (this did not decrease when adults attendance changed),

and (2), the changed form of attendance stimulated by this UNSUCCESSFUL BEGGING DID NOT INCREASE the amount of food reaching the chicks, but served only to remove the adults from the close proximity of the chicks.

So it was reasoned that excess UNSUCCESSFUL BEGGING was not concerned directly with increased food demands of the growing chicks.

The possibility that the over-reaction of the full grown chicks to the presence of the adults on the ledge could actually be inhiniting the transfer of available food to them was briefly considered in conjunction with the observation that chicks reached a peak of weight at 28-29 days yet finally abandoned the nest at about 52 days.

An alternative hypothesis was that, like PECKING behaviour that increased throughout chick care and was never food rewarded, chicks pecked increasingly at the powerful stimulus of the adults bill while engaged in a behaviour, indistinguishable from UNSUCCESSFUL BEGGING, that was important to the development of the co-ordinated eye and bill movements so necessary to a predator of a fast moving prey.

Unlike the large and varied environment of the chicks of ground-nesting gulls, kittiwake chicks developed in a cramped environment starved of stimuli where adults attending in the ON position provided a mobile and dominant feature ideally positioned for the attention of the chicks.

Hailman (1967) proposed a simple scheme to describe the dynamics of PECKING in gull chicks. Put simply, this model predicted that as a chick becomes hungry so it increases its rate of pecking at the adults bill which induces the adult to regurgitate food, which the chick then eats. When the chick is full, it then stops PECKING and the adult reingests any food remaining. This scheme depends on a hungry chick signalling its food 'needs' by increased PECKING. Weidmann and Weidmann (1958) reported that the responsiveness to stimuli associated with the adults bill decreases when black-headed gull chicks are fed and gradually recovers with time. Hailmann (1967) claimed to have demonstrated that PECKING rate increased with the time of food deprivation. Of his four groups of chicks three showed an absolute increase in PECKING rate after 2 hours of food deprevation, although only one of these was significant (not the control group) and the other group showed an absolute decrease in PECKING rate. Evans (1970b) showed in the black-billed gull that the length of food deprivation enhanced the approach of chicks to the feeding call. Of particular interest in understanding the problem of demonstrating increased hunger by increased PECKING rates was the work of Hogan (1972) who worked with chicks of the Burmese red jungle fowl (*Gallus gallus spadiceus*). He showed that over the first 8 days of life, chicks that were not deprived of food increased their pecking rates to food in a similar, although somewhat reduced way to the large increases seen in those that had been deprived of food for 5 hours. When the same two groups were tested on sand somewhat lower increases were recorded with a similar difference between the deprived and non-deprived group. When the chicks were tested in empty cages only a very slight increase in pecking rate was recorded with no difference between the 2 groups. When chicks were weighed after the experiments only deprived chicks tested on food were seen to have ingested the stimulus object. Although these increasing pecking rates were only recorded over the first 8 days of life the study did indicate that, under certain circumstances, pecking rates of fowl chicks were only slightly affected by their state of hunger. Further, it showed that the stimulus object itself rather than its nutritional 'feedback' could be an important determinant of pecking rates as pecking was only poorly correlated with ingestion. Hogan concluded that after hatching, pecking is largely controlled by novel releasing stimuli and pecking drive and that these factors probably remain effective throughout life.

This work and the present study indicate that simplistic models of chick pecking are inadequate to explain the observed results, particularly when chicks other than very young and inexperienced ones are considered.

DISCUSSION

Nelson (1970) stressed that "behaviour is the mechanism by which adaptions to the total environment are forged and maintained". Recently the study of the ways in which selection pressures give survival value to major ecological features, like colonial breeding, (which in themselves select for certain types of behaviour, as a reciprocal relationship) has provided an evolutionary approach to ecology and behaviour.

Several recent investigations of single seabird species have demonstrated the intricacy of some interactions between behaviour and ecology e.g. kittiwake. (Coulson and White 1958a,b, 1960, 1961 and Coulson.1966, 1968, 1971, and 1972 and the adelie penguin (*Pygoscelis adelias*) Penney, 1968, Penney and Lowry, 1967, Sladen 1953, 1958, Sladen, LeResche and Wood, 1968, Tailor, 1962, Ainley and Schlatter, 1972 and LeResche and Sladen, 1970. Only one family of seabirds however, the Sulidae, have ever been extensively studied from this point of view. For this group of birds Nelson (complete references in Nelson 1970) has provided detailed descriptions of all but two members of the family stressing the relationships between behaviour, habitat and population dynamics and emphasizing particularly their coloniality as a central theme. In all of these studies, attempts are made to show mechanisms *and* functions of behaviour traits and this has also been the aim of the present work. Two main methods have been used to study behaviour/ecology interaction in the field: (1) the experimental approach, pioneered by Tinbergen (1951) - see Tinbergen (1953) Tinbergen et al (1961) Hailman (1967) Weidman (1961) Weidman (1956) and Beer (1961, 1966a) for examples and (2) the observational approach used in the long-term studies, cited above and in the present study. This second technique depends on long and detailed observations over many consecutive breeding seasons of individually colour-ringed individuals of known age and breeding history.

The second method suffers from many difficulties inherent in the types of problems studied. Many of these arise directly from an inability to manipulate a free-living population of birds experimentally. Some of the most important problems are given below.

(a) Seabirds spend the majority of their time in areas scarcely open to observation, i.e. at sea, and thus virtually all behaviour studied is breeding behaviour.

(b) It is not possible to control immigration, emigration or mortality at a colony.

(c) Studied are necessarily long-term as seabirds tend to be long lived animals and age and experience have been shown considerably to affect seabird behaviour, (Coulson 1972, LeResche and Sladen, 1970, Nelson, 1966a).

(d) It is unsafe to assume homogeneity of performance without careful checking of representative samples of the whole population, (Coulson, 1971).

(e) Many behaviours are exceedingly complex and inter-related with many others e.g. the pair-bond, (Coulson, 1972).

Due to the lack of possible experimentation (although the work of Coulson et al 1968, and Coulson, 1971 are exceptions), hypotheses must often be derived directly from the data and then tested with the same data. This is unsatisfactory as it is often very difficult to carry out observations that can be used to verify or revise that hypothesis. For example it is impossible to test if pairs of adults that are unable to lay or incubate eggs can successfully rear chicks, or to discover whether pairs of adults that are not allowed to carry out mutual courtship feeding can form a pair-bond. However, suppose a population is studied which shows differences in behaviour from another population, presumably related phyletically. This in itself is not a valid demonstration that the characters are under selective pressures due to observed environmental differences between the populations. Any correlation can however function as a prediction of what may happen in another population with the same or similar environment to either of the populations already known. The third population can only be used to test the hypothesis (i.e. causal relationships between environment and behaviour) if its characters were unknown before the conception of the hypothesis.

Often the best that can be achieved by an individual study is to illustrate a collection of correlations that may then be interpreted within the restraints of natural selection and keeping the results of related studies in mind. As Nelson (1970) commented "this approach requires imagination and the only inviolable rule should be to ensure that the reader is easily able to distinguish fact from interpretation."

Although the measurement of behaviour by automatic methods in the laboratory has become well established practice, relatively few successful attempts have been made to utilize these methods in the field. An exception was reported by Royama (1959, 1966a) where all the food items brought to the nest box of a number of great tits (Parus major) were automatically photographed. As already mentioned, Coulson (1972) utilized an automatic method of recording the attendance of breeding kittiwakes at the nest site by a radio-active tagging technique. As far as I know, this present study represents the only successful attempt to measure quantitative changes in adult and chick behaviour at a colony of breeding seabirds by time-lapse photographic methods.

Although some of the difficulties of time-lapse techniques have already been discussed in Section 1, other problems become apparent from the preceeding Sections and should therefore be mentioned. Constraints dictated by the cost of cine-film meant that events could only be filmed at a single time-lapse interval. Although specific problems like the measurement of the structure and duration of BEGGING bouts required more ideally to be investigated at short time-lapse intervals whereas the measurement of attendance stints only required a relatively long time-lapse interval, all measurements were taken from the same film. The choice of time-lapse interval, therefore, was often not directly related to specific problems but represented a compromise. This difficulty had to be weighed against the advantages of the method. One of these was the permanent nature of the record that recorded all of the events in the visual mode whether or not their recording was the intention of the exercise at the time of filming. This is particularly important in the present type of study where repeat observations of events necessary to test hypotheses at best can occur at 1 year intervals or at worst can never be repeated. Death of a bird (or its mate), egg robbing by small boys, or merely the effects of increased breeding experience of a bird from year to year, can all make a particular observation during a particular season unique.

Another obvious advantage of this type of information is that a large amount of data is generated with relatively little field labour so that other types of observations may be carried out at the same time e.g. spot observations of the other breeding pairs in the colony and of the club area. Filming at inconvenient times (sunrise is at 4.30 a.m. during July) and over greater periods than could be possible for a single observer means that accurate measurement of fledging behaviour (see Coulson 1958b) could easily be achieved. The measurement of behaviour from time-lapse film is, however, a very time consuming business. The filmed records of the 4 time-lapse pairs that form the basis of this study represented about 2,750 feet (about half a mile) of film that contained over 109,000 individual frames to be analysed.

Not only filming, but all observations at the colony were made more simple by the convenient habit of the birds of nesting on the window ledges of a warehouse. This allowed swift and detailed observations to be made at very close range (from behind the nest sites where the chicks were most easily observed - see Section 2) without disturbing the birds. Nelson (1966a) suggested that human interference was a major factor accounting for egg loss in gannets as the parents atypically left the nest site allowing predatory gulls to take the unprotected eggs. Although there were no predators of kittiwake eggs at North Shields, either chilling of the eggs or accidental spillage could have been a major problem if disturbances had been common. Both Coulson (1958b) and Nelson (1964) note that interference, particularly close to the time when chicks reach their maximum weight, can cause chicks to abandon their nest site prematurely. Because of this practical difficulty much less is known about the final third of the growth process of chicks than of the first two-thirds. At no stage in the present study was the fledging behaviour of chicks affected by observer activity.

Attention is finally drawn to the special features arising from the study of a few pairs in great detail rather than many pairs at a more superficial level. In the present study two criteria were used to choose pairs for filming. These were: (1) that they would be likely to succeed in rearing young and (2) that the nest site could be conveniently situated to an electricity power point and not be cluttered with the contents of the warehouse. In no way did these criteria pre-empt the hypotheses that were to be tested and there was no reason to expect a priori that their behaviour could be any more atypical than any of the other successful pairs. One of the strengths of the study was that an idea would be gained of which ~~the~~ features of kittiwake breeding behaviour showed the greatest variation as it was reasoned that these were just the areas most likely to indicate where pair-bonds and differences in quality operated (see Coulson 1968, 1972). Spot observations (Coulson 1958a and the present study) give an 'average' picture of equally shared attendance by the adults of a pair during breeding while time-lapse techniques reveal that one adult may carry out 1.8 times the amount of the other adult's daylight attendance (Information for Pair 3 during the Main breeding stage, from Table II).

Except for the study by Coulson and White (1958a) with additional observations by Paludan (1955) Cullen (1957) Maunder and Threlfall (1972) and McLannahan (1973), no overall description of the pattern of the quantitative changes in adult behaviour at the nest site through the breeding season exists in the literature. This study goes some way to remedy this deficiency (that also is found for most other species of "well-observed" seabirds although Beer's investigations of black-headed gulls (Beer, 1961,1962,1963a,1963b,1966a) is a noteworthy exception.

Present study showed that for successful breeding pairs of kittiwake, adult behaviour at the nest site could be described in three ways; by the type of attendance, by the type of behaviour category or the type of orientation relative to the precipice. Each of these measures showed a pattern through the breeding cycle such that periods of stability followed one another by changing more or less abruptly at certain points. These periods of stability (as separate stages as shown below) could be related to the changed stimulus environment of the nest site.

(1) Stages of attendance

Pre-breeding, Incubation with Early chick-care, Late chick-care, Post chicks

(2) Stages of behaviour

Pre-breeding, Incubation, Very early chick-care, chick-care and fledging, post chicks.

(3) Stages of orientation

Pre-breeding, Incubation, very early chick-care, chick-care and fledging, post chicks.

Many of the changes in adult behaviour tended not to be abrupt but rather some of the behaviour patterns of one stage tended to change in frequency of occurrence, over short periods, to levels typical of the nest stage e.g. standing and sitting (Beer, 1963a, 1966a). Other categories of behaviour, however, appeared to be restricted to one stage only e.g. copulation and squatting. The same type of graded change was seen in adult facing orientation (except at hatching of the chicks) and also in attendance between all stages. Perhaps the most abrupt change in attendance was at egg laying, when there was a particularly marked decrease in attendance of both birds together.

The similarity in the timing of these changes suggested that there was an association between the three measures. Pre-breeding was essentially a period when the nest site was guarded, with behaviour directed both towards the outside of the nest site (advertisement in choking) and towards the inside between the members of the pair (copulation, begging, courtship feeding and nest building). Incubation was accompanied by a change in emphasis, such that the requirements of the eggs seemed to be the dominant and constant influence with little or no indication that interaction was occurring with either pair or colony outside the nest site. At hatching the behaviour and orientation of adults radically altered so that the weak and uncoordinated but mobile, chicks received the greatest degree of protection both from chilling and the danger of falling. This degree of protection decreased with the age of the brood due to changes in the facing orientation of the adults, and in their behaviour.

At some stage during chick-care adults attended to one side of the nest structure (if there was room) and/or left the site unattended (males initiating this before females). Increasing avoidance of interaction with chicks was indicated during this period by the direction of facing, location of the adult relative to the chicks (see above) and behaviour of adults. However, during their reduced contact adults tended to orientate more obviously towards the brood, possibly for safety during feeding.

After the first flight the site became progressively devoid of chicks and under this condition only, both single and occasionally pair adult attendance increased. The avoidance of chicks continued to increase but this was influenced by the chick number present. SIDE attendance was less frequent when the freely mobile flighted chicks could interact with adults away from the nest structure. The attendance during the post chick stage consisted of a brief period when the orientation and behaviour (individually and together) were again directed outside of the nest site, reminiscent of a less complete version of Pre-breeding.

When adults were absent from their sites, non-breeding strangers landed on them, irrespective of the resident chicks' presence or absence. Their visits tended to be short. Adults away from the nest ledge did not leave the colony but remained in the club area and periodically visited the site when strangers would be removed.

After Cullen's (1957) classic study of the cliff-nesting adaptations of the kittiwake (followed by McLannahan, 1973) several authors have demonstrated similar adaptions in other cliff-nesting species; Bateson and Plowright (1959) in the ivory gull, Cullen and Ashmole (1963) in the black noddy, Smith (1966) in cliff-nesting individuals of thayer's, iceland and glaucous gulls, Hailman (1965) Snow and Snow (1967) and Nelson (1968a) in the swallow-tailed gull and Nelson (1968b) in the gannet. All of these authors have stressed the relaxation of predator pressure as a primary advantage of the habit (only Hailman, 1965, suggested that the nocturnal fishing in swallow-tailed gulls was developed to allow adults to guard chicks from aerial predators during daylight).

Cullen (1957) stressed that there was intense competition in kittiwakes for the limited numbers of nest sites. This required them to guard the sites vigilantly before breeding began. Coulson (1968), However, pointed out that competition was most pronounced for certain sites in the colony only: those that had been occupied earliest in the history of the colony. A somewhat similar situation was found in gannets, where sites in those areas with the highest nest density were keenly sought after when equally 'suitable' areas (with similar terrain) were ignored (Nelson, 1966a). Although it is not known if the differences in breeding success and male mortality found between the central and edge areas of kittiwake colonies is under genetic control or socially induced (Coulson, 1971), competition for sites segregates birds in this way. In gannets, Nelson (1966a) thought that the 'social stimulation' of high breeding density induced synchronous breeding by providing an accurate proximate factor (Lack, 1966) for the timing of breeding so that the chicks left the sites at the most advantageous time. In most of the studies above the authors have stressed the large amount of nest guarding before egg laying. Typically this is not seen in ground-nesting gulls e.g. the black-headed gull (Moynihan, 1955, Cullen, 1957). This difference between cliff and ground-nesters is particularly well shown in those species which nest in both habitats (Smith, 1966, and McLannahan 1973). This difference is particularly interesting as it might be expected that in ground-nesting gulls (where the relative importance of ground predators was more important at a later stage) there would be strong advantage in pairs defending and guarding particular territories in the middle of the colony against usurpers. The difference in size between cliff ledges and ground territories may go some way to explain the differences.

Small territory size in kittiwake colonies ensures intense social interactions as there is no leeway for retreat except by leaving the ledge. This means that kittiwakes tend to be very aggressive towards conspecifics at the site and show specialised fighting methods and appeasement postures (Cullen, 1957). This in itself brings problems, as for successful breeding the mate must be tolerated on the cramped ledge. At a later stage recognition must be quick and accurate as disputes or energetic greeting ceremonies could endanger young chicks or eggs. In order to resolve this problem appeasement and pair-bond behaviours during pre-breeding would be expected to be well developed. (In another type of situation, where the dependence of the chicks is particularly prolonged, pair-bond behaviour is complex before breeding but an elaborate greeting ceremony is lacking e.g. some albatrosses, penguins and the red-footed booby, Sula sula). Nelson (1970) reviews in detail the specialisations imposed by the habitat on the behavioural expression of aggression and pair-bond formation in sulids.

The present study showed that nest guarding was intense during pre-breeding from soon after pairing and that a great deal of time was spent by the pair together (protracted pair-bond formation). The orientation of adults tended to be away from the nest and choking and begging appeared to be the most ritualised behaviour patterns representing site ownership and appeasement respectively. However, even the period of nest building was shown to be unnecessarily long (Maunder and Threlfall, 1972, noted that nests could be completely rebuilt in 2-9 days) so that this too may have had ritual significance. Cullen (1957) described the 'trampling' of dry grass or even bare rock that could not have affected the security of the nest structure. The formation of the pair-bond itself may well depend on the performance of all of these behaviour patterns (in conjunction with the biological requirements of copulation, courtship feeding and nest building). The sequence of changes in emphasis during pre-breeding may well depend on a complex cycle of hormonal and experimental changes in the adults that are necessary to prime the individual for the more dramatic cycle of changes in behaviour seen during the later stages where 'reinforcement' is not derived from the mate (see Lott and Comerford 1968).

The incubation stage of kittiwakes has been shown to represent a major change in the attendance and behaviour pattern of the adults. The new behaviour is essentially simple (incubation-sitting and movement of eggs) but the requirements of the developing embryo are rigid, viz. regular turning and a fairly high constant temperature (10.6° C.)above ambient, Maunder and Threlfall, 1972). These must be maintained throughout the 27 day period without respite even though the egg itself (except towards the latter part of incubation) provides an unvarying stimulus. Attendance of the pair must be perfectly co-ordinated even though they have little opportunity to reinforce the pair-bond by anything more than brief choking bouts at changeover (personal observation), in contrast to the preceding stage.

In the highly aggressive gannet, Nelson (1965) reported a highly developed greeting ceremony on the nest site at changeover that was thought to serve this function. In this species uniparous clutches are the rule and an incubating adult holds the egg securely in the feet (Nelson, 1966a). In the typical ground-nesting black-headed gull, Beer (1966a) described how, at changeover, adults occasionally arrived with small pieces of nest material. This behaviour could have had ritual pair-bond reinforcing significance (see Nelson, 1968, for pair-bond nest building in the swallow-tailed gull). It would not be appropriate to the cliff ledge habitat of the kittiwake, where indeed it was not observed.

One marked difference between the kittiwake and the black-headed gull (Beer, 1961) was the pattern of change in the orientation of the adult at the cliff nest site that, in conjunction with the incubation, brooding and standing behaviour, served to protect the eggs, and particularly the very young mobile chicks (McLannahan 1973) at a time when they were at greatest risk from falling. I know of no other demonstration of this behaviour in any other species but it would be interesting to make comparable observations on other cliff-nesting species. The present study shows that kittiwake chicks are constantly guarded for at least the period that they receive some brooding. McLannahan (1973) showed that the intensity and length of the chick-care period where guarding was observed was greater in kittiwakes than in cliff-nesting herring gulls which in turn was greater than in ground-nesting herring gulls. Nelson (1966a) showed that gannets constantly attended their chick right up to the time that they left. Other cliff-nesting species, however, are not constantly guarded after the first few days of life, as has been shown by Cullen and Ashmole (1963) in the black noddy and by Hailman (1965) in the swallow-tailed gull. In these species the pattern is closer to that of ground-nesting gulls, e.g. the black-headed gull (Beer, 1966a) the ring-billed gull (Evans, 1970) and the black-billed gull (Beer, 1966b) where all are closely attended for only a few days after hatching. However, the nest site conditions of swallow-tailed gulls are not the same as those of kittiwakes or gannets.

Both Snow and Snow (1967) and Nelson (1968) reported that the nest was usually close to boulders where chicks hid when the adults ceased to guard them. In this respect they are similar to ground-nesting species.

One factor which could affect guarding might be food availability. Only these species for which food is in plenty can 'afford' to have half the food gathering potential of a pair ~~which is~~ inactive during guarding. Nelson (1970) quotes the example of the great frigate bird (Fregeta minor) and the red-footed booby where a sparse food supply reduces guarding to a minimum. Pearson (1968) showed that two species of medium-sized terms in temperate climates, the arctic tern (Sterna paradisaea) and the common tern (Sterna hirundo) appeared to be at about the limit where it was possible or economical to rear chicks by typical tern feeding methods. This might suggest that ~~in~~ the black noddy tern may find it difficult to provide sufficient food and guard the brood, unlike the cliff-nesting kittiwakes and gannets. Neither the gannet (Nelson, 1966a) nor the kittiwake (Coulson, 1958b and the present study) or 7 other large species of temperate seabirds (Pearson, 1968) appear to have any difficulty in providing sufficient food for their growing brood as they spent relatively so little of their available time fishing.

The present study showed that kittiwake adults shifted their position off the nest and onto the ledge where there was room and/or, left the ledge altogether during chick-care. This change in attendance was a response to the increased begging pressure of the chicks but it tended to affect males sooner than females. Earlier, it was pointed out that after mutual begging bouts during pre-breeding, males fed females but the converse was never observed. This may have indicated that males had a lower threshold for tolerance of begging pressure than females and thus would be expected to respond to begging by the chicks earlier than females. Adults in the SIDE position could not directly protect the chicks from falling as their position, and facing direction respectively neither hindered the chicks access to the precipice or indicated close surveillance. As the chicks developed so the adults reacted more often to their begging, which became more frequent, so that close guarding became increasingly rare.

Nelson (1964) stressed that young gannets were hardly ever left unguarded as the extreme aggression of the species (useful in site establishment and maintenance) mediated against this. On the rare occasions where it was observed e.g. where one of a pair died, the chicks were killed by neighbouring breeding birds. This difference between gannets and kittiwakes will be referred to later, but it should be noted that no instances of chick murder were ever recorded in kittiwakes.

Table 35 shows the amounts of guarding after hatching, the occurrence of interactions of the chicks with adults other than their parents, and the habitat types, of several species of seabirds. The corresponding behaviour of the chicks and their fledging methods is also included. This table shows that generally the cliff-nesting habit predisposes chicks to interact with conspecific strange adults on the cramped nest ledges, whereas most ground-nesting chicks can either run away or hide when in this situation. Presumably, as an adaption to this, the chicks of cliff-nesting species are shown to exhibit marked appeasement behaviour. The chicks of the ground-nesting white booby appear to be an exception to this. Nelson (1967) however, maintained that in this species both chicks (which practice sibling murder) and adults are very aggressive. He vividly demonstrated that chick appeasement was a necessary behaviour in this species, which nested on bare slopes, for any chicks of red-footed boobies (which did

TABLE 35 INCIDENCE OF GUARDING IN SEABIRDS

SPECIES	AMOUNTS OF GUARDING AFTER HATCHING	AMOUNT OF INTERACTION AND EFFECT	CHICK BEHAVIOUR	FLEDGING METHOD	HABITAT TYPE	REFERENCES AND COMMENTS OF AUTHORS
1. Gannet	Full Guarding	If it occurs chick killed	Appeasement	Single Flight to sea	Cliff Ledge	Nelson (1966a,1970) (Highly specialised)
2. Kittiwake	Partial Guarding (BEGGING Pressure)	Attacked frequently (May fall, premature fledging)	Appeasement	*Prolonged Fledging Period	Cliff Ledge	Cullen (1954) Present Study (Highly specialised)
3. Black Noddy	Not Guarded (Food shortage?)	Attacked frequently (may fall or be killed)	Appeasement (May defend site)	Prolonged Fledging Period	Cliff Ledge	Cullen & Ashmole (1963) (Less perfect adaptions than kittiwake)
4. Swallow-Tailed Gull	Not Guarded (Can hide)	Attacked? May fall?	Hides Not known if appeasement. But has Black neck band like kittiwake chick (Cullen 1954)	Prolonged Fledging Period	Cliff Ledge with Boulders	Hailman (1965) (Not nearly so specialised as kittiwake)

TABLE 35 INCIDENCE OF GUARDING IN SEABIRDS (CONT.)

SPECIES	AMOUNT OF GUARDING AFTER HATCHING	AMOUNT OF INTERACTION AND EFFECT	CHICK BEHAVIOUR	FLEDGING METHOD	HABITAT TYPE	REFERENCES AND COMMENTS OF AUTHORS
5. White Booby (Sula dactylatra)	Partial Guarding (BEGGING Pressure)	Attacked frequently and vigourously	Appeasement (May defend site)	Prolonged Fledging Period	Fairly Bare Slopes	Nelson (1967,1970) (Very aggressive adults and chicks)
6. Ground Nesting Gull on cliffs (Herring Gull)	Hardly Guarded	Attacked? May Fall?	No Appeasement	Prolonged Fledging Period?	Cliff Ledge	McLannahan (1973) (Much less perfect than kittiwake)
7. Ground Nesting Gull on Ground (Herring and Black-headed gull)	Not Guarded	Rarely Attacked	Runs away and hides	Prolonged Fledging Period	Ground with adjacent plant cover	Cullen (1957) McLannahan (1973)

* Prolonged fledging period means chicks are not independent after their first flight.

not show appeasement) were pecked to death by white booby adults. This table also shows that, typically, seabirds have a prolonged fledging stage (as described for the kittiwake) such that chicks are not independent after their first flight. Thus in all cases of cliff-nesting species (even with appeasement behaviour) chicks left alone by parents run the risk of (a) being pecked and injured and/or being forcibly removed from the site (with fatal consequences) or (b) taking their first flight prematurely or suffering a disturbed fledging stage. (b) will not affect gannet chicks but will be particularly damaging to the other species as cliff-nesting chicks have to 'home' on their own sites to be fed. Both of these forms of disturbance have been shown in the present study to affect kittiwakes. Cullen and Ashmole (1963) recorded observations of small black noddy chicks that were pecked and injured by strange adults on their nest sites. Further, "many" young were found below the nest ledges bearing signs of attacks that could well have removed them from their ledges.

Thus the evidence presented suggests that an important potential source of chick mortality, either directly or indirectly, might arise from the interference by conspecific adults of the chicks of cliff-nesting species. It would be expected that compensation for this danger would result from marked appeasement behaviour by the chicks and from their constant guarding by the parents. The extent of the development of these two behaviours may be thought of as a measure of successful adapting to the cliff ledge habitat.

An alternative strategy might be for chicks to react aggressively towards strange adults. This was reported to occur in well-grown black noddies, white boobies and blue-footed boobies (see Table 35 for references). However, as adult birds tend to be more mobile and experienced than chicks then to be efficient this strategy must be able to revert to appeasement should retaliation become intense. In a cliff-nesting species like the black noddy it would be expected that the dangers inherent in the strategy, coupled with the precarious nest site, might make the risks correspondingly greater than in the two ground-nesting species cited above. Attacks by chicks against strange adults were never recorded in kittiwakes.

When chicks were absent during their fledging stage, and after they had left the site, a short resurgence of adult attendance could be demonstrated in kittiwakes. This attendance by one or both members of the pair involved choking as an important element, just as it did in the pre-breeding stage. An increase in pair occupation of the sites after the chicks had fledged was also recorded by Nelson (1966a, 1967) in the gannet and white booby. Coulson (1958a) showed that the fledging and post-chick stage of successful kittiwake breeding cycles coincided with an influx of non-breeders into the colony which might breed in the following season. The increased activity of pairs may well represent the reinforcing of the pair bond for the following season after the stresses of breeding in the present season when pair attendance was minimal. Thus those pairs which maintained their guard over their sites throughout the breeding cycle would also be expected to stand the greatest chance of retaining those sites from season to season.

The pattern of chick behaviour in kittiwakes has been shown to be mainly one of a gradual increase in coordinated activities as they developed with a corresponding decrease in sitting. Wing flapping formed consistently a relatively insignificant fraction of their behaviour, and preening (although increasing over the early period of feather growth) remained thereafter at a fairly constant level.

Pecking at the nest bottom and particularly UNSUCCESSFUL BEGGING came to dominate chick behaviour with adults in close attendance. The effect of this latter behaviour was eventually to drive the adults off the nest structure itself and onto the nest ledge (if there was room) and, maybe, off the site completely. SIDE attendance only reduced the pestering while chicks could not fly. After this time the adults left the chicks more and more. There was no evidence of increased fishing activity by adults which had been driven from the nest site.

An interesting parallel can be drawn between the observations above and those made by Nelson on the white booby (1967). He believed that the adults of this ground-nesting species needed to shelter the young chicks from the fierce sun and from the cool nights. At a later stage(as previously mentioned) there was also interference to the young by strange adults. Somewhere between 22 and 62 days of age (variable from pair to pair) chicks were first left unattended. It was noted that during the later stages of chick development the adults only stayed with the chick long enough to feed it and then moved to another part of the territory (perhaps homologous with SIDE attendance in kittiwakes). Nelson noted that adult boobies were "obviously discomfited by the chicks passionate begging", and moved away as soon as possible. After the chicks were free-flying they elicited overt aggression (from particularly the male) by their pestering, but this might then be followed by feeding. The pestering became stronger and more elaborate with age and even "occurred in vacuo" at low intensity for protracted periods. Like kittiwake chicks intense 'feeding movements' could be evoked from isolated booby chicks by holding the fingers over them like a beak.

Nelson pointed out that the dgree of pestering in the gannet was less vigorous than in what he took to be the hungrier white booby chick. However, Nelson (1966a) describes high intensity gannet begging as chicks stabbing and caressing the adult's bill with their own, which was so stimulating that regurgitation movements were elicited even "when no food was available". Adults made no attempts to stimulate the chicks but if ready to feed would stand motionless and allow the chicks to beg; otherwise they would avoid the chicks' attentions (like kittiwake head turning). Nelson (1964) reported that pairs of adults with artificially enlarged broods of 2 chicks spent less time together than was normal, at the nest site, and occasionally left the site completely unattended. This was particularly unusual for this species. Although the growth rates of twins and their peak weights were equal to those of singletons he maintained that both (1) the occasional absences of adults, and (2) the apparently greater intensity in twins of pestering which often elicited futile regurgitation movements,were evidence that adults were responding fully with their food gathering capacity to double broods. But see above for the effects due to singletons.

The interpretation of these data, in the light of the present study, was that in the case of the artificially enlarged 2 chick broods of gannets the pestering by well-grown chicks on the confined site was so potent that adults were driven off. The nesting density and aggression of neighbours was such that SIDE attendance was impossible. This interpretation gains credence as it does not require that adults were incapable of obtaining sufficient food for their enlarged broods, and for which there was no real evidence. Nelson (1964) has shown that gannet chicks reach a peak of 1.3 times the adult weight at about 3 weeks before fledging.

Two chicks of this size must present a formidable stimulus to the adults when both beg at high intensity. Nelson (1966b) could "give no satisfactory reason why gannets had not taken advantage of their capacity to raise two chicks". However, site tenacity was an important facet of gannet breeding,(Nelson, 1964). This, coupled with the extreme aggression required to retain those sites, may have provided a sufficiently powerful selective pressure to prevent adults from reducing their nest guarding as would occur with 2 chick broods. Adult aggression was shown to be so extreme that unguarded gannet chicks could be pecked to death. The present study has indicated another possible source of mortality (or at least decreased viability) that might be particularly serious in this species. Table 35 indicates that the chicks of gannets fledged atypically. (Nelson, 1970, discusses how the strategy might have been evolved of feeding past the point where the chicks are capable of returning to their ledges). If unguarded gannet chicks were encouraged to leave their ledges by strangers, as in the kittiwake, then there would be no chance for them to return, unlike the kittiwake. This could well predispose such gannet chicks to become part of the group which makes up the 80% mortality in the first year, in this species (Nelson 1966a).

Thus a cliff-nesting species that showed pronounced site tenacity, chick murder and a non-return fledging pattern might be expected to be restricted to that brood size where guarding could remain constant. Although the problem has appeared to have stimulated little study, chicks that beg from their parents, particularly as in seabirds where this involves physical contact with the bill, must present an increasingly threatening stimulus to their parents as they develop. The adaptations of juvenile plumage and characteristic appeasement behaviour may all help to reduce such aggression, (Cullen, 1957, Nelson 1970) but nevertheless the late chick-care period must be particularly stressful to adults after the previous rigours of the breeding cycle. This is demonstrated by the present study.

The development and refinement of the pecking response during early chick-care has been extensively investigated but little is known about the begging responses of well-grown chicks. Let us imagine the situation where (1) begging had been food-reinforced for the whole of early chick-care, (2) this was the only food available to the chick and (3) the food requirements (and hunger?) could be expected to increase with age. In this case, even if the profitability of the exercise became reduced (by driving away the adult) this would not be expected to reduce begging by the chicks when they had the chance, but rather to encourage it. This appeared to be typical of kittiwakes. Obviously, careful experimental verification of these points is required.

Although these points apply equally to all seabirds, in contrast to cliff-nesters, it may be that those with large territories may less obviously be required to leave those territories unguarded-they can retire from the chicks (Nelson, 1967). Furthermore, the dangers to chicks from strangers will potentially be less severe if there is no steep drop or difficult landing for the chick, and if in any case the chicks can run away.

The stress of feeding large chicks might still be reflected in their weights which would be particularly important at the point of achieving independence. Coulson and White(1959 and 1958b) showed that kittiwakes suffered a 21% mortality during their first year of life (compared with a 15% mortality during chick-care) and Nelson (1964) gave the even greater figure of 80% for gannets (of which 12% was during chick-care and the first flight). This shows that post-chick mortality can be of great importance in seabird population studies. If post-chick survival depended on some correlate of their weight at independence, then any factor affecting this would also be important. Nelson (1970) for many sulids and Coulson and White (1958b), and Maunder and Threlfall (1972) for the kittiwake, showed that chicks reach a peak weight before achieving independence. In the latter case this occurs about 10 days before the first flight and the weight continues to decrease through the fledging stage. Although it may be possible to explain the terminal part of this drop in weight as a result of chance lack of co-ordination between adult and chick attendance, caused by the adult's avoidance of the chicks, the earlier decrease in weight could not be caused in this way as chicks were always present at the site. In the simpler situation with gannets, adults and chicks are in close proximity for the whole period up to flying yet the chick weight decreases (by 10% of the final weight) over the last 3-4 weeks prior to flying (Nelson, 1964). Ricklefs (1968) shows a relationship between this pattern of growth and aerial foraging. He demonstrated that in one species of swallow (Hirundo rustica) the drop in weight could be accounted for by the loss of water from the feathers and other tissues as they matured. There is no indication in the literature that this is the case in seabirds. Rather it seems that the resources gained during late chick-care are necessary to tide fledglings over the period before they become self-sufficient (Nelson, 1966a). There is also no indication in the literature of the reasons why chicks should not merely increase their food demands, by begging, if increased physical activity calls for this.

Thus neither in kittiwakes or gannets was there:

(1) any suggestion that the food available to the adults was limited.

or (2) that there was an obvious a priori reason why (from the chicks point of view) they should decrease their feeding from well before their first flight, and even in kittiwakes, during the fledging stage. On the contrary there was, probably a good reason for them to maintain a high final weight in that this would increase their potential viability. Any advantage of a low weight for the first flight in kittiwake chicks must be offset by the even lower weight at final abandoning of the site, since chick weight was found here to decrease progressively.

The interpretation of these data in terms of the present study is that adults have difficulty in transferring optimum quantities of food to the well-grown chicks due to the repellent (and perhaps aggressive) stimuli from the chicks in the begging situation. This was particularly important in kittiwakes and gannets where all feeding occurred at the confined nest ledge. These stimuli increase with age of the brood.

This process may well serve to encourage the hungry chicks of both species to make their first flight from the nest site and eventually to abandon the nest site completely (in kittiwakes). Differences in potential viability of individual chicks might be indicated by their peak weight, the age of the chicks at peak weight and by their rates of decrease in weight after this peak. Nelson (1964) stated that gannet chicks were sometimes fed right up to the point of fledging and were therefore not starved off the ledge. He also stated that it was difficult to decide when food had actually been passed from adult to chick. However, as shown above, although feeding interactions between chicks and adults would increase up to fledging the amounts of food transferred could well become increasingly inadequate.

Potential studies that could test the predictions of the hypothesis expressed above, but which have not yet been carried out could be concerned with:

(1) Comparative accounts of the changes with age of ALL feeding interactions, particularly in older chicks of other species of seabirds.

(2) Quantified accounts of the effects of (1) on the adult's behaviour.

(3) Accurate measures of the weight changes in chicks as they developed and an analysis of which body materials accounted for the changes.

(4) Quantified accounts of the relationship between the effects of (1) and (2) on (3).

In order to evaluate the importance of chick/adult interactions (as illustrated in the present study) to chick survival or adult breeding success then results would be required from studies concerned with:

(1) The relationship between the condition of chicks at fledging and their subsequent survival

and (2) The effects of lack of chick guarding both on chicks and the retention of the nest site by the pair.

One of the practical problems that affects the study of well-grown seabird chicks (particularly on cliff ledges) has already been mentioned. This is that there may be premature abandonment of the site when disturbed. This, in conjunction with the considerations given below, may well explain why so little is known about the problems above.

The kittiwake, in common with the vast majority of seabirds, shows colonial breeding. No instances have ever been recorded of pairs nesting in isolation and even at the earliest stages of colony formation numbers of young adults are present together at a potential colony a whole season before they actually start breeding (Coulson and White, 1956).

Large concentrations of seabirds of one species on land at the time typical for breeding indicates a strong common motivation. That the strength of the motivation, or the abilities to breed, or both, vary individually is obvious from the instances cited in the literature of large numbers of non-breeding members of colonies, e.g. by Cullen and Ashmole (1963) for the black noddy, Coulson and White (1956, 1958a) for the kittiwake and Moynihan (1955) for the black-headed gull. Nelson (1966a, 1966b) provides the best attempt to quantify and identify the non-breeding fraction of the colony population. He showed that about 20% of the site-holding adults in a gannetry made no attempt to breed. Coulson and White estimated 19% in a kittiwake colony. Nelson's figure did not include the 2,000 - 3,000 mobile club members of the Bass Rock colony. Of this 20%, some were young adults on immatures which had paired and held a site and nest. Others paired and held a site but without a nest. The club birds consisted both of adults and immatures which did not appear to hold sites even though these were available. Of the birds that bred, 22% failed to raise eggs to hatching and although some of these must have been due to chance accidents others must have been due to poor ability to incubate. Only 17% of pairs reared young in 4 successive seasons and 41% in 3 successive seasons. Richdale (1949) for the yellow-eyed penguin (Megadyptes antipodes) Coulson and White (1958a) for kittiwakes and later Nelson (loc.cit.) for the gannet, ~~for~~ all found a relationship between the age of breeding adults and their subsequent breeding success, such that first-time breeders were less successful than older birds. Coulson and White also showed that older birds returned to the colony sooner and bred before younger birds, a feature which had also been found in the gannet by Nelson. Subsequently, Coulson (1966,1968,1972) showed that in the kittiwake much of the variation in breeding performance was related to age, duration of the pair-bond and to the position occupied in the colony. He concluded that pairs found it difficult to develop into full breeding condition. Few pairs breed as well as the more successful, some miss a breeding season and many, usually young birds pair but fail at some stage of breeding. (See above for the description of gannets by Nelson). In relation to these differences there was clearly an advantage for potentially good breeding birds to breed together. Coulson thought that this was achieved by the best birds returning earliest and segregating to the centre of the colony where they paired with potentially good mates. The retention of a good mate from year to year enhanced the breeding performance. It was thought that the pair bond resulted in complex relationship which improved with experience. Similar advantages of high breeding success with pair-bond development have also been demonstrated in the adelie penguin by Penney (1968) and Leresche and Sladen (1970). These latter authors also showed that early and synchronised arrival at the colony was essential to the maintainence of pair-bonds.

Coulson and White (1958a) found that kittiwakes exhibited considerable nest site tenacity but that this varied with breeding experience. Birds breeding for the first time and ringed the previous year on a particular nest, were over twice as likely to change sites than birds which were breeding for at least the third time. All of the nests in the North Shields colony were on identical window ledges and there was no adult or chick predation so that the differences demonstrated in breeding success between the centre and edge of the colony (Coulson 1968) were all due to the quality of the adults recruited. The older, more experienced and central birds showed the greates site tenacity. Nest site tenacity has also been shown to be an important feature in other seabird species e.g. the gannet (Nelson 1966a) and the adelie penguin (Penney, 1968). I know of only two examples, both of which are obvious specialisations to peculiar niches, where nest tenacity was not found; in the black-billed gull (Beer, 1966b) and in the great frigate bird (Nelson 1970). At least in the kittiwake and the adelie penguin (and probably the gannet) the retention of nest sites appears to play a central role in pair-bond maintenance, particularly during the earliest part of the breeding season.

The relationship between the pre-breeding behaviour and pair-bond formation has already been discussed. In general, with the exception of attendance together before pre-breeding, the adults of a pair showed patterns of behaviour which were very similar in form for all attendance categories. It was clear from the earlier discussion on incubation behaviour that there was no possibility of either adult diverging from the simple pattern required by the needs of the developing embryo. Any such divergence would result in a failure of the eggs to hatch. The results from the individual pairs showed that the attendance may not necessarily be equally shared during the daylight hours. This suggested the possibility that pair-bonds may not only exist between 'good quality birds with very similar performances', the good breeding stereotype, but also between 'night sitters' and 'day sitters', and if the discrepancy between sharing were maintained through the night, between 'long sitters' and 'short sitters' also. The important feature would be that the members of a pair mutually complemented each others' performance.

Most of the studies on seabird breeding have used the ability of adults to hatch eggs as the criterion of success. This involves, not only the mutual behaviour of producing fertile eggs, synchronisation of behaviour changes in preparation for them (nest building) and their incubation, but also the co-ordination of two potentially idiosyncratic attendance schedules to form a viable whole. Some studies have also quoted estimates of 'fledging success' according to the percentage of hatchlings which reach an age close to that at which they would be expected to disappear. It was suggested earlier that this latter coarse measure may well give only a poor indication of the viability of the chicks and therefore an inaccurate estimate of breeding SUCCESS defined as the rearing of chicks that will enter the breeding population. The hatching of the egg, in contrast, is an unequivocable measure of the success up to this stage of breeding.

Although the behaviour patterns of all individual kittiwakes have been shown broadly to be similar during chick-care, the attendance patterns exhibit a great deal of individual variation. The present study has shown that although the timing and amount of SIDE attendance depends largely on the degree of crowding at the nest site, yet the early breeding, high quality, pairs tended to leave their broods unattended at a later stage of development than the later breeding, low quality pairs. This indicates that high quality birds could endure (or avoid) the pestering of chicks more successfully than low quality birds. Nelson (1967) found that adult white boobies, which also reacted to chick pestering, tended to leave their chicks unattended at a progressively earlier stage of development as the season progressed. He assumed that this was due to a waning of motivation due to the lateness of the season although if the high quality adults bred early in this species, as they do in the gannet, there would be a close similarity to the kittiwake. Nelson (1966a) also showed in the gannet that the total length of the fledging period depended on the lateness in the season, and decreased as the season progressed. This might also indicate that the 'quality' of the chick-care period depended on the quality of the adults.

From the present study it appears that fledging mortality tends to be higher in the broods of those adults which leave their sites relatively early. It has also been suggested that the susceptibility of adults to chick begging might significantly lower the chicks fledging weight. The highest quality birds which are also those most resistant to chick pestering, might therefore be likely to raise chicks with a higher chance of SUCCESS. This difference in chick rearing capabilities would not be shown by the measures used in previous studies (see Coulson 1966).

Successful kittiwake pairs tend to retain their main pattern of attendance sharing during chick-care even if, as individuals, they show periodic absences from the nest site, (this study). The site is also regularly revisited at which time any strange adults will be removed. After the chicks have finally left, pairs increase their attendance (see earlier) although the intensity and duration of this stage is variable. An indication of the likelihood of a pair bond surviving to the next season may well be found in the length of this period. The control of whether this stage occurs or not may well depend on the 'survival' of the main pattern of attendance sharing through chick care. Guarding of the site might enhance the 'survival' of the pattern.

In a similar way to the incubation period individual attendance patterns during chick-care can be highly variable. This means that the pair-bond and quality of the pair may well be a function of the compatibility of their individual attendance patterns rather than their absolute form. The actual patterns of attendance depend on the susceptibility of the adult to chick pestering, so that the viability of the pair bond may also depend on this factor.

Thus, the use of an intensive study method on a few selected pairs of kittiwakes has indicated a striking similarity of individual behaviour patterns yet a great variation in attendance patterns. Much of the chick-care variation arese from the individual levels of tolerance for chick pestering. This may well alter with experience. The sparse and confined cliff-ledge habitat predisposes the chicks to become a major factor in the regulation of the breeding biology of kittiwakes.

SUMMARY

Certain aspects of the behaviour of breeding kittiwake gulls were studied at a colony of individually colour-ringed birds which nested on the window ledges of a riverside warehouse in North Shields, Northumberland.

A technique is described whereby 4 pairs of successful breeding birds were time-lapse filmed at the nest site during daylight hours: one pair was observed from their arrival at the colony until their abandonment of the site and three further pairs from soon after their chicks had hatched until the sites were abandoned.

The resulting film gave a long series of instantaneous observations of the attendance and behaviour of adults and chicks. Spot observations on all of the other breeding pairs in the colony were compared with the detailed records of time-lapse pairs.

It was decided that of the lapse intervals available film of 80 seconds/lapse gave the best compromise between accuracy, discrimination, time taken for analysis and cost of film.

The analysis of the film showed that breeding adults did not orientate randomly at the nest site but showed a pattern of orientation that was profoundly affected by the prevailing nest site conditions. Adults rarely faced the precipice when incubating eggs and faced essentially only one direction (directly away from the precipice) when young chicks were present. This orientation, in conjunction with the position adopted by brooding adults (between the precipice and the brood) ensured the greatest degree of protection for the uncoordinated chicks on the cliff-face habitat.

Adults attended their sites alone or together either ON the nest

structure itself or to one SIDE on the nest ledge. Sites were also left unattended.

A consideration of the changes in the relative amounts of these different categories of attendance suggested that the breeding cycle could be divided into 5 stages. The extensive periods of attendance by adults alone or together during pre-breeding were thought to represent nest site guarding, synchronisation of physiological and behavioural rhythms, pair-bond formation and preparation for laying the eggs.

The main breeding stage (which started shortly before egg-laying and continued well into chick care) was a period of perfectly co-ordinated attendance. The nest site, for the first time, was constantly attended. Each adult of the pair taking turns with the other, with brief changeovers. The pattern was consistent as although neither sex typically carried out more attendance than the other, in particular cases one of the pair habitually attended for the majority of the daylight hours (64% in one case).

By incorporating SIDE attendance into the attendance pattern of the previous stage or leaving the site unguarded particular adults showed highly individual patterns of attendance during Late chick-care. As both the timing (males before females) and the extent of the changes were independent of those of the mate, so the total patterns of attendance at different sites varied (in contrast to the earlier stage). Different sites were unguarded from 8 to 39% of the daylight hours.

During the fledging stage the same individuality of attendance pattern was seen but there was a shift in emphasis of the different categories.

The pattern of attendance after the departure of the chicks was simpler and showed, less inter-pair variation, indicating the effect of their presence on adult attendance. The post chick stage was variable in length and females attended more often than males.

Detailed investigation showed that after the initiation of both of the new forms of attendance during late chick-care (SIDE attendance and leaving the chicks unattended) these became increasingly important components of individual attendance patterns (although rates of increase were similar in most cases). There was no evidence of compensation by any individual for the shortcomings of the mate, and so it was concluded that the basic pattern of attendance sharing (seen during the Main breeding stage) was maintained, and that individuals modified their own pattern within this framework. All broods were left unattended at some stage (beginning at a mean of 33.1 days after hatching) although only 66% of individuals SIDE attended (beginning at a mean of 33.1 days after hatching). The probability of a change in attendance pattern increased with the age of the broods and there was no seasonal difference in the mean age of broods at the onset of the two changes. The presence of pairs of conspecifics on adjacent sites tended to inhibit SIDE attendance yet hardly affected the initiation of leaving the site. Where adults were free to carry out both forms of attendance, SIDE attendance was initiated before broods were first left unattended. Males appeared mainly to be responsible for the earliest leaving of the brood. Individual differences in these two measures were consistent from year to year when pairs retained their site and brood size. In general, early broods (mainly from high quality parents) were first left unattended (and probably exposed to

SIDE attendance also) at a later stage in their development than broods from later in the season (whose parents were mainly of lower quality). The timing of the initiation of both types of attendance was affected by brood size, and occurred in 2 chick broods before 1 chick broods.

Kittiwake chicks made their maiden flight a mean 40.8 days after hatching. There then followed a period during which they might return to the nest site for feeding (at gradually increasing intervals) which finally terminated a mean 51.8 days after hatching when they permanently quit the site. The presence of chicks was shown to inhibit the attendance of the parents (2 chicks more strongly than 1 chick) yet the sites were not abandoned for protracted periods as a decrease in chick numbers at the site was accompanied by an accurate 'response' of increased attendance by the adults. Adults that had left their sites unguarded were present in the 'club' areas and thus could periodically visit their sites.

Differences between the attendance patterns of the adults of a pair tended only to be seen when chicks were present. Thus both the basic pattern of attendance sharing and the modification of individual patterns within this framework mainly depended on the presence of the chicks for their expression. Adults did not SIDE attend empty sites but did attend as a pair.

During the post-chick period attendance was similar to that during fledging with no chicks present. The absolute daily amounts of attendance together and alone increased for a brief period, as adult attendance was no longer inhibited at any part of the day by chick presence. The breeding cycle was terminated by the progressive abandonment of the site by the pair, the males tending to leave earlier and more abruptly than the females.

It was concluded that adults altered their attendance to avoid close interaction with the chicks. The older were the chicks or the larger was the brood size, so the greater was this avoidance. It was first achieved by SIDE attendance (where possible) and later, when chicks became more mobile, by leaving them unattended.

Strange adults attended the unguarded nest sites of breeding pairs although the extent of interference varied from pair to pair. These adults attended sites without regard to the chick numbers present during Late chick-care (10.7% of all unguarded sites). During Fledging periods relatively more interference was seen with fewer chicks present (14.6% of all unguarded sites). A scheme was proposed which could explain this difference in which adults were taken to attend sites at random and where a constant 36% of chicks would respond to the arrival of an adult by leaving the ledge. Chicks showed various modifications of behaviour to minimise their premature removal (11.4% were attacked) but it was concluded that the greatest danger from the generally short (14 mins.) bouts of stranger attendance came from the disruption of a chicks fledging stage when their waterproofing and independent foraging capabilities were most poorly developed. During 1970 48% of the expected first year mortality occurred in the Fledging stage (mainly by drowning) and chicks that had been left unattended earlier than average were over-represented in this group. The changes in the pattern of adult behaviour through the breeding season are described with particular reference to cliff-nesting adaptations, the requirements of the pair-bond and the changing conditions at the nest site. The behaviour of individuals was strikingly similar with only small differences in the detailed pattern of brooding. HEAD TURNING (from begging chicks) became an important behaviour during the later stages of chick growth but levels were lower (up to the time of flying) when adults SIDE attended. Chick behaviour is described from hatching until quitting of the site. This was unaffected by whichever of the parents attended or according to whether one or two chicks were present. After an early and relatively long period of inactivity during brooding (a cliff-nesting adaptation) chicks became more active, yet their mobility was restricted. With increasing age UNSUCCESSFUL BEGGING came to dominate chick behaviour patterns with adults ON attending.

This was the behaviour where chicks and adults intimately interacted, when there was no simple relationship to the amounts of SUCCESSFUL BEGGING (it was 4.7 times more frequent during early chick care yet 15 times more frequent during fledging) and where the frequency of interaction was reduced by HEAD TURNING, SIDE attendance and adults leaving the site (in order of increasing effectiveness). The inter-relationships between chick behaviour and adult attendance on the crowded nest site is fully discussed.

APPENDIX

STATISTICAL ANALYSIS

As adults varied from day to day in the absolute amounts of their attendance then all counts of time-lapse frames had to be converted into percentages in order to carry out comparisons. Two particular difficulties arose from their analysis. 1) A population of percentages follows a binomial distribution that is particularly different from a normal distribution when the number of replicates is small. 2) Some of the percentage values were calculated from small total numbers of time-lapse frames (as few as 10 frames in rare cases) where chance events could seriously distort a percentage value. An attempt was made to overcome these difficulties by transforming percentage values (taking account of the number of frames used to calculate the percentage) by the arcsine square root of percentage transformation (Snedecor and Cochran 1957, Mosteller and Youtz, 1961). This tended to reduce the disturbing influence of the very high and very low scores thus making distributions more nearly normal and allowing the use of robust parametric tests. Where doubt existed over the shape of frequency distributions then distribution-free non-parametric tests were used (Siegel 1956). Generally transformation had the effect of reducing the variation both within and between populations so that the bias was towards a conservative interpretation of a difference.

Overall statistical analysis of the information over the period of development was generally avoided for several reasons. (1) When a period of time is split into fractions then the size of one of those fractions may well not be independant of the size of the other fractions. (2) Different types of behaviour tend not to be independant of one another; such features as shared causal factors e.g. UNSUCCESSFUL and SUCCESSFUL BEGGING or mutual exclusion e.g. PECKING and PREENING at the same time, all affect independance. Instead individual tests were mainly used to clarify particular points and attempts were made to allow for the problems of lack of independance in the interpretation.

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