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ASPECTS OF THE BREEDING BEHAVIOUR OF THE KITTIWAKE (Rissa tridactyla) BEFORE EGG-LAYING

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....being a thesis presented in candidature for the degree
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CORRIGENDA

1. Page 9, Line 4: change "periods as whole" to read: "periods as a whole"
2. Page 40, Line 1: change "affect" to read "effect"
3. Page 50, Line 23: change "reduces" to read "reduce"
4. Page 71, bottom line: change "The" to read "the"
5. Page 78, Line 22: change "pairs incorporated" to read "pairs of Gannets incorporated"
6. Page 86, Figure 7.2: number above solid dot, second from right, should read "29" not "2"
7. Page 119, Line 7: change "with incompatible" to read "with an incompatible"

ABSTRACT

The breeding behaviour of individually marked Kittiwakes (Rissa tridactyla) that retained mates from the previous year (SAME) was compared, over the period from pair-formation to egg-laying, with those that changed mates (CHANGE). Courtship behaviour and sequences are described. Position of nest-site in colony and breeding experience did not differ in the two groups. Pair-formation was later in CHANGE pairs but dates of egg-laying were similar. Birds in CHANGE pairs used a less efficient means of nest-site defense by incorporating up to 19% more attendance as a pair. Birds in CHANGE pairs left their nest-sites unattended up to 13% less often. Rates of greeting were up to 2.5 times higher in CHANGE pairs and energy requirements were probably higher as a result. There was no evidence that frequency and timing of courtship feeding or copulation differed in a manner that could explain the lower reproductive success in CHANGE pairs reported by other workers. Breeding and non-breeding males interfered in the copulations of others. Breeding males were more often than expected members of CHANGE pairs and interfered most often during the two week period before their females laid eggs. The effects of interference on disrupted pairs was minimal. The adaptive significance of interference is discussed. In general, there was greater variance in measures of behaviour in CHANGE pairs and differences between the two groups were usually greatest during the first two weeks after pair-formation. The causation of these differences are discussed in terms of mate familiarity and presumed differences in paternity assurance in the two groups. The consequences are discussed in terms of breeding efficiency and the costs of mate change.

ACKNOWLEDGEMENTS

Many people assisted me in every phase of this work and I am indebted to all. Dr. John Coulson supervised the study and I especially thank him for his help and for allowing me the privilege of working at the unique warehouse colony of Kittiwakes at North Shields. Prof. D. Barker provided logistic support through the facilities in the Department of Zoology, University of Durham. The thesis was written at Brock University, St. Catharines, Canada and Prof. M. Manocha allowed the use of facilities there. Dr. Ralph Morris encouraged me throughout and provided stimulating discussion on many topics. Dr. Callum Thomas, Nigel Grist, Dr. Richard Knapton, David Wiggins and others also discussed many aspects of the study. Special thanks are due to Callum for his generous supply of sanity. John Steele advised on the use of the computer and Dr. Eric Muller, on statistical techniques. Swan Hunter Ship Repairers, their employees, and Messrs. Jim and Mike Pepper allowed access to the colony at all times. I should particularly thank the security staff at the shipyard for many cups of tea and for attempting to protect the colony from the ravages of young egg collectors. Eric Henderson, Mike Bone and Alf Bowman helped with a variety of technical matters. Walter Giesbrecht and David Wiggins assisted with the figures. Jean Elizabeth Chardine (Ruddell) was my companion throughout and helped in a myriad of ways. During my stay at Durham I was supported by a Commonwealth Scholarship, without which, this work would not have been possible.

CHAPTER 1: INTRODUCTION

Background and aims

One of many features that sets the class Aves apart from other animal taxa is the predominance of monogamy as a mating system (Lack, 1968). Monogamy is characterized by a "prolonged and essentially exclusive mating relationship between one male and one female" (Wittenberger and Tilson, 1981). Polygamous mating systems also involve mating relationships or pair-bonds between male and female but they are not exclusive. Regardless of the mating system, if an individual can expect to reproduce more than once, the opportunity arises to re-pair with the same mate from the previous breeding attempt.

Gulls (Laridae) are monogamous, long-lived water-birds and studies of uniquely marked individuals have shown that re-pairing with the same partner, year after year, is common. For example, Mills (1973) found that over 80 percent of female Red-billed Gulls pair with the same male from one year to the next, and Coulson and Thomas (1980) found that in the Kittiwake, about half the pair-bonds in any one year remain intact in the following year. Data for other seabird species also show mate retention to be a common phenomenon (Adélie Penguin: LeResche and Sladen, 1970; Gannet: Nelson, 1972; Buller's Mollymawk: Richdale and Warham, 1973; Manx Shearwater: Brooke, 1978; Fulmar: Ollason and Dunnet, 1978; Ring-billed Gull: Southern and Southern, 1982).

The apparent ubiquity of mate retention in birds (Rowley, 1983) suggests that it is generally adaptive to re-pair with the same individual from year to year. Higher reproductive success through larger clutch size, larger egg-size, earlier laying, and higher hatching success characterize pairs formed in years prior to study, compared to new pairs (Coulson, 1966, 1972; Nelson, 1972; Mills, 1973, 1979; Ollason and Dunnet, 1978; Cooke _et al._, 1981). The specific mechanisms responsible for these differences are unknown but it is generally agreed that mate retention permits a higher degree of co-ordination of activities between male and female, which results in higher reproductive success (Coulson, 1966, 1972; Coulson and Wooller, in prep.). Cooke _et al._, (1981) found Lesser Snow Geese that had changed mates to be less co-ordinated in nest defense activities than those that had retained their mates. Mills (1973) and Rowley (1983) suggested that reduced reproductive success seen in birds that have changed mates may be a result of the extra time needed to form new pair relationships in comparison to that needed when re-mating with the same individual.

Mate change usually results from one of two causes: either one member of the pair dies or both survive but take different mates. This latter form of mate change has been termed divorce (Coulson, 1966). In long-lived species such as gulls, divorce usually accounts for the greater proportion of mate change (Coulson, 1966; Mills, 1973). If mate retention is so clearly adaptive (see above), it is difficult to understand why divorce ever occurs. The dilemma is answered if divorce is viewed in the context of mate choice. Divorce is seen more frequently following years of reproductive failure (Coulson, 1966; Brooke, 1978; Rowley, 1983). Such failure may the result of incompatibility between male and female (Coulson, 1966) and divorce can be seen as a method of dissolving incompatible pairings. The net advantage of divorce is a trade-off between the demonstrated costs in decreased reproductive success associated with mate change in general, and the benefits gained by dissolving a partnership with an inappropriate mate.

The majority of work on the effects of mate retention and mate change in birds has centred on reproductive biology (i.e. clutch size, laying date, reproductive success) and much of the knowledge in this area has come from studies of the Kittiwake undertaken by John Coulson and his students at the warehouse colony, North Shields, England. Based on their work, it was considered important for several reasons, to extend the study in a comparison of the breeding behaviour of Kittiwakes that retained mates from the previous season (SAME pairs) with those that changed mates (CHANGE pairs). In particular, it was thought that differences in the reproductive biology of SAME and CHANGE pairs of Kittiwakes noted previously (Coulson, 1966, 1972) might be explained by differences in breeding behaviour occurring before egg-laying. This thesis describes the results of this investigation.

Certain biological aspects of the Kittiwake and physical aspects of the warehouse colony made them ideal for this study. Of course, the study would not have been possible at all without the historical data base that is available on every bird in the colony. This has been a result of the yearly recording of breeding information for all pairs in conjunction with a colour ringing programme that has produced an almost completely marked population. An important physical attribute of the colony is that the effect of the observer is probably negligible, since the colony is not entered during observation (see Methods below). In contrast, similar activities in a ground-nesting gull colony would likely entail significant observer effect (Fetterolf, 1983a). It is important to note that unlike many other gulls that interact as pairs in "clubs" or in areas other than the nest-site (Tinbergen, 1960; Niebuhr, 1981), the Kittiwake returns directly to the nest-site upon arrival from wintering areas (Cullen, 1957). Thus, all pair interactions in the Kittiwake are likely to occur at the nest-site where, at least at the warehouse colony, they can be easily observed and quantified.

Methods

1. The study site.

The warehouse colony of Kittiwakes is situated on the north shore of the River Tyne at North Shields, Tyne and Wear, England (55°00' N, 01°27' W: Figure 1.1). Kittiwakes nest on the window ledges on all five floors and four sides of the building, although the top three floors of the west and south sides are most heavily colonised. Once a brewery, the warehouse is now used for storage and a limited amount of small boat construction on the bottom two floors.

The west-side of the warehouse was chosen for behavioural study mainly due to the visibility of the nests from the shipyard below. Ledges are arranged in an array of ten columns and five rows (corresponding to floors of the building). No kittiwakes have nested on the bottom floor of this side, presumably because it is only about 1.5 m above ground level. During the study, a few pairs nested on the second floor, but they were often obscured from view by machinery and only those nesting on the top three floors were studied. The window ledges are about 0.75 m wide by 0.3 m deep and support either one or two nests. The physical attributes of each nest-site are identical.

The warehouse was first colonised by Kittiwakes in 1949. The colony increased in size to about 100 pairs in 1967, and has since declined to about 80 pairs in recent times (Wooller and Coulson, 1977; Thomas, 1980). Approximately 40 pairs now nest on the west-side.

Figure 1.1: The warehouse Kittiwake colony at North Shields, Tyne and Wear, England. The west-side of the building is to the left and the south-side in to the right. Picture taken in July, 1980.


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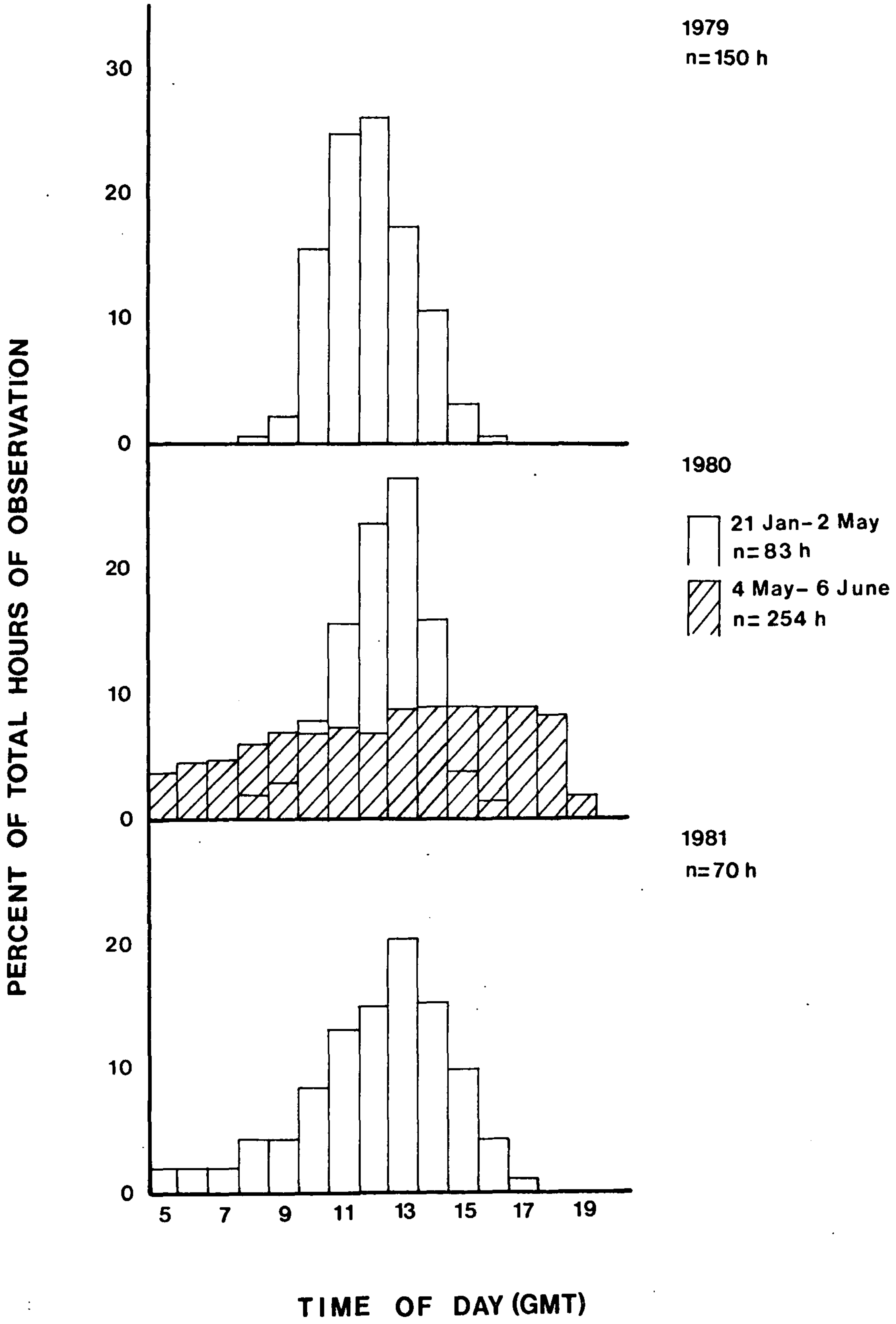
2. Fieldwork.

The colony was visited about once every two days from 3 January to 29 August 1979, from 2 January to 29 August 1980 and from 5 February to 1 July 1981. Between 4 May and 6 June 1980, visits were made daily. On each occasion, routine collection of data associated with the long-term investigation at North Shields, was carried out (see Coulson and Thomas, in prep., for details). Behaviour of SAME pairs (1979: n=14; 1980: n=14; 1981: n=17) and CHANGE pairs (1979: n=8; 1980: n=9; 1981: n=7) was recorded on alternate visits except during the period from 4 May to 6 June, 1980, when daily records were kept. Behaviour was not recorded during periods of inclement weather such as high winds, snow or heavy rain. Observations were made from a car parked about 25 m from the base of the building.

Observation periods lasted 3 to 4 hours except during the period from 4 May to 6 June in 1980, when they lasted for about 7 or 14 hours. The west-side of the colony was observed for a total of 150 hours in 1979, 337 hours in 1980 and 70 hours in 1981. Most of the observation periods were carried out during the same part of the day (i.e. between 0900 and 1500 hours, GMT, Figure 1.2). At this time, activity was relatively stable and the sampling of time periods during which rapid changes in activity levels occurred, was avoided. Half-day watches occurring between 4 May and 6 June 1980, started between 0500 and 0600 hours or between 1200 and 1300 hours, while full-day watches started between 0500 and 0600 hours. The purpose of these extended observation periods, which were made before egg-laying in 1980, was to increase the sample size of observed courtship feedings and copulations and to spread observations over daylight hours. Observations were confined to daylight as it was found that there was virtually no nocturnal activity at the colony. An initial task of the

Figure 1.2: Percent distribution of observation periods over daylight hours in each year.


1979
n=150 h
1980
21 Jan-2 May
n=83 h
4 May- 6 June
n= 254 h
1981
n=70 h
30
20
10
0
20
10
0
20
10
0
5
7
9
11
13
15
17
19
PERCENT OF TOTAL HOURS OF OBSERVATION
TIME OF DAY (GMT)

1979 field season was to compile and describe Kittiwake courtship behaviour. This was achieved in several ways. Direct observations of behaviour were recorded into a tape recorder. Behaviour was also filmed using both still and cine cameras.

Spot observations of birds at nest-sites were used to determine attendance patterns of SAME and CHANGE pairs during the period between pair-formation and egg-laying. At the beginning of each observation period and at one hour intervals thereafter, the identity of birds at each nest-site was recorded.

As a result of the relatively low frequency at which courtship feedings and copulations occurred, all such events in SAME and CHANGE pairs were recorded throughout the observation periods. Courtship feedings were scored only if food was actually seen passed from male to female, or, based on the behaviour of the female, there was good evidence of a successful feeding. During copulations, cloacal contact was assumed to have occurred if the male was seen to bring his (wagging) tail under the cloacal region of the female. In 1979 and 1981, copulations were scored as either unsuccessful (no cloacal contact) or successful (termed contact copulation), while in 1980 the actual number of cloacal contacts per copulation was recorded.

During each observation period and usually immediately after the spot observations of attendance, all west-side pairs were intensively observed for 5 minute periods in 1979 and 30 minute periods in 1980 and 1981. These periods are called sessions. Sessions of intensive observation were performed in order to sample behaviours that, because of their relatively high rate of occurrence, could not be observed continuously throughout each observation period. A total of 152, 5 minute sessions in 1979, 165, 30 minute sessions in 1980 and 21, 30 minute sessions in 1981 resulted in 760, 4950, and 630 minutes of intensive observation of each pair, in each year respectively. Since sessions occurred evenly within observation periods, their distribution over daylight hours was similar to that of observation periods as whole (Figure 1.2).

All occurrences of returns to the mate at the nest-site, greeting ceremonies and bouts of head-tossing were recorded during every session of intensive observation. The occurrence of facing-away and intra-pair aggression such as head-pecking was only recorded in 1980 (see Chapter 2 for descriptions). The sex of all breeding birds in the colony is known and was recorded in conjunction with each observation.

The timing of reproductive events for SAME and CHANGE pairs was determined by observation from inside and outside the warehouse. The date of arrival at the colony from wintering grounds was considered to be the first day an individual was seen at the colony. The date of pair-formation was taken as the first day a pair was observed together on a nest-site. Dates of egg-laying were determined by visits either daily (1980) or every other day (1979 and 1981) inside the warehouse. The term "date of egg-laying" describes the day first eggs were laid.

3. Analysis of data.

Tape recorded data were transcribed and prepared for input to the computer facility at the University of Durham. MIDAS (Michigan Interactive Data Analysis System: Fox and Guire, 1976) and SPSS (Statistical Package for the Social Sciences: Nie _et_ _al_., 1970) were used for data management and statistical analysis.

Spot observation data on attendance of SAME and CHANGE pairs were treated as follows. For a particular period (e.g. first two weeks after pair-formation) and for each pair, the proportions of observations of the male, female (both single or with mate), pair or neither bird were calculated and arcsine square-root transformed. This transformation served to eliminate the dependency between the mean and variance of a sample of proportions (Sokal and Rohlf, 1969). The transformed proportions were then used in calculating mean proportions (and variances) of each type of attendance for SAME and CHANGE samples of pairs. When reporting these statistics in tabular form, the mean and standard deviation of the transformed proportions are given with the mean percent, back-transformed. In graph form, the mean percent and asymmetric standard errors are given. When the proportion before transformation equalled zero and the number of spot observations (n) equalled 50 or less, the proportion was taken as 1/(4n) (Snedecor and Cochran, 1967). These authors also suggest a modification for proportions that equal one, however, these were rare in the data and the modification was not used.

In order to evaluate seasonal trends in behavioural differences between SAME and CHANGE pairs, the time between pair-formation and egg-laying was divided into three periods (numbered 1, 2 and 3): Period 1 comprised the first two weeks after pair-formation, Period 3, the last two weeks before egg-laying, and Period 2, the middle period between first and last two week periods.

The daily observation regime carried out in May and early June, 1980, made possible a close examination of behavioural changes taking place up to and immediately after egg-laying. For this purpose, data were pooled over two day intervals starting 14 days before first eggs were laid and ending five days after.

Hypothesis testing was carried out using both parametric and non-parametric techniques. Variance homogeneity between SAME and CHANGE pairs was not assumed when t-tests were conducted, and Welch's approximation for degrees of freedom was used (Remington and Schork, 1970). When calculating a Chi-square value on a 2X2 table (df=1), Yates correction for continuity was not used (Fox and Guire, 1976). Throughout, the null hypothesis was rejected if $p < 0.05$. If $p \geq 0.05$, the result was noted as not significant (ns). F-tests for variance homogeneity were performed where appropriate and the results given as either "yes" (i.e. variances were homogeneous, $p \geq 0.05$) or "no" ($p < 0.05$). Parametric tests (e.g. t-tests, ANOVA) of the mean proportions of each type of attendance were performed on the arcsine square-root transformed statistics (Sokal and Rohlf, 1969).

CHAPTER 2. COURTSHIP BEHAVIOUR OF THE KITTIWAKE

Introduction

Courtship behaviour can be defined as "the heterosexual reproductive communication system leading up to the consummatory sexual act" (Morris, 1956). The definition delineates courtship as those behaviours performed by male and female in the context of reproduction and communication. It has generally been held that systems of communication of information evolved because of mutual benefits gained both by the sender and receiver of the information (Wittenberger, 1981). However, Dawkins and Krebs (1978) have suggested that a more appropriate way of considering communication is to think of it as a method by which the sender of the information manipulates, to its advantage, the behaviour of the receiver. Regardless of which view is most appropriate, a common denominator in each approach is that communication at least benefits the sender of information.

How then does courtship benefit the courting bird? Both during and after pair-formation, there is a necessary requirement for male and female to be in relatively close proximity to one another and information regarding the intentions of each bird at any particular time may serve to breakdown natural distance barriers that are normally in operation between individuals outside the breeding season. Male birds in general show more aggression in their intra-specific interactions than females (e.g. Pierotti, 1981; Burger, 1981; Southern, 1981; Morris and Bidochka, 1982) and this trend is also apparent in interactions between male and female in a pair (Tinbergen, 1959; Nelson, 1972). Thus, in order to facilitate the close physical contact required between male and female during each phase of courtship, it may benefit both to communicate their internal states (e.g. aggression, fear, sexual) to one another. In this way the male can suppress fear in the female, and the female can reduce aggression in the male. There should be strong selection for behaviour that would accomplish these functions, particularly in monogamous species where both sexes usually invest substantially in the reproductive effort and some level of co-operation between pair members is essential for successful reproduction (Coulson, 1972)

Once the pair has formed, the performance of courtship in male and female probably functions to maintain and strengthen the relationship between partners (e.g. Morris and Erickson, 1971; Hale and Ashcroft, 1982). Additionally, courtship may provide a means by which both intra- and inter-pair synchrony of reproductive cycles is achieved (Bastock, 1967; Hunt, 1980). The communication of information regarding the physiological state of male and female would facilitate the synchronization of reproductive cycles within a pair. Conspicuous courtship behaviours may have a social stimulation effect on other birds in the colony (e.g. Southern, 1974), which could act to enhance inter-pair reproductive synchrony and, thus, the reproductive success of courting individuals (Darling, 1938; Kruuk, 1964; Patterson, 1965)

The courtship behaviour of gulls has been studied from a variety of view points. Early reports were descriptive in nature (e.g. Noble and Wurm, 1943). Later, Tinbergen (1959) used a comparative approach to study the evolution and function of gull displays. It was the view of Tinbergen and others that courtship behaviour has been derived, via the process of ritualization (for more efficient communication), from behaviour patterns unrelated directly to courtship, and often include indications of internal conflict (i.e. flee, fight or copulate) within the individual. More recent studies have rightly emphasized the adaptive nature of courtship in terms of its direct effects reproductive success (e.g. Brown, 1967; Nisbet, 1973, 1977; Hunt, 1980; Tasker and Mills, 1981).

There are only a few reports on the courtship behaviour of the Kittiwake. Descriptions can be found in Paludan (1955). Cullen (1957) contrasted the behaviour of the Kittiwake with that of typical ground-nesting gulls such as the Herring Gull and showed that courtship behaviour seen in the Kittiwake has been shaped over evolutionary time, by the habit of nesting on small cliff ledges and the consequent protection this gives from predation.

The aims of this chapter are first to give descriptions of Kittiwake courtship behaviour based on observations of birds of known sex. The investigation has been limited only to courtship that is conspicuous and performed in the context of the pair together at the nest-site. These are: the greeting ceremony, head-tossing, courtship feeding and copulation. Second, the probabilistic relationships between each behaviour as they occur in sequence, will be presented. This will provide a framework within which each behaviour can be studied in relation to the status of the pair (i.e. SAME or CHANGE).

Results

1. Descriptions of courtship behaviour.

a. The greeting ceremony.

Probably the most visually and aurally conspicuous courtship behaviour seen in the Kittiwake is the greeting ceremony. As its name implies, the greeting ceremony is seen after a bird returns to its mate at the nest-site (return greeting). However, it also occurs in an almost identical form in pairs already together at the nest-site (spontaneous greeting). The vocalization associated with the ceremony is that from which the Kittiwake derives its name and will be referred to as "kittiwaaking".

The "kittiwaaking" vocalization usually starts first in the returning bird as it flies around the colony before returning to the mate at the nest-site. Before "kittiwaaking" begins in the returning bird, it often utters one or several "owe" vocalizations. These usually elicit a clear response of recognition in the mate at the nest-site, who then starts "kittiwaaking" as well. After the birds come together at the nest-site, "kittiwaaking" continues and the greeting ceremony is performed. Both birds stand with their body axes varying from parallel to perpendicular. If parallel, the birds are usually head-to-head. Regardless of their relative orientation, the bodies of both birds, particularly the head and bill regions, are normally in close proximity throughout the greeting ceremony. While "kittiwaaking" the bill is held open, revealing the vermilion coloured inner lining of the mouth and the tongue held up in the mouth cavity. The head and neck regions of male and female are repeatedly moved up and down or side to side, in synchrony with the vocalization. At the end of the greeting, "kittiwaaking" stops and both birds normally raise their bills while bobbing the head up and down (termed upward choking; Tinbergen, 1959).

There was some variability in the form of the greeting ceremony. Most notably, ceremonies varied in length, depending on the number of "kittiwaaks" performed (see Heath et al., 1982). Sometimes only the "upward choking" component was performed, although in these cases, a full greeting ceremony was not considered to have occurred.

Few differences in the greeting ceremony as performed by male and female were apparent. The relative attitudes of each bird were often such that the male stood above the female. Various forms of aggressive behaviour were noted during greeting and in all cases the aggression was directed from the male toward the female. For example, the male was observed to direct his bill at the female's bill and this often ended in the female being pecked. The reaction in the female to this aggression was to turn her bill away from the male and avoid his head and bill region (facing-away). However, facing-away in the female was also observed out of this context with no apparent cause. Facing-away was observed in 18 percent (n=3067) of greeting ceremonies seen in 1980.

b. Head-tossing.

Head-tossing occurred either spontaneously or after a greeting ceremony. It was never seen in single birds at the nest-site. At the start of a bout of head-tossing the female usually takes up a position below that of the male. This is accomplished by the female either bending her legs in a squatting posture or sitting on the nest-site. With body axis horizontal and head drawn in, the bill is moved (tossed) quickly up and more slowly down in a rhythmical fashion. At the highest point of the head-toss, the angle of the bill varies from somewhat above the horizontal to vertical. During the upward movement of the bill the female produces a thin, squeek vocalization.

Most frequently the female head-tossed alone (72 percent of 1058 bouts of head-tossing) but sometimes the male also performed the behaviour with the female (27 percent). On three occasions the male head-tossed alone. In addition to frequency of occurrence, the form and duration of the behaviour was different in males and females. The male's head-toss was usually much shallower than the female's, and on 98 percent of occasions when both head-tossed (n=286), the female performed the behaviour for a longer period than the male.

c. Courtship feeding.

After head-tossing, the male frequently fed the female. This behaviour is termed courtship feeding. During a feeding, the male first regurgitates a food bolus into his throat region and then opens his bill. The female then feeds from the throat of the male. Food was very rarely regurgitated onto the nest-site before feeding. Several feedings sometimes took place in rapid succession, but these were recorded as single bouts of courtship feeding.

d. Copulation.

Copulation occurred only after head-tossing and rarely after courtship feeding. Copulation starts with the female sitting down on or near the nest-site with tail pointing outward. The male then mounts the female with a few flaps of his wings and after a pause of varying length, usually begins to "tread" on the female's back. At the same time, the female often looks around at the male and pecks or nibbles at his breast feathers. At the time of mounting the female's tail rests flat on the rim of the nest but sometime after she raises her tail to an angle approximately 30-40 degrees above the horizontal. After varying lengths of time the male then begins to wag his tail back and forth in a rhythmical fashion, and shortly thereafter, pushes his cloacal region under the female's tail in order to make cloacal contact. During tail-wagging and particularly cloacal contact, the male usually utters a series of short, muffled "ehee" vocalizations (termed copulation call) while vigourously flapping his wings. Cloacal contact is usually repeated several times, after which the male remains on the female's back before dismounting.

Considerable variation in copulatory behaviour was seen. Sometimes the male mounted after only a short period of head-tossing by the female and at other times the male never achieved a mounting. Some males almost immediately started to tail-wag before cloacal contact while others spent several minutes on the female before contact occurred. Frequently, cloacal contact was not attempted by the male. Sometimes the female prevented cloacal contact by failing to raise her tail above the nest.

2. Sequences of courtship behaviour.

Courtship behaviour described in a-d above, occurred in a well defined sequence. First one bird returned to the other at the nest-site and a greeting usually occurred. Greetings also occurred spontaneously in a pair already together at the nest-site. Head-tossing sometimes followed, or it also occurred spontaneously. Following head-tossing, courtship feeding or copulation took place. Copulation also followed courtship feeding. Courtship feeding or copulation were never seen to occur spontaneously.

Greetings were much less common after a return with nest material than one without. Of 166 returns with nest material seen in all three years of study, 53 percent were followed by a greeting ceremony. In contrast, almost all returns without nest material were followed by a greeting (see below). For this reason, returns with nest material were excluded from the analysis of sequences of courtship behaviour. The sex of the returning bird could not always be determined (usually because the colour-rings were obscured from view). These returns were also excluded. All such sequences seen in study pairs in 1979, 1980 and 1981 were pooled as there was no significant between year variation in transition probabilities between points in the sequence (2X2 contingency Chi-square tests, df=1). A sequence started either by a return to the mate at the nest, a spontaneous greeting or spontaneous head-tossing. Sequences were categorised into groups according to these methods of commencement and graphically represented in Figures 2.1 and 2.2. Arrows indicate the temporal flow through each sequence. Differences between transition probabilities were tested using a 2X2 Chi-square with one degree of freedom.

Of 2078 returns observed in all years, 95 percent were followed by a greeting. Female head-tossing occurred more than four times as often after a return greeting than after a spontaneous greeting

Figure 2.1: Outcome of all returns to mate seen between pair-formation and egg-laying. 1979-81 combined. Returns of birds of undetermined sex were excluded, as were those involving nest material. Arrows indicate temporal flow through sequence.

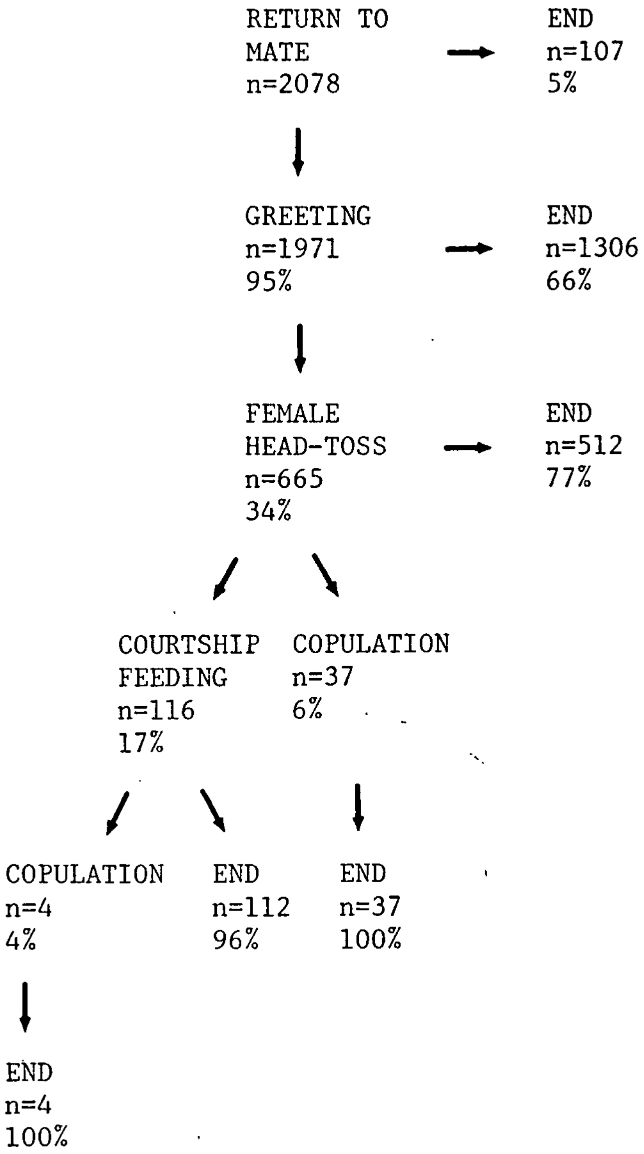
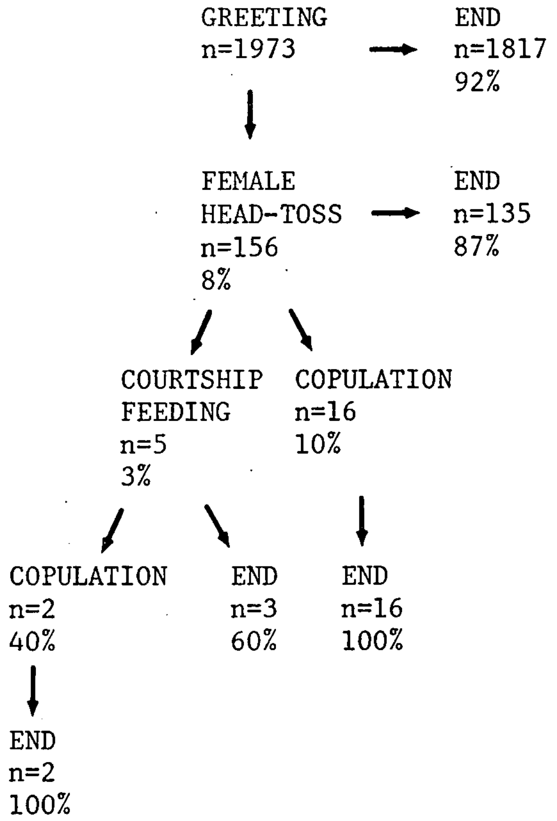
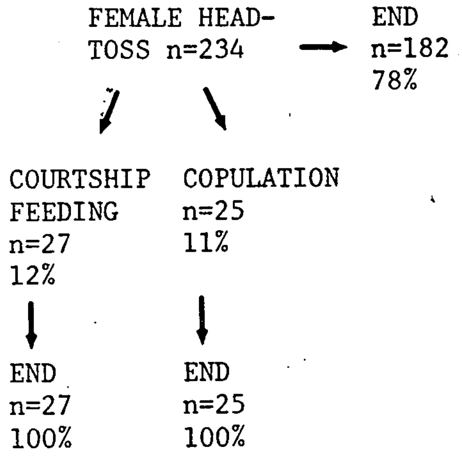

RETURN TO MATE n=2078
END n=107 5%
GREETING n=1971 95%
END n=1306 66%
FEMALE HEAD-TOSS n=665 34%
END n=512 77%
COURTSHIP FEEDING n=116 17%
COPULATION n=37 6%
COPULATION n=4 4%
END n=112 96%
END n=37 100%
END n=4 100%

Figure 2.2: Outcome of all spontaneous greetings and bouts of spontaneous female head-tossing seen between pair-formation and egg-laying. 1979-81 combined. Arrows indicate temporal flow through sequence.

SPONTANEOUS GREETINGS



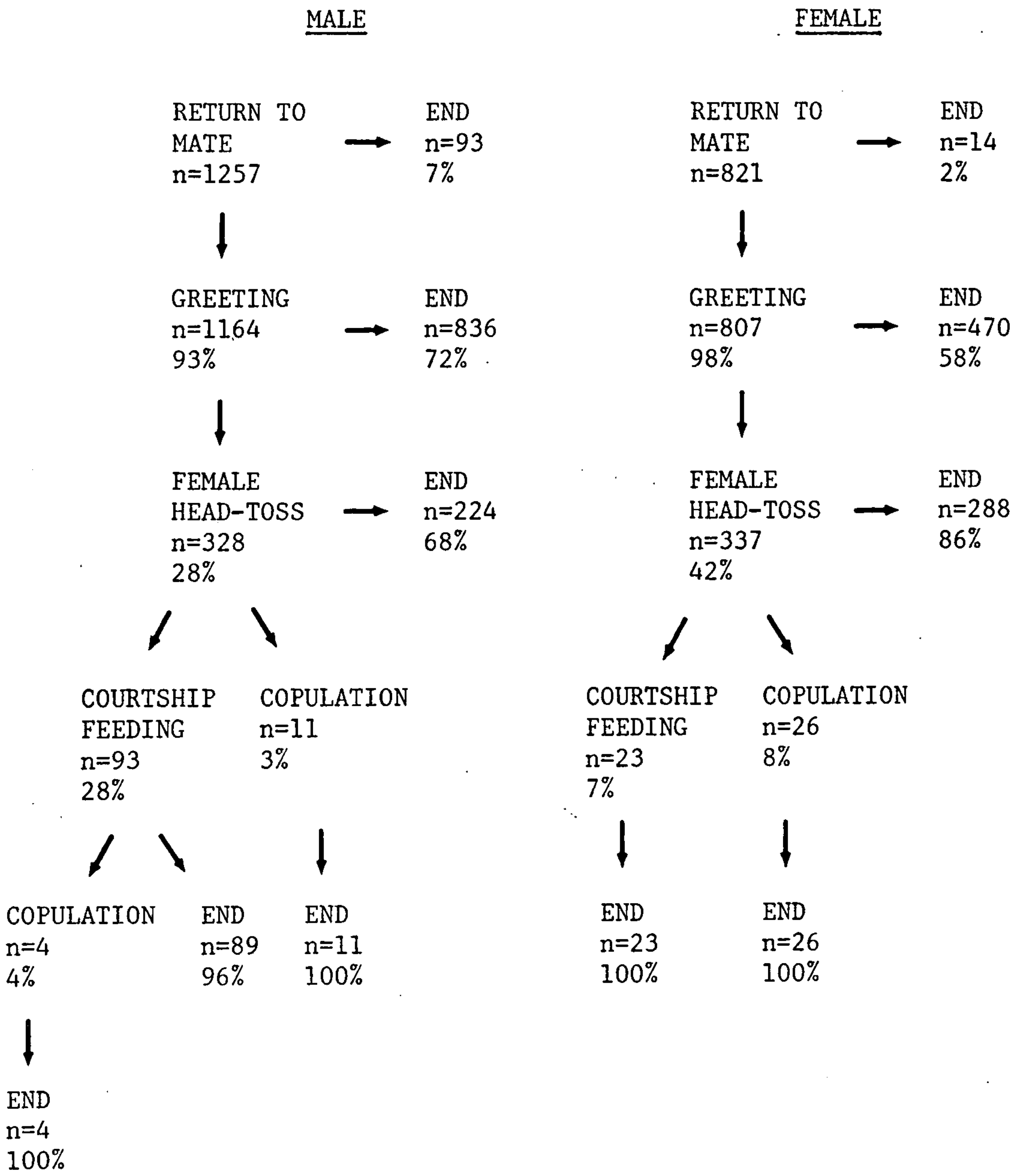
SPONTANEOUS FEMALE HEAD-TOSSING



(Chi-square=399.2, $p < 0.005$). Courtship feeding followed female head-tossing almost six times as often in return greeting sequences than in spontaneous greeting sequences (Chi-square=20.4, $p < 0.005$), and about 1.5 times as often in spontaneous head-tossing sequences (Chi-square=4.5, $p < 0.05$). Courtship feeding followed female head-tossing four times more frequently in spontaneous head-tossing sequences than in spontaneous greeting sequences (Chi-square=8.6, $p < 0.005$). Copulation followed female head-tossing about half as often in return greeting sequences than in either spontaneous greeting sequences (Chi-square=4.6, $p < 0.05$) or spontaneous head-tossing sequences (Chi-square=7.1, $p < 0.01$). There was no significant difference in the frequency with which copulation followed female head-tossing in spontaneous greeting and spontaneous head-tossing sequences (Chi-square=0, ns).

The return sequences used in Figure 2.1 were segregated according to the sex of the returning bird and presented in a similar fashion in Figure 2.3. For every female return, about 1.5 male returns were observed. This ratio deviated significantly from unity (Chi-square= 46.3, $p < 0.005$). Greeting followed the return of the female more often than the return of the male. The difference was small but significant (Chi-square=33.0, $p < 0.005$). Head-tossing occurred 1.5 times as often after a female return greeting than after a male return greeting (Chi-square=39.3, $p < 0.005$). Courtship feeding followed female head-tossing four times more often in male return sequences than in female return sequences (Chi-square=53.5, $p < 0.005$). In contrast, copulation followed female head-tossing over twice as often in female return sequences than in male return sequences (Chi-square=6.0, $p < 0.05$).

Figure 2.3: Outcome of all returns to mate seen between pair-formation and egg-laying in relation to the sex of the returning bird. 1979-81 combined. Returns with nest material were excluded. Arrows indicate temporal flow through sequence.


MALE
RETURN TO MATE n=1257
END n=93 7%
GREETING n=1164 93%
END n=836 72%
FEMALE HEAD-TOSS n=328 28%
END n=224 68%
COURTSHIP FEEDING n=93 28%
COPULATION n=11 3%
COPULATION n=4 4%
END n=89 96%
END n=11 100%
END n=4 100%
FEMALE
RETURN TO MATE n=821
END n=14 2%
GREETING n=807 98%
END n=470 58%
FEMALE HEAD-TOSS n=337 42%
END n=288 86%
COURTSHIP FEEDING n=23 7%
COPULATION n=26 8%
END n=23 100%
END n=26 100%

Discussion

Paludan (1955), Cullen (1957) and Tinbergen (1959) have reported on aspects of the courtship behaviour of the Kittiwake. In terms of descriptions of behaviour and behavioural sequences, the observations presented here differ in only minor respects from those given by these workers. What has been added is derived from the fact that a quantitative approach was used in describing behavioural sequences and the sex of the birds under observation was known

An important observation in this chapter is that courtship behaviour in the Kittiwake occurred in a particular sequence: return to mate at nest-site, greeting ceremony, head-tossing, courtship feeding or copulation, (or both in that order). Just as each of these behaviour patterns is represented in most gull species, so too is the sequence (e.g. Noble and Wurm, 1943; Moynihan, 1957; Tinbergen, 1959; Brown, 1967; Tasker and Mills, 1981). Thus, despite the form of the courtship behaviour being somewhat different through adaptation to the cliff-nesting habit (Cullen, 1957), the Kittiwake appears to have retained sequences of behaviour common to other Larids. This suggests that the sequence of courtship is, in evolutionary terms, less plastic than the form of each behaviour and further that it probably has an important function transcending that of its constituent parts. A possibility is that the sequence functions to "allow" courtship feeding and copulation to occur at an appropriate frequency and time during the nesting cycle. This would be important in terms of reproductive success (Brown, 1967; Tasker and Mills, 1981). Courtship feeding and copulation were the end points of the sequence and were never observed to occur spontaneously. By there very nature, both require considerable physical contact between partners, which may be impossible without the performance of preliminary behaviour such as greeting and/or head-tossing. This may function to reduce natural aggressive tendencies in male and female and gradually prepare partners for subsequent contact.

However, if it is assumed that it is more efficient to perform courtship feeding or copulation spontaneously, one may ask why individuals behaving in such a way have not been favoured by selection. The answer may lie in the high costs of having to reduce aggressive tendencies in order to allow courtship feeding and copulation to occur spontaneously. Aggressive individuals are probably more successful in competing for food, a mate or a nest-site and are better able to defend a nest-site once found. The costs of being less successful in this regard, may outweigh the benefits gained by the ability to perform courtship feeding and copulation without preliminary activities.

Data presented in this chapter suggest that there is an asymmetry of aggressive tendencies within a pair of Kittiwakes and further that the male is the more aggressive bird within a pair. Intra-pair aggression during greeting was always directed at the female from the male and only females were seen to face-away. Facing-away is considered a classic appeasement behaviour (Tinbergen, 1960; Nelson, 1965) because it functions to hide the bill (the most important offensive "weapon" in the Kittiwake: Cullen, 1957) from the view of the aggressive bird. Male Kittiwakes compete keenly among themselves for nest-sites, which they commonly retain from year to year (Coulson, 1971; Coulson and Thomas, 1980). There is probably a greater requirement for males to be aggressive toward conspecifics and this aggressiveness appears to "spill over" into the pair relationship (see Nelson, 1972).

It was found that transition probabilities between each behaviour in the sequence depended upon the point at which the sequence was entered. Differences in probabilities can be explained largely in proximate terms. For example, females head-tossed much more frequently after return greetings than after spontaneous greetings. This reflects the fact that the cause of spontaneous greetings was probably extrinsic (i.e. behaviour of other birds in colony: see Coulson and Dixon, 1979), while the cause of a return of a bird to its mate and subsequent greeting was presumably a result of intrinsic factors controlling behaviour in the male and female. Head-tossing also occurred more frequently after a female return than after a male return greeting. The direction of this trend is unexpected, as the male is likely to be in a better position to feed the female after a return from an absence away, rather than vice versa. The reason for the difference may derive from differences in the proximate reasons for returning to the mate at the nest-site. One reason a female returns to a male may be to procure food or a copulation from him and this may have resulted in a higher proportion of female return greetings followed by head-tossing. Courtship feeding occurred proportionately more frequently in male return sequences than those of the female. An obvious reason for this trend is that, while away from the colony, the male is probably feeding and is thus more capable of feeding the female upon his return.

This chapter has shown that courtship behaviour in the Kittiwake occurs in a specific sequence leading to courtship feeding and/or copulation and that transition probabilities between behaviour in the sequence are dependent upon the point at which the sequence is entered. This information is used in the following chapters as a partial guide to the analysis of behavioural differences between SAME and CHANGE pairs.

CHAPTER 3. BREEDING EXPERIENCE AND POSITION IN COLONY

Introduction

In studying the influence of pair-status on behaviour of Kittiwake pairs, the approach used was non-manipulative and relied on the "natural experiment" provided by birds either retaining mates from the previous year (SAME pairs) or changing mates (CHANGE pairs). In such an approach, control of potential confounding variables is often difficult and it is thus, incumbent upon the investigator to attempt to identify these variables and assess their possible effects on the planned comparisons. Two such variables were identified here: position of pair in colony (centre or edge) and breeding experience (number of years bred at North Shields) of the birds making up each pair.

There is reason to believe that these variables may influence the behaviour of Kittiwakes. Coulson (1968) found significant differences in adult (male) survival and reproductive success, between individuals nesting in the centre compared to those nesting at the edge of the warehouse colony. He attributed the trends to either differences inherent in the particular area of the colony or to differences in the "quality" of birds recruited into each area. Wooller (1979) found that greeting rates were higher in pairs nesting in the centre of the colony than those nesting at the edge, and further that fewer greetings were followed by female head-tossing in pairs nesting at the edge. The author suggested that these behavioural differences may have been a result of higher nesting density in the centre of the colony producing more social facilitation of behaviours such as greeting and head-tossing.

Age or breeding experience has been found to influence many aspects of the reproductive biology of the Kittiwake (Coulson, 1966;

Thomas, 1980) and other seabirds (see Ryder [1980] for review). Relationships between age and reproductive behaviour are less well documented, however, there is little doubt that they do exist in some bird species and that they are probably of biological importance (e.g. Ryan and Dinsmore, 1980; Bruggers and Jackson, 1981; Pugesek, 1981).

Results

Nest locations and the mean breeding experience of birds in SAME and CHANGE pairs did not differ significantly between years (Chi-square tests and ANOVA) and data from each year were pooled.

There was no significant difference in the proportion of SAME and CHANGE pairs nesting at centre or the edge of the colony (Table 3.1). Figure 3.1 shows the percent distribution of male and female breeding experience in SAME and CHANGE pairs. Few differences in the distributions for SAME and CHANGE pairs are apparent. A little under half the males and females in each group had bred at North Shields for 2 to 4 years. In "middle aged" birds (5 to 10 years breeding experience), males and females in CHANGE pairs were over-represented, while birds with more than 10 years of breeding experience were more likely to be members of SAME pairs.

The mean breeding experience of males and females in SAME and CHANGE pairs is in Table 3.2. On average, males and females in CHANGE pairs had bred for fewer years than those in SAME pairs but the differences were not significant. Variance in breeding experience was smaller in CHANGE pairs and the difference was significant for females.

Discussion

Similar proportions of SAME and CHANGE pairs nested in the centre

Table 3.1: Nest location in relation to pair-status. 1979-81 combined.

NEST LOCATION[1]	SAME		CHANGE		
	Pairs (n)	Percent	Pairs (n)	Percent	Chi-square df=1
CENTRE	16	36	9	38	0.02 ns
EDGE	29	64	15	62	

1. After Coulson (1968)

Figure 3.1: Percent distribution of breeding experience of males and females in SAME (n=45) and CHANGE (n=24) pairs. 1979-81 combined. Numbers above bars indicate sample size of birds in each category of experience.

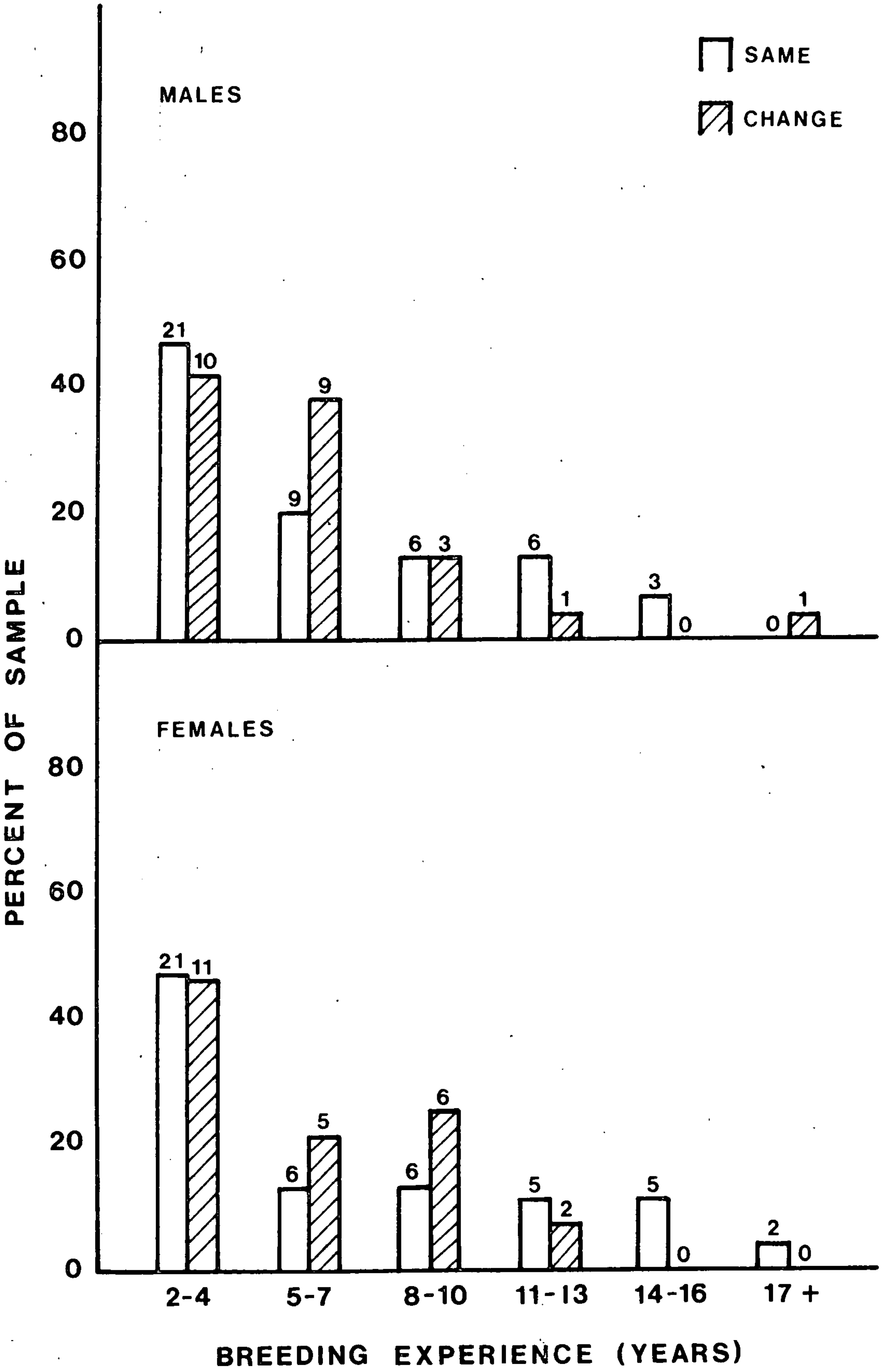

SAME
CHANGE
MALES
FEMALES
PERCENT OF SAMPLE
80
60
40
20
0
21
10
9
9
6
3
6
1
3
0
0
1
21
11
5
6
6
6
5
2
5
0
2
0
2-4
5-7
8-10
11-13
14-16
17 +
BREEDING EXPERIENCE (YEARS)

Table 3.2: Breeding age of males and females in relation to pair-status. 1979-81 combined.

	BREEDING AGE (years)							
SEX	SAME n=45		CHANGE n=24					
	Mean	s.d.	Mean	s.d.	t[1]	df	p	VH[2]
Male	6.1	4.2	5.6	3.7	0.51	55	ns	yes
Female	7.2	5.1	5.7	3.0	1.54	69	ns	no

1. Welch's modification for assumption of unequal variance: degrees of freedom approximate

2. Variance homogeneity (F test)

and edge of the colony. This observation was unexpected, as Coulson (1966) and Coulson and Wooller (1976) showed that during the growth phase of the colony (1954 to 1966), both rates of divorce and mortality were higher at the edge of the colony. This would result in overall rates of mate change being higher at the edge of the colony than at the centre and CHANGE pairs should have more likely nested at the edge (see Coulson, 1966). The reason for the discrepancy in the findings presented here and those reported in the literature may lie in the fact that the colony has experienced growth and stable phases (1967 to present) and that in each phase there were different trends in mortality rates of males (Coulson and Wooller, 1976). In the growth phase, male mortality rates were higher at the edge of the colony and this would have resulted in higher rates of mate change. Data presented in this thesis are taken from the stable phase when male mortality rates in the centre and at the edge of the colony were similar. This would result in rates of mate change being more similar between the two areas and any differences would be due to differences in divorce rates between centre and edge.

It was considered of particular importance to establish that comparisons of behaviour in relation to pair-status were not confounded by differences in breeding experience. It was found that, on average, birds in CHANGE pairs had bred for fewer years than birds in SAME pairs, but differences were small and not significant. Neither were there important differences in the proportion of birds in each category of breeding experience. In establishing the similarity of breeding experience of birds in SAME and CHANGE pairs, it is of particular significance to point out that birds with 2 to 4 years of experience were represented at similar frequencies in both groups. It is in these birds that one finds the largest improvement in reproductive success from one year to the next (Thomas, 1980) and it follows that changes in behaviour would also be greatest over this period of life. On the other hand, "middle aged" birds (those with 5 to 8 years of experience) were somewhat over-represented in CHANGE pairs and "older" birds were under represented. This difference is of little importance in terms of possible confounding effects on comparisons of behaviour in relation to pair-status, since few changes in biology, and presumably behaviour, take place in these later years (Thomas, 1980).

In conclusion, it has been shown that, with respect to position in colony and breeding experience, there were no major differences between SAME and CHANGE pairs and thus, behavioural differences revealed by comparisons of SAME and CHANGE pairs can with greater confidence be attributed to pair-status.

CHAPTER 4. TIMING OF ARRIVAL AT THE COLONY, PAIR-FORMATION AND EGG-LAYING

Introduction

In evolutionary terms, birds have adjusted the timing of reproduction to coincide with environmental conditions necessary for successful reproduction. One important environmental factor determining reproductive success is food availability during the chick rearing phase and many birds lay eggs at such a time that subsequent food availability is optimal when chicks are being fed (Perrins, 1970).

In proximate terms, the timing of reproductive events is influenced by a variety of factors such as photoperiod, weather and food availability (e.g. Lofts and Murton, 1968; Perrins, 1970; Sealy, 1975; Brown, 1967; Wingfield _et_ _al_., 1983). In many gull species, the date of egg-laying is inversely related to breeding experience (Coulson and White, 1958; Chabrzyk and Coulson, 1976; Haymes and Blokpoel, 1980; Ryder, 1980). Older birds lay, on average, earlier in the season than younger birds. The proximate mechanism responsible for this trend is thought to be hormonal. Young birds generally show later development of the gonads compared to older birds (e.g. Brown, 1967; Mills, 1973) and, as a result, reproduce later in the season.

Pair-status influences laying date in the Kittiwake (Coulson, 1966; Thomas, 1980), Red-billed Gull (Mills, 1973), Manx Shearwater (Brooke, 1978) and Fulmar (Ollason and Dunnet, 1978). In general, females that change mates breed, on average, later than those that retain the same mate from the previous year. Coulson (1966) suggested that a hormonal difference caused by mate change may be a factor contributing to later laying. Mills (1973) suggested that the longer time required to establish a pair-bond in birds that change mate may be responsible for the observed trend. Thomas (1980) showed that an important factor influencing date of egg-laying in females that changed mate was the difference in breeding experience of the new male, compared to the previous partner. If the new male was younger than the previous male, females tended to lay eggs relatively later than in the previous year, while the reverse was the case among females taking a relatively older partner.

In many colonial species of gulls, reproductive success is related to the timing of egg-laying. Later laying birds tend to lay smaller clutches, hatch fewer eggs and fledge fewer chicks (e.g. Coulson and White, 1961; Coulson _et_ _al_., 1969; Morris and Haymes, 1977). There is also evidence that in some species, very early layers also do poorly in terms of reproductive success and it is those birds laying at the peak for the colony as a whole that show the highest reproductive success (Patterson, 1965; Parsons, 1975; Chardine and Morris, 1983). Thus, the optimal strategy for a colonial nesting bird may be to synchronize laying with other birds in the colony and not to lay eggs too early or too late. This involves making the necessary preparations for breeding (e.g. returning to the colony, finding a mate) at an appropriate length of time in advance of actual egg-laying.

The aims of this chapter are to determine the relationships between pair-status and timing of arrival at the colony, timing of pair-formation and timing of egg-laying. The potential for late pairing to cause late egg-laying will be investigated.

Results

Since the mean absolute dates of arrival, pair-formation and egg-laying differed significantly between years (ANOVA, $p < 0.05$) dates were expressed as deviations from the mean dates for SAME and CHANGE pairs combined. For example, the mean date of laying (first eggs) in 1979 was 23 May and a female laying on 26 May would be considered to have laid on day +3. Dates occurring before the mean are expressed as negative numbers. As a result of the conversion to relative dates, there was no significant between year variation in the parameters dealt with in this chapter (ANOVA) and data for each year were pooled.

In terms of absolute dates, birds in study pairs arrived back to the colony from January to April in all three years. Pairing occurred on the day of arrival or sometime thereafter, while egg-laying occurred during May and early June. Mean absolute dates of arrival, pair-formation and egg-laying for SAME and CHANGE pairs in each year are in Appendix B.

The relative dates of arrival, pair-formation and egg-laying for SAME and CHANGE pairs are in Table 4.1. There were no significant differences between SAME and CHANGE pairs in any of the parameters, however, some trends were apparent. Despite relatively similar dates of arrival, CHANGE pairs formed, on average, 12 days after SAME pairs. The mean date of egg-laying was very similar in both groups, the difference being less than one day.

Table 4.2 shows the mean times between arrival, pair-formation and egg-laying for SAME and CHANGE pairs. After arrival, it took, on average, over six days longer for males to take a new mate, than to re-pair with a partner from the previous year. The difference was significant. It took females, on average, about 12 days longer to take a new mate, but possibly due to large variance in the data, the difference was not significant. The period from pair-formation to egg-laying was, on average, nine days shorter in CHANGE pairs compared

Table 4.1: Relative dates of arrival, pair-formation and egg-laying in relation to pair-status. 1979-81 combined.

		RELATIVE DATE[1]							
		SAME n=45		CHANGE n=24					
EVENT		Mean	s.d.	Mean	s.d.	t[2]	df	p	VH[3]
Arrival	Male	-1.7	28.5	3.4	32.7	0.65	43	ns	yes
	Female	-1.0	20.9	0.3	22.0	0.24	47	ns	yes
Pair-formation		-4.1	26.7	7.9	31.0	1.61	43	ns	yes
Egg-laying		-0.8	4.8	0.0	6.7	0.52	37	ns	yes

1. Dates relative to mean for SAME and CHANGE combined. A minus sign signifies a date before the mean

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

3. Variance homogeneity (F test)

Table 4.2: Time between events in the reproductive cycle in relation to pair-status. 1979-81 combined.

EVENTS		SAME n=45 Mean	SAME n=45 s.d.	CHANGE n=24 Mean	CHANGE n=24 s.d.	t[1]	df	p	VH[2]
Arrival to pair-formation	Male	3.0	5.6	9.9	8.4	3.62	35	<.001	yes
	Female	13.6	21.2	25.3	29.8	1.71	37	ns	yes
Pair-formation to egg-laying		89.5	33.0	80.5	35.1	1.04	46	ns	yes

TIME (Days)

1. Welch's modification for assumption of unequal variance: degrees of freedom approximate

2. Variance homogeneity (F test)

to SAME pairs, but the difference was not significant.

In order to determine whether late pairing caused late laying, and whether the relationship depended on pair-status, dates of egg-laying were plotted against the dates of pair-formation for SAME and CHANGE pairs (Figure 4.1). There was no significant correlation between date of pair-formation and date of egg-laying for either group (SAME: r=-0.20, df=43; CHANGE: r=0.29, df=22) and the slopes of the lines did not differ significantly (SAME: slope=-0.034, se=0.03, n=45; CHANGE: slope=0.052, se=0.04, n=24; t=1.72, df=50). However, the positive slope for CHANGE pairs suggests that late egg-laying may be related, to a stronger degree, with late pairing in this group.

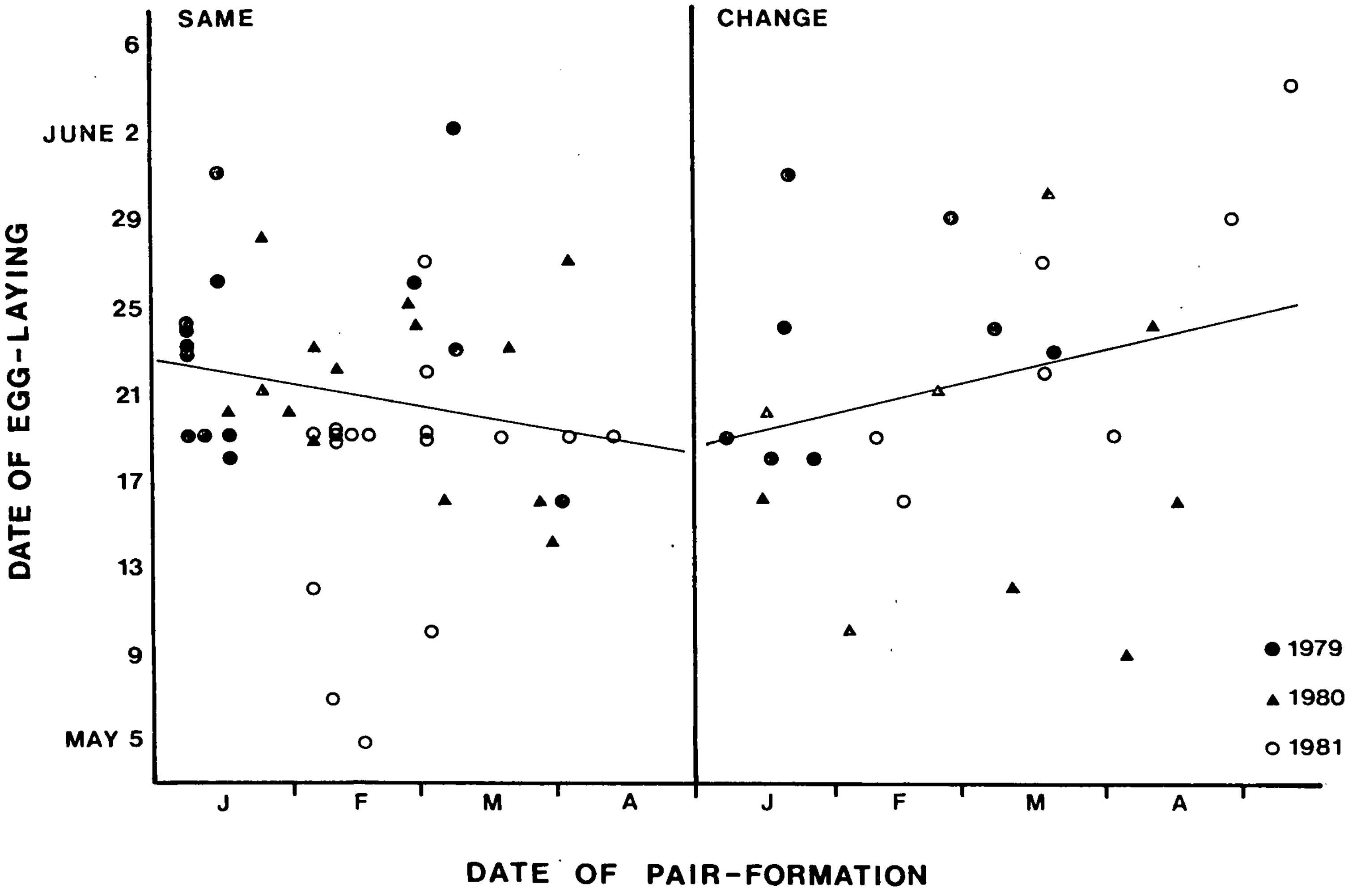
Discussion

Coulson (1966) found that female Kittiwakes in CHANGE pairs laid, on average, later in the season than those in SAME pairs. Mills (1973) found a similar trend in Red-billed Gulls and suggested that the difference was a result of the extra time needed to find a new mate and form a partnership. The results presented here are not in accord with these findings, or Mills' (1973) suggestion. Despite pairing with their mates, on average, 12 days later (not significant), females in CHANGE pairs laid eggs less than one day later than females in SAME pairs. Thus, females that changed mates appeared to be able to compensate for relatively late pairing and did not lay eggs correspondingly late.

On an individual pair basis, there was no significant correlation between date of pair-formation and date of egg-laying. However, there was a suggestion that the relationship, albeit not significant, was stronger in a positive direction for CHANGE pairs than for SAME pairs. Thomas (1980) found that late pairing caused relatively late laying in

Figure 4.1: Relationship between date of pair-formation and date of egg-laying in SAME (n=45) and CHANGE (n=24) pairs. Equations for lines: SAME Y=-0.034X + 142.47, r=-0.20, df=43, ns; CHANGE Y=0.052X + 138.50, r=0.29, df=22, ns.

What is
X
Y


SAME
CHANGE
DATE OF EGG-LAYING
6
JUNE 2
29
25
21
17
13
9
MAY 5
J
F
M
A
J
F
M
A
DATE OF PAIR-FORMATION
● 1979
▲ 1980
○ 1981

CHANGE pairs, but had no affect on SAME pairs. Therefore, in years when birds return to the colony and pair-up relatively late, one might expect to find CHANGE pairs laying later than SAME pairs, but in early years, the differences would be smaller. The mean date of return of Kittiwakes to the warehouse has advanced (become earlier) over the history of the colony, although recently it has become later (Coulson and Thomas, in prep.). This may explain why in this study, no relationship between pair-status and laying date was found, whereas, in an earlier study at the same colony (Coulson, 1966), females in CHANGE pairs laid consistently later than SAME pairs. During the present study, birds in CHANGE pairs presumably arrived back to the colony early enough to lay at a similar time to birds in SAME pairs. Before 1966, mean dates of return were later (Coulson and Thomas, in prep.), which may have resulted in later laying in CHANGE pairs compared to SAME pairs.

The tendency for CHANGE pairs to form later than SAME pairs was not entirely the result of birds in the former group arriving back to the colony later. The period between arrival and pair-formation was, on average, longer in both males (significant) and females (not significant) in CHANGE pairs compared to those in SAME pairs. Later pairing in CHANGE pairs can likely be attributed to the longer time required to find a new mate compared to the time required to reform a partnership with a previous mate.

CHAPTER 5. ATTENDANCE AT THE NEST-SITE

Introduction

Many Kittiwakes return to the colony from the winter season up to four months in advance of egg-laying (Coulson and White, 1958; Chapter 4, this thesis). As a seabird, the Kittiwake is by no means unusual in this respect. Coulson and Horobin (1972) found that Fulmars occupied their nest-sites up to six months prior to egg-laying. Gannets (Nelson, 1978) and Common Guillemots (Birkhead, 1978) return to their colonies and attend nest-sites several months before eggs are laid.

Why do Kittiwakes return so early? Since there is always a chance that divorce will occur or a mate will die between breeding seasons, early arrival may ensure that a mate is found far enough in advance of egg-laying to allow for successful reproduction. Cullen (1957) suggested that Kittiwakes, unlike other gulls, return directly to their nest-sites upon return from winter quarters because of the shortage of suitable ledges upon which to build a nest. This, together with the high densities at which Kittiwakes breed (Coulson and White, 1960) results in heavy competition for nest-sites (Coulson, 1971). For birds returning to a previously used (by them) nest-site, an early return would be important in terms of securing the site and defending it from other birds in search of a new site. For this latter group of birds, an early return may function to increase the chances of finding a good quality nest-site. This would be particularly important in the natural cliff-nesting situation where nest-site quality probably varies substantially more than at the warehouse colony.

The Kittiwake defends its nest-site by occupation. Attendance at the nest-site during the period between pair-formation and egg-laying has not been studied in detail in this species. Coulson and White (1958) showed that between arrival and laying, Kittiwakes, on average, spend about two-thirds of their time occupying their nest-sites and that experienced breeders spend more time on the nest-site than birds breeding for the first time.

The Kittiwake rarely leaves its nest-site unattended during the pre-egg period (Coulson and Horobin, 1972), and one can infer that most or all of the interactions between pair members take place at the nest-site. Thus, the amount of pair attendance in the Kittiwake is an important factor determining the opportunity for interaction of partners. Attendance patterns of male and female dictate the availability of "off-duty" time during which feeding and other self-maintenance activities occur. The aim of this chapter is to present nest-site attendance patterns for birds in SAME and CHANGE pairs and evaluate differences in terms of their possible causes and effects.

Results

There was no significant between year variation in attendance patterns of birds in SAME and CHANGE pairs (ANOVA) and data from each year were pooled. Sample sizes of spot observations of attendance (see Methods, Chapter 1) are in Appendix C.

1. Number of nest-sites occupied between pair-formation and egg-laying.

After pair-formation, the majority of study pairs attended a single nest-site and eventually laid eggs there. However, several attended other nest-sites in addition to those upon which they laid eggs. Only pairs seen on alternate nest-sites on more than two visits to the colony were classed as attending more than one nest-site.

Some window ledges on the warehouse supported two nests close together, often with rims touching; these were not considered separate sites in this analysis.

Twenty-six percent of CHANGE pairs (n=24) and 18 percent of SAME pairs (n=45) occupied more than one nest-site. The difference was not significant (Chi-square=0.30, df=1). All alternate nest-sites were on the west-side of the warehouse and no pairs from elsewhere in the colony were ever seen to occupy alternate sites on the west-side.

2. Attendance between pair-formation and egg-laying.

Attendance at the nest-site over this time is presented for each of three periods (see Methods, Chapter 1). Without regard for the sex of the bird at the nest-site, attendance was separated into three categories: the pair, a single bird or neither bird. Observations of a single bird are not presented as they simply represent the balance of observations after those of the pair and neither bird at the nest-site have been taken into account.

Attendance as a pair is presented in Table 5.1. Birds in CHANGE pairs were seen together more often than birds in SAME pairs in each of the periods. Differences were significant in the first two periods. During the first two weeks after pair-formation, birds in CHANGE pairs were seen together, on average, about twice as often as birds in SAME pairs. Differences decreased in the two subsequent periods.

The proportion of observations of neither bird (nest-site unattended) is in Table 5.2. During the first two weeks after pair-formation, SAME pairs were observed to leave their nest-site unattended three times more often than CHANGE pairs. The difference was significant. This trend persisted in the next period but the

Table 5.1: Percent of observations of the pair at the nest-site. 1979-81 combined.

PERIOD[1]	PROPORTION OF OBSERVATIONS OF PAIR							
	SAME				CHANGE			
	Mean Percent	Mean (Arcsine	s.d. scale)	Pairs n	Mean Percent	Mean (Arcsine	s.d. scale)	Pairs n
1	23	0.50	0.30	45	44	0.73	0.27	23
2	18	0.43	0.20	45	31	0.59	0.27	21
3	15	0.40	0.27	44	20	0.46	0.28	21

	SAME vs. CHANGE			
PERIOD	t[2]	df	p	VH[3]
1	3.20	51	<.01	yes
2	2.42	32	<.05	yes
3	0.82	40	ns	yes

1. Period 1: first two weeks after pair-formation
   Period 2: intervening period
   Period 3: last two weeks before egg-laying

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

3. Variance homogeneity (F test)

Table 5.2: Percent of observations of neither bird at the nest-site.
1979-81 combined.

PERIOD[1]	PROPORTION OF OBSERVATIONS OF NEITHER BIRD							
	SAME				CHANGE			
	Mean Percent	Mean (Arcsine	s.d. scale)	Pairs n	Mean Percent	Mean (Arcsine	s.d. scale)	Pairs n
1	19	0.45	0.32	45	6	0.25	0.23	23
2	11	0.34	0.20	45	8	0.28	0.14	21
3	1	0.12	0.19	44	2	0.14	0.15	21

PERIOD	SAME vs. CHANGE			
	t[2]	df	p	VH[3]
1	2.96	61	<.01	yes
2	1.41	57	ns	yes
3	0.46	51	ns	yes

1. Period 1: first two weeks after pair-formation
   Period 2: intervening period
   Period 3: last two weeks before egg-laying

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

3. Variance homogeneity (F test)

difference was not significant. During the two weeks before egg-laying, the nest-site was almost never left unattended by either group of birds.

The proportion of observations of the male or female, either with its partner or as a single bird, gives the total amount of attendance at the nest-site. Total attendance for birds in SAME and CHANGE pairs is in Table 5.3. During the first two weeks after pair-formation, males and females in CHANGE pairs were seen, respectively, 15 and 18 percent more frequently than counterparts in SAME pairs. Both differences were significant. In the two subsequent periods, males in SAME and CHANGE pairs were seen on about half of occasions and differences were not significant. In contrast, females in CHANGE pairs were seen, respectively, 19 and 10 percent more often than females in SAME pairs, in the two subsequent periods. Both differences were significant.

2. Patterns of attendance during the two week period before, and five day period after egg-laying in 1980.

The daily observation periods undertaken before and after egg-laying in 1980 made possible a closer analysis of attendance patterns during this period (day 0 indicates the day first eggs were laid and either a minus or a plus sign indicate days before or after this day, respectively: see Methods, Chapter 1). Figure 5.1 shows the pattern of attendance for SAME and CHANGE pairs over the period in question. Before egg-laying, birds in CHANGE pairs were observed together about twice as often as birds in SAME pairs. None of the differences between individual pairs of points was significant (Appendix D), however, if the 14-day period before egg-laying is taken as a whole, the difference between SAME and CHANGE pairs is significant (t=2.91,

Table 5.3: Total attendance of male and female in relation to pair-status. 1979-81 combined.

PERIOD[1]	PROPORTION OF TOTAL ATTENDANCE							
	SAME				CHANGE			
	Mean Percent	Mean (Arcsine	s.d. scale)	Pairs n	Mean Percent	Mean (Arcsine	s.d. scale)	Pairs n
MALES								
1	54	0.83	0.27	45	69	0.98	0.26	23
2	57	0.86	0.18	45	57	0.86	0.22	21
3	48	0.76	0.23	44	42	0.70	0.28	21
FEMALES								
1	51	0.79	0.32	45	69	0.98	0.25	23
2	49	0.78	0.19	45	68	0.97	0.19	21
3	69	0.98	0.25	44	79	1.09	0.15	21

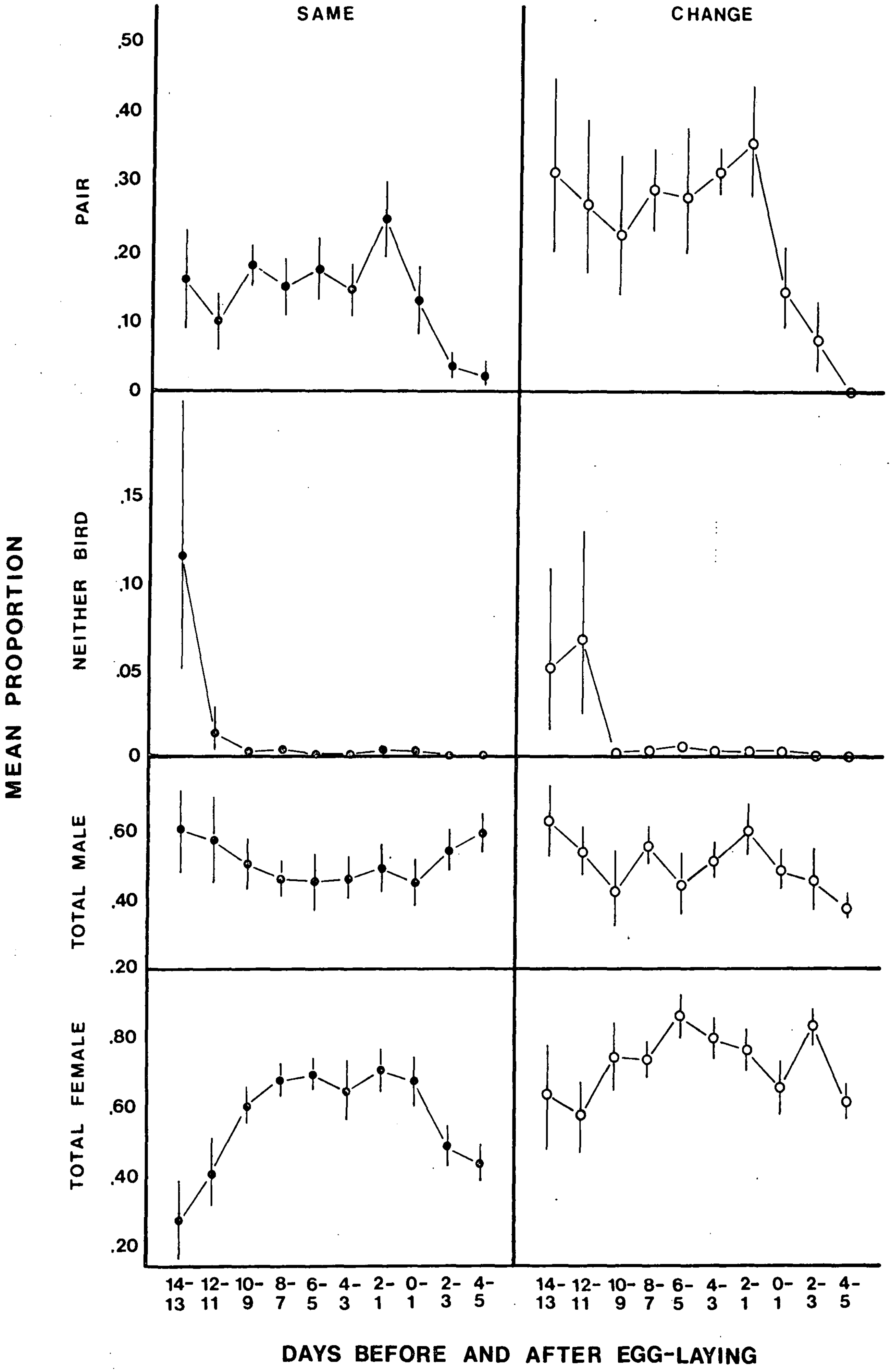
	SAME vs CHANGE			
PERIOD	t[2]	df	p	VH[3]
MALES				
1	2.22	48	<.05	yes
2	0	34	ns	yes
3	0.85	35	ns	yes
FEMALES				
1	2.69	57	<.01	yes
2	3.78	41	<.001	yes
3	2.20	62	<.05	no

1. Period 1: first two weeks after pair-formation
   Period 2: intervening period
   Period 3: last two weeks before egg-laying

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

3. Variance homogeneity (F test)

Figure 5.1: Changes in attendance patterns of birds in SAME (n=14) and CHANGE (n=9) pairs before and after egg-laying in 1980. Attendance in expressed as the mean proportion of observations of the pair, neither bird, male or female (singly and with mate). Bars are standard errors. Results of t-tests comparing means are in Appendix D.



SAME
CHANGE
MEAN PROPORTION
PAIR
.50
.40
.30
.20
.10
0
NEITHER BIRD
.15
.10
.05
0
TOTAL MALE
.60
.40
.20
TOTAL FEMALE
.80
.60
.40
.20
14-13
12-11
10-9
8-7
6-5
4-3
2-1
0-1
2-3
4-5
DAYS BEFORE AND AFTER EGG-LAYING

df=18, $p < 0.01$). Pair attendance in both groups dropped dramatically once the first egg had been laid and by five days later, was near zero. Throughout the 14 day period before, and five day period after egg-laying, the nest-site was left unattended at low frequencies in both SAME and CHANGE pairs. The nest-site was left unattended more often early in the period than late. None of the differences between SAME and CHANGE pairs was significant (Appendix D). There was no obvious seasonal trend in total male attendance in either SAME or CHANGE pairs. In both groups there was a trend for total female attendance to increase from day -14 to a peak about three or four days before egg-laying and decrease thereafter. Males in SAME and CHANGE pairs occupied the nest-site, on average, at relatively similar frequencies during the period, whereas, females in CHANGE pairs were seen consistently more often (up to over 30 percent) than females in SAME pairs. However, the majority of differences between SAME and CHANGE pairs were not significant (Appendix D).

Discussion

It is clear that attendance patterns of SAME and CHANGE pairs were different over the period between pair-formation and egg-laying. Birds in CHANGE pairs spent more time together at the nest-site than birds in SAME pairs and left the nest-site unattended less often. This either caused, or was a result of higher levels of attendance for individuals in CHANGE pairs. Females, in particular, were affected and were seen consistently more often at the nest-site than females in SAME pairs. Differences in attendance patterns between SAME and CHANGE pairs were greatest during the first two weeks after pair-formation and decreased toward egg-laying.

In proximate terms, the higher levels of pair attendance seen in

CHANGE pairs may have been a result of higher levels of individual male and female attendance in CHANGE pairs. If it is assumed that both partners attend the nest-site independently of one another, then the result of higher levels of individual attendance would be a larger overlap of male and female attendance; i.e. more attendance as a pair. This could also explain the observation that birds in CHANGE pairs left their nest-sites unattended less frequently than birds in SAME pairs. As with pair attendance, this was especially true during the first two weeks after pair-formation. Higher levels of individual attendance in CHANGE pairs may have been the result of the fact that mate change is often associated with a change of nest-site (Coulson and Thomas, 1980). Securing "ownership" of a new nest-site, that has probably been used by another pair in the previous year, may require levels of attendance higher than that required to re-occupy a site used in the previous year, especially during the initial stages of occupation.

The higher levels of pair attendance seen in CHANGE pairs could have been the cause rather than the result of higher levels of individual attendance. It may be adaptive for birds in CHANGE pairs to spend more time together with their mates because they are in the process of developing new pair relationships in contrast to reforming old bonds with a previous mate. Higher levels of pair attendance probably reduces the time required for new mates to become familiar with one another. Behaviour such as the greeting ceremony and head-tossing, can occur only while partners are together and may have important symbolic functions in reducing the natural aggressive responses between the male and female (Chapter 2). The need to perform these behaviours may be higher in CHANGE pairs than in SAME pairs, which would require higher levels of pair attendance in the former group. Differences between SAME and CHANGE pairs, in the levels of pair attendance, were greatest just after pair-formation, when male and female in CHANGE pairs were presumably unfamiliar with each other, and the requirement for aggression reducing behaviours would be correspondingly high.

If it is assumed that in order to defend the nest-site from intruders, one bird in attendance is all that is required, then an efficient system of defense would be to minimize the amount of time the pair is together at the nest-site. This would allow more "off-duty" time for both male and female during which feeding and other self-maintenance activities could be pursued. The system of nest-site defense seen in CHANGE pairs was thus, less efficient than that seen in SAME pairs, due to higher levels of pair attendance.

Attendance patterns may have implications with regard to the energy budgets of birds in SAME and CHANGE pairs because they determine the amounts of "off-duty" time available for activities such as feeding. On average, females in CHANGE pairs were seen at the nest-site on 10 to 19 percent more occasions than females in SAME pairs (depending on time of season in relation to pair-formation and egg-laying) and had correspondingly less "off-duty" time. This difference may have significantly reduced the amount of time available to females in CHANGE pairs for feeding and in turn reduce the their overall body condition. There is evidence, from field and laboratory studies, that nutrition and female body condition can affect reproductive parameters such as egg size, clutch size and the timing of egg-laying in several species (Jones and Ward, 1974; Kjallander, 1974; Dijkstra et al., 1982). These studies show that females obtaining adequate amounts of food (or food supplements), or who are in good body condition (in terms of protein and fat reserves), produce larger eggs, larger clutches and lay earlier than females receiving less food or who are in poorer condition. Thus, if females that change mates are in relatively poor body condition, this could explain the observation that they tend to lay smaller eggs and clutches and lay later than females that have retained mates from the previous year (Coulson, 1966; Mills, 1973, 1979; Cooke _et_ _al_., 1981; Ollason and Dunnet, 1978).

Examination of attendance patterns over the two week period before, and five day period after first eggs were laid (in 1980) showed differences over time and differences related to pair-status. Consistently higher levels of pair attendance were maintained by CHANGE pairs until egg-laying when pair attendance dropped dramatically to near zero in both SAME and CHANGE pairs. Pair attendance before egg-laying has been interpreted as male surveillance of the female in order to reduce the chances of cuckoldry (Beecher and Beecher, 1979; Birkhead, 1979; Zenone _et_ _al_., 1979; Lumpkin _et_ _al_., 1982). This hypothesis may apply to the the Kittiwake, even though levels of pair attendance during the last two weeks before egg-laying, ranged from only about 15 to 30 percent depending on pair-status. This is possibly the maximum amount of time the male could spend with the female due the demands imposed by having to feed himself and the female (through courtship feeding, see Chapter 7) and supply most of the material required for nest construction (unpubl. obs.). On the other hand, in terms of surveillance of the female, the levels of pair attendance noted above, are likely to be minima, since the male can potentially keep the female within his visual ambit by flying by or circling around the colony; this behaviour was seen very often, although the identity of the birds could not be determined since colour rings are usually not visible during flight. The dramatic drop to almost zero pair attendance at clutch completion would be predicted by the surveillance hypothesis, since the chances of cuckoldry at this time would be minimal. In the final chapter of this thesis it is argued that the chances of cuckoldry might be higher in CHANGE pairs than in SAME pairs and further that this may explain why the former group of birds spent more time together at the nest-site.

CHAPTER 6. THE GREETING CEREMONY AND HEAD-TOSSING

Introduction

Of all the courtship displays performed by the Kittiwake, the greeting ceremony is probably most characteristic. The sound of a Kittiwake colony is made up mostly of the "kittiwaak" vocalization associated with the ceremony and one can infer that, during the breeding season, the display is probably performed more frequently than any other in the repertoire of the species. Perhaps for this reason, considerable attention has been paid to the Kittiwake's greeting ceremony in the literature.

Wooller (1978) studied the "kittiwaak" vocalization associated with greeting and found that paired males and females recognize each other's call from one breeding season to the next. He suggested at least two functions for vocal recognition. First, Kittiwakes nest at high density on cliffs and vocal recognition of mates may serve as a means by which male and female can communicate during the return of one bird to the other at the nest-site. Second, vocal recognition between mates is important in the process of reforming pair relationships, as birds are able to find each other by voice, even if the nest-site changes from one breeding season to the next. Heath _et al._ (1982) studied quantitative aspects of the ceremony in the Kittiwake and found that the duration increased as a function of the length of time male and female had been separated.

Greeting or meeting ceremonies are seen in a variety of bird species (e.g. Gannet and several species of Booby: Nelson, 1966, 1978; Lesser Black-backed Gull: Brown, 1967; Common Guillemot and Razorbill: Birkhead, 1978; Redshank: Hale and Ashcroft, 1982) and often involve elements of aggression and appeasement in the participating birds.

There is general agreement that greeting functions to reduce aggression within the pair during meeting, and through repetition, maintain the pair relationship after initial pair-formation. There is also evidence that courtship vocalization (such as that associated with the greeting ceremony in the Kittiwake) may stimulate the female into reproductive condition and eventually to ovulation (Lehrman, 1959; Brockway, 1965; Wooller, 1973).

In established pairs of gulls, courtship feeding and copulation are usually preceded by some form of female solicitation. (Moynihan, 1957; Tinbergen, 1959). This usually takes the form of head-tossing behaviour and associated vocalizations, both reminiscent of chicks begging for food from their parents (Tinbergen, 1959). Relatively little has been written about the function of head-tossing; however, one can infer function both from context and from its effect on other individuals. Through head-tossing, the female communicates her requirements for courtship feeding and copulation to the male, and the behaviour probably stimulates the male to either feed, or copulate with, the female. Head-tossing may also act to prepare both male and female for the physical contact involved in courtship feeding and copulation, thereby reducing possible aggression within the pair.

The aims of this chapter are to present data on the timing and frequency of return, greeting and head-tossing, and occurrence of intra-pair aggression in SAME and CHANGE pairs and evaluate differences in terms of their possible causes and effects.

Results

Between year variation in behavioural parameters reported in this chapter was tested (ANOVA) and found to be not significant. Thus, data from the three years were pooled. As in Chapter 5, data taken during the time between pair-formation and egg-laying were separated into three periods (see Chapter 1, Methods) and rates of return, greeting, head-tossing and other behavioural measures are presented for each. The duration of sessions of intensive observation periods during which the data were recorded are in Appendix C.

1. Return to mate, greeting and head-tossing between pair-formation and egg-laying.

a. Return to mate at nest-site.

The return of one bird to its mate at the nest-site almost always resulted in a greeting ceremony between members of the pair. However, on only about half of occasions did a greeting occur after the return of a bird carrying nest material (Chapter 2). It is clear that the underlying reasons for a return with nest material were quite different from a return without and thus, when considering rates of return to the nest-site, those involving nest material were excluded from the analysis. However, when rates of greeting after return were considered (see 1b. below), all returns, regardless of whether or not nest material was involved, were included in the analysis. For this reason, reported rates of return greeting are sometimes higher than rates of return.

The mean rate of return (per pair per hour) of a bird of either sex to its mate at the nest-site for SAME and CHANGE pairs is in Table 6.1. Birds in CHANGE pairs returned to their mates almost three times more often than birds in SAME pairs during Period 1. The difference was significant. The same trend was also apparent during Periods 2 and 3, although the differences were smaller and only significant in Period 2. There was significantly greater variance of rates of return

Table 6.1: Rate of all returns to mate at nest-site in relation to pair-status. 1979-81 combined.

	RATE PER PAIR PER HOUR									
	SAME			CHANGE						
PERIOD[1]	Mean	s.d.	n	Mean	s.d.	n	t[2]	df	p	VH[3]
1	0.69	0.73	44	1.78	1.83	22	2.69	25	<.05	no
2	0.83	0.60	45	1.15	0.60	21	2.02	41	<.05	yes
3	0.81	1.14	45	1.05	1.20	23	0.79	44	ns	yes

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

3. Variance homogeneity (F test)

in CHANGE pairs compared to SAME pairs during Period 1, while variances were homogeneous in the subsequent periods.

In order to establish which sex was responsible for the higher rates of return in CHANGE pairs, data in Table 6.1 were segregated according to the sex of the returning bird and results displayed in Table 6.2. In general, the higher rates of return found in CHANGE pairs were caused by higher return rates of both male and female, although, the only significant difference between SAME and CHANGE pairs occurred during Period 1 and involved returns by the male. Variance in rates of return, according to sex, were in general higher in CHANGE pairs than in SAME pairs and differences were significant for both sexes in Period 1 and for females in Period 3.

On many occasions birds were seen to leave their mate at the nest-site only to return after a few seconds (see Chapter 2 for description). This behaviour is termed a "circuit" and its occurrence was systematically recorded in 1980. "Circuits" were only scored as having occurred if the bird returned within one minute from leaving the nest-site. Table 6.3 shows the number and proportion of returns to the mate at the nest-site that involved "circuits" in SAME and CHANGE pairs for each of the three time periods. The proportion of returns involving "circuits" was over three times greater among CHANGE pairs than SAME pairs in Period 1 and almost twice as great in Period 2. Both differences were significant. There was no significant difference in Period 3.

b. Greeting.

In Chapter 2 it was shown that Kittiwakes almost always performed a greeting ceremony after the return of one bird to another. Table 6.4 shows the proportion of returns followed by greeting in each of the three periods according to pair-status. There were no consistent or

Table 6.2: Rate of return of male or female to mate at nest-site in relation to pair-status. 1979-81 combined.

		RATE PER PAIR PER HOUR									
		SAME			CHANGE						
PERIOD[1]	SEX	Mean	s.d.	n	Mean	s.d.	n	t[2]	df	p	VH[3]
1	M	0.29	0.40	44	0.85	0.99	22	2.55	25	<.05	no
	F	0.38	0.46	44	0.93	1.27	22	1.97	24	ns	no
2	M	0.47	0.47	45	0.69	0.46	21	1.80	42	ns	yes
	F	0.34	0.34	45	0.46	0.37	21	1.26	38	ns	yes
3	M	0.55	1.07	45	0.66	0.77	23	0.49	61	ns	yes
	F	0.24	0.54	45	0.37	0.96	23	0.60	30	ns	no

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

3. Variance homogeneity (F test)

Table 6.3: Proportion of returns to mate at nest-site involving "circuits" in 1980, in relation to pair-status.

	SAME n=14 pairs		CHANGE n=9 pairs			
PERIOD	RETURNS (n)	PERCENT CIRCUITS	RETURNS (n)	PERCENT CIRCUITS	CHI-SQUARE[1] df=1	p
1	59	7	91	25	8.30	<.005
2	326	15	248	27	12.55	<.005
3	104	16	127	17	0.04	ns

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

Table 6.4: Proportion of returns followed by greeting in relation to pair-status. 1979-81 combined.

		SAME n=45 pairs		CHANGE n=24 pairs	
PERIOD[1]	SEX	RETURNS (n)	PERCENT FOLLOWED BY GREETING	RETURNS (n)	PERCENT FOLLOWED BY GREETING
1	M	33	100	73	100
	F	59	100	46	100
2	M	227	96	189	97
	F	185	99	115	96
3	M	84	80	104	85
	F	33	97	29	100

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

significant differences between SAME and CHANGE pairs in this regard. Greeting followed the great majority of returns in both groups.

Mean rates of return greeting for SAME and CHANGE pairs in each of the three periods are in Table 6.5. CHANGE pairs showed higher rates of return greeting in all three periods. In Period 1, CHANGE pairs greeted after return almost three times more often than SAME pairs. This difference was significant. In subsequent periods differences between the two groups decreased and were not significant. Mean rates of spontaneous greeting for SAME and CHANGE pairs in each period are in Table 6.6. CHANGE pairs spontaneously greeted more often than SAME pairs in all three periods but none of the differences was significant. The variance in rates of return greeting was significantly higher in CHANGE pairs in Period 1.

Males were seen to aggressively peck at the head and bill region of the female, and females, regardless of whether or not they were pecked at, often faced away from the male in what appeared to be an attempt to avoid the male's bill (descriptions are in Chapter 2). Table 6.7 shows the proportion of greetings seen in SAME and CHANGE pairs, during which the male actively pecked at the head and/or bill region of the female. The greetings are broken down into those following the return of the male, those following the return of the female and spontaneous greetings. The behaviour was observed at very low levels (0 to 7 percent of greetings) and there was no indication that it was observed proportionately more often in SAME or CHANGE pairs.

Table 6.8 shows a similar analysis for facing-away in the female. In general, females in SAME and CHANGE pairs did not differ with respect to the frequency of facing-away during greeting, and there was no consistent numerical trend one way or the other. The only

Table 6.5: Rate of greeting after all returns to mate at nest-site in relation to pair-status. 1979-81 combined.

	RATE PER PAIR PER HOUR									
	SAME			CHANGE						
PERIOD[1]	Mean	s.d.	n	Mean	s.d.	n	t[2]	df	p	VH[3]
1	0.68	0.73	44	1.80	1.89	22	2.68	25	<.05	no
2	0.83	0.60	45	1.14	0.60	21	1.96	41	ns	yes
3	0.88	1.14	45	1.10	1.25	23	0.71	43	ns	yes

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

3. Variance homogeneity (F test)

Table 6.6: Rate of spontaneous greeting in relation to pair-status.

1979-81 combined.

	RATE PER PAIR PER HOUR									
	SAME			CHANGE						
PERIOD[1]	Mean	s.d.	n	Mean	s.d.	n	t[2]	df	p	VH[3]
1	0.75	1.26	44	1.45	2.20	22	1.38	29	ns	no
2	0.81	0.94	45	0.95	0.73	21	0.66	52	ns	yes
3	0.26	0.54	45	0.62	1.01	23	1.60	29	ns	no

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

3. Variance homogeneity (F test)

Table 6.7: Occurrence of male pecking at the head and bill region of the female during greeting in 1980, in relation to pair-status.

GREETING TYPE	PERIOD[1]	SAME n=14 pairs		CHANGE n=9 pairs	
		GREETINGS (n)	PERCENT PECKING	GREETINGS (n)	PERCENT PECKING
After male return	1	18	6	62	2
	2	174	3	160	7
	3	74	0	101	0
After female return	1	41	5	29	3
	2	152	5	79	3
	3	30	0	26	0
Spontaneous	1	58	3	115	4
	2	314	2	260	3
	3	68	0	92	1

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

Table 6.8: Occurrence of facing-away during greeting in relation to pair-status in 1980.

		SAME n=14 pairs		CHANGE n=9 pairs			
GREETING TYPE	PERIOD[1]	GREETINGS (n)	PERCENT FACING-AWAY	GREETINGS (n)	PERCENT FACING-AWAY	CHI-SQUARE[2] df=1	p
After male return	1	18	44	62	29	1.51	ns
	2	174	18	160	35	11.85	<.005
	3	74	4	101	12	-	
After female return	1	41	49	29	28	3.18	ns
	2	152	27	79	28	0.02	ns
	3	30	13	26	12	-	
Spontaneous greeting	1	58	16	115	14	0.08	ns
	2	314	11	260	12	0.08	ns
	3	68	6	92	7	-	

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

2. Missing Chi-square values indicate where data too few to test

significant difference occurred during Period 2, in greetings following the return of the male, when females in CHANGE pairs faced-away almost twice as often as females in SAME pairs. There was a trend in both SAME and CHANGE pairs for facing-away to be much less frequent during spontaneous greetings than during greetings that followed the return of a bird to its mate.

c. Female head-tossing.

Head-tossing in the female occurred after a greeting ceremony or spontaneously. Two measures of female head-tossing following greeting were evaluated in SAME and CHANGE pairs. The proportion of greetings followed by head-tossing is in Table 6.9 and the rate (per pair per hour) of head-tossing following greeting is in Table 6.10. There was a consistent trend for greetings to be followed proportionately more often by head-tossing in SAME pairs than in CHANGE pairs (Table 6.9). In Period 1, females in SAME pairs head-tossed more than twice as often after greeting than females in CHANGE pairs and the difference was significant. This trend continued in the two subsequent periods but the differences were smaller and not significant. Mean rates of female head-tossing after greeting were higher in CHANGE pairs than SAME pairs (Table 6.10), however, none of the differences was statistically significant.

Rates of spontaneous head-tossing for SAME and CHANGE pairs are in Table 6.11. There were no consistent or significant differences between the means for each group. The variance in the parameter was significantly larger in CHANGE pairs in Periods 1 and 2, and significantly smaller in Period 3.

Table 6.9: Proportion of all greetings followed by female head-tossing in relation to pair-status. 1979-81 combined.

	SAME n=45 pairs		CHANGE n=24 pairs			
PERIOD[1]	GREETINGS (n)	PERCENT HEAD-TOSSING	GREETINGS (n)	PERCENT HEAD-TOSSING	CHI-SQUARE df=1	p
1	195	27	265	12	17.0	<.005
2	835	21	573	17	2.6	ns
3	239	28	230	24	1.0	ns

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

Table 6.10: Rate of female head-tossing after all greetings. 1979-81 combined.

	RATE PER PAIR PER HOUR									
	SAME			CHANGE						
PERIOD[1]	Mean	s.d.	n	Mean	s.d.	n	t[2]	df	p	VH[3]
1	0.33	0.40	44	0.41	0.52	22	0.63	35	ns	yes
2	0.34	0.36	45	0.37	0.28	21	0.37	52	ns	yes
3	0.40	0.60	45	0.54	0.77	23	0.76	37	ns	yes

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

3. Variance homogeneity (F test)

Table 6.11: Rate of spontaneous female head-tossing in relation to pair-status. 1979-81 combined.

	RATE PER PAIR PER HOUR									
	SAME			CHANGE						
PERIOD[1]	Mean	s.d.	n	Mean	s.d.	n	t[2]	df	p	VH[3]
1	0.12	0.27	44	0.15	0.42	22	0.31	31	ns	no
2	0.05	0.07	45	0.13	0.18	21	1.97	23	ns	no
3	0.30	0.81	45	0.09	0.14	23	1.69	49	ns	no

1. Period 1: first 2-weeks after pair-formation
   Period 2: intervening period between 1 and 3
   Period 3: last 2-weeks before egg-laying

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

3. Variance homogeneity (F test)

2. Patterns of return to mate, greeting and head-tossing during two week period before, and five day period after egg-laying, in 1980.

a. Return to mate at nest-site.

The pattern of mean rates of return (excluding returns with nest material) for SAME and CHANGE pairs is in Figure 6.1 (day 0 is the date first eggs were laid and either a minus or plus sign indicate days before or after this date, respectively). From day -14 to -5, birds in CHANGE pairs returned to their mates from two to four times more often than birds in SAME pairs; however, with one exception the differences were not significant (Appendix D). Neither was the difference significant if the period is considered as a whole. At day -6, rates of return in both groups started increasing to a peak just before egg-laying and then decreased thereafter.

Rates of return according to the sex of the returning bird are also in Figure 6.1. It is clear that the difference between SAME and CHANGE pairs seen when all returns were considered was due mainly to differences in the rate of return of males to females and not vice versa. From day -14 to -5, males in CHANGE pairs returned to their mates at consistently higher rates than those in SAME pairs, and two of the differences were significant (Appendix D). If the period is considered as a whole the difference between the two groups was not significant. There was very little difference in the rates of return of females in SAME and CHANGE pairs over the same period. The peak in rates of return that occurred before egg-laying was entirely due to a peak in the rate of return of the male to the female at that time.

b. Greeting.

Figure 6.2 shows the pattern of mean rates of return greeting (returns with and without nest material) and spontaneous greeting for SAME and CHANGE pairs. With respect to return greetings, The trends

Figure 6.1: Changes in the mean rate of return (per pair per hour) of birds in SAME (n=14) and CHANGE (n=9) pairs before and after egg-laying in 1980. Graph of all returns includes the return of birds of undetermined sex. Returns with nest-material have been excluded. Bars are standard errors. Results of t-tests comparing means are in Appendix D.

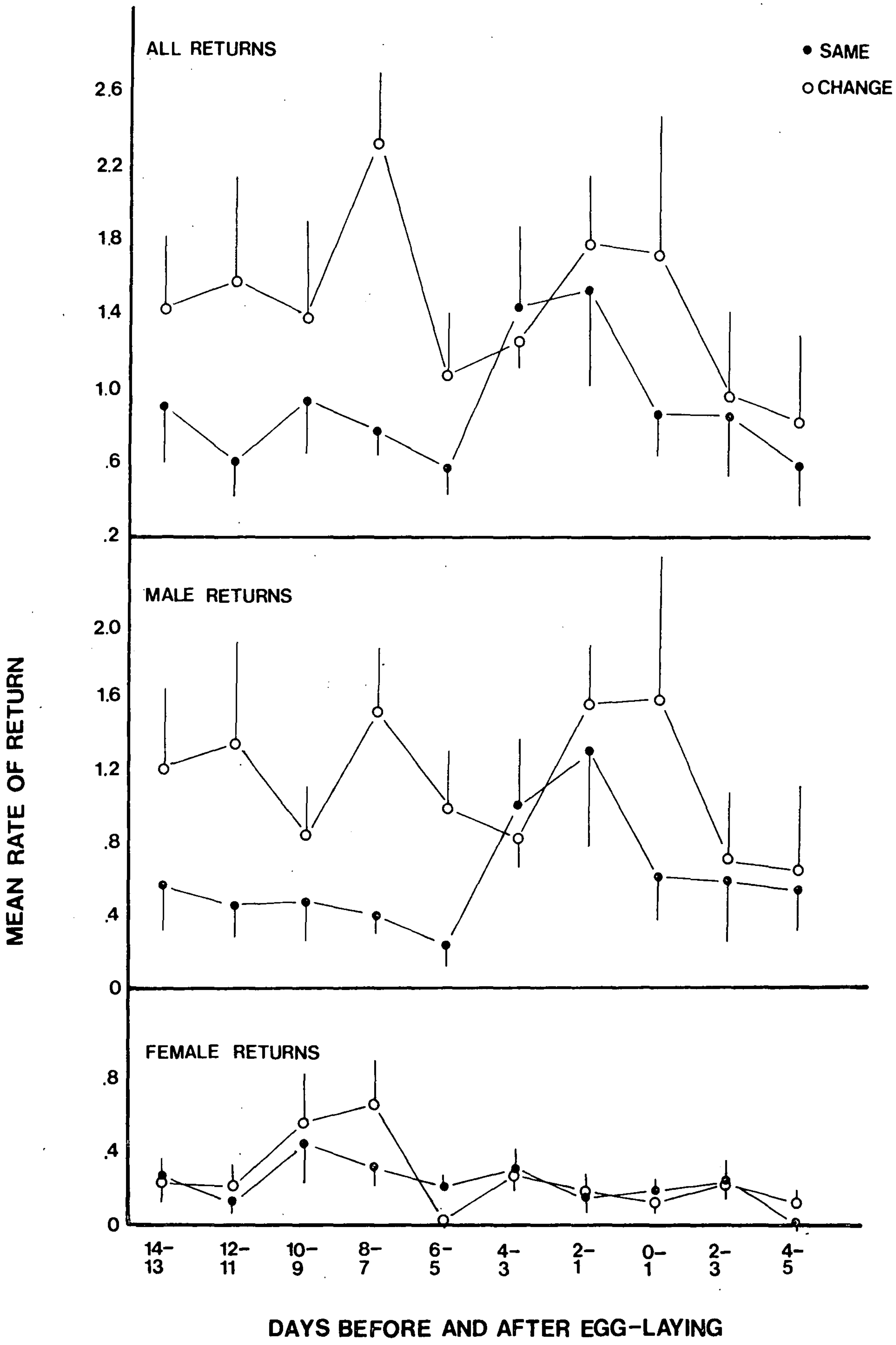
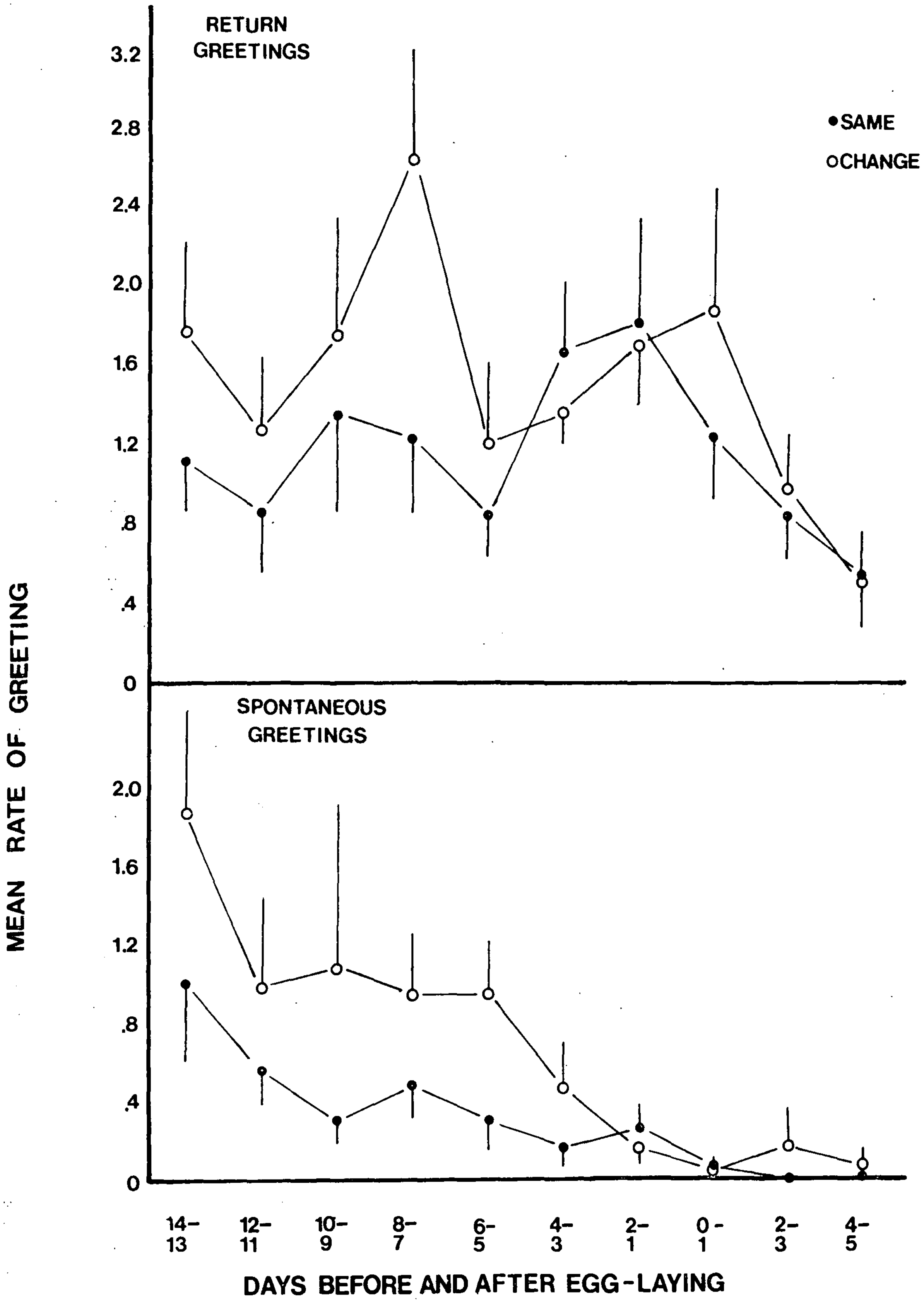

ALL RETURNS
● SAME
○ CHANGE
2.6
2.2
1.8
1.4
1.0
.6
.2
MALE RETURNS
2.0
1.6
1.2
.8
.4
0
FEMALE RETURNS
.8
.4
0
MEAN RATE OF RETURN
14–13
12–11
10–9
8–7
6–5
4–3
2–1
0–1
2–3
4–5
DAYS BEFORE AND AFTER EGG-LAYING

Figure 6.2: Changes in the mean rate of greeting (per pair per hour) in SAME (n=14) and CHANGE (n=9) pairs before and after egg-laying in 1980. Greetings after returns with nest material are included. Bars are standard errors. Results of t-tests comparing means in Appendix D.

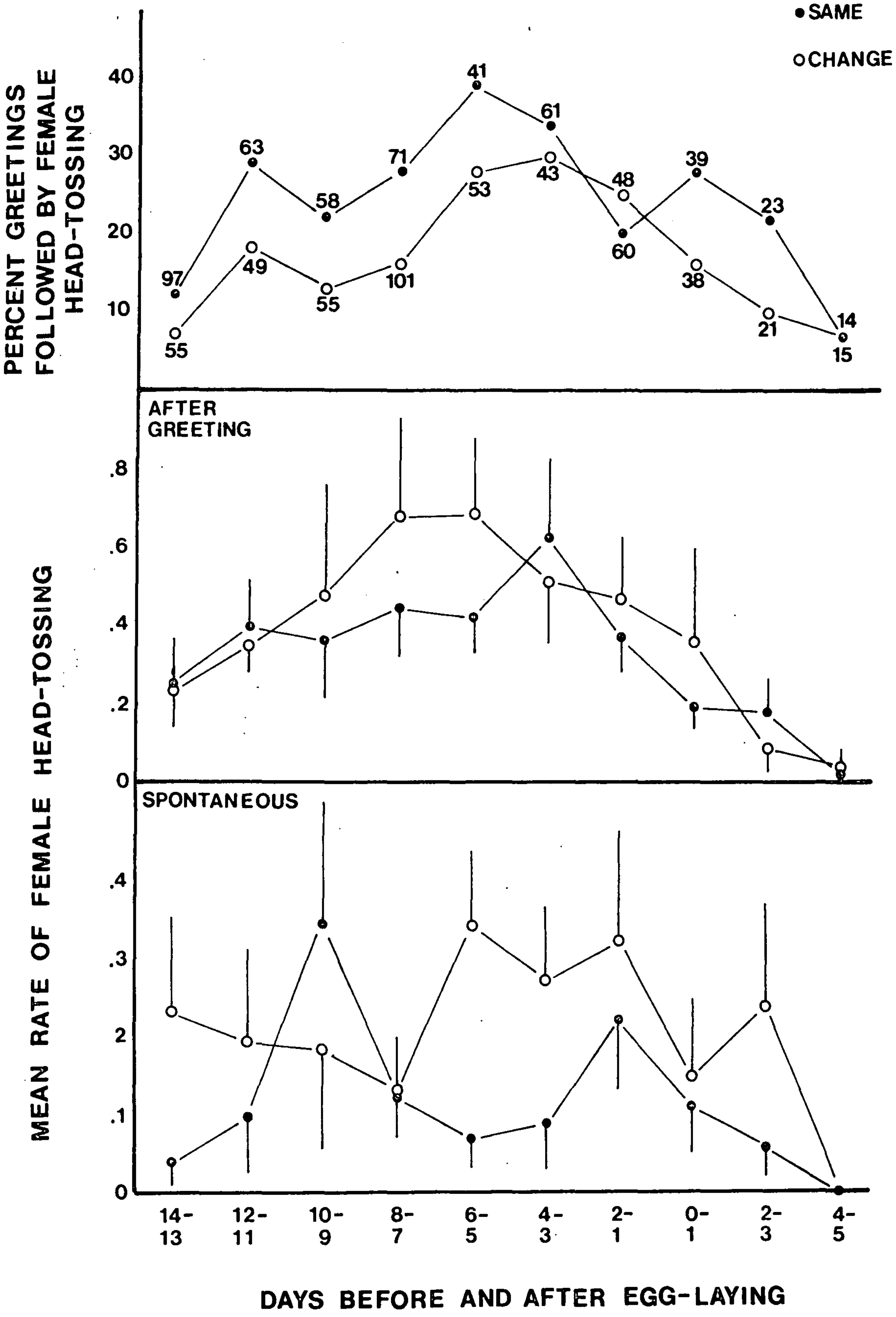

RETURN GREETINGS
SPONTANEOUS GREETINGS
●SAME
○CHANGE
MEAN RATE OF GREETING
3.2
2.8
2.4
2.0
1.6
1.2
.8
.4
0
2.0
1.6
1.2
.8
.4
0
14- 13
12- 11
10- 9
8- 7
6- 5
4- 3
2- 1
0 - 1
2- 3
4- 5
DAYS BEFORE AND AFTER EGG-LAYING

followed those seen when rates of return were considered (Figure 6.1). CHANGE pairs showed higher mean rates of return greeting than SAME pairs, from day -14 to -5, but differences were significant on only one occasion (Appendix D). From day -5, mean rates of return greeting increased to a peak just before egg-laying in SAME pairs and at the start of egg-laying in CHANGE pairs, before decreasing dramatically in both groups. CHANGE pairs greeted spontaneously at a consistently higher rate than SAME pairs, from day -14 to -3, but only one of the differences was significant (Appendix D). Rates were relatively constant in both groups from day -12 to -5; however, differences were not significant when data were pooled over this period. Rates of spontaneous greeting in both SAME and CHANGE pairs decreased steadily throughout the period and reached almost zero during and after egg-laying.

c. Female head-tossing.

Patterns of female head-tossing are in Figure 6.3. The figure shows three different measures of female head-tossing: the proportion of all greetings that were followed by head-tossing, the rate of head-tossing after greeting and the rate of spontaneous head-tossing. Females in SAME pairs head-tossed consistently more frequently after greeting than those in CHANGE pairs from day -14 to -3, and when the period was taken as a whole, the difference was significant (Chi-square=6.28, df=1, $p < 0.05$). Over this period the proportion of greetings that were followed by female head-tossing increased in both SAME and CHANGE pairs to peaks at day -3 to -4 in SAME pairs and day -5 to -6 in CHANGE pairs, after which the proportion decreased in both groups. Rates of female head-tossing were not consistently different between SAME and CHANGE pairs. The pattern for both groups was for rates to increase from day -14 to a peak occurring at day -3 to -4 in

Figure 6.3: Changes in the occurrence of female head-tossing in SAME (n=14) and CHANGE (n=9) pairs before and after egg-laying in 1980. Rates are expressed per pair per hour. Numbers on plot of percent of all greetings followed by head-tossing are sample sizes of greetings. Results of Chi-square tests (percents) and t-tests (means) in Appendix D.


● SAME
○ CHANGE
PERCENT GREETINGS FOLLOWED BY FEMALE HEAD-TOSSING
40
30
20
10
97
63
58
71
41
61
60
39
23
14
55
49
55
101
53
43
48
38
21
15
AFTER GREETING
.8
.6
.4
.2
0
SPONTANEOUS
.4
.3
2
.1
0
MEAN RATE OF FEMALE HEAD-TOSSING
14-13
12-11
10-9
8-7
6-5
4-3
2-1
0-1
2-3
4-5
DAYS BEFORE AND AFTER EGG-LAYING

SAME pairs and day -5 to -6 in CHANGE pairs. Subsequently, rates of female head-tossing decreased in both groups. There was a trend for rates of spontaneous head-tossing to be higher in CHANGE pairs than in SAME pairs, but differences were significant on only one occasion (Appendix D). There was no overall pattern in rates of spontaneous female head-tossing for either SAME or CHANGE pairs: unlike head-tossing following greeting, no peak rates were seen. In both groups, there was a decrease in rates of spontaneous female head-tossing from day -1 to -2, through egg-laying.

Discussion

A clear trend in this chapter was that birds in CHANGE pairs were observed to greet more frequently than birds in SAME pairs. The proportion of returns that were followed by greeting did not differ between the two groups and the trend was primarily due to higher rates of return of one bird to the other in CHANGE pairs. A higher proportion of these returns in CHANGE pairs involved "circuits", i.e. birds returning to, and leaving the nest-site in quick succession. Both males and females were responsible for the higher rates of return in CHANGE pairs. Similar observations of higher levels of vocalization in newly paired birds compared to those previously paired have been reported in several species (Ring Dove: Erickson and Morris, 1972; Stilt Sandpiper: Jehl, 1973; Greenshank: Nethersole-Thompson, 1951 in Jehl, 1973).

Differences in return greeting rates were greatest and usually significant in the two weeks after pair-formation, and decreased thereafter. The most obvious explanation for the difference occurring at this time is that birds in CHANGE pairs were relatively unfamiliar with each other just after pair-formation and performed more greetings than birds in SAME pairs as a result. Aggressive tendencies between members of a pair may be higher during this initial period and the greeting ceremony may act to reduce these tendencies. Another explanation for the observed differences may lie in the fact that Kittiwakes recognize and remember the vocalizations of their mates from year to year (Wooller, 1978). Clearly, birds in CHANGE pairs initially will not know the calls of their mates, and presumably, a period of learning is required. The higher rates of greeting seen in CHANGE pairs may be important in making the period of learning as short as possible.

The observation that Kittiwakes perform "circuits" suggests that they often return to their mates for no other reason but to perform a greeting ceremony. Birds in CHANGE pairs performed "circuits" proportionately more often than birds in SAME pairs (except during the last two weeks before egg-laying). Nelson (1978) suggested that a important function of "circuits" seen in the Gannet (referred to as "leave and returns") was to familiarize the female with returns by the male, thereby strengthening the pair relationship and also the female's attachment to the nest-site. The performance of "circuits" may thus, be much more important for birds in CHANGE pairs, who are relatively unfamiliar with one another, and who have more than likely changed nest-sites from the previous year (Coulson and Thomas, 1980).

Although SAME pairs greeted less frequently than CHANGE pairs, female head-tossing in the former group occurred more often after greeting than in the latter. Again this effect was most pronounced during the two week period after pair-formation. The result of the interaction of these differences was that rates of female head-tossing did not differ significantly between the two groups in each of the three time periods studied. A possible explanation for why females in

SAME pairs head-tossed proportionately more often after greeting may lie in the context in which head-tossing occurs. Head-tossing in gulls is considered a female solicitation behaviour for courtship feeding and/or copulation (Tinbergen, 1959). Recently, Smith (1980) presented evidence that female solicitation for courtship feeding should be viewed as a "demand" for male parental contribution and further that solicitation is indicative of female dominance over the male. If this is the case, then female Kittiwakes in CHANGE pairs, being less familiar with their mates than females in SAME pairs, may be much less willing to perform head-tossing. Furthermore, the reluctance of females in CHANGE pairs to head-toss should diminish as male and female become more familiar, and differences between SAME and CHANGE pairs should be greatest just after pair-formation. The data support these predictions: the proportion of greetings followed by head-tossing increased in CHANGE pairs, from pair-formation to egg-laying, while the proportion in SAME pairs did not. Differences between the two groups were greatest during the two week period after pair-formation.

No consistent differences in levels of aggression (male peck female) or appeasement (female face-away) during the greeting ceremony were seen in SAME and CHANGE pairs. In contrast, Nelson (1972) found that "new" pairs incorporated more aggression into the meeting (greeting) ceremony than did established pairs. A possible reason for the different observations may lie in the fact that, in this study, all birds in SAME and CHANGE pairs had bred in previous years, whereas, Nelson's "new" pairs were likely made up of inexperienced as well as experienced birds. Part of the process of gaining breeding experience may involve learning to distinguish between interactions with a mate and those with other birds and reducing aggressive tendencies in the former interactions.

There were few significant differences between SAME and CHANGE pairs in the patterns of returning to the nest-site, greeting or head-tossing during the two weeks before, and five days after first eggs were laid in 1980. However, trends seen when the two week period before egg-laying was considered as a whole (Period 3) were also evident in the more detailed analysis of the period.

Egg-laying was both preceded and followed by a definite pattern of behaviour in both male and female. From five days before egg-laying, rates of male return and greeting increased to a peak at or just before egg-laying and then decreased to original levels. Both the rate of female head-tossing and the proportion of greetings followed by female head-tossing increased from 14 days before egg-laying to a peak at about three to six days before egg-laying and then decreased to almost zero after clutch completion. A question arises as to how the male and female co-ordinate their activities in this way. Either information regarding the timing of egg-laying is passed from female to male or the male may be capable of controlling the timing egg-laying in the female.

It is known that males are capable of affecting the timing of reproductive events in the female, through courtship vocalizations (Brockway, 1965; Lehrman, 1959). Wooller (1973, 1978) suggested that the greeting ceremony in the Kittiwake stimulated ovulation in the female. Ovulation, at least in gulls, probably occurs about 48 hours before egg-laying (Parsons, 1976) and this coincides with the increase in rates of return in the male reported here. At best, however, this trend could be responsible only for "fine tuning" the timing of ovulation in the female since the increase occurred so close to egg-laying.

The female could communicate her reproductive state to the male in several ways. Casual observations suggest that the female was often able to attract the male to the nest-site by calling ("kittiwaaking") to him as he flew by. Thus, the female may be able to control, to some extent, the frequency and timing of male returns and greetings. Once a greeting has occurred the female has the option of head-tossing and this, in turn, may lead to courtship feeding or copulation. The proportion of greetings that were followed by female head-tossing peaked several days before egg-laying, and this could have provided an ample cue to the male that the female was about to lay eggs.

The adaptive value of co-ordination of activities between partners seems clear. Both male and female Kittiwakes co-operate in building the nest (Wooller, 1973) and a nest, fully built at an appropriate time before egg-laying, is an essential prerequisite for successful reproduction in a cliff-nesting species such as the Kittiwake. Optimum reproductive success may depend on the appropriate timing of courtship feeding and copulation to coincide with ovulation in the female, and to this end, an efficient means of communication between members of a pair is essential (Tasker and Mills, 1981).

CHAPTER 7. COURTSHIP FEEDING AND COPULATION

Introduction

In contrast to the behaviour dealt with previously in this thesis, courtship feeding and copulation are likely to have direct effects on reproductive performance through their potential to influence parameters such as egg and clutch size, fertility rates and timing of laying (see Taneja and Gowe, 1962; Nisbet, 1973, 1977).

The feeding of the female by the male is termed courtship feeding because it was originally thought to have only a symbolic function, resulting in the strengthening of the relationship between pair members. Lack (1940) argued, for a variety of species, that this may be the most appropriate functional interpretation of the behaviour. More recently, several authors have presented evidence suggesting that courtship feeding before egg-laying serves an important function in supplementing the female's diet (Royama, 1966; Nisbet, 1973, 1977; Tasker and Mills, 1981).

The function of copulation is more immediately obvious: the fertilization of eggs through the transmission of sperm from male to female. The fertility of eggs depends on whether or not copulation has occurred, however, the extent to which higher rates of copulation result in higher fertility rates in wild birds is not known (but see Taneja and Gowe [1962] for domestic birds). The timing of copulation relative to egg-laying, rather than absolute rates, may be more important in terms of fertility. Although some gulls have been seen to copulate many weeks in advance of egg-laying, they show peak rates of copulation just before egg-laying, which probably coincide with the female's fertile period (Brown, 1967; Tasker and Mills, 1981).

Pair-status has been shown to have important effects on reproductive success in some bird species. Birds that change mates from the previous year, on average, lay smaller eggs, smaller clutches and experience lower hatching success than birds retaining the same mate (Coulson, 1966; Mills, 1973, 1979; Cooke et al., 1981). These trends could be the result of lower rates, or inappropriate timing of courtship feeding and copulation in CHANGE pairs. The aim of this chapter is to present courtship feeding and copulation data for SAME and CHANGE pairs and evaluate differences in terms of possible causes and effects.

Results

Although all observed courtship feedings and copulations were recorded in the three years of study, only in 1980 were they studied in detail. Seven or 14 hour, daily observation periods were conducted starting 4 May 1980 (five days before the first study pair laid eggs) and lasted several days after the last study pairs had laid eggs (see Chapter 1, Methods). In proportion to the other two years, many more courtship feedings and copulations were sampled in 1980 and most of the observations and data that follow, come from that year. Whenever, data were available from all three years, between year variation was tested using ANOVA and found to be not significant. Accordingly, data from each year were pooled. Duration of observation periods from which data are used in the following analyses are in Appendix C.

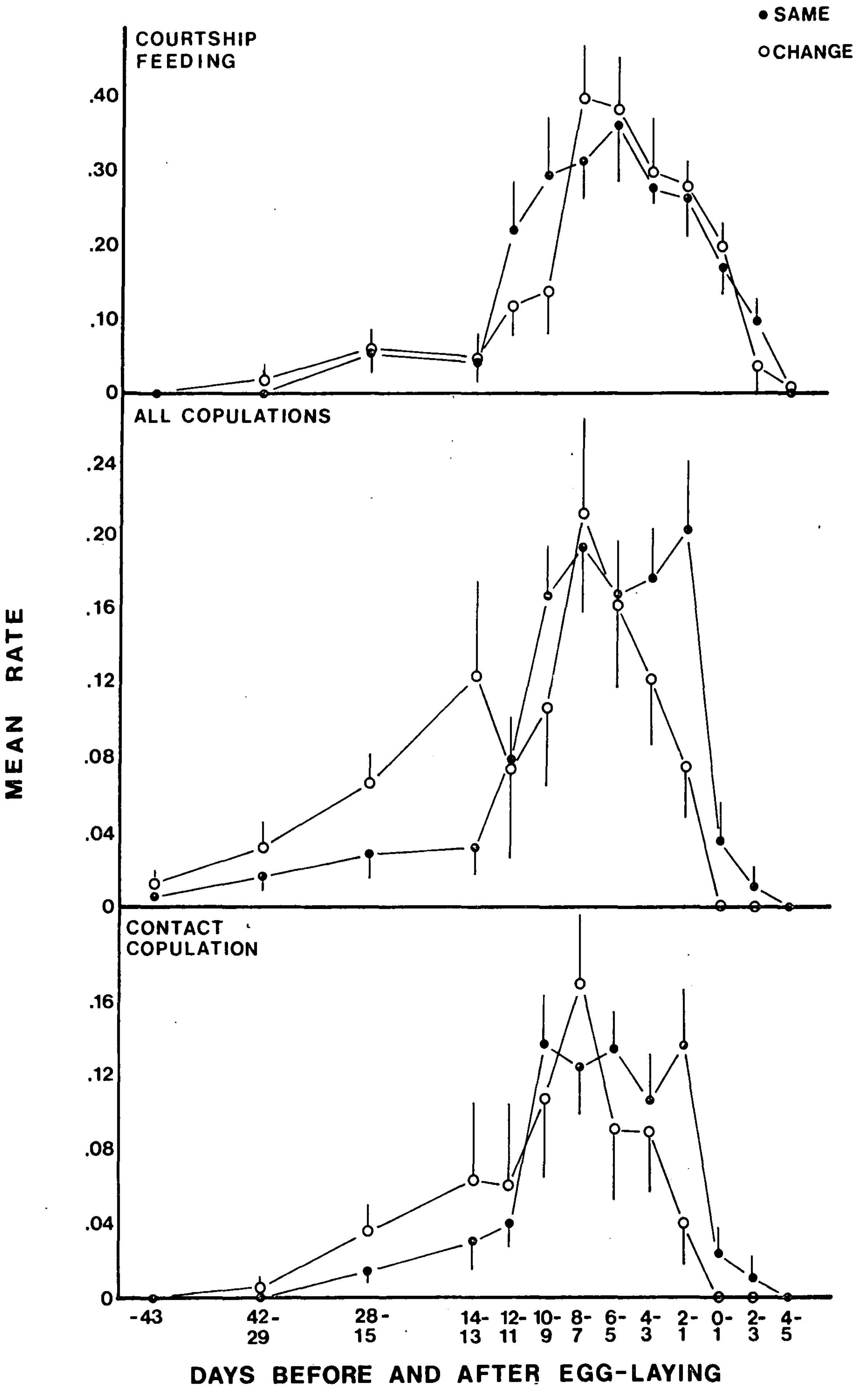
1. Timing of courtship feeding and copulation.

Mean rates of courtship feeding and copulation relative to the date first eggs were laid (Day 0, minus sign indicates days before egg-laying and plus sign indicates after) were calculated for SAME and CHANGE pairs in 1980. Data were partitioned into two day periods from two weeks before to five days after first eggs were laid. Prior to 14 days before egg-laying, data were partitioned into three periods: 15 to 28 days, 29 to 42 days, and 43 days before egg-laying or earlier.

Figure 7.1 shows mean rates of courtship feeding, copulation and contact copulation for SAME and CHANGE pairs. The pattern of courtship feeding was very similar in each group and there were no significant differences between the mean rates in any of the time periods (Appendix D). The earliest courtship feeding seen in SAME pairs was on day -24 and that for CHANGE pairs was on day -31. Courtship feeding rates remained low until two weeks before egg-laying at which time rates increased about eight times in both groups to a peak between day -5 and -8. From the peak, rates steadily decreased to zero at day +5.

In contrast to courtship feeding, the patterns of copulation differed in SAME and CHANGE pairs (Figure 7.1). A low rate of copulations was observed in both groups before day -43. Subsequently, rates of copulation increased faster in CHANGE than in SAME pairs up to day -13. Over this period rates of copulation were two to four times higher in CHANGE pairs than in SAME pairs, although none of the differences was significant (Appendix D). Neither was the difference significant if data for the period were pooled. From day -12 to -7 rates of copulation increased about five times in SAME pairs and about twice in CHANGE pairs. Subsequently, rates of copulation in CHANGE pairs decreased to zero on the day first eggs were laid, whereas in SAME pairs, rates remained high until first eggs were laid. Over the four day period before egg-laying, rates of copulation were, on average, about twice as high in SAME pairs than in CHANGE pairs and the difference was significant ($t=2.12$, $df=22$, $p < 0.05$). The higher rates of copulation seen in CHANGE pairs in the period prior to day -13 were evident when contact copulations were considered, however,

Figure 7.1: Changes in mean rate (per pair per hour) of courtship feeding, all copulation and contact copulation (those involving cloacal contact) for SAME (n=14) and CHANGE (n=9) pairs over period between pair-formation and egg-laying in 1980. Bars are standard errors. Results of t-tests comparing means in Appendix D.


● SAME
○ CHANGE
COURTSHIP FEEDING
.40
.30
.20
.10
0
ALL COPULATIONS
.24
.20
.16
.12
.08
.04
0
CONTACT COPULATION
.16
.12
.08
.04
0
MEAN RATE
-43
42-29
28-15
14-13
12-11
10-9
8-7
6-5
4-3
2-1
0-1
2-3
4-5
DAYS BEFORE AND AFTER EGG-LAYING

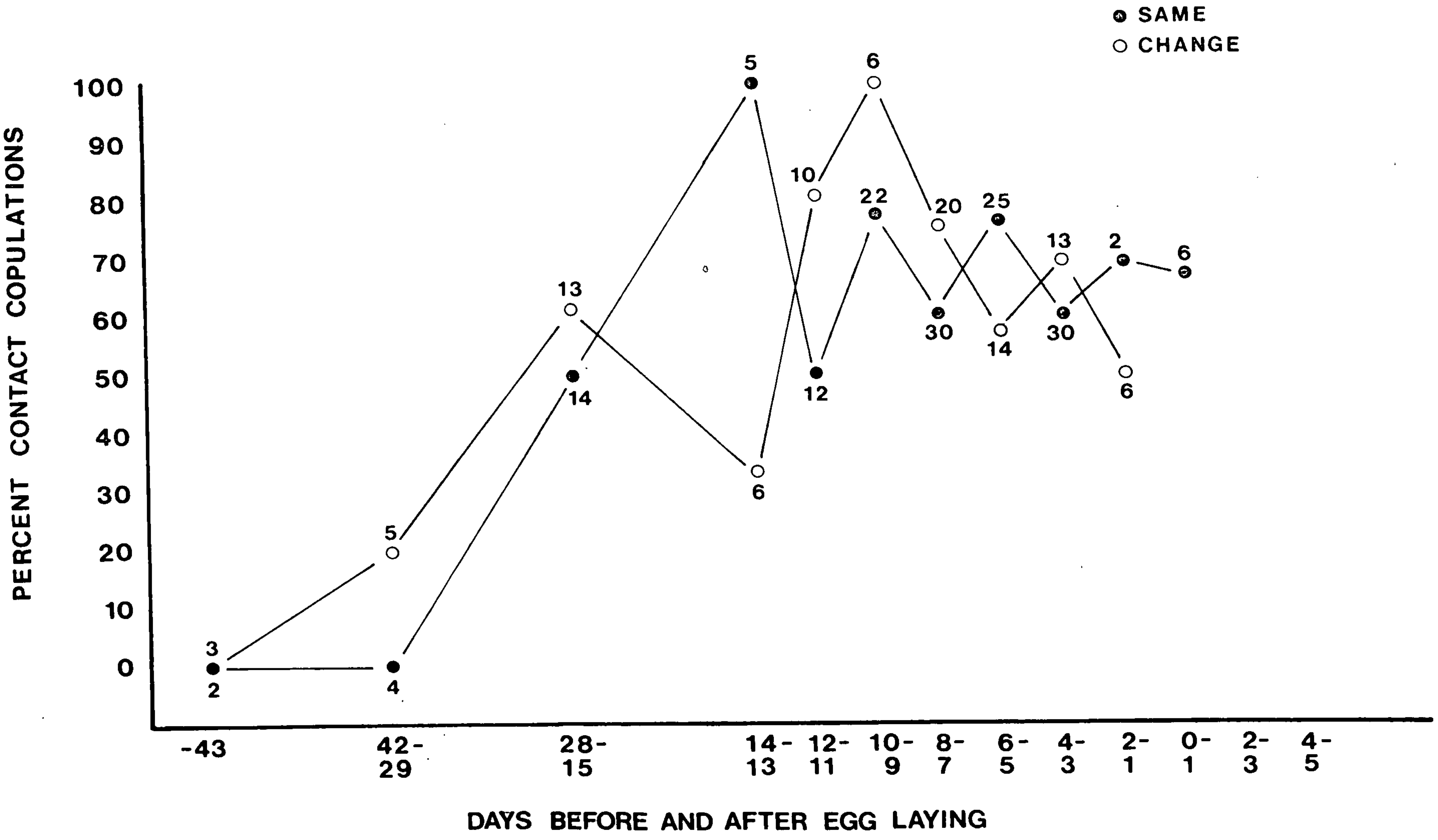
the differences were smaller (Figure 7.1). The difference between SAME and CHANGE pairs in the rate of copulation during the last four days before egg-laying was not significant for contact copulations; however, the difference was significant over the last two days (Appendix D).

Seasonal changes in the proportion of all copulations that involved cloacal contact in SAME and CHANGE pairs are in Figure 7.2. Cloacal contacts did not occur in any of the early (before day -43) copulations performed by birds in both groups. Subsequently, the proportion of contact copulations increased to about 65 percent in both groups over the period from day -14 to egg-laying.

The preceding analysis showed that there were differences between SAME and CHANGE pairs in both the onset and cessation of copulation. The rate of copulation was higher in CHANGE pairs early in the season, relative to egg-laying, and higher in SAME pairs just before first eggs were laid. The first effect is analysed further in Table 7.1 where mean times (in days) between first copulation and egg-laying, and first contact copulation and egg-laying are shown for SAME and CHANGE pairs. The mean times between first copulation and egg-laying were almost twice as long in CHANGE pairs compared to SAME pairs and the difference was significant. When contact copulations were considered, mean times were again higher in CHANGE pairs but the differences between the two groups were much smaller and not significant. Variance of these parameters was significantly higher in CHANGE pairs than in SAME pairs.

The higher rates of copulation seen in SAME pairs before egg-laying suggests that they may have continued to copulate for longer than CHANGE pairs. Figure 7.3 shows a plot of the date of the last observed copulation or contact copulation against the date first eggs

Figure 7.2: Changes in the proportion all copulations involving cloacal contact (contact copulation) for SAME (n=14) and CHANGE (n=9) pairs over period between pair-formation and egg-laying in 1980. Sample sizes of copulations for each group are given next to each point.



● SAME
○ CHANGE
PERCENT CONTACT COPULATIONS
100
90
80
70
60
50
40
30
20
10
0
DAYS BEFORE AND AFTER EGG LAYING
-43
42-29
28-15
14-13
12-11
10-9
8-7
6-5
4-3
2-1
0-1
2-3
4-5
3
2
5
4
13
14
5
6
10
12
6
22
20
30
25
14
13
30
2
6
6

Table 7.1: Time between first copulation and egg-laying

1979-81 combined.

	TIME (days)							
	SAME n=42[1]		CHANGE n=23[2]					
	Mean	s.d.	Mean	s.d.	t[3]	df	p	VH[4]
All copulations	21.7	17.2	39.0	29.2	2.61	31	$< .05$	no
Contact copulations	14.1	8.9	17.9	13.0	1.25	35	ns	no

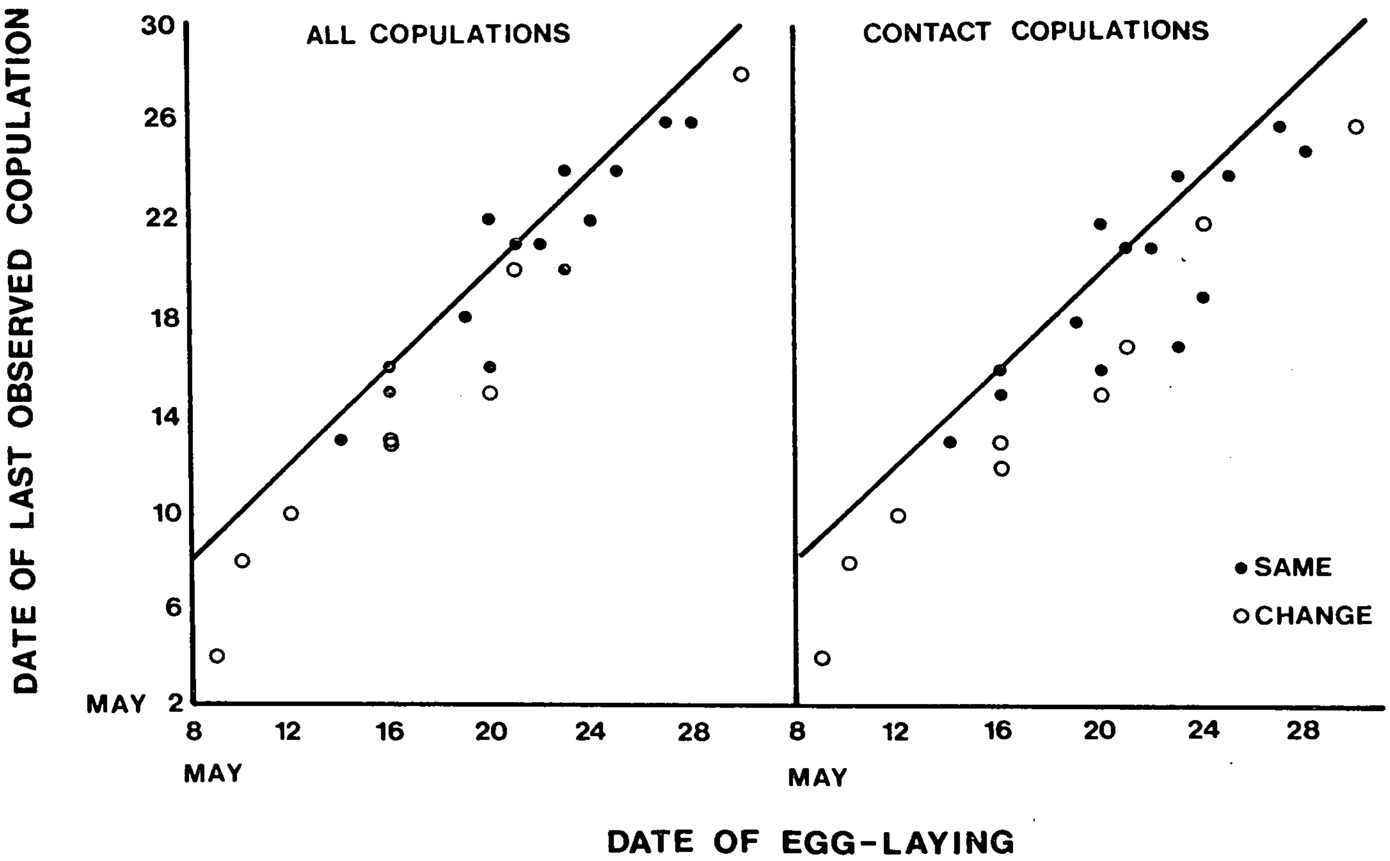
1. Three pairs never seen to copulate

2. One pair never seen to copulate

3. Welch's modification for assumption of unequal variance: degrees of freedom approximate

4. Variance homogeneity (F test)

Figure 7.3: Date of last observed copulation or contact copulation in relation to date of egg-laying for SAME and CHANGE pairs in 1980. Diagonal denotes line of equal dates.


ALL COPULATIONS
CONTACT COPULATIONS
DATE OF LAST OBSERVED COPULATION
30
26
22
18
14
10
6
MAY 2
8
12
16
20
24
28
MAY
8
12
16
20
24
28
MAY
● SAME
○ CHANGE
DATE OF EGG-LAYING

were laid for SAME and CHANGE pairs in 1980. Coverage of this period in 1979 and 1981 did not allow a similar analysis for these years. The diagonal indicates the line of equal dates (i.e. copulations last seen on day of egg-laying). Nineteen of the 23 pairs (83 percent) apparently stopped copulating prior to the laying of first eggs. All CHANGE pairs and ten SAME pairs did so. On average copulations stopped significantly earlier relative to egg-laying in CHANGE pairs compared to SAME pairs (mean relative date of last copulation: SAME -1.0, s.d.=1.5, n=14; CHANGE -2.8, s.d.=1.4, n=9; t=2.93 df=20, $p < 0.01$). Contact copulations also stopped significantly earlier in CHANGE pairs (mean relative date of last contact copulation: SAME -1.5, s.d.=2.3, n=14; CHANGE -3.4, s.d.=1.2, n=9; t=2.59, df=22, $p < 0.05$).

2. Courtship feeding and copulation during the two week period before egg-laying in 1980.

Table 7.2 shows mean rates of courtship feeding, copulation and contact copulation for SAME and CHANGE pairs during the two week period before egg-laying. Mean rates of each behaviour were very similar between SAME and CHANGE pairs and no significant differences were found.

The number of cloacal contacts per copulation was recorded in 1980. A comparison of this parameter in SAME and CHANGE pairs is in Table 7.3. Copulations are grouped according to number of cloacal contacts (0, 1 to 2, 3 to 4, more than 5). Cloacal contact did not occur in about one third of copulations in both groups. There was a significant tendency for SAME pairs to perform more cloacal contacts per copulation than CHANGE pairs.

Table 7.2: Rates of courtship feeding and copulation during last 14-days before egg-laying in 1980, in relation to pair-status.

	RATE PER PAIR PER HOUR							
	SAME n=14		CHANGE n=9					
	Mean	s.d.	Mean	s.d.	t[1]	df	p	VH[2]
Courtship feedings	0.26	0.41	0.29	0.30	0.20	23	ns	yes
All copulations	0.15	0.23	0.14	0.27	0.09	17	ns	yes
Contact copulations	0.10	0.11	0.09	0.18	0.15	13	ns	yes

1. Welch's modification for assumption of unequal variance: degrees of freedom approximate

2. Variance homogeneity (F test)

Table 7.3: Number of cloacal contacts per copulation during last 14-days before egg-laying in 1980, in relation to pair-status.

		CLOACAL CONTACTS PER COPULATION				
		0	1-2	3-4	5 or more	Total
SAME	n	50	23	31	49	153
	%	33	15	20	32	100
CHANGE	n	24	21	19	11	75
	%	32	28	25	15	100

Chi-square=10.75 d.f.=3 $p<0.05$

3. Extra-pair copulation.

Copulations occurring outside the context of the pair are termed extra-pair copulations (EPC). EPC's were rare: 17 were seen over the three years of study. This figure represented only two percent of all copulations observed (n=737). A total of seven males and seven females were involved in the EPC's; six of the seven males and two of the seven females bred in the year during which the EPC's were seen. With regard to the two females that eventually bred, the EPC's occurred several weeks before egg-laying. Three EPC's occurred on the male's nest-site while 14 occurred elsewhere. Only five of the 17 EPC's involved cloacal contacts. In general, this was not due to the male failing to attempt contact but was usually a result of the female not co-operating in the copulation attempt, either by standing on the site rather than sitting, not raising her tail while mounted, or reacting aggressively toward the male.

Nine of the 17 EPC's involved a single male and the context of these copulations is noteworthy. The male in question had divorced his mate of the previous year and took a new mate. He attended his new mate's nest-site but occasionally was observed to return to his mate of the previous year. It was during these visits that the EPC's occurred. None of the EPC's involved cloacal contact because the female never raised her tail during mounting. The forced nature of the EPC's was illustrated by the fact that frequently the male mounted the female while she remained standing on the nest-site. This contrasted to the usual observation that the male does not mount the female until such time as she has positioned herself in a sitting posture on the nest-site (Chapter 2).

Discussion

There were very few differences between SAME and CHANGE pairs in either the timing or frequency of courtship feeding. Both groups showed a dramatic increase in the rate of courtship feeding starting 14 days before first eggs were laid. Rates increased to a peak between five and eight days before egg-laying and then sharply declined to zero at clutch completion. This pattern is very similar to that reported for the Red-billed Gull by Tasker and Mills (1981) and the Lesser Black-backed Gull by Brown (1967). Of particular interest is these species and the Kittiwake, is that courtship feeding rates peaked in advance of egg-laying. The increase before egg-laying suggests that courtship feeding in these species functions to supplement the female's diet. The peak occurring before egg-laying may be an indication of the probable delay between ingestion of nutrients and their mobilization for egg production. Furthermore, yolk formation in the Kittiwake takes about nine days (Roudybush _et_ _al_., 1979) and the ovum, with fully formed yolk is probably expelled from the ovary about 48 hours before egg-laying (Parsons, 1976). Thus, the first egg is being formed over a period of about 11 days before laying and it is at this time that rates of courtship feeding were found to be on the increase to a peak about 5-6 days before egg-laying.

In contrast to courtship feeding, there were some differences between SAME and CHANGE pairs in the timing and frequency of copulation in relation to egg-laying. First copulations were seen significantly earlier in CHANGE pairs than in SAME pairs and rates of copulation were higher in SAME pairs just prior to egg-laying. The overall trend in rates of copulation paralleled with few exceptions that found for Red-billed Gulls (Tasker and Mills, 1981) and Lesser Black-backed Gulls (Brown, 1967). An important difference was that rates of copulation declined much more dramatically in the Kittiwake, such that copulation was seen very infrequently once the first egg in the clutch had been laid. In contrast, rates of copulation in the other two species remain relatively high throughout egg-laying and only decline to near zero when the clutch is complete. The difference probably relates to different nesting habitat. Nelson (1978) found that the cliff-nesting Gannet does not copulate once an egg is laid and he suggested that this was an adaptation to avoid damage to the eggs when, perforce, the pair has to copulate on or very close to the nest. The same must surely apply to the Kittiwake, whereas, the ground-nesting Red-billed and Lesser Black-backed Gulls can copulate beyond the nest and thus not jeopardize the safety of eggs.

Copulation was observed over several weeks prior to egg-laying. This suggests that the behaviour has a function beyond insemination. Cloacal contacts were not attempted in many of these early copulations, and even if they were, it is highly unlikely that mature gametes would have been present in the reproductive tracts of male and female at this time. Early copulation may function as "practice" for both male and female (Brown, 1967) and this may be the reason why CHANGE pairs were seen to copulate much earlier, in relation to egg-laying, than SAME pairs. Birds in CHANGE pairs are presumably less familiar with one another than those in SAME pairs and it may be advantageous for birds in the former group to engage in early copulation and thus gain experience of each other. The fact that few early copulations involved cloacal contact suggests that the act of the male mounting the female may be of importance. Mounting requires an exceptional level of physical contact between male and female and its repetition may act to suppress aggression and fear in both birds.

There are several other explanations for why Kittiwakes in both SAME and CHANGE pairs were observed to copulate over such an extended period before egg-laying. Extended copulation might increase the chances of fertilization by decreasing the chances of the male "missing" the female's fertile period. Birkhead (1979) suggested that if there is a chance that extra-pair copulation might occur, then males should copulate frequently with their females for a considerable period before egg-laying in order to disguise the female's fertile period from other males. Also, frequent copulation would act to maintain a relatively high concentration of fresh sperm in the female's reproductive tract, thus reducing the chances of sperm from another male having the opportunity to fertilize an ovum. Both explanations assume that it is adaptive for males that invest substantially in offspring (e.g. Kittiwake), to decrease the chances of cuckoldry (Trivers, 1972). However, extra-pair copulations were observed relatively rarely in this study. This was due mainly to infrequent attempts on the part of males and not to avoidance of extra-pair copulations by the female. Thus, the probability of a male Kittiwake at the warehouse colony being cuckolded was relatively small, and one might expect that the occurrence of cuckoldry avoidance behaviours in the male would be correspondingly low. On the other hand, the costs of cuckoldry for a male Kittiwake may be high enough that any amount of extra-pair copulation may cause strong selection for individuals who perform cuckoldry-avoidance behaviour.

Rates of copulation over the two week period before egg-laying were very similar in SAME and CHANGE pairs; however, the timing of copulations was somewhat different, with SAME pairs maintaining a much higher rate of copulation, both during the four days before first eggs were laid and after. The proximate reasons for the difference are not clear. If females in CHANGE pairs head-tossed less frequently during this period, then this may have resulted in fewer copulations; however, rates of head-tossing in SAME and CHANGE pairs were very similar (Chapter 6). The difference in copulation rates might have been due to males in CHANGE pairs not responding to head-tossing as frequently as males in SAME pairs. The reason for this difference is unknown.

Coulson (1966) found that CHANGE pairs of Kittiwakes hatch proportionately fewer eggs than SAME pairs and suggested that the difference was a result less co-ordinated incubation behaviour in CHANGE pairs. The higher rates of copulation seen in SAME pairs over the four day period before egg-laying could cause higher rates of fertility in these pairs and provide a possible alternate explanation for the difference in hatching success. It is doubtful whether this is the case, however, because CHANGE pairs copulated at high rates prior to the four days before egg-laying, and sperm storage is known to occur in several bird species (Hatch, 1983; Howarth, 1974; Zenone _et al._, 1979). If Kittiwakes also exhibit sperm storage capabilities then there may have been adequate amounts of viable sperm in the oviducts of females in CHANGE pairs at the time of ovulation. The low copulation rates seen just before and during egg-laying have a greater potential to affect the fertility of the second egg laid in a clutch, as the viability of sperm is known to decrease as time of storage in the female's oviduct increases (Warren and Kilpatrick, 1929).

CHAPTER 8. INTERFERENCE

Introduction

The colonial nesting habit brings with it greater opportunity for conspecific interference over that experienced by birds whose breeding distribution is more dispersed. Such interference can take many forms. For example, Parsons (1971) reported widespread cannibalism of eggs and chicks in Herring Gull colonies (see also Pierotti, 1980). The stealing of nest material is common in gull colonies (pers. obs.; Cullen, 1957). Fetterolf (1983b) observed adult Ring-billed Gulls stealing food from neighbouring adults during chick feeding. Conspecific aggression in colonies can act to disrupt courtship activities (Gochfeld, 1980), and local competition for nest-sites and mates is probably more intense than that experienced by more solitary breeders. In communally mating, lek species, various workers have observed males and females disrupt or interfere with the courtship activities (including copulation) of conspecifics (various references in Foster, 1983).

During all three years of study reported here, Kittiwakes were observed to interfere with the copulations of other colony members. The aims of this chapter are to provide descriptions of interference and, based on observations of interference by marked individuals, appraise various hypotheses for the adaptive function of the behaviour.

Results

Although interference was seen in all three years, the behaviour was studied in detail only in 1980. The analysis that follows is based solely on data from that year.

1. Description of interference.

Of 596 copulations seen in 1980, 27 percent (n=158) involved interference. Most (89 percent) involved either one or two interferences, but up to six were observed on one occasion. Thus, although 158 copulations were interfered with, a total of 223 actual interferences were observed.

Several types of interference were identified (Table 8.1). "Approach" interference occurred when the interfering bird flew up to a copulating pair on a track perpendicular to the face of the colony and did not come into physical contact with the pair. Birds usually approached the copulating pair to within 0.5 m or less before veering sharply away. This was the most commonly observed type of interference. "Flyby" interference describes a situation where the interfering bird approached the copulating pair on a track parallel to the face of the colony and flew by the pair to within 0.5 m or less. "Contact" interference was similar in every respect to "approach" interference except that actual physical contact took place between the interfering bird and the copulating pair. Frequently the contact was violent in nature and usually the interfering bird left immediately upon contact. "Site" interference was similar to "contact" interference except that the interfering bird landed on the ledge immediately adjacent to the copulating pair. Usually the interfering bird remained on the site for several seconds before leaving.

On many occasions, birds were seen to leave their nest-site on the west-side of the warehouse and subsequently interfere with a copulation. It was at this time that many of the birds were identified by colour-rings (see part 2 below). Frequently, they were with their mates before leaving to interfere. Although no quantitative data were recorded, certain characteristic movements and calls made during the

Table 8.1: Frequency of different types of copulation interference seen in 1980.

	TYPE OF INTERFERENCE					
	Approach	Flyby	Contact	Site	Not Recorded	Total
n	106	49	27	21	20	223
%	48	22	12	9	9	100

copulation, such as wing-flapping by the male or copulation calling, frequently attracted the attention of the interfering bird while still on the nest-site. Typically, the bird then flew off the nest-site and circled the area adjacent to the colony before interference.

At no time were interfering birds ever observed to attempt to copulate with the female of the disrupted pair.

2. Description of identified birds seen interfering.

Birds both with and without colour-rings were seen to interfere. Those with no colour-rings were assumed to be young birds that had never bred before, whereas, colour-ringed individuals had either bred at the warehouse or had been trapped as "prospectors" in a previous year (Wooller and Coulson, 1977).

The identity of interfering birds was determined on 45 percent of occasions (n=158), by either colour-rings or other unique feature such as primary moult or marks on feathers. Table 8.2 lists these birds together with details regarding their breeding status and the number of observed copulations interfered with by each. Fifteen different birds were seen to interfere and all were males. The sex of unringed birds was determined by behavioural interactions (courtship) with other birds. The males did not interfere with similar frequency. Male 1 accounted for 45 percent of observations, and the males that ranked top three, in terms of number of copulations interfered with, together accounted for 75 percent of observations of identified birds. Twelve of the fifteen bred in 1980 and all bred on west-side nest-sites. No bird that bred elsewhere in the colony (i.e. on another side) was ever seen to interfere with a pair that occupied a nest-site on the west-side. Male 6 mated bigamously with his female from the previous year and a new female. Where appropriate this male was

Table 8.2: Details of identified birds seen interfering with copulations in 1980.

BIRD NUMBER	SEX	BRED in 1980?	PAIR-STATUS[1]	BREEDING EXPERIENCE (Years)	INTERFERENCES OBSERVED (n)
1	Male	Yes	C	2	32
2	Male	Yes	C	6	12
3	Male	Yes	S (2)	2	9
4	Male	Yes	S (2)	11	2
5	Male	Yes	C	2	2
6	Male	Yes	B	13	2
7	Male	Yes	S (2)	2	2
8	Male	No	-	-	2
9	Male	No	-	-	2
10	Male	Yes	C	10	1
11	Male	Yes	C	6	1
12	Male	Yes	C	6	1
13	Male	Yes	F	1	1
14	Male	Yes	F	1	1
15	Male	No	-	-	1

1. S=SAME, C=CHANGE, F=First-time breeder. Numbers in parentheses are years pair has been together. B denotes a bigamous male.

excluded from the analysis below.

Males with one to 13 years of breeding experience interfered with copulations. The breeding experience of males that were seen to interfere was compared to those that were not. Only males with more than one year of breeding experience were used in the comparison, as younger individuals were unringed and thus would have likely been under-represented in the sample of identified birds. There was no difference in the mean breeding experience of the two groups (interferers: mean=6.0 years, s.d.=4.1, n=10; non-interferers: mean=5.6 years, s.d.=4.3, n=16; t=0.24, df=22, ns).

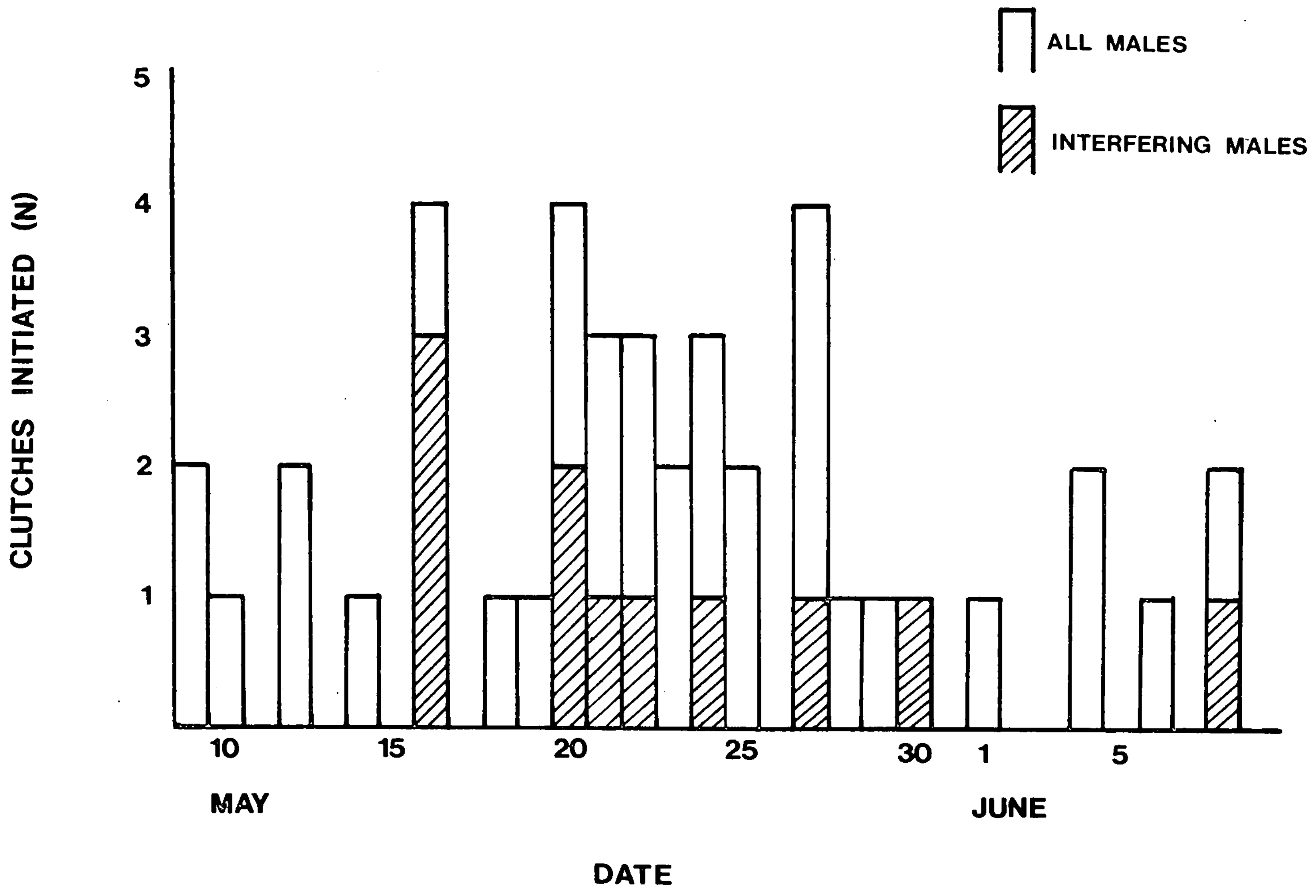
All pair-status types (SAME and CHANGE pairs and those birds breeding for the first time) were represented in the sample of interfering males in Table 8.2. Excluding first-time breeders for reasons given above, interfering males were significantly more likely to be members of CHANGE pairs rather than SAME pairs (Fisher Exact Probability Test, p=0.04). It is worthwhile noting further that all interfering males in SAME pairs had paired with their females for the first time in the previous year.

Figure 8.1 shows the distribution of laying dates of first eggs in all west-side pairs in 1980. Also indicated are the laying dates of first eggs in the interfering male's clutches. There was no tendency for interfering male's clutches to be laid either early or late relative the all pairs.

3. Timing of interference.

The mean date of interference by colour-ringed birds was compared to that of unringed birds (includes first-time and non-breeders), as breeding experience was higher in the former group, and young birds are generally later in their activities at the colony (Coulson and

Figure 8.1: Temporal distribution of egg-laying (first eggs) in all west-side pairs (clear bars) and in those pairs containing a male seen to interfere in copulations in 1980 (shaded bars)


ALL MALES
INTERFERING MALES
CLUTCHES INITIATED (N)
1
2
3
4
5
10
15
20
25
30
1
5
MAY
JUNE
DATE

White, 1958; Coulson, 1959). The mean date of interference by unringed birds (23 May, s.d.=6.8, n=34) was significantly later (t=2.56, df=55, $p < 0.05$) than that for colour-ringed birds (19 May, s.d.=5.3, n=69).

Twelve of the fifteen identified males bred in 1980 (Table 8.2). Thus, timing of interferences engaged in by these males could be expressed in terms relative to their female's reproductive cycle. Figure 8.2 shows the mean rate of interference (per bird per hour) by these males, relative to when their females each laid eggs (Day 0; minus or plus sign indicates days before or after egg-laying respectively; bigamous male excluded). No interferences occurred earlier than day -29. From day -14, interference rate increased about eight fold to a peak occurring in the last two days before eggs were laid. From that point on, interference rate decreased dramatically to near zero on day +5.

4. Location of interferences on the west-side of the warehouse.

Figure 8.3 shows the locations of the pairs interfered with by males 1, 2 and 3. There was no particular trend in the location of interferences with respect to either absolute position in the colony or the position relative to each interfering male's nest-site.

5. Effect of interference.

The direct effect of interference was measured in terms of how much the behaviour disrupted the act of copulation. Fifty-one percent of interferences (n=158) resulted in the copulation coming to an abrupt end, either with the male dismounting and remaining on the window ledge (n=72), or flying off the female in pursuit of the interfering bird (n=8). The balance of the interferences (n=78, 49 percent) did not cause the copulation to stop, but most (74 percent)

Figure 8.2: Changes in the rate of interference of 11 breeding males (see Table 8.2) over the period from pair-formation to egg-laying in 1980. Dates are in relation to the day first eggs were laid (day 0) by the male's partners. Bars are standard errors.

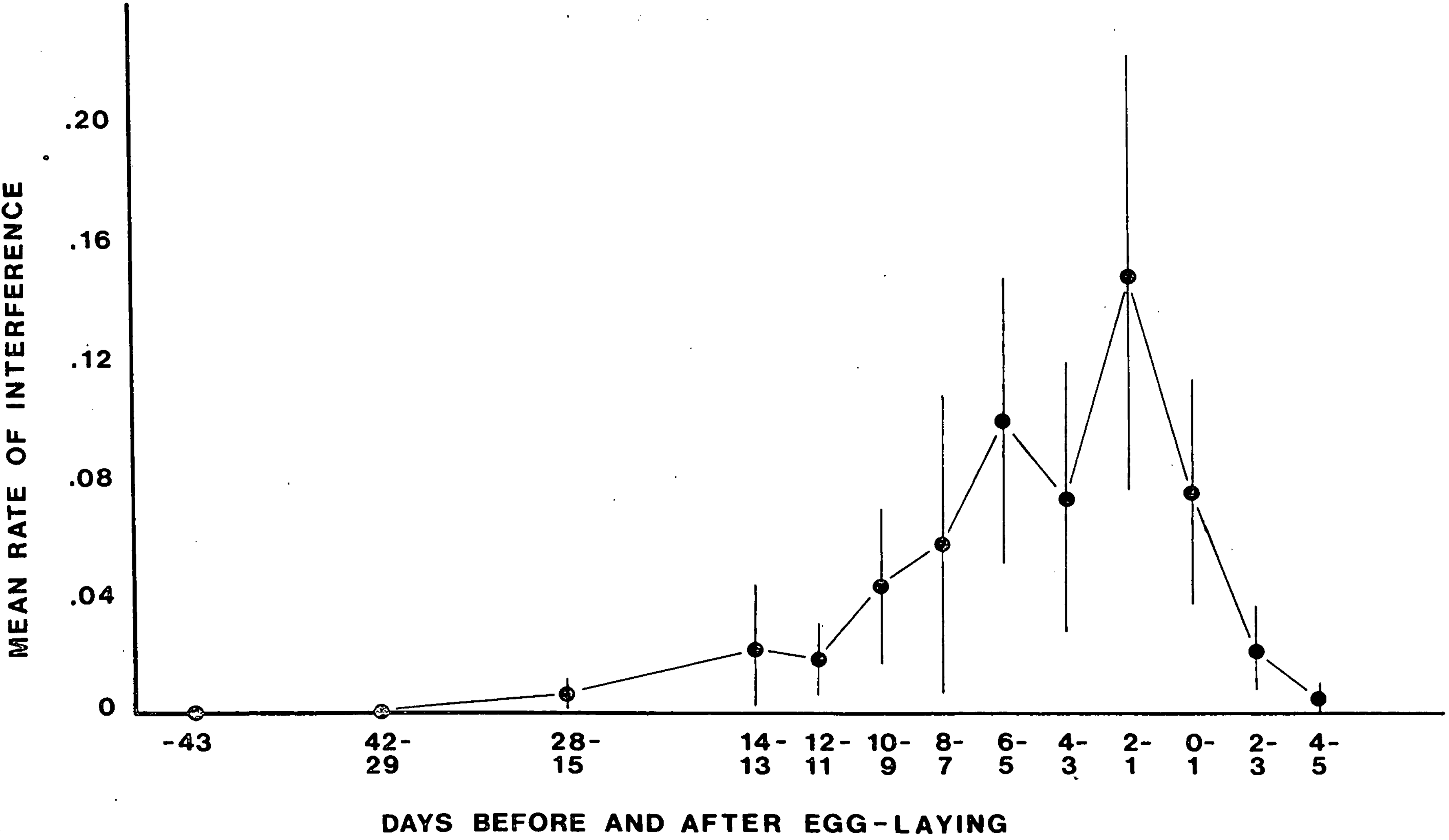
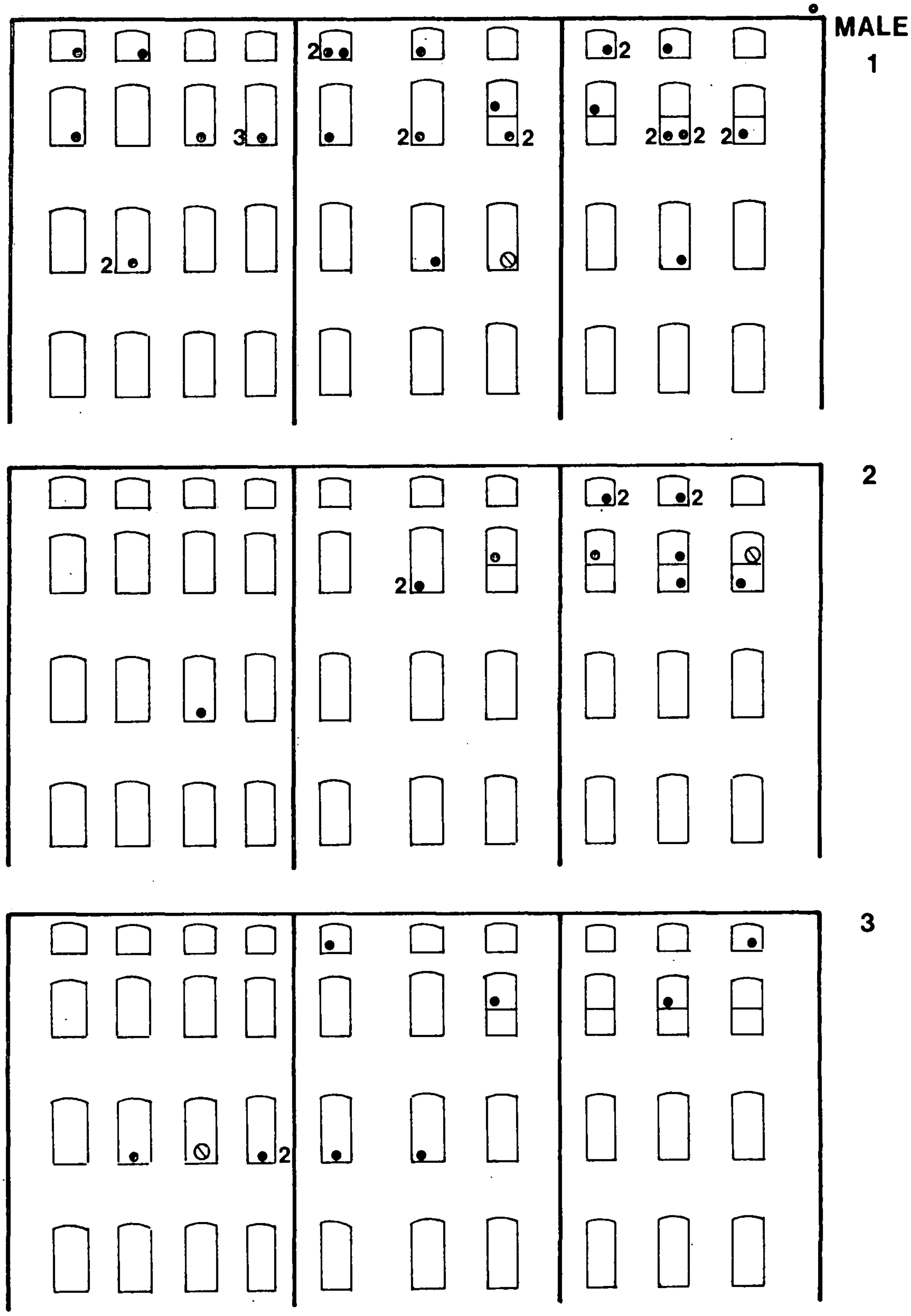

MEAN RATE OF INTERFERENCE
.20
.16
.12
.08
.04
0
-43
42-29
28-15
14-13
12-11
10-9
8-7
6-5
4-3
2-1
0-1
2-3
4-5
DAYS BEFORE AND AFTER EGG-LAYING

Figure 8.3: The west-side of the warehouse showing locations of nest-sites of pairs interfered with by males 1, 2 and 3 (see Table 8.2). ⦸ = nest-site of interfering male. ● = location of interference. Numbers of interferences (if greater than one) are indicated by locations.


MALE
1
2
3

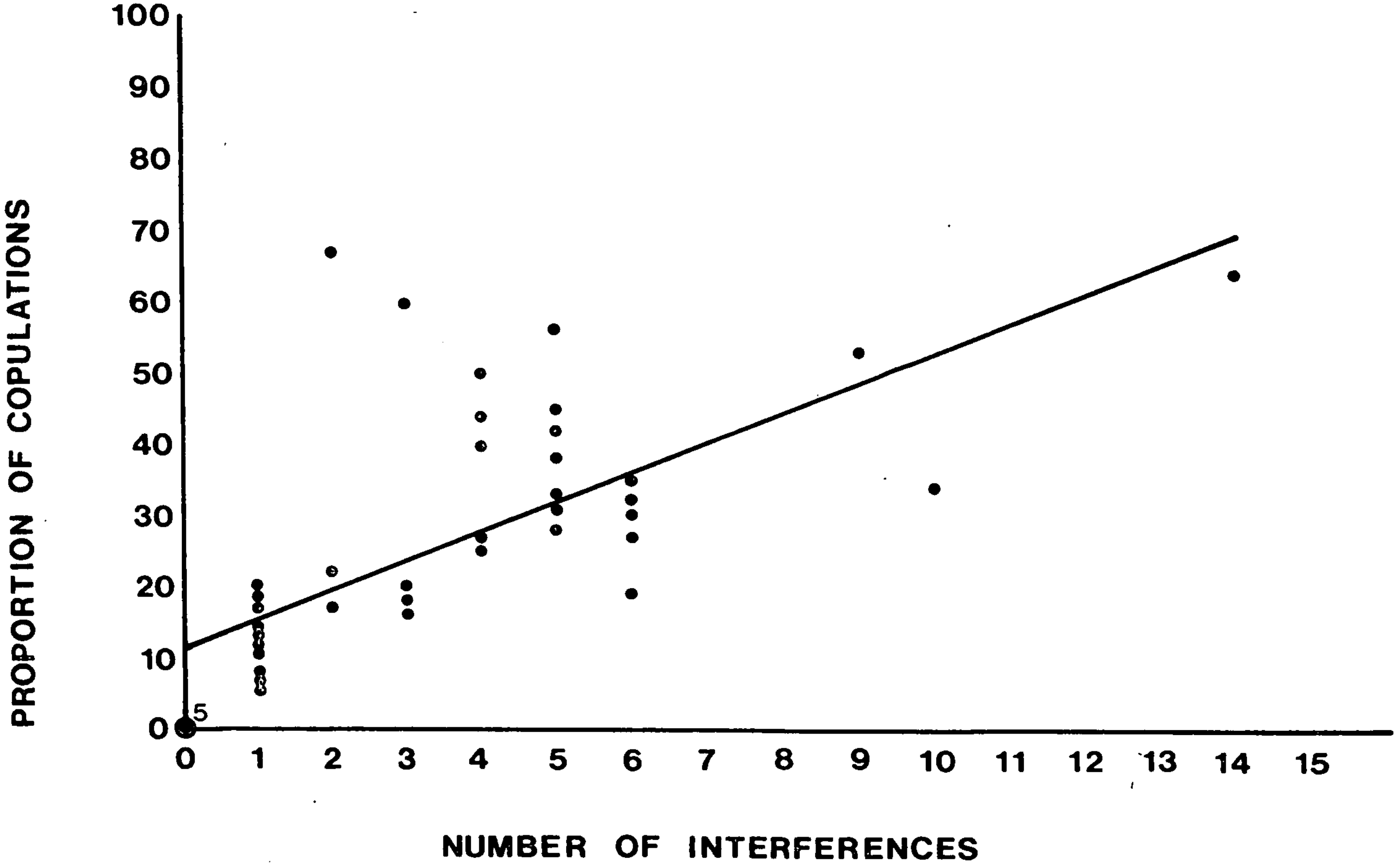
were disturbing to some degree. Typically, either the male or both birds reacted to the incoming bird by looking around and temporarily halting all activity before continuing. Fifteen instances of "approach" and five instances of "flyby" interference caused no overt disturbance, primarily because neither member of the copulating pair saw, or otherwise detected, the incoming bird. They were included as cases of interference because of their potential for some degree of disturbance.

Interference occurred throughout the act of copulation. The timing of interference during copulations was recorded on 140 of 158 cases of interference. On 63 occasions (45 percent), interference occurred after the male mounted the female but before cloacal contact. The balance of interferences (n=77, 55 percent) took place after cloacal contacts had started. Therefore, interference had the potential to reduce the number of cloacal contacts occurring during a particular copulation (copulation success).

In order to examine the effect of interference on copulation success, west-side pairs were grouped according to the number of interfered copulations each experienced over the period between pair-formation and egg-laying (Low: 0-1, Medium: 2-4, High: 5-14). This parameter was used as an index of the "amount" of interference experienced by each pair. The number of interferences experienced by each pair correlated with the proportion of copulations that were interfered with ($r=0.69$, $df=40$, $p<0.01$; Figure 8.4).

The relationship between the "amount" of interference and copulation success (cloacal contacts per copulation) is shown in Table 8.3. Interference did not significantly affect the number of cloacal contacts per copulation. Unsuccessful copulations (no cloacal contact) represented about one third of copulation attempts, regardless of the

Figure 8.4: Relationship between number of interferences experienced and the proportion of copulations interfered with for all west-side pairs (n=42) in 1980: $r=0.69$, $df=40$, $p< 0.05$.



PROPORTION OF COPULATIONS
100
90
80
70
60
50
40
30
20
10
0
5
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
NUMBER OF INTERFERENCES

Table 8.3: Effect of number of interfered copulations on the number of cloacal contacts per copulation in 1980.

NUMBER OF DISRUPTED COPULATIONS			NUMBER OF CLOACAL CONTACTS PER COPULATION					
			0	1	2	3	4	5+
LOW (0-1) n=13 pairs	Copulations	n	36	8	6	12	14	24
		%	36	8	6	12	14	24
MEDIUM (2-4) n=12 pairs	Copulations	n	49	9	13	12	10	45
		%	36	7	9	9	7	33
HIGH (5-14) n=14 pairs	Copulations	n	83	23	22	25	32	65
		%	33	9	9	10	13	26

Chi-square=7.9 df=10 ns

number of interfered copulations experienced by a pair.

Interference also has the potential to influence laying dates and hatching success through a reduction in the number of successful copulations performed (see Brown, 1967). The relationship between the "amount" of interference, laying dates (first eggs) and hatching success (eggs hatched per egg laid) is shown in Table 8.4. There was no significant relationship between the "amount" of interference and either parameter.

Discussion

Kittiwakes at the warehouse colony frequently interfered with one another's copulations. This behaviour has not been reported for this species. Individuals of other avian species are known to interfere in conspecific copulations (e.g. Rook: Goodwin, 1955; Feral Pigeon: Goodwin, 1967; Brown, 1968; Gray Gull: Howell et al., 1974; Ring-billed Gull: Fetterolf, 1979; Common Guillemot: T.R. Birkhead, pers. comm.; a variety of lek species: Foster, 1983).

Some of the above authors speculated on the adaptive significance of interference in copulations. Goodwin (1955) suggested that interference in the Rook served as a means by which males acquire extra-pair copulations. Goodwin (1967) suggested that interference by male Feral Pigeons was an adaptation preventing the insemination of the male's mate by another bird (cuckoldry). This would be particularly important if male parental investment were substantial (Trivers, 1972). Interference may reduce the chances of other males successfully inseminating females and may serve to increase the relative fitness of the interferer (Foster, 1983).

Viable hypotheses for the adaptive significance of interference in the Kittiwake should be compatible with the various aspects of the

Table 8.4: Effect of the number of interfered copulations on laying date and hatching success in 1980.

	NUMBER OF INTERFERED COPULATIONS			
	LOW (0-1) n=13 pairs	MEDIUM (2-4) n=12	HIGH (5-14) n=14	
Laying date Mean	22 May	22 May	24 May	ANOVA F=0.23 df=2,36
s.d.	11.5	6.9	3.5	ns
Hatching success Eggs hatched/ egg laid (2-egg clutches)	0.59	0.72	0.75	CHI-SQUARE[1]= 1.49, df=2 ns

[1] Chi-square calculated on the number of eggs hatched and not hatched in Low, Medium and High groups (3X2 table)

data. Only males (breeding and non-breeding) were seen to interfere and breeding males interfered most frequently during the two week period before their females laid eggs. Within this period, rates of interference increased steadily to a peak immediately before egg-laying and decreased dramatically thereafter. Although interference caused disturbance of copulation, the behaviour did not affect the number of cloacal contacts per copulation, laying date and hatching success of disturbed pairs. Extra-pair copulation attempts were never observed in association with an interference.

Of the adaptive explanations for interference mentioned above, the "cuckoldry-avoidance" hypothesis suggested by Goodwin (1967) appears to be most favourably supported by the data. Clearly, Kittiwake males do not interfere with copulations in order obtain extra-pair copulations since attempts by the interfering male were never observed. Disrupted pairs of Kittiwakes were not adversely affected either in terms of copulation success (cloacal contacts per copulation), laying date or hatching success. Thus, interference in the Kittiwake is not likely to function in reducing the relative fitness of conspecifics.

If there is a risk of cuckoldry at the colony then it may benefit male Kittiwakes to interfere with copulations, as these copulations may involve their mates. Although relatively rare, extra-pair copulations were observed in the three years of study (Chapter 7). Over the two week period before egg-laying, males in both SAME and CHANGE pairs spent about half their time away from the colony (Chapter 5), at which time the female was often left alone at the nest-site. These observations suggest that there is a risk of cuckoldry for male Kittiwakes at the warehouse colony. The "cuckoldry-avoidance" hypothesis predicts two striking features of the data: 1) only males interfered with copulations and 2) they interfered most often during their female's fertile period (i.e. just before egg-laying). However, observations are not entirely compatible with the hypothesis. The risks of cuckoldry are likely to be higher during a male's absence from the colony and interference should be more common directly after the male's return. On many occasions, however, males were at the nest-site with their partners immediately before interference took place and in these circumstances it is difficult to see the value of the behaviour in terms of cuckoldry avoidance. Over half the interferences occurred after cloacal contact but, in order to be effective, they should have occurred most frequently before any cloacal contact had taken place.

An alternative hypothesis is that interference functions to delay egg-laying in disrupted pairs, thus bringing them into closer reproductive synchrony with the interfering bird. The hypothesis assumes that inter-pair reproductive synchrony has a positive effect on reproductive success of participating individuals and that disruption of copulation delays egg-laying in the interfered pair. There is some support for these assumptions in the literature (Kruuk, 1964; Patterson, 1965; Brown, 1967; Gochfeld, 1980; Findlay and Cooke, 1982). Predictions of the hypothesis are that interference should delay egg-laying in disrupted pairs and that interfering males should be paired with females that eventually lay during times of the season when synchrony is low and when there is the opportunity to bring pairs into reproductive synchrony with themselves (i.e. late in the season, after the peak of laying). There is little support for this hypothesis in the data. Interfering male's clutches were not laid late in the season relative to other west-side birds. Mean laying dates of pairs experiencing different numbers of interferences did not differ significantly. Of course, there is a problem in testing this because it is difficult to predict when a female will lay eggs in a given year and correspondingly difficult to evaluate a certain laying date in terms of it being either early or late. Interestingly, many unringed (young) birds interfered in copulations. Young birds would have most to gain from enhancing local synchrony late in the season as that is the time they most frequently lay eggs (Coulson and White, 1958).

A final consideration is that interference may have no function in an evolutionary sense. In other words, its selective effects may be neutral and its occurrence would be mediated solely by proximate factors. Interference may be caused by an attraction to copulating pairs brought about by the heightened hormonal state of the male prior to egg-laying. Indeed, the most common types of interference ("flyby" and "approach") looked very much like a bird being attracted to and inspecting the act of copulation, rather than a bird trying to actively disrupt the copulation.

The suggestion that interference is a result of an attraction of males to the act of copulation, and further that it has no ultimate function is, in general, supported by the data. The occurrence of interference would be expected to follow hormonal changes in the male, of the kind that would occur at the time of year interference was seen (i.e. two week period prior to egg-laying). Young, unringed birds may also undergo hormonal changes similar to breeders, albeit probably later in the season (Brown, 1967, Mills, 1973). This may explain why they were seen to interfere, on average, later than more experienced, colour-ringed birds.

An interesting difference between interfering and non-interfering males was that the former group were much more likely than expected by chance, to be members of CHANGE pairs. Further, interfering males that were members of SAME pairs (n=3) had paired with their females for the first time in the year prior to study. Males that had recently changed mates appeared to show a greater tendency to interfere in copulations. The reasons for the trend are unclear. Males paired with females that lay eggs relatively early would have less chance to interfere because there would be fewer copulations taking place at this time. However, females in SAME and CHANGE pairs did not differ with respect to dates of egg-laying in 1980 (Appendix B). Males in CHANGE pairs may differ hormonally from those in SAME pairs (see Coulson, 1966), which may affect their tendency to interfere. If interference functions to reduce the chances of cuckoldry then the difference might be caused by a higher probability of cuckoldry in CHANGE pairs. This possibility is developed further in the final discussion of this thesis (Chapter 9).

CHAPTER 9. FINAL DISCUSSION

Individuals of most bird species mate monogamously and many breed more than once in their lifetime (Lack, 1968, Rowley, 1983). It is common for mates to be retained from year to year (references in Rowley, 1983) and thus, in birds, the opportunity arises for a complex relationship to develop between male and female breeding partners. This is not the case for many species in other taxa since mating systems are primarily promiscuous or polygynous (Wilson, 1975) with relatively little interaction between male and female except for copulation.

Most of the work addressing the significance of the pair relationship or "pair-bond" with respect to reproductive biology has involved birds. In general, work has shown that individuals retaining their mates from the previous year reproduce with greater success than those changing mates (Coulson, 1966, 1972; Mills, 1973, 1979; Ollason and Dunnet, 1978). Regardless of breeding experience, birds that have changed mates (CHANGE) lay smaller eggs and smaller clutches later in the season and hatch fewer eggs than those retaining mates (SAME). Although the reasons for the differences are unclear, they are likely to stem either from behavioural differences before egg-laying or from differences in parental care abilities in the two groups (see Coulson, 1972; Mills, 1973; Rowley, 1983).

This thesis has shown that behavioural differences between SAME and CHANGE pairs occurring before egg-laying, may explain some of the differences in reproductive parameters noted above. Over the period from pair-formation to egg-laying, female Kittiwakes in CHANGE pairs were seen up to 19 percent more frequently at the nest-site than females in SAME pairs and, as a result, probably had less "off-duty" during which to forage. This was also the case for males during the two weeks after pair-formation when those in CHANGE pairs were seen 15 percent more frequently than those in SAME pairs. More frequent courtship feeding could compensate for reduced foraging time in the female (although this would put higher demands on the male) but there was no evidence that this was the case in CHANGE pairs. The higher rates of return and greeting seen in CHANGE pairs (up to 2.5 times) may increase energy requirements and in conjunction with less foraging time, reduce the nutrient reserves of these birds. This, in turn, could have a depressive effect on reproductive success and adult survival.

Coulson (1966) suggested that mate change in the Kittiwake results in less efficient breeding. Presumably, this means that for a certain unit of reproductive output, birds in CHANGE pairs expend greater effort than birds in SAME pairs. Although reproductive success was not studied in this thesis, it appears that CHANGE pairs did expend greater effort than SAME pairs, due to a less efficient system of nest-site attendance and higher rates of some courtship behaviour. However, the observation that CHANGE pairs behaved more like SAME pairs as the season progressed indicates that CHANGE pairs were able to adjust their breeding behaviour toward a more efficient system as egg-laying approached. To some extent this reduces the importance of behavioural differences between the two groups as it would be expected that behaviour occurring immediately before egg-laying would have more effect on reproductive success than behaviour occurring earlier.

Data for the Kittiwake do not support the suggestion that birds in SAME pairs are at an advantage over those in CHANGE pairs because of the time they save by not having to find a new mate (Mills, 1973; Rowley, 1983). CHANGE pairs formed later than SAME pairs yet mean dates of egg-laying were very similar in both groups. It is possible that, although CHANGE pairs formed later in the season, the higher levels of pair attendance and higher rates of greeting seen in these birds may have increased stimulation and accelerated hormonal changes preceding egg-laying. This may have resulted in dates of egg-laying being relatively similar in the two groups. There was also no evidence that, once the pair has formed, the progression through stages of behaviour toward egg-laying was different in SAME and CHANGE pairs. Rowley (1983) suggested that, in general, birds retaining the same mate could dispense with courtship because they are familiar with each other. This was clearly not the case in the Kittiwake. Both SAME and CHANGE pairs performed courtship behaviour from pair-formation to egg-laying and quantitative differences were not as obvious as Rowley suggests they might have been. This author's comments may be more applicable to individuals of perennially monogamous species that do not split up between breeding attempts. There is no evidence that Kittiwake partners stay together during the winter months (Coulson and Thomas, 1983) and it appears that regardless of whether individuals are re-pairing with the same bird or changing mates, there is a requirement for the performance of courtship behaviour after pair-formation.

Mate change results from either the death of a partner or divorce (both birds return to breed but take different mates). A bird is forced to change mates if its partner dies, but divorce can be considered an active (unconscious) "decision" on the part of one or both partners. The costs of divorce are those associated with mate change and have been outlined above: they entail significant reductions in reproductive success. The benefits of divorce are suggested from the observation that pairs more often break up, even though both partners survive, following a year of reproductive failure (e.g. Coulson, 1966; Brooke, 1978). Coulson (1966) suggested that reproductive failure may be the result of incompatibility between partners. Although by divorcing, individuals forfeit the potential for increased reproductive success through re-mating with the same individual, they presumably benefit by dissolving a pair relationship with incompatible or otherwise inappropriate mate. In this context, divorce can be seen as an integral component of the process of mate choice.

Depending upon the method by which individuals choose mates, the best possible choice may be made only infrequently (Gladstone, 1979; Wittenberger, 1983) and incompatibility of partners might be a common phenomenon. For example, Coulson and Thomas (1983) showed that Kittiwakes at the warehouse colony have a very limited choice of birds from which to select a partner after mate change because of physical and temporal constraints imposed on birds in search of a mate. Under these conditions of mate choice it may be highly adaptive for birds to have the option of divorce, if indications of incompatibility or generally inappropriate pairing can be detected during the first breeding attempt.

An interesting question with regard to the role divorce plays in the process of mate choice is why the incompatibility or unsuitability of mates is not detected and acted upon before the first breeding attempt. It may be that the required information regarding the general suitability of a partner is not available in time to choose another mate before breeding commences. Even if such information were available before egg-laying (see Nisbet, 1973; Niebuhr, 1981), the likelihood of finding a more suitable mate in time to breed might be small. In the study reported here, once a pair of Kittiwakes had formed, a separation was never observed. Similarly, Nisbet (1973) never saw Common Tern pairs break up in the later phases of courtship. It appears that once these birds have paired, they are committed to continue together at least for one breeding season. In long-lived birds such as gulls and terns, the costs in terms of lifetime reproductive success, of "experimenting" with a partner for one breeding bout, may be small compared to the potential benefits of finding a suitable mate with which to breed for several years.

In terms of causation, two possible interpretations of the behavioural differences between SAME and CHANGE pairs will be considered. Generally, the data are compatible with the notion that birds in CHANGE pairs are unfamiliar with one another (see Erickson, 1973; Lumpkin *et al.*, 1982). Unfamiliar partners might be expected to spend more time together at the nest-site and perform more courtship behaviour (such as the greeting ceremony) than those familiar with one another through previous breeding experience, since the result would be an increase in the duration and frequency of interaction of male and female. This may decrease the period over which the pair relationship is established and allow these birds to divert more time and energy into activities such as nest-site defense and feeding. The observation that differences between SAME and CHANGE pairs were, in general, greatest during the two week period after pair-formation is predicted since initially unfamiliar partners should develop familiarity as the breeding season progresses.

A second interpretation of the behavioural differences observed between SAME and CHANGE pairs involves the notion that paternity assurance is lower for males in CHANGE pairs. This concept was alluded to in Chapter 8, in a discussion of the adaptive significance of interference. Trivers (1972) argued that in species where male investment is substantial, selection should favour males who show behaviour that enhances paternity assurance (decreases the chances of cuckoldry), as the costs of wasting parental investment are high.

A question arises as to why paternity assurance should be lower for males in CHANGE pairs than for males in SAME pairs. First, assume that there is variation in females with regard to their tendency to accept extra-pair copulations. If so, then selection should favour males that choose as mates, those females who repel the sexual advances of other males. During previous breeding attempts, males in SAME pairs have had the opportunity to assess their females with respect to this factor, while males in CHANGE pairs have not. Females in CHANGE pairs are, in a sense, "unknown quantities", and it may benefit males paired with females for the first time, to modify behaviour patterns in order to increase paternity assurance.

Males in CHANGE pairs may have increased paternity assurance in several ways. These males were seen more often with their partners than were males in SAME pairs, throughout the period from pair-formation to egg-laying. In so doing, they could potentially keep their mates under surveillance for longer and reduce the chances of other males copulating with their females. In this context, surveillance is of importance only during the fertile period of the female, yet as mentioned above, males in CHANGE pairs were seen with their females more often throughout the period from pair-formation to egg-laying. The duration of the fertile period in the Kittiwake is unknown, but it may be relatively long if females are able to store sperm. (Recently, Hatch (1983) has shown that sperm storage glands exist in the Horned Puffin, a species in the same order as the Kittiwake: Charadriiformes). If this is the case then male Kittiwakes may have to attend their females several weeks before egg-laying, in in order to assure their paternity. Surveillance of females in CHANGE pairs may have been more intense than that indicated by levels of pair attendance, as a result of males remaining closer to the colony during absences away. Evidence for this is given by the observation that rates of male return were higher in CHANGE pairs. In order to maintain higher rates of return, these males would have probably had to remain in the vicinity of the colony for longer periods than males in SAME pairs and could have kept their females under more continuous surveillance.

In relation to egg-laying, CHANGE pairs first copulated much earlier than SAME pairs. They also maintained numerically higher rates of copulation early in the season. Birkhead (1979) suggested that, in general, males copulate with females for extended periods before egg-laying in order to disguise the fertile period of the female from other males and thus increase paternity assurance. If males copulated only during a short period close to egg-laying, it would be easy for other males to detect copulation in a pair and time their extra-pair copulation attempts more appropriately. If there is lower paternity assurance for males in CHANGE pairs then it may benefit them to disguise their female's fertile period more effectively (by copulating earlier) than if their paternity assurance were higher.

Breeding males were seen to interfere with copulations of other pairs of Kittiwakes and these males were significantly more likely to have changed their mates in the year of study. Goodwin (1967) suggested that interference in Feral Pigeons may have evolved as a mechanism to reduce the chances of cuckoldry, and in Chapter 8 of this thesis, the cuckoldry-avoidance hypothesis for interference in the Kittiwake received some support. Taken together, the three lines of evidence presented above, suggests that some of the behavioural differences between SAME and CHANGE pairs can be explained in terms of presumed differences in paternity assurance. An interesting footnote is that in monogamous, colonial birds, females in many species react aggressively and repel the advances of males attempting extra-pair copulations (MacRoberts, 1973; Gladstone, 1979). It was suggested earlier that males should choose as mates, females that react in this way. If there is heritable variability in the way females react to the advances of other males then it is possible that the trend noted by the above authors was a result of inter-sexual selection for aggressive females caused by male choice.

A general trend found in this study was that variation in behavioural measures was often significantly larger in CHANGE pairs than in SAME pairs. Both Coulson (1966) and Mills (1973) found consistently greater variation in CHANGE pairs with respect to laying dates. Cooke et al. (1981) found greater variation in clutch size of Lesser Snow Geese that changed mates. None of these authors suggested a reason for the observed trend in variance. It is possible that CHANGE pairs are in general more variable than SAME pairs with respect to biological and behavioural parameters due to the selective effects of certain pairs divorcing and certain pairs staying together. Presumably, a sample of CHANGE pairs would contain both compatible and incompatible combinations, so if one assumes that the incompatible pairs split up through divorce, then the result may be lower variability in characteristics of the pair types that persist over time (SAME) compared to those that split up more frequently (CHANGE). In species where the major cause of the break up of pairs is the death of a partner, differences in variability between SAME and CHANGE pairs would not be expected. This is because the pairs that break up are not likely to be different from the pairs that remain together.

This study represents a preliminary investigation of the relationships between breeding behaviour prior to egg-laying, and pair-status, which to my knowledge has never been attempted before, under natural conditions. Since the results and conclusions are based on only three years of data (and one year in a few cases), they are necessarily tentative. An investigation such as this, conducted over a relatively short period of time, is at best representative of the period of study only: extrapolation may be inappropriate.

Clearly, there is scope for continuing and expanding this study. Of particular importance is the elucidation of components of compatibility between pair members, which until now have only been speculated upon (e.g. Coulson, 1972; Tasker and Mills, 1981). This kind of study would lead to a fuller understanding of the reasons for divorce in the Kittiwake. The study of parental care patterns in relation to pair-status may provide answers to the question of why CHANGE pairs experience lower reproductive success than SAME pairs. Biologists are realizing the importance of long-term studies of individually marked individuals and the frequency of these sorts of investigations appears to be on the increase. It is hoped that out these studies will flow information regarding the significance of pair-status in relation to behaviour and a fuller understanding of the complex relationships that exist between pair members in monogamous, long-lived species.

SUMMARY

1. The breeding behaviour of Kittiwakes that retained mates from the previous breeding attempt (SAME) was compared to those that changed mates (CHANGE), over the period between pair-formation and egg-laying. Unless otherwise noted the differences referred to below are significant ($p < 0.05$).

2. Descriptions of Kittiwake courtship behaviour are given. Courtship behaviour occurred in a specific sequence: return to mate, greeting ceremony, female head-tossing, courtship feeding or copulation. Rarely, copulation followed courtship feeding. Both the greeting ceremony and female head-tossing occurred spontaneously, whereas, courtship feeding or copulation never did. The probability of one behaviour being followed by another depended on the point of entry into the sequence (i.e. either through return, spontaneous greeting or spontaneous head-tossing). Males were responsible for all cases of intra-pair aggression.

3. SAME and CHANGE pairs did not differ significantly in either position of nest-site in colony (i.e. centre or edge) or breeding experience and the comparison of SAME and CHANGE pairs was not confounded by these variables.

4. The period from the arrival of the male to pair-formation was longer in CHANGE pairs (difference=6.9 days). Although not significant, the difference was even larger in females (d=12 days). This was probably a result of the longer time required to find a new mate compared to retaining the same mate. Birds in SAME and CHANGE

pairs did not differ significantly in relative dates (compared to mean for SAME and CHANGE combined) of arrival, pair-formation or egg-laying, however, some trends were apparent. CHANGE pairs formed 12 days later than SAME pairs despite relatively similar dates of arrival of males and females in each group. Late pair-formation did not appear to cause late egg-laying in either group.

5. The time between pair-formation and egg-laying was divided in three periods: Period 1- first two weeks after pair formation, Period 2- intervening period, Period 3- last two weeks before egg-laying. Birds in CHANGE pairs were seen more often together at the nest-site during Periods 1 (d=21%) and 2 (d=13%) and less often away from the nest-site during Period 1 (d=13%). Males in CHANGE pairs were seen more often at the nest-site, either singly or with mate, during Period 1 (d=15%). This was the case for females in CHANGE pairs during all three periods (1: d=18%; 2: d=19%; 3: d=10%). Over the 14 day period before, and five day period after the start of egg-laying, levels of pair attendance were consistently higher in CHANGE pairs before egg-laying and decreased in both groups thereafter. The proportion of time the nest-site was left unoccupied, was consistently low in SAME and CHANGE pairs. In both groups, males were seen (either singly or with mate) at similar frequencies while female attendance increased to a peak about 5-6 days before egg-laying and was generally higher in CHANGE pairs. Since only one bird is necessary to defend the nest-site, it is suggested that CHANGE pairs use a less efficient method of nest-site defense through the incorporation of more pair attendance. This may have lead to birds in CHANGE pairs having less "off-duty" time during which to forage and pursue other self-maintenance activities. This may reduce the overall body condition of

birds in CHANGE pairs and in turn, reduce reproductive success. Trends in pair attendance before and after egg-laying suggest a surveillance function for pair attendance whereby the male is attempting prevent other males from inseminating their mates.

6. Birds in CHANGE pairs returned to their mates about 2.5 times more often in Period 1 (d=1.09 returns/pair/hour) and almost 1.5 times more often in Period 2 (d=0.32). This was partly the result of birds in CHANGE pairs performing proportionately more "circuits" (leave and return to nest-site within 1 min.) in these periods (1: d=18%, 2: d=12%). The rate of greeting after return was over 2.5 times higher in CHANGE pairs during Period 1 (d=1.12 greetings/pair/hour). A lower proportion of greetings in CHANGE pairs were followed by female head-tossing in Period 1 (d=15%). These differences between SAME and CHANGE pairs were also apparent during the 14 day period before and five day period after egg-laying in 1980. Trends in these parameters, over the period, were similar in both groups. In general, rates of return and greeting increased to a peak during the two days before egg-laying and declined thereafter. The frequency of female head-tossing increased to a peak about 5-6 days before egg-laying and decreased thereafter. The observations are in keeping with those of several other authors who note higher rates of courtship in new pairs compared to established pairs. Kittiwakes recognize the greeting call ("kittiwaak") of their mates and it is suggested that the higher rates of greeting in CHANGE pairs serves to shorten the period of learning of these calls in pairs of unfamiliar birds. Trends in return, greeting and head-tossing before and after egg-laying are discussed in terms of the co-ordination of activities and communication between male and female.

7. Rates of courtship feeding and copulation were relatively low in SAME and CHANGE up to 14 days before egg-laying. Rates then increased to a peak about 5-6 days before egg-laying and decreased thereafter. The exception was rates of copulation in SAME pairs, which remained at peak levels until first eggs were laid. The timing of courtship feeding and copulation relative to egg-laying appear to be similar to other gulls with the exception that copulation ends sooner in the Kittiwake. This may be a result of the cliff nesting habit. The timing of these behaviours is considered in a functional context with regard to egg production and fertility. Early copulations were generally unsuccessful (cloacal contact did not occur). In both groups, the proportion of contact copulations increased toward egg-laying and stabilized at about 70% of attempted copulations. The period from the first attempted copulation to egg-laying was almost twice as long (d=17 days) in CHANGE pairs. The rate of copulation was almost three times higher in CHANGE pairs (d=0.04 cops/pair/hour, not significant) over the period from pair-formation to 12 days before egg-laying. It is suggested that these early copulations function as "practice" for birds unfamiliar with each other. Copulation rates were twice as high in SAME pairs (d=0.09) over the last 4 days before egg-laying. Similar trends were found when contact copulations were considered, however, differences between SAME and CHANGE pairs were smaller. No such differences in rates of courtship feeding were observed between the two groups. The last 14 days before egg-laying was considered as a whole and rates of courtship feeding and copulation did not differ in the two groups. Over this time period, SAME pairs performed more cloacal contacts per copulation than CHANGE pairs. It is doubtful whether lower reproductive success reported for CHANGE pairs by other workers can be explained by differences in the frequency and timing of

courtship feeding or copulation.

8. Behavioural differences between SAME and CHANGE pairs were usually greatest during the first two weeks after pair-formation and decreased toward egg-laying. Variation in behavioural parameters was usually greatest in CHANGE pairs.

9. Both breeding and non-breeding males were seen to interfere in copulations of other pairs. Breeding males interfered most frequently over the 14 day period before their females laid eggs, and were, more frequently than expected, members of CHANGE rather than SAME pairs. There was no relationship between breeding experience and the tendency for males to interfere. Males never attempted copulation during interference. Interference had no effect on timing of egg-laying, cloacal contacts per copulation or hatching success of disrupted pairs. Several hypotheses for the adaptive significance of interference are considered. The data provide some support for the hypothesis that interference functions to reduce the chances of cuckoldry. Alternatively, interference may have no ultimate function and its occurrence may be mediated by proximate factors such as the hormonal state of interfering males.

10. Behavioural differences between SAME and CHANGE pairs are discussed in terms of cause and effect. Two possible causes of the differences are considered. First, the data fit very well to the notion that birds in CHANGE pairs are unfamiliar with each other and as a result spend more time together as a pair and more frequently perform courtship behaviour such as greeting. Initially unfamiliar partners become more familiar with each other as the season progresses

and this explains why differences between SAME and CHANGE pairs decreased from pair-formation to egg-laying. Second, an argument is presented to suggest that differences in attendance patterns, timing of copulation and the tendency to interfere in copulations in the two groups is the result of lower paternity assurance for males in CHANGE pairs. The effects of the differences between SAME and CHANGE pairs are discussed in terms of breeding efficiency in the two groups. Birds in CHANGE pairs appeared to expend more energy in the reproductive effort by adhering to a less efficient method of nest-site defense and by performing courtship behaviour such as greeting, more frequently. The data do not support the suggestion that CHANGE pairs are at a disadvantage due to the loss in time caused by having to find a new mate. It is suggested that variation in behavioural parameters was greatest in CHANGE pairs due to the selective effects of certain pair types (e.g. those involving incompatible partners) breaking up more frequently than others.

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APPENDICES

Appendix A. Scientific names of species referred to in this thesis.

Adélie Penguin	*Pygoscelis adeliae* (Hombron & Jacquinot)
Booby	*Sula* spp.
Buller's Mollymawk	*Diomedea bulleri* Rothschild
Common Guillemot	*Uria aalge* (Pontoppidan)
Feral Pigeon	*Columba livia* Gmelin
Fulmar	*Fulmarus glacialis* (L.)
Gannet	*Sula bassana* (L.)
Greenshank	*Tringa nebularia* Gunner.
Gulls	
Gray	*Larus modestus* Tschudi
Herring	*Larus argentatus* Pontoppidan
Kittiwake	*Rissa tridactyla* (L.)
Lesser Black-backed	*Larus fuscus* L.
Red-billed	*Larus novaehollandiae* Forster
Ring-billed	*Larus delawarensis* Ord
Lesser Snow Goose	*Anser caerulescens* (L.)
Manx Shearwater	*Puffinus puffinus* (Brunnich)
Horned Puffin	*Fratercula corniculata* (Naumann)
Razorbill	*Alca torda* L.
Redshank	*Tringa totanus* (L.)
Ring Dove	*Streptopelia risoria* L.
Rook	*Corvus frugilegus* L.
Stilt Sandpiper	*Micropalama himantopus* (Bonaparte)

Appendix B: Mean dates of arrival at the colony, pair-formation and egg-laying for SAME and CHANGE pairs in each year.

Table B.1: Arrival at the colony.

	DATE					
	SAME			CHANGE		
	Mean	s.d.	n	Mean	s.d.	n
1979						
Male	26 Jan	28.6	14	27 Jan	26.4	8
Female	13 Jan	13.5	14	23 Jan	25.0	8
1980						
Male	18 Feb	30.3	14	25 Feb	36.8	9
Female	6 Feb	22.6	14	3 Feb	20.8	9
1981						
Male	7 Mar	28.5	17	15 Mar	38.4	7
Female	28 Feb	25.0	17	27 Feb	22.1	7

Table B.2: Pair-formation

	DATE					
	SAME			CHANGE		
	Mean	s.d.	n	Mean	s.d.	n
1979	28 Jan	29.1	14	6 Feb	26.6	8
1980	22 Feb	26.8	14	6 Mar	35.9	9
1981	9 Mar	26.1	17	25 Mar	33.6	7

Table B.3: Egg-laying (first eggs)

	DATE					
	SAME			CHANGE		
	Mean	s.d.	n	Mean	s.d.	n
1979	23 May	4.9	14	23 May	4.9	8
1980	22 May	4.1	14	19 May	6.9	9
1981	18 May	5.1	17	24 May	6.7	7

Appendix C: Sample sizes of spot observations of attendance and duration of observation periods for each pair in each year. Pairs are identified by their nest-site code.

Table C.1: Sample size of spot observations of each pair for three periods from pair-formation to egg-laying in 1979.

NEST-SITE	NUMBER OF SPOT OBSERVATIONS		
	First 2-weeks after pair-formation	Middle period	Last 2-weeks before egg-laying
SAME			
W1Aa	11	86	13
W1Bb	23	84	7
W1Eb	15	82	13
W1Fb	21	72	11
W2Aa	8	93	13
W2Da	8	94	12
W2Fb	8	92	14
W2H	8	92	14
W3A	21	71	13
W3Ba	23	78	12
W2Ja	7	44	12
W1Ab	6	38	14
W1Fa	5	50	4
W3Da	14	14	12
CHANGE			
W1Ga	8	88	13
W2ATa	21	72	11
W2Ba	19	58	11
W2Bb	21	71	13
W2Ea	21	79	7
W3Fb	7	49	8
W2G	10	29	14
W3Db	8	40	12

Table C.2: Sample size of spot observations of each pair for three periods from pair-formation to egg-laying in 1980.

NEST-SITE	NUMBER OF SPOT OBSERVATIONS		
	First 2-weeks after pair-formation	Middle period	Last 2-weeks before egg-laying
SAME			
W2Ab	14	110	91
W2Ba	8	111	90
W2Da	11	153	103
W1Eb	13	94	82
W1Fa	14	97	90
W1H	5	99	103
W2H	13	108	101
W2Eb	17	97	98
W2Ja	13	110	101
W1Ab	16	34	71
W1Ea	21	26	61
W2BTa	13	57	71
W3Fb	10	78	101
W3H	24	76	111
CHANGE			
W2ATa	8	110	90
W2C	5	100	71
W1Ga	11	76	44
W2Fb	14	86	91
W3G	10	121	105
W2CTb	13	46	51
W2Ib	26	5	40
W3Ba	26	0	71
W3Da	27	44	98

Table C.3: Sample size of spot observations of each study pair for three periods from pair- formation to egg-laying in 1981.

NEST-SITE	NUMBER OF SPOT OBSERVATIONS		
	First 2-weeks after pair-formation	Middle period	Last 2-weeks before egg-laying
SAME			
W1Bb	13	26	8
W1Da	13	10	8
W1Eb	14	35	8
W1Fa	16	29	8
W1Fb	13	10	8
W1G	16	31	12
W1Jb	5	14	10
W2Ab	14	35	8
W2BTa	13	19	7
W2Da	8	4	8
W2Eb	14	35	8
W2G	16	34	8
W2Ia	13	9	8
W2Ib	14	18	0
W3Ba	12	6	4
W3Bb	13	10	8
W3Fb	7	23	8
CHANGE			
W1Ab	12	0	0
W1Ba	0	0	0
W1Ja	8	32	0
W2C	14	35	8
W2Fb	13	25	9
W3G	6	23	8
W3H	13	10	8

Table C.4: Sample size of spot observations of each pair for ten, 2-day periods before and after egg-laying in 1980.

NEST-SITE	NUMBER OF SPOT OBSERVATIONS Days before and after egg-laying[1]									
	14-13	12-11	10-9	8-7	6-5	4-3	2-1	0-1	2-3	4-5
SAME										
W2Ab	8	16	6	14	18	14	15	18	16	6
W2Ba	6	17	7	14	13	19	14	19	12	10
W2Da	13	19	14	19	12	16	10	15	16	7
W1Eb	6	8	16	6	14	18	14	15	18	6
W1Fa	6	17	7	14	13	19	14	19	12	10
W1H	17	7	14	13	19	14	19	12	16	10
W2H	16	6	14	18	14	15	18	16	16	0
W2Eb	7	14	13	19	14	19	12	16	10	9
W2Ja	6	14	18	14	15	18	16	16	9	6
W1Ab	4	10	6	17	7	14	13	19	14	7
W1Ea	3	4	10	6	17	7	14	13	19	6
W2BTa	4	10	6	17	7	14	13	19	14	19
W3Fb	16	6	14	18	14	15	18	16	16	0
W3H	14	18	14	15	18	16	16	9	12	17
CHANGE										
W2ATa	6	17	7	14	13	19	14	19	12	10
W2C	4	10	6	17	7	14	13	19	12	7
W1Ga	0	4	3	4	10	6	17	7	14	6
W2Fb	8	16	6	14	18	14	15	18	14	6
W3G	19	14	19	12	16	10	15	16	16	6
W2CTb	4	3	4	10	6	17	7	14	7	11
W2Ib	5	4	3	4	10	6	8	16	13	0
W3Ba	4	10	6	17	7	14	13	19	14	19
W3Da	7	14	13	19	14	19	12	16	10	9

1. Day first eggs laid is Day 0

Table C.5: Duration of sessions of intensive observation for each pair during three periods from pair-formation to egg-laying in 1979.

NEST-SITE	DURATION (Minutes) First 2-weeks after pair-formation	Middle period	Last 2-weeks before egg-laying
SAME			
W1Aa	65	365	45
W1Bb	125	345	25
W1Eb	85	345	45
W1Fb	105	295	40
W2Aa	50	395	50
W2Da	50	395	50
W2Fb	50	390	50
W2H	50	390	50
W3A	105	295	45
W3Ba	125	320	50
W2Ja	32	148	50
W1Ab	26	132	50
W1Fa	26	162	20
W3Da	45	40	45
CHANGE			
W1Ga	50	380	45
W2ATa	105	295	40
W2Ba	95	230	40
W2Bb	105	290	50
W2Ea	105	315	25
W3Fb	32	163	35
W2G	47	90	50
W3Db	36	132	50

Table C.6: Duration of sessions of intensive observation for each pair during three periods from pair-formation to egg-laying in 1980.

NEST-SITE	DURATION (Minutes) First 2-weeks after pair-formation	Middle period	Last 2-weeks before egg-laying
SAME			
W2Ab	180	2505	1166
W2Ba	100	2504	1255
W2Da	190	3159	963
W1Eb	345	2054	1165
W1Fa	360	2144	1256
W1H	180	2145	1256
W2H	345	2378	1083
W2Eb	318	2031	992
W2Ja	363	2196	992
W1Ab	315	682	1256
W1Ea	406	526	1141
W2BTa	243	1150	1256
W3Fb	228	1652	1083
W3H	496	1457	1083
CHANGE			
W2ATa	100	2504	1256
W2C	90	2183	1256
W1Ga	270	1748	870
W2Fb	423	1782	1166
W3G	228	2253	903
W2CTb	243	992	961
W2Ib	612	120	845
W3Ba	501	0	1256
W3Da	617	871	992

Table C.7: Duration of sessions of intensive observation for each pair during three periods from pair-formation to egg-laying in 1981.

NEST-SITE	DURATION (Minutes) First 2-weeks after pair-formation	Middle period	Last 2-weeks before egg-laying
SAME			
W1Bb	240	222	30
W1Da	117	105	30
W1Eb	180	402	30
W1Fa	300	282	30
W1Fb	117	105	30
W1G	180	372	30
W1Jb	42	150	30
W2Ab	180	402	30
W2BTa	240	162	60
W2Da	90	30	30
W2Eb	180	402	30
W2G	180	402	30
W2Ia	117	105	30
W2Ib	117	105	30
W3Ba	117	75	30
W3Bb	117	105	30
W3Fb	0	222	30
CHANGE			
W1Ab	30	0	30
W1Ba	30	0	30
W1Ja	0	222	30
W2C	180	402	30
W2Fb	0	222	30
W3G	117	105	30
W3H	240	222	0

Table C.8: Duration of sessions of intensive observation for each pair during ten, two day periods before and after egg-laying in 1980.

NEST-SITE	DURATION (Minutes)									
	Days before and after egg-laying[1]									
	14-13	12-11	10-9	8-7	6-5	4-3	2-1	0-1	2-3	4-5
SAME										
W2Ab	173	241	60	210	210	120	152	90	150	151
W2Ba	151	324	90	180	180	210	120	152	60	150
W2Da	180	210	120	152	60	150	91	120	120	60
W1Eb	151	173	241	60	210	210	120	152	90	150
W1Fa	151	324	90	180	180	210	120	152	60	150
W1H	324	90	180	180	210	120	152	60	150	91
W2H	241	60	210	210	120	152	90	150	151	30
W2Eb	90	180	180	210	120	152	60	150	91	120
W2Ja	60	210	210	120	152	90	150	151	30	120
W1Ab	91	240	150	324	90	180	180	210	120	152
W1Ea	65	91	240	151	324	90	180	180	210	120
W2BTa	91	240	150	324	90	180	180	210	120	152
W3Fb	241	60	210	210	120	152	90	150	151	30
W3H	210	210	120	152	90	150	151	30	120	150
CHANGE										
W2ATa	151	324	90	180	180	210	120	152	60	150
W2C	91	240	151	324	90	180	180	210	120	152
W1Ga	0	0	65	91	240	151	324	90	180	180
W2Fb	173	241	60	210	210	120	152	90	150	151
W3G	210	120	152	60	150	91	120	120	60	120
W2CTb	0	65	91	240	151	324	90	180	180	210
W2Ib	125	0	65	91	240	151	173	241	60	210
W3Ba	91	240	151	324	90	180	180	210	120	152
W3Da	90	180	180	210	120	152	60	150	91	120

1. Day 0 is day first eggs were laid

Table C.9: Duration of observation periods for each pair, over four periods from pair-formation to egg-laying in 1980.

NEST-SITE	DURATION (Hours) Pair-formation to 43 days before eggs[1]	42-29 days before eggs	28-15 days before eggs	14-1 day before eggs
SAME				
W2Ab	53.0	16.8	23.5	71.0
W2Ba	52.2	15.8	22.4	71.1
W2Da	60.4	17.3	51.9	70.9
W1Eb	42.8	15.8	22.4	65.6
W1Fa	47.6	15.8	22.4	71.1
W1H	37.1	16.8	23.5	79.0
W2H	44.8	16.8	29.3	76.3
W2Eb	28.6	20.5	33.6	71.5
W2Ja	34.1	17.3	41.6	71.5
W1Ab	4.0	16.7	14.8	57.5
W1Ea	np	16.4	17.3	51.9
W2BTa	19.4	16.7	14.8	57.5
W3Fb	16.6	16.8	29.3	76.3
W3H	13.4	20.3	43.9	78.9
CHANGE				
W2ATa	52.2	15.8	22.4	71.1
W2C	47.9	16.7	14.8	57.5
W1Ga	36.7	10.3	20.5	33.6
W2Fb	31.9	16.8	23.5	71.0
W3G	27.1	14.8	57.5	74.6
W2CTb	13.6	13.4	17.3	41.6
W2Ib	np	6.3	16.8	29.3
W3Ba	np	4.3	14.8	57.5
W3Da	np	20.5	33.6	71.5

1. np: not paired at any time during period

Table C.10: Duration of observation periods of each pair for ten, two day periods before and after egg-laying in 1980.

NEST-SITE	DURATION (Hours) Days before and after egg-laying[1]									
	14-13	12-11	10-9	8-7	6-5	4-3	2-1	0-1	2-3	4-5
SAME										
W2Ab	5.8	16.0	5.3	11.5	11.9	11.1	9.5	11.0	11.3	12.7
W2Ba	4.1	13.8	8.0	13.3	7.4	16.0	8.6	12.0	6.3	12.7
W2Da	7.4	16.0	8.6	12.0	6.3	12.7	8.0	11.0	11.7	5.0
W1Eb	4.1	5.8	16.0	5.3	11.5	11.9	11.1	9.5	11.0	11.3
W1Fa	4.1	13.8	8.0	13.3	7.4	16.0	8.6	12.0	6.3	12.7
W1H	13.8	8.0	13.3	7.4	16.0	8.6	12.0	6.3	12.7	8.0
W2H	16.0	5.3	11.5	11.9	11.1	9.5	11.0	11.3	12.7	8.0
W2Eb	8.0	13.3	7.4	16.0	8.6	12.0	6.3	12.7	8.0	11.0
W2Ja	5.3	11.5	11.9	11.1	9.5	11.0	11.3	12.7	8.0	6.7
W1Ab	3.0	8.0	4.1	13.8	8.0	13.3	7.4	16.0	8.6	12.0
W1Ea	1.8	3.0	8.0	4.1	13.8	8.0	13.3	7.4	16.0	8.6
W2BTa	3.0	8.0	4.1	13.8	8.0	13.3	7.4	16.0	8.6	12.0
W3Fb	16.0	5.3	11.5	11.9	11.1	9.5	11.0	11.3	12.7	8.0
W3H	11.5	11.9	11.1	9.5	11.0	11.3	12.7	8.0	6.7	13.0
CHANGE										
W2ATa	4.1	13.8	8.0	13.3	7.4	16.0	8.6	12.0	6.3	12.7
W2C	3.0	8.0	4.1	13.8	8.0	13.3	7.4	16.0	8.6	12.0
W1Ga	0	3.0	1.8	3.0	8.0	4.1	13.8	8.0	13.3	7.4
W2Fb	5.8	16.0	5.3	11.5	11.9	11.1	9.5	11.0	11.3	12.7
W3G	16.0	8.6	12.0	6.3	12.7	8.0	11.0	11.7	5.0	7.2
W2CTb	3.0	1.8	3.0	8.0	4.1	13.8	8.0	13.3	7.4	16.0
W2Ib	3.7	3.0	1.8	3.0	8.0	4.1	5.8	16.0	5.3	11.5
W3Ba	3.0	8.0	4.1	13.8	8.0	13.3	7.4	16.0	8.6	12.0
W3Da	8.0	13.3	7.4	16.0	8.6	12.0	6.3	12.7	8.0	11.0

1. First eggs laid on Day 0

Appendix D: Results of statistical tests comparing SAME and CHANGE pairs with respect to patterns of attendance and courtship behaviour during 14 days before and 5 days after egg-laying in 1980.

Table D.1: Results of t-tests comparing SAME and CHANGE pairs with respect to mean proportions of each type of attendance (arcsine square-root transformed) during 14 days before and 5 days after egg-laying in 1980.

DAYS BEFORE AND AFTER EGG-LAYING[1]	PAIR ATTENDANCE			NEST-SITE UNATTENDED		
	t[2]	df	p	t	df	p
Before						
14-13	1.16	17	ns	0.73	22	ns
12-11	1.70	16	ns	1.20	12	ns
10-9	0.54	12	ns	0.49	12	ns
8-7	1.99	21	ns	0.62	22	ns
6-5	1.11	15	ns	1.33	8	ns
4-3	3.17	22	< .01	0.33	19	ns
2-1	1.19	19	ns	1.56	13	ns
After						
0-1	0.26	21	ns	1.40	13	ns
2-3	0.93	12	ns	-	-	-
4-5	2.19	11	ns	-	-	-

	TOTAL ATTENDANCE					
	MALE			FEMALE		
	t	df	p	t	df	p
Before						
14-13	0.18	21	ns	1.80	18	ns
12-11	0.22	19	ns	1.13	22	ns
10-9	0.54	16	ns	1.24	12	ns
8-7	1.41	22	ns	0.85	22	ns
6-5	0	21	ns	2.04	14	ns
4-3	0.83	22	ns	1.51	23	ns
2-1	1.21	22	ns	0.71	22	ns
After						
0-1	0.43	23	ns	0.19	20	ns
2-3	0.74	15	ns	4.12	19	<.001
4-5	3.77	18	< .01	2.40	19	< .05

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1. Day first egg laid is Day 0

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

Table D.2: Results of t-tests comparing SAME and CHANGE pairs with respect to mean rates of return and greeting during 14 days before and 5 days after egg-laying in 1980.

DAYS BEFORE AND AFTER EGG-LAYING[1]	ALL RETURNS			MALE RETURNS			FEMALE RETURNS		
	t[2]	df	p	t	df	p	t	df	p
Before									
14-13	1.03	15	ns	1.23	11	ns	0.29	19	ns
12-11	1.60	8	ns	1.45	7	ns	0.65	9	ns
10-9	0.75	15	ns	1.01	18	ns	0.34	19	ns
8-7	3.72	11	< .01	2.93	10	< .05	1.43	13	ns
6-5	1.39	11	ns	2.30	10	< .05	2.27	18	< .05
4-3	0.49	17	ns	0.46	18	ns	0.24	23	ns
2-1	0.38	22	ns	0.41	21	ns	0.38	20	ns
After									
0-1	1.13	10	ns	1.19	10	ns	0.74	22	ns
2-3	0.19	19	ns	0.21	20	ns	0.05	22	ns
4-5	0.43	13	ns	0.20	13	ns	1.37	12	ns

	RETURN GREETING			SPONTANEOUS GREETING		
	t	df	p	t	df	p
Before						
14-13	1.17	13	ns	1.32	15	ns
12-11	0.87	17	ns	0.88	9	ns
10-9	0.48	20	ns	0.95	8	ns
8-7	2.10	17	ns	1.34	14	ns
6-5	0.77	12	ns	2.16	14	<.05
4-3	0.75	18	ns	1.24	11	ns
2-1	0.17	20	ns	0.69	22	ns
After						
0-1	0.90	13	ns	0.29	17	ns
2-3	0.36	20	ns	1.00	8	ns
4-5	0.12	21	ns	1.48	8	ns

1. Day first eggs laid is Day 0

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

Table D.3: Results of statistical tests comparing SAME and CHANGE pairs with respect to mean rates and proportions of female head-tossing after greeting and spontaneous female head-tossing during 14 days before and 5 days after egg-laying in 1980.

DAYS BEFORE AND AFTER EGG-LAYING[1]	RATE OF HEAD-TOSSING AFTER GREETING			PROPORTION OF FEMALE HEAD-TOSSING AFTER GREETING		SPONTANEOUS HEAD-TOSSING		
	t[2]	df	p	Chi-square df=1	p	t	df	p
Before								
14-13	0.10	21	ns	0.97	ns	1.54	7	ns
12-11	0.36	20	ns	1.57	ns	0.71	12	ns
10-9	0.35	12	ns	1.82	ns	0.94	20	ns
8-7	0.82	12	ns	3.83	ns	0.07	17	ns
6-5	1.14	13	ns	1.20	ns	3.28	12	$<.01$
4-3	0.43	23	ns	0.20	ns	1.74	16	ns
2-1	0.53	13	ns	0.39	ns	0.62	16	ns
After								
0-1	0.68	9	ns	0.06	ns	0.33	15	ns
2-3	0.84	23	ns	1.22	ns	1.35	10	ns
4-5	0.31	16	ns	0.00	ns	-	-	

1. Day first eggs laid is Day 0

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate

Table D.4: Results of t-tests comparing SAME and CHANGE pairs with respect to mean rates of copulation and courtship feeding.

DAYS BEFORE AND AFTER EGG-LAYING[1]	ALL COPULATIONS[2]			CONTACT COPULATIONS			COURTSHIP FEEDINGS		
	t	df	p	t	df	p	t	df	p
Before									
P-43	0.75	12	ns	-			-		
42-29	0.96	16	ns	0.94	8	ns	1.02	8	ns
28-15	1.82	20	ns	1.33	11	ns	0.11	23	ns
14-13	1.61	8	ns	0.69	9	ns	0.12	17	ns
12-11	0.09	12	ns	0.43	10	ns	1.26	22	ns
10-9	1.16	15	ns	0.57	16	ns	1.73	23	ns
8-7	0.30	17	ns	0.98	18	ns	0.93	18	ns
6-5	0.12	16	ns	1.00	14	ns	0.18	22	ns
4-3	1.18	20	ns	0.42	19	ns	0.27	10	ns
2-1	2.70	23	<.05	2.55	23	.05	0.24	23	ns
After									
0-1	1.66	13	ns	1.69	13	ns	0.52	21	ns
2-3	0.96	13	ns	0.96	13	ns	1.05	22	ns
4-5	-			-			0.96	8	ns

1. Day first eggs laid is Day 0. P refers to the day of pair-formation

2. Welch's modification for assumption of unequal variance: degrees of freedom approximate