A study of colonial organisation of the kittiwake Rissa tridactyla

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Jacqueline Anne Fairweather

Abstract

Kittiwakes have been studied in detail at North Shields, Tyne and Wear, England since 1954. I investigated the effect of mate change (due to divorce or mate death) on reproductive performance. Below average productivity in the year of divorce and in the preceding year, coupled with a low adult survival rate in the year following divorce, suggested birds which divorced were poorer quality individuals than birds which retained their mate. Productivity was reduced if one or both members of a pair were in their last year of life and was indicative of a decline in fitness.

Dispersal, breeding and the importance of nest site tenacity to mate retention were studied when kittiwakes were prevented from returning to their original nest sites in 1991. In 1991, extensive non-breeding (57%) and low productivity resulted. Of the birds which bred, 54 (83%) nested in the immediate colony area and only 11 moved to other colonies. Despite moving site, many birds retained their mate of the previous breeding season. In the following year, a further 61 kittiwakes moved and nested at other colonies and about a third retained their mate. This, and other evidence, suggests that individual recognition is important in mate retention.

Reproductive performance, in relation to nest position in the colony and proximity to other nesting pairs, was compared with a kittiwake colony at Marsden, NE England. Productivity was highest at the centre of the colonies and, at the edge, was highest for pairs which nested adjacent to another pair. It is suggested that social stimulation, arising from nesting adjacent to another pair, advanced the date of laying.

Adult attendance at the nest during chick-rearing was monitored at Marsden in three years. During comparable time periods in 1991 and 1993, 93% and 75% of the broods, respectively, were attended by an adult, compared to only 51% during the same period in 1992. Attendance decreased in relation to hatching date, chick age and brood size and increased with parental age and/or quality.

A study of colonial organisation of the kittiwake *Rissa tridactyla*

By

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A thesis presented in candidature for the degree of Doctor of Philosophy in the
University of Durham. 1994.

I declare that this thesis is original and entirely my own work, except where otherwise stated. No part of it has been submitted previously for a degree at any other university.

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GENERAL INTRODUCTION

As a consequence of long-term studies of uniquely marked animals it has become possible to monitor the breeding performance of individuals throughout their lives (e.g. Hoogland & Foltz 1982; Coulson & Thomas 1985a; Newton 1985; Le Boeuf & Reiter 1988; Clutton-Brock, Albon & Guinness 1988; McCleery & Perrins 1988; Ollason & Dunnet 1988; Packer *et al.* 1988; Mills 1989; Wooller *et al.* 1989; Oring, Colwell & Reed 1991; Holland & Yalden 1994). Detailed studies have been carried out on birds as many species are conspicuous and diurnal and are readily trapped and marked. Hence, it is often possible to measure the breeding performance of individuals at each and every breeding attempt. This has enabled the measurement of lifetime reproductive success; the total number of young raised by recognisable individuals during their life span (Newton 1989). For any individual, lifetime reproductive success is limited by the number of breeding years, the number of broods per year, the number of young per brood and the number of offspring which survive to breed. Factors which affect the annual reproduction and/or adult survival rates of birds consequently influence lifetime reproductive success. The influence of social and environmental factors are discussed below, with special reference to the kittiwake *Rissa tridactyla.*

Several studies of birds have shown that the reproductive success of pairs formed as a result of divorce or death of the previous mate was lower than in mate faithful pairs (Coulson 1966; Mills 1973; Davis 1976; Perrins & McCleery 1985; Bradley *et al.* 1990; Weimerskirch 1990; for review see Johnston & Ryder 1987). It has been suggested that mate change may not directly lead to lower reproductive success, as poorer quality individuals may be both poor breeders and have a lower tendency for mate retention (Perrins & McCleery 1985). Hence, the implication is that mate change is correlated with low breeding success, but is not an effect of it. By considering reproductive performance before and after an event, the influence of individual quality on mate retention and lifetime reproductive success can be considered. Similarly, the reproductive performance of individuals in their last breeding year is of interest as it can be used to indicate whether birds die suddenly, for example as a result of predation, or suffer a progressive loss of fitness which reduces their breeding success.

Few studies have had the opportunity to consider the impact of preventing animals from returning to their breeding sites at the beginning of a breeding season. In 1991, the development of a warehouse at North Shields, Tyne and Wear, England prevented kittiwakes from returning to their nest sites at the beginning of the breeding season. As this kittiwake colony has been studied in detail since 1954, the behaviour of the birds, in terms of breeding site fidelity and mate retention, is known (Coulson & White 1958a; Coulson 1972; Coulson & Thomas 1983; Aebischer & Coulson 1990). Although opportunities to study movements of birds are relatively common, for example, as a result of land use change, effective monitoring is dependent on having a population of marked individuals. Obvious advantages arise from studies which encompass both the period before and after the disturbance, as the usual behaviour of the individuals prior to the event is known. Colonial nesting seabirds rarely change colony after their first breeding attempt (Austin 1949; Coulson & White 1958a; Birkhead 1977; Harris & Wanless 1991; Aebischer *et al.* in press, but see Danchin & Monnat 1992), hence the movement of individuals to new colonies has not been monitored. As breeding site fidelity and nest site tenacity of birds are important factors influencing mate retention (Soikkeli 1967; Holmes 1971; Coulson 1972; Richdale & Warham 1973; Morse & Kress 1984; Ollason & Dunnet 1988; Cuthbert 1985; Gratto, Morrison & Cooke 1985; Ainley, Ribic & Wood 1990) which subsequently influences reproductive performance, it is essential to understand the effect that a forced site change will have. The closure of the warehouse to nesting kittiwakes was a natural experiment, allowing analysis of the effect of the disturbance to the birds in terms of dispersal, non-breeding and mate retention.

Social factors play an important role in determining lifetime reproductive success. Since Darling (1938) suggested that colonial breeding enhanced the performance of the individual through social stimulation, reproductive performance in relation to density and position in the colony has been considered for many species of colonial seabird (Coulson 1968, 1971; Tenaza 1971; Nettleship 1972; Parsons 1976; Birkhead 1977; Nelson 1978a;

Potts, Coulson & Deans 1980; Ryder & Ryder 1981; Furness 1984). In colonial species, high productivity is generally associated with nesting at high density (Coulson 1968; Birkhead 1977; Harris 1980), although for some species increased nest density is associated with decreased reproductive performance (Parsons 1976; Butler & Trivelpiece 1981; Hill 1988; Kilpi 1989). As individual kittiwakes have been studied in detail at North Shields, account can be taken of the influence of position in the colony and proximity to other nesting pairs on reproductive performance. Hence, in association with these factors, assessment can be made of the importance of social stimulation to the breeding birds.

Factors determining lifetime reproductive success, such as adult survival rates and the number of young surviving are influenced by environmental factors. The partial or total breeding failure which occurred at a number of seabird colonies in Britain and northern Europe in recent years has been associated with a decrease in fish stocks (Barrett *et al.* 1987; Heubeck 1988; Monaghan *et al.* 1989; Harris & Wanless 1990; Hamer, Furness & Caldow 1991; Danchin 1992). Studies such as these, which relate the breeding biology of birds to environmental conditions, have served to focus attention on the use of birds as monitors of environmental change (see Furness & Greenwood 1993). Although avian populations may show an immediate response to an environmental change (eg. "red-tides", Coulson *et al.* 1968; Armstrong *et al.* 1978), avian population fluctuations are not generally considered to be useful monitors of environmental change as there may be a time lag in the population response (Morrison 1986). However, there are opportunities to use birds for other forms of environmental monitoring (Montevecchi 1993). As the behaviour and reproductive performance of birds is highly responsive to small fluctuations in the environment, studies carried out over a period of years can be useful in revealing changes in the breeding biology of the birds brought about by changes in environmental conditions. Previous studies have revealed the effects of pollutants and long term changes in fish stocks and oceanographic conditions on birds (Coulson & Thomas 1985b; Newton, Bogan & Rothery 1986; Aebischer, Coulson & Colebrook 1990; Hamer *et al.* 1991; Klomp & Furness 1992; Furness 1993).

As suggested by Montevecchi (1993), progress will be made in understanding the effects of fisheries, physical processes and ocean and climate change on avian behavioural ecology by conducting studies within and outside spheres of commercial fishing activity, and making efforts to standardise comparative studies. Hence, whilst causal links between bird numbers and environmental changes are not clear, studies of adult behaviour and productivity in each breeding season can serve as useful indicators of changes in environmental conditions.

Seabirds are long-lived, exhibit delayed maturity and, in general, produce only one, two or three offspring in any year. As a result, small changes in social and environmental factors which affect breeding success and/or adult survival rates can have prolonged effects upon their breeding biology. At North Shields, kittiwakes return to the colony in late February (the actual date depends on breeding experience, Coulson & Thomas 1985b) and egg-laying typically starts in early May (Coulson 1974). Both members of the pair participate in chick-rearing until the young fledge in July/August, but considerable variation occurs between individuals in the extent of participation (Coulson & Wooller 1984; Coulson & Johnson 1993). As kittiwakes are associated with the colony for 5 - 6 months, detailed studies can be carried out on the behaviour and breeding biology throughout the breeding season. For example, the long term study of kittiwakes at North Shields has shown that many factors influence the reproductive success of individuals; age, breeding experience, timing of breeding, pair status, position in the colony and individual quality (Coulson & White 1958a, 1960; Coulson 1968; Coulson & Porter 1985; Coulson & Thomas 1980, 1985a). Although some kittiwake colonies experience a high incidence of predation, it was minimal at North Shields (Coulson 1988) and Marsden (Chapter 5). During the study, long term changes have taken place in the breeding parameters and adult survival rates, explicable only in terms of changes in the environment (Coulson & Thomas 1985b; Aebischer & Coulson 1990). More recent studies at this colony have examined behavioural aspects of the breeding biology of the kittiwake, such as patterns of recruitment, behaviour before egg-laying and the attendance of adults at the nest during chick rearing (Chardine 1987; Porter 1990; Coulson & Johnson 1993). All of these factors have a marked effect upon the breeding biology of the pair and hence, the colony as a whole.

Many hypotheses have been advanced to explain the evolution of coloniality (e.g. the information centre hypothesis, Ward & Zahavi 1973; deterral of predators, Darling 1938; breeding site availability, Wittenberger & Hunt 1985), but they have received little support as none has been adequately tested (Wittenberger & Hunt 1985; Danchin & Boulinier in press). The costs and benefits of group living however, have been well documented (Wittenberger & Hunt 1985). As a consequence of coloniality, the behaviour of individuals is influenced by social factors arising from the presence of conspecifics (e.g. nest position in the colony and pair status influence the laying date; established breeders influence recruitment). Further, environmental factors exert an effect. For example, low productivity caused by unfavourable environmental conditions may result in a change of breeding site (Danchin & Monnat 1992). Hence, both social and environmental factors influence colonial organisation through their influence on reproduction and adult survival rates. This thesis considers the influence of social and environmental factors on the annual reproduction, adult survival rates and lifetime reproductive success of the kittiwake. It is presented as a series of scientific papers involving the following five aspects:

1. An analysis of data from the long term study of kittiwakes at North Shields to investigate the effect of mate change on the reproductive performance and adult survival rates of the kittiwake.
2. A study of the dispersal and breeding of the adult kittiwakes prevented from returning to their nest sites at the warehouse at the beginning of the 1991 breeding season.
3. The importance of nest site tenacity to mate retention was evaluated by using data from the long term study at North Shields .
4. The influence of nest position in the colony and proximity to other nesting pairs on reproductive performance at North Shields (1954 - 90) was studied. The findings were tested with kittiwakes nesting at Marsden in northeast England (1991 - 93).
5. By monitoring the productivity and attendance of adult kittiwakes at the nest at Marsden, factors influencing the attendance of adults were considered.

CHAPTER 1

THE INFLUENCE OF DIVORCE AND IMPENDING DEATH ON THE BREEDING SUCCESS OF THE KITTIWAKE

Introduction

In a number of studies of the effect of mate change in birds, reproductive success following the formation of new pairs was lower than in mate faithful pairs (Coulson 1966; Mills 1973; Davis 1976; Perrins & McCleery 1985; Bradley *et al.* 1990; Weimerskirch 1990). Several studies have looked at the effect of mate change due to divorce, i.e. where the partners are still alive but not paired together, and have focussed attention on the relationship between reproductive failure and an increased likelihood of divorce in the subsequent season (Coulson 1966; Mills 1973; Brooke 1978a; Harris *et al.* 1987; Ollason & Dunnet 1988; Bradley *et al.* 1990; Weimerskirch 1990).

In the kittiwake *Rissa tridactyla* L., reproductive failure was associated particularly with the level of compatibility of the members of the pair during the incubation period (Coulson 1972). In contrast, Ens, Safriel and Harris (1993), in their work on the oystercatcher *Haematopus ostralegus*, suggested that divorce did not occur because the mates were incompatible, but because one individual of the pair had a better option. Although they could not disprove the incompatibility hypothesis, they suggested that the expected benefits of changing mate outweighed the expected costs for one rather than both partners. The better option hypothesis takes account of active choice and competition for good mates and/or good territories. However, the practical distinctions between the two hypotheses are small and in practice both, either or neither members of the pair may benefit from a change of mate.

It has generally been assumed that there is a direct relationship between divorce and reproductive success. However, it is possible that mate change does not directly lead to lower reproductive success, as birds which are in some ways inferior individuals may be both poor breeders and have a lower tendency for mate retention (Perrins & McCleery 1985). The tendency to separate is then only a correlate of low breeding success and not an effect of it.

In some bird species, individuals which bred successfully were significantly more likely to survive to the next breeding season than those which bred unsuccessfully (e.g. shag *Phalacrocorax aristotelis*, Potts 1969; great tit *Parus major*, McCleery & Perrins 1989). Similarly, in the kittiwake, birds which fledged three young had a higher survival rate during the following year than those which fledged one or two young, which again indicates a difference in quality between individual birds (Coulson & Porter 1985) and conceals any "costs" in being more productive. The existence of variation in quality of individual kittiwakes has also been examined by Coulson & Thomas (1985a).

The average number of chicks fledged per pair each year in kittiwakes increased with age, reaching a plateau in the birds that had previously bred for four to nine years (Thomas & Coulson 1988). Reproductive success in kittiwakes also increased with the duration of the pair bond (Coulson 1972), as repeated breeding attempts with the same mate lead to an increased familiarity and co-ordination in breeding activities (Coulson 1972; Coulson & Thomas 1983; Chardine 1987). Kittiwakes which retained their mate from the previous year bred earlier than birds which changed their mate (Coulson & Thomas 1980) and early laying tended to be correlated with high reproductive success (Wooller & Coulson 1977). The implication that reproductive success increased with the duration of the pair bond also implies that reproductive success will be lower in new pairs formed after mate change.

In the barnacle goose *Branta leucopsis,* there is evidence that individuals which acquired a young new mate had a lower reproductive success than individuals which acquired an older new mate (Forslund & Larsson 1991). The reproductive success of this latter group did not differ from that in birds which retained their mate. Similarly, in the manx shearwater *Puffinus puffinus*, individuals which acquired an experienced new mate achieved as high a hatching success as that in established pairs (Brooke 1978a). In the manx shearwater, there was therefore selection for experienced breeders to pair with other experienced breeders when forming a new pair.

Previous studies of birds have shown a decline in annual productivity later in life, although most are not significant (Arctic tern *Sterna paradisaea,* Coulson & Horobin 1976; great tits, Perrins 1979; sparrowhawks *Accipter nisus,* Newton, Marquiss & Moss 1981; short-tailed shearwaters *Puffinus tenuirostris,* Wooller *et al.* 1989). For the sparrowhawk and short-tailed shearwater, it was suggested that the decrease in reproductive performance near the end of the breeding career was due to senescence (the tendency for all aspects of performance, including survival probability and fertility, to decline with advancing age, Partridge 1989). In the kittiwake, a significant decline in the number of chicks fledged was found for males with breeding experience of between 5 and 10 years, and those with 11 - 19 years experience, but no significant difference was shown for females of the same breeding age (Thomas & Coulson 1988). The reduced male productivity corresponded to the slight decrease in the adult survival rate which occurred after 12 breeding years (Aebischer & Coulson 1990).

This study investigates whether divorce affects the reproductive performance of all individual kittiwakes, and evaluates the effect the breeding age of the new partner has on productivity following divorce. In order to investigate whether factors other than senescence affect the reproductive performance of individuals in their last breeding year, I analysed the reproductive performance in relation to female breeding age, when one or both members of the pair were in their last year of life.

Methods

The study colony is situated on a warehouse at North Shields, Tyne and Wear, England. Details of the methods of study have been presented previously (Coulson & Thomas 1980, 1985b; Aebischer & Coulson 1990). Since 1954, virtually all kittiwakes breeding in the colony (and many potential recruits) have been marked with unique combinations of Darvic colour rings (Coulson 1963) and are thus recognisable as individuals. This allows detailed information to be accumulated about the mate and breeding performance in a series of years.

Kittiwakes which return to the colony for a new breeding season either retain the same mate as they had in the previous breeding season (**same mate**) or change mate. There is no evidence to suggest that after the adults desert the colony at the end of the breeding season each year, members of the pair remain together. Change of mate is evident at the beginning of the breeding season when nest sites are first occupied and occurs when both members of a pair from the previous year return to the colony but select different mates (**divorce**) or when one member of the pair has died since the last breeding season (**mate death**). It is assumed that the divorce took place in the year in which a new pair has been formed.

In this study we consider the relative date of laying, clutch size and productivity of birds after they have taken a new mate (due to divorce or mate death) or after they have retained the same mate. As divorce has been associated with breeding failure, we also examine the above reproductive parameters for birds in the year prior to changing or retaining their mate. Data in the results section are presented as:

Year preceding mate change (i.e. divorce or mate death) or mate retention - considers the breeding performance in the breeding season before the mate change or mate retention occurred.

Year of mate change (i.e. divorce or mate death) or mate retention - considers the breeding performance which followed mate change or mate retention at the start of the current breeding season.

The movement of breeding adults from North Shields to other colonies was virtually non-existent (Aebischer & Coulson 1990), and so it could be confidently assumed that adults which did not return to the colony in the following breeding season, and were not seen again, had died. The rates of divorce and mate retention are calculated only for those birds in which both members of the previous pair survived from one breeding season to the next and so were potentially able to reform the same pair. Thus, mates of birds who had died in the intervening period were excluded.

Since adults in this and neighbouring colonies did not interchange (c.f. Danchin & Monnat 1992), it can reasonably be assumed that new breeding birds were young individuals breeding for the first time. The "age" of the bird used in this chapter is the number of breeding years (i.e. breeding experience). Most kittiwakes breed for the first time when 3 - 4 years old (Wooller & Coulson 1977; Porter & Coulson 1987). Therefore, "age" underestimates true age usually by 3 or 4 years.

Over the whole period of study no kittiwake above the age of 12 divorced. Therefore, in Tables 1.1 - 1.3, the analysis of females which changed or retained their mate is restricted to females of age 1 - 12 in order that the groups are comparable in terms of breeding experience. Table 1.5 shows the reproductive performance of divorced females aged 2 - 3 and 4 - 8 with mates aged 2 - 3 or 4 - 8. As only 6% (n = 332) of the males which were the new partners were aged 9 or older, and 7% (n = 332) of the females which divorced were aged 9 or older, the data could not be sub-divided into further groups with respect to female and male age.

Over the period of study, 1954 - 85, male survival rate was consistently lower than that of females by about 4 percentage points, averaging 78% compared to 82% per year (Aebischer & Coulson 1990). In Tables 1.6 - 1.8 and Figure 1.6, only the data for females and males up to, and including, the breeding age of 12 has been used in order to avoid effects arising from possible senescence in kittiwakes over the age of 12.

The mean date of laying in this colony (1954 - 90) was 19 May ± 9 days (SD; $n = 2655$). The earliest mean date of laying in any year was 14 May in 1984, the latest was 25 May in 1982. To exclude annual variations (which were typically small), the relative date of laying has been used in the calculations. The relative date of laying is the deviation of the laying date of a pair from the mean for the whole colony in that year. Positive figures indicate the number of days before the mean date that the pair laid, whilst negative figures indicate the number of days after the mean.

In 2 by 2 χ^2 calculations, Yates' correction has been used. All means are presented as mean ± SE, unless otherwise stated. Where appropriate, the data have been transformed.

Results

Over the 37 years of the study, 935 of the pairs (59.4%) which existed in one breeding season (1954 - 89) were reformed in the following year. A further 338 (21.5%) female kittiwakes changed mate due to divorce and 300 (19.1%) changed mate because their mate had died since the last breeding season.

Figure 1.1 shows the rate of divorce of female kittiwakes in each year between 1955 - 90. The rate of divorce did not change significantly with time ($r_{34} = 0.22$, slope = 0.23% per year ± 0.18). Of the occasions when males and females could have retained their mate, 27% divorced ($n = 1273$ females).

Divorce frequency declined progressively and significantly with the age of the female (Fig. 1.2), from 36% of 1-year old females to 8% of 12-year old females. Above the age of 12, no females ($n = 45$) divorced. Of all the females which divorced, 31% did so in the year immediately following first breeding ($n = 338$) (Fig. 1.3).

Reproductive performance in the year preceding mate change

Females (age 1 - 12) which would divorce in the next year laid significantly later in the current year (relative date = +0.16 days ± 0.50, $n = 338$) and laid smaller clutches (mean = 2.02, $n = 338$) than females (age 1 - 12) which would keep the same mate in the next year (relative date = +1.58 days ± 0.26, mean clutch = 2.12, $n = 890$) (Table 1.1). Similarly, the mean number of young fledged was significantly lower in females which would divorce (mean = 1.22, $n = 316$) than in females which would keep the same mate in the next year (mean = 1.43, $n = 843$) (Table 1.1). Of females which would divorce in the next year, 27% ± 2% failed to fledge any young ($n = 316$), compared to 14% ± 1% of the females which would keep the same mate ($n = 843$) ($\chi^2 = 23.9$, df = 1, $P < 0.001$), whilst the proportion of females which fledged one or more (2 or 3) young did not differ significantly ($\chi^2 = 0.03$, df = 1, NS). In relation to female age, females which would divorce in the next year laid later, had a smaller clutch size and lower productivity than females of the same age which would keep the same mate in the next

Figure 1.1 Rate of divorce of female kittiwakes in relation to year. Data for all years, 1955 - 90.

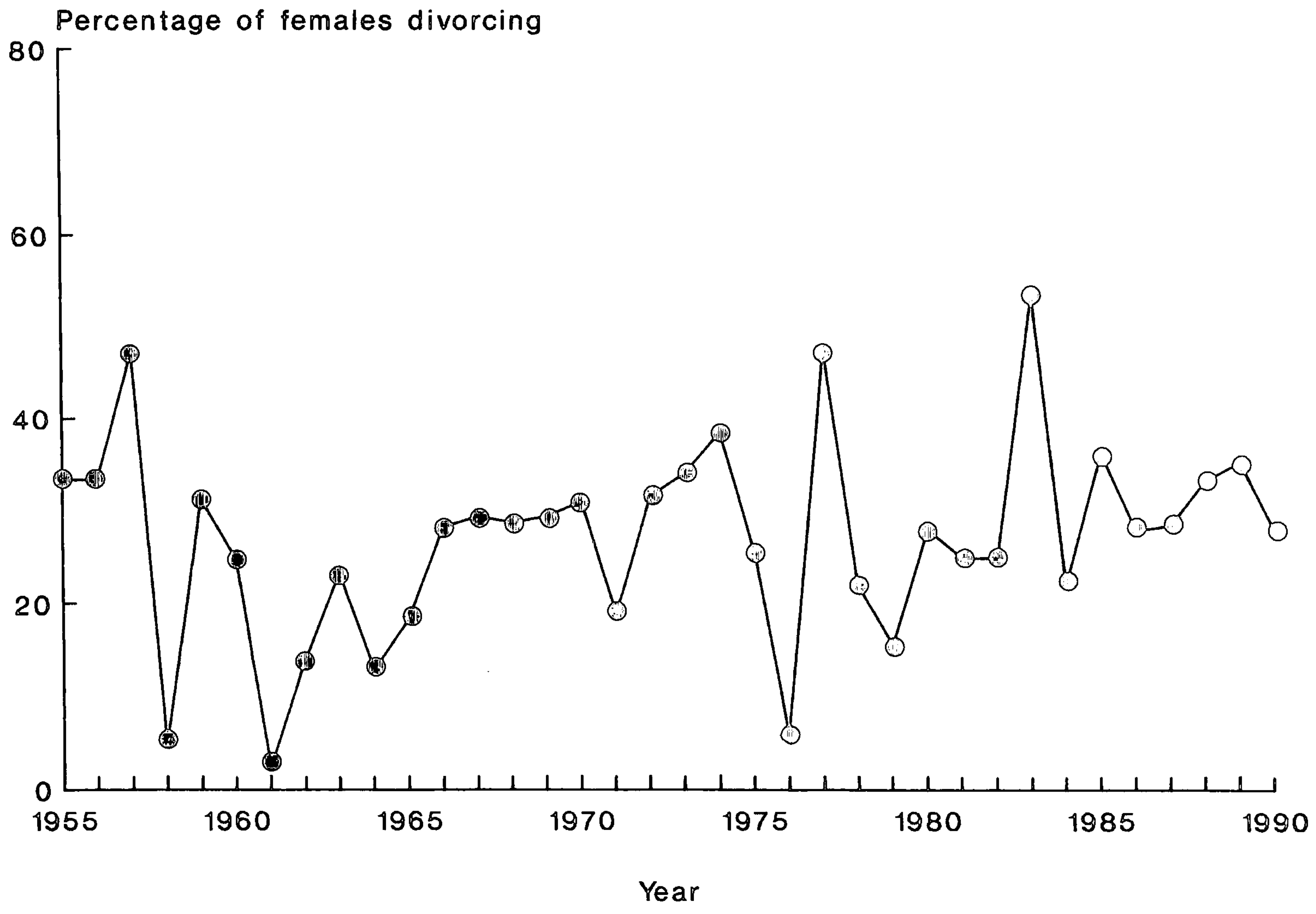

Percentage of females divorcing
80
60
40
20
0
1955
1960
1965
1970
1975
1980
1985
1990
Year

Figure 1.2 Divorce rate of female kittiwakes in relation to age ($r_{10} = -0.93$). Numbers for each point are sample sizes.

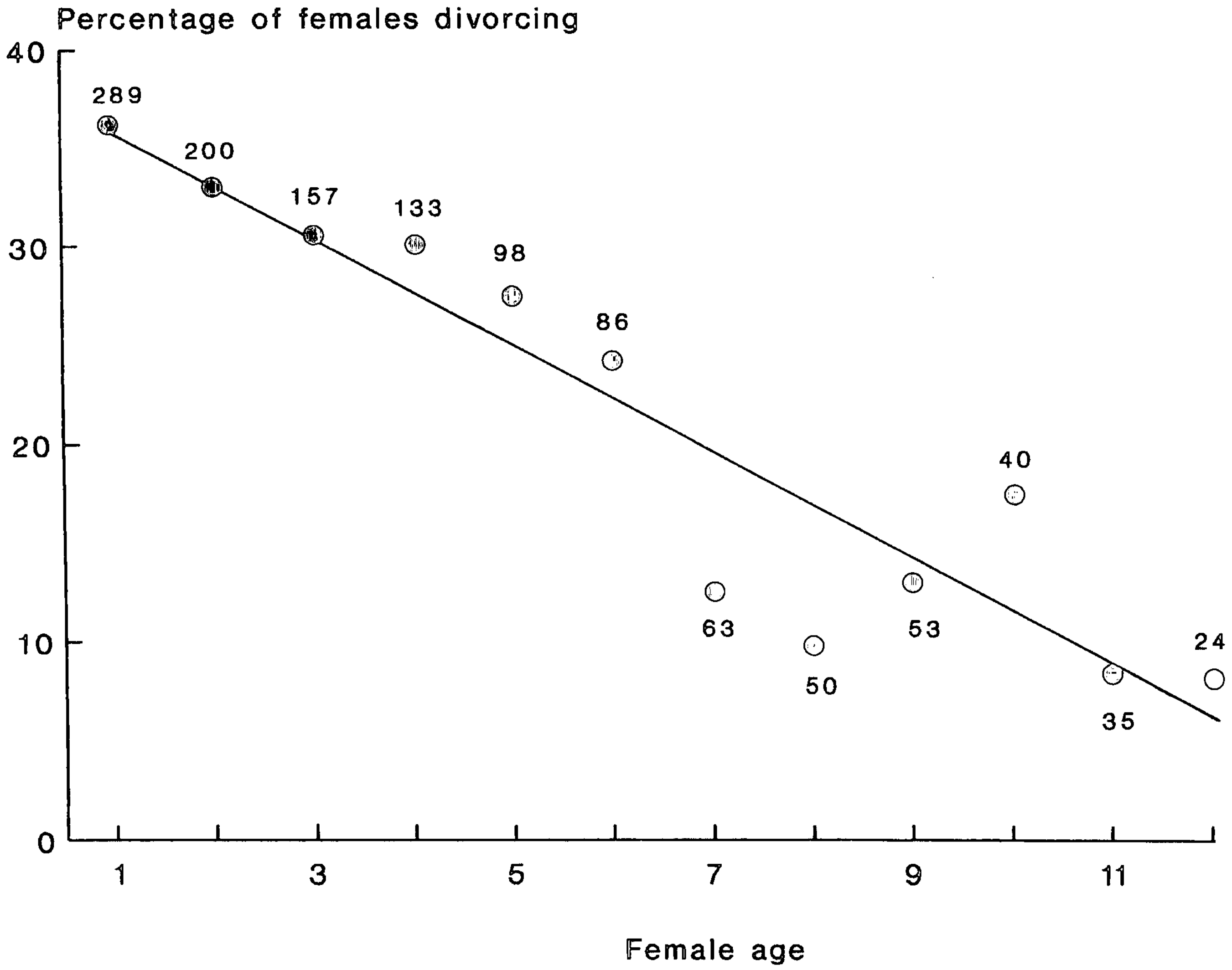

Percentage of females divorcing
40
30
20
10
0
289
200
157
133
98
86
63
50
53
40
35
24
1
3
5
7
9
11
Female age

Figure 1.3 Frequency distribution of the age of female kittiwakes which divorced. Data for all years, 1955 - 90.

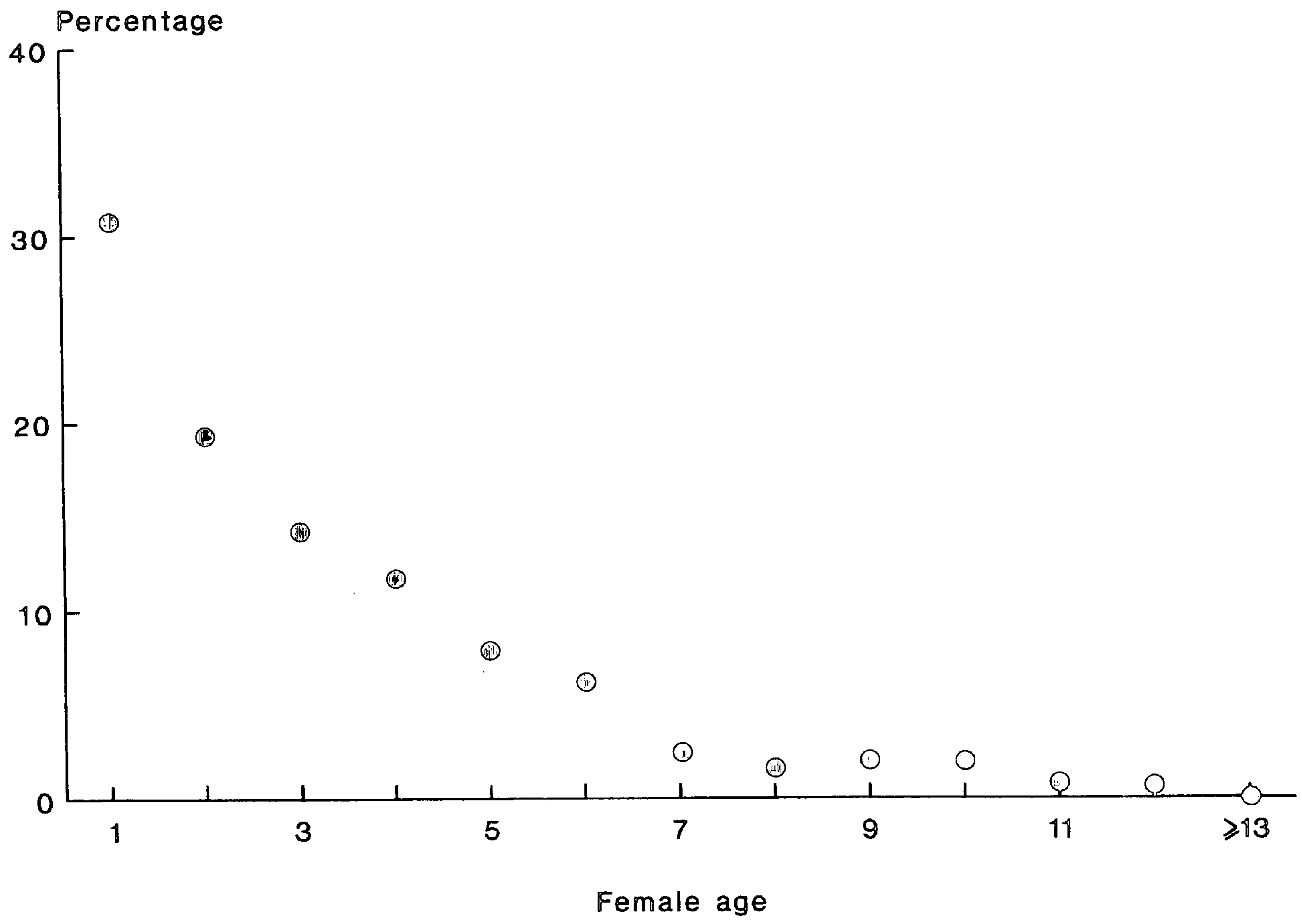

Percentage
40
30
20
10
0
1
3
5
7
9
11
≥13
Female age

Table 1.1. Reproductive performance of female kittiwakes (age = 1 - 12) in relation to female age in the breeding season preceding mate retention or mate change, with respect to pair status in the next breeding season. Data for all years, 1954 - 89.

		Relative date of laying			Clutch size				Number young fledged				
		Mean (days)	SE	*n*	1	2	3	Mean	0	1	2	3	Mean
	Age 1 - 2												
i	Same mate	0.53	0.50	319	29	255	35	2.02	52	117	130	8	1.31
ii	Divorce	-0.38	0.77	170	19	140	11	1.95	50	40	63	2	1.11
iii	Mate death	0.22	0.79	114	11	98	5	1.95	36	30	41	0	1.05
	Age 3 - 6												
i	Same mate	2.18	0.41	338	13	263	62	2.14	38	97	173	12	1.50
ii	Divorce	1.53	0.65	136	6	112	18	2.09	27	37	60	7	1.36
iii	Mate death	1.72	0.66	119	10	94	16	2.05	18	33	58	3	1.41
	Age 7 - 12												
i	Same mate	2.15	0.44	233	9	159	65	2.24	31	58	111	16	1.52
ii	Divorce	-2.78	1.68	32	1	28	3	2.06	8	8	14	0	1.20
iii	Mate death	-0.22	0.94	55	3	45	7	2.07	14	16	18	1	1.12

No. fledged: 0 v 1 v 2 or 3

Combined data						
	i v *ii*	*i* v *iii*	*i* v *ii*	*i* v *iii*	*i* v *ii*	*i* v *iii*
	z = 2.5*	z = 1.6 NS	$\chi^2_2 = 14.8^{***}$	$\chi^2_2 = 13.1^{**}$	$\chi^2_2 = 24.8^{***}$	$\chi^2_2 = 17.7^{***}$

NS = not significant, $^{*} = P < 0.05$, $^{**} = P < 0.01$, $^{***} = P < 0.001$
z-test of relative date of laying: divorce v mate death = NS
χ^2_2 test of clutch size and number young fledged: divorce v mate death = NS

year (Table 1.1). Compared to females which would retain their mate in the next year, females which would lose their mate through death before the next year (Table 1.1) laid later (relative date = +0.76 days ± 0.45, $n = 288$), produced smaller clutches (mean = 2.01, $n = 289$) and fledged significantly fewer young (mean = 1.21, $n = 268$). This trend was also evident for females of comparable age (Table 1.1). The date of laying, clutch size and number of young fledged did not differ significantly between females which would divorce or lose their mate through death in the next year (Table 1.1).

Reproductive performance in the year of mate change

Divorced females (age 2 - 13) laid later (mean = +0.19 days ± 0.43, $n = 338$), produced smaller clutches (mean = 2.05, $n = 338$) and fledged fewer young (mean = 1.17, $n = 313$) than females of the same age which retained their mate (relative date = +1.73 days ± 0.23, $n = 890$, mean clutch = 2.15, $n = 890$, mean young fledged = 1.44, $n = 833$) (Table 1.2). Of the females which divorced, 27% ± 2% failed to fledge any young ($n = 313$), compared to 16% ± 1% of those which kept the same mate ($n = 833$) ($\chi^2 = 15.5$, df = 1, $P < 0.001$). Of females which fledged young, a significantly higher proportion of the females which divorced fledged only one young (43% ± 3%, $n = 230$), compared with females which retained their mate (34% ± 2%, $n = 699$) (no. fledged 1 v 2 or 3, $\chi^2 = 6.3$, df = 1, $P < 0.05$). Compared to females which retained their mate, divorced birds of comparable age laid consistently later, had smaller clutches and lower productivity (Table 1.2). The same effect was shown when birds which lost their mate through death were compared to females which retained their mate (Table 1.2).

Productivity by year, in relation to mate retention and divorce

The mean fledging success each year from 1955 - 90, in relation to pair status, is shown in Figures 1.4 and 1.5. The figures show the reduced productivity of female kittiwakes in the year of divorce (Fig. 1.4) and in the year prior to divorce (Fig. 1.5) when compared to females which retained their mates (Fig. 1.4) or which would retain their mate (Fig. 1.5) in the next year. Females which divorced had lower productivity than females of the same age (2 - 13) which retained their mate in 11 of the 12 time

Table 1.2. Reproductive performance of female kittiwakes (age = 2 - 13) in the breeding season of mate retention or mate change, in relation to female age and pair status. Data for all years, 1955 - 90.

		Relative date of laying			Clutch size				Number young fledged				
		Mean (days)	SE	*n*	1	2	3	Mean	0	1	2	3	Mean
	Age 2 - 3												
i	Same mate	1.61	0.39	319	25	248	46	2.07	52	90	150	6	1.37
ii	Divorce	0.08	0.63	171	9	149	13	2.02	40	52	60	2	1.16
iii	Mate death	1.03	0.73	115	9	98	8	1.99	33	33	44	3	1.15
	Age 4 - 7												
i	Same mate	1.82	0.38	338	17	250	71	2.16	42	94	165	21	1.51
ii	Divorce	0.86	0.63	135	8	108	19	2.08	33	38	55	3	1.22
iii	Mate death	1.00	0.79	118	13	89	17	2.03	24	32	50	6	1.34
	Age 8 - 13												
i	Same mate	1.75	0.43	233	7	159	67	2.26	40	54	104	15	1.44
ii	Divorce	-2.09	1.32	32	2	26	4	2.06	10	10	9	1	1.03
iii	Mate death	-1.13	1.10	55	4	47	4	2.00	17	12	21	2	1.15
									No. fledged: 0 v 1 v 2 or 3				
	<u>Combined data</u>	*i* v *ii*	*i* v *iii*		*i* v *ii*		*i* v *iii*		*i* v *ii*		*i* v *iii*		
		$z = 3.2^{**}$	$z = 2.1^{*}$		$\chi^2_2 = 16.9^{***}$		$\chi^2_2 = 19.3^{***}$		$\chi^2_2 = 22.4^{***}$		$\chi^2_2 = 16.4^{***}$		

NS = not significant, $^{*} = P < 0.05$, $^{**} = P < 0.01$, $^{***} = P < 0.001$

z-test of relative date of laying: divorce v mate death = NS

χ^2_2 test of clutch size and number young fledged: divorce v mate death = NS

Figure 1.4 Mean number of young fledged by female kittiwakes which divorced (○) or retained their mate (□). Data for all years, 1955 - 90, pooled in 3-year time periods. Numbers for each point are sample sizes.

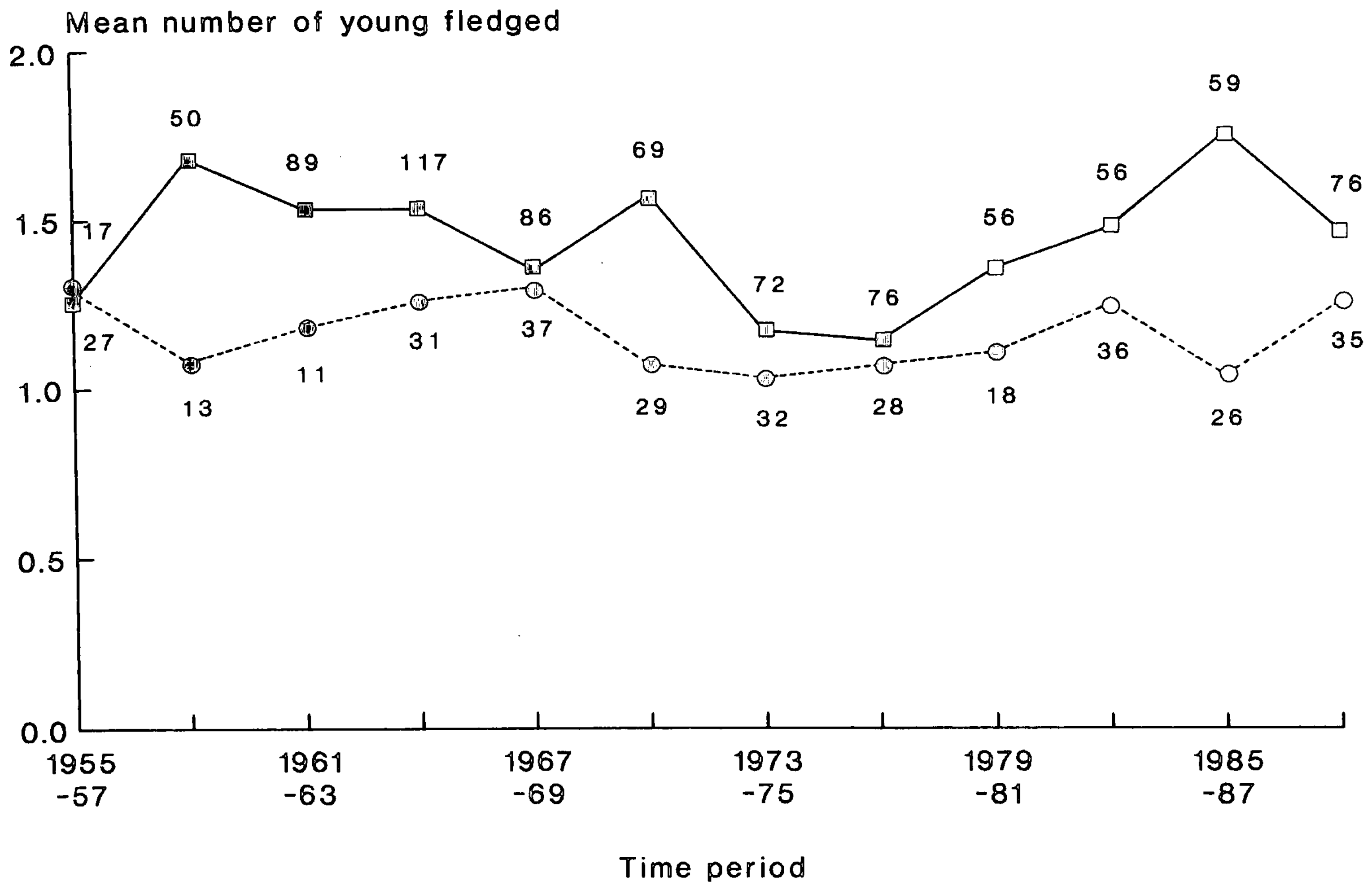
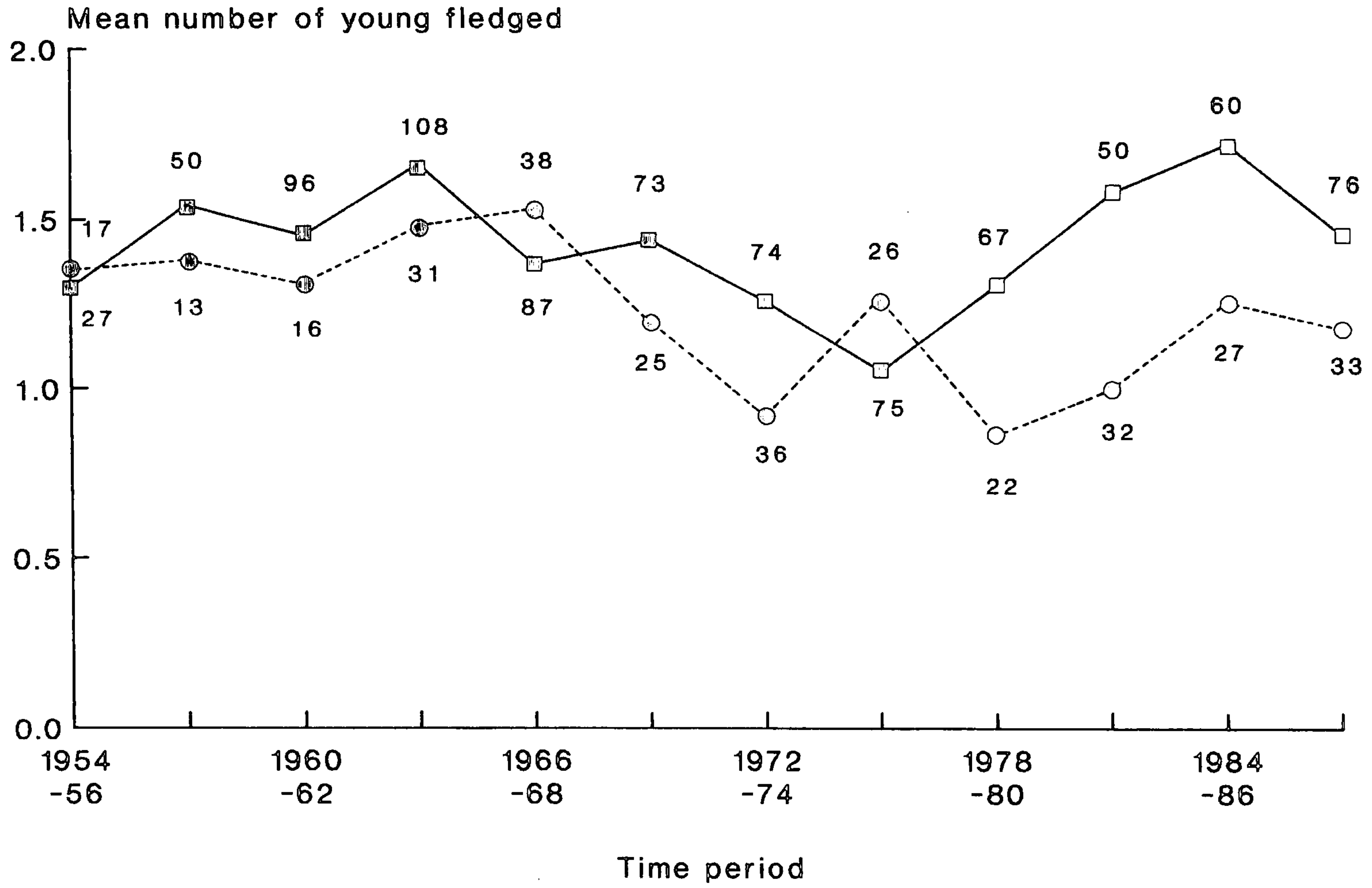

Mean number of young fledged
2.0
1.5
1.0
0.5
0.0
17
27
50
13
89
11
117
31
86
37
69
29
72
32
76
28
56
18
56
36
59
26
76
35
1955
-57
1961
-63
1967
-69
1973
-75
1979
-81
1985
-87
Time period

Figure 1.5 Mean number of young fledged by female kittiwakes which would divorce (○) or retain their mate (□) in the next breeding season. Data for all years, 1954 - 89, pooled in 3-year time periods. Numbers for each point are sample sizes.


Mean number of young fledged
2.0
1.5
1.0
0.5
0.0
1954
-56
1960
-62
1966
-68
1972
-74
1978
-80
1984
-86
Time period
17
27
50
13
96
16
108
31
38
87
73
25
74
36
26
75
67
22
50
32
60
27
76
33

periods (Fig. 1.4). In the year preceding their divorce, females had lower productivity than females which would retain their mate in the next year in 9 of the 12 time periods (Fig. 1.5).

Survival following divorce and mate retention

For kittiwakes (age ≤ 12) of both sexes, the average annual survival rate in each year following divorce was lower than for those which retained their mate in all eight time periods (Fig. 1.6) (sign test, $n = 8$, $P < 0.01$). The average annual survival rate (1956 - 90) for females (age ≤ 12) following divorce was 74.4% ± 2.1% ($n = 313$), for males it was 73.8% ± 2.4% ($n = 346$). The average annual survival rate for both sexes (age ≤ 12) following divorce was 74.0% ± 1.7% ($n = 659$) compared to 79.6% ± 1.2% following mate retention ($n = 1643$), a difference of 5.6 percentage points, resulting in a 25% reduction in expectation of further life for the divorced birds (expectation of further life: divorced birds = 3.3 years, birds which retained the same mate = 4.4 years).

Reproductive performance of divorced females in relation to pair status in the following year

Table 1.3 shows the reproductive performance of females in the year of their divorce, in relation to their pair status in the following year. Divorced females which would retain the same mate in the next year did not lay significantly earlier or larger clutches than females which would divorce again in the next year, but fledged significantly more young. A significantly smaller proportion of females which would retain their mate in the next year failed to fledge any young in the year of divorce (14% ± 4%, $n = 95$), compared to females which would divorce again in the next year (33% ± 6%, $n = 57$) ($\chi^2 = 7.1$, df = 1, $P < 0.01$).

Divorced females which would retain the same mate in the next year laid earlier, had larger clutches and fledged more young than females which would die before the next breeding season commenced. A third (33% ± 5%, $n = 84$) of the divorced females in their last breeding year failed to fledge any young in the year of divorce, compared to

Figure 1.6 Average annual adult survival rates (1959 - 90) for kittiwakes of both sexes in the year following divorce (●) or mate retention (▤). Age ≤ 12 in the year following divorce or mate retention. Data pooled in 4-year time periods. Numbers for each point are sample sizes.

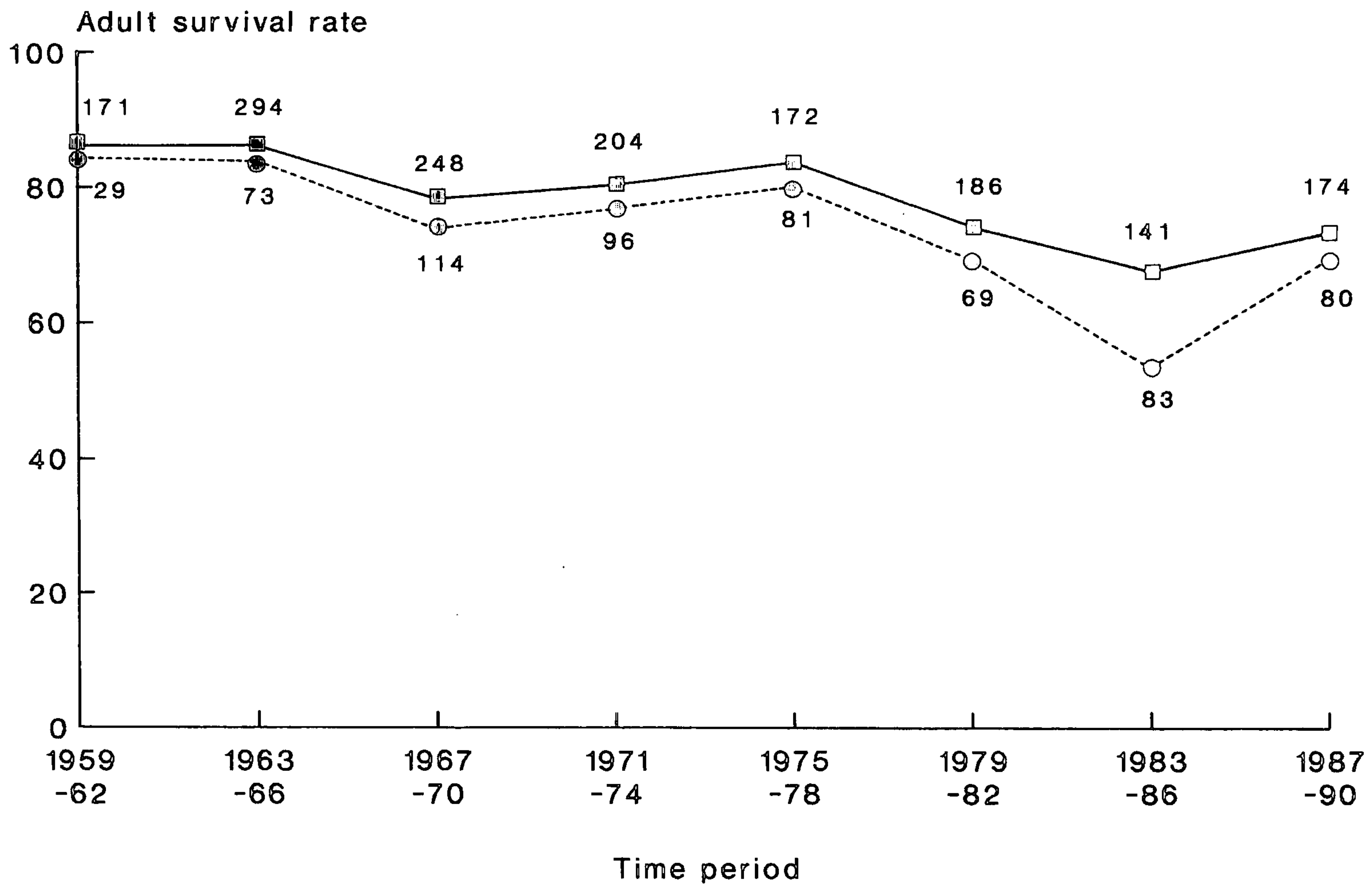

Adult survival rate
100
80
60
40
20
0
171
29
294
73
248
114
204
96
172
81
186
69
141
83
174
80
1959 -62
1963 -66
1967 -70
1971 -74
1975 -78
1979 -82
1983 -86
1987 -90
Time period

Table 1.3. Reproductive performance of female kittiwakes in the breeding season of divorce (this year) in relation to pair status which occurred in the next breeding season.

			Reproductive performance this year												
			Relative date of laying			Clutch size				Number young fledged					
	This year	Next year	Mean (days)	SE	*n*	1	2	3	Mean	0	1	2	3	Mean	% failed breeding
i	Divorce	Same mate	1.61	0.80	101	2	84	15	2.13	13	32	48	2	1.41	14 ± 4
ii	Divorce	Divorce	-0.08	1.12	61	2	55	4	2.03	19	15	22	1	1.09	33 ± 6
iii	Divorce	Mate death	0.77	1.23	31	1	27	3	2.06	7	6	14	0	1.26	26 ± 9
iv	Divorce	Die	-1.37	0.79	91	8	77	6	1.98	28	31	23	2	0.99	33 ± 5
										No. fledged: 0 v 1 v 2 or 3					
		i v *ii*	$z = 1.2$ NS			$\chi^2_2 = 2.7$ NS				$\chi^2_2 = 8.3^*$					
		i v *iii*	$z = 0.6$ NS			$\chi^2_2 = 0.7$ NS				$\chi^2_2 = 2.8$ NS					
		i v *iv*	$z = 2.7^{**}$			$\chi^2_2 = 7.3^*$				$\chi^2_2 = 13.2^{**}$					

NS = not significant, $^* = P < 0.05$, $^{**} = P < 0.01$

14% ± 4% of the divorced females which would return to breed with the same mate ($n = 95$) ($\chi^2 = 8.7$, df = 1, $P < 0.01$).

There was no significant difference in the relative date of laying, clutch size and productivity between divorced females which would retain the same mate in the following year, and females which had bred with the same mate for at least two years (Table 1.4). When the data were sub-divided according to female breeding age (Table 1.4), both young (age 2 - 3) and old divorced females (age 4 - 13) which would retain the same mate in the next year, had similar dates of laying, clutch size and productivity to females of a similar age (2 - 3 or 4 - 13) which had retained their mate for at least two years.

Reproductive performance of divorced females in relation to male age

Following divorce, a proportion of the females tended to take a young male as their new mate (Fig. 1.7); 65% ($n = 332$) of the divorced females took a mate with only 0 - 2 years of previous breeding experience. To determine whether the reproductive success of divorced females was affected by the age of the male, the data were divided by female and male ages (Table 1.5).

The relative date of laying, clutch size and productivity of divorced young females (age 2 - 3) with young males (age 1 - 3) or older males (age 4 - 8) did not differ significantly (Table 1.5). Older female (age 4 - 8) and young male pairs laid significantly later than older female and older male pairs (mean difference = 3.6 days) but the mean clutch size was not significantly different (Table 1.5). Older female and young male pairs fledged significantly fewer young (mean = 1.13) than older female and older male pairs (mean = 1.50) (Table 1.5). Of the older females which fledged young, a significantly higher proportion of the older female and young male pairs fledged only one young (48% ± 7%, $n = 56$), compared to older female and older male pairs (22% ± 7%, $n = 36$) ($\chi^2 = 5.2$, df = 1, $P < 0.05$).

Table 1.4. Reproductive performance of female kittiwakes in the breeding season of divorce (this year) which retained their mate in the next breeding season, compared to the reproductive performance of females which kept the same mate this breeding season. Data sub-divided by female age.

		Reproductive performance this year											
		Relative date of laying			Clutch size				Number young fledged				
This year	Next year	Mean (days)	SE	*n*	1	2	3	Mean	0	1	2	3	Mean
Divorce	Same mate	1.61	0.80	101	2	84	15	2.13	13	32	48	2	1.41
Same mate		1.73	0.23	890	49	657	184	2.15	134	238	419	42	1.44
Age 2 - 3													
Divorce	Same mate	0.22	1.49	45	2	39	4	2.04	6	12	25	0	1.44
Same mate		1.61	0.39	319	25	248	46	2.07	52	90	150	6	1.37
Age 4 - 13													
Divorce	Same mate	2.73	0.79	56	0	45	11	2.20	7	20	23	2	1.38
Same mate		1.79	0.28	571	24	409	138	2.20	82	148	269	36	1.48

z-test of relative date of laying: divorce-same mate v same mate = NS
χ^2 test of number young fledged (0 v 1 v 2 or 3): divorce-same mate v same mate = NS

Figure 1.7 The age at divorce of female kittiwakes, in relation to the age of their new partner. The dotted line emphasizes that 216 (65%) of the divorced female kittiwakes took a 0 - 2 year old male as their new partner. A bird about to breed for the first time is age 0.

Male age	1	2	3	4	5	6	7	8	9	10	11	12
16							1					
15							1					
14												
13			1									
12					2	1	1					
11						1						
10		2						1				
9	1	1	1			1						
8	1		1		1	1		1	1			
7	1	1	1	3	1	1						
6	2	4	2	1	2	2	1				1	
5	3	1	4	3	1			1	1		1	
4	5	5	5	2	2	1				1		2
3	13	7	5	3	2	1	2	1				
2	17	12	7	4	3	4			2	3	1	
1	21	14	10	8	8	1	1		1	1		
0	39	18	10	15	5	6	1		2	2		

Female age

Table 1.5. Reproductive performance of (a) female kittiwakes in the breeding season of divorce, in relation to female age and the age of the new partner and (b) the reproductive performance of females which kept the same mate.

		Relative date of laying					Clutch size					Number young fledged					
		Male age	Mean (days)	SE	n	z	1	2	3	Mean	χ^2_2	0	1	2	3	Mean	χ^2_2
(a)	Female: Age 2 - 3																
	New mate	1 - 3	-0.50	0.82	121		7	104	10	2.02		26	36	44	2	1.20	
						1.6 NS					1.4 NS						0.7 NS
	New mate	4 - 8	1.45	0.87	42		1	39	2	2.02		12	12	15	0	1.08	
	Female: Age 4 - 8																
	New mate	1 - 3	-0.46	0.87	82		5	69	8	2.04		21	27	27	2	1.13	
						3.1**					3.8 NS						7.7*
	New mate	4 - 8	3.16	0.76	45		2	33	10	2.18		8	8	26	2	1.50	
						1.2 NS					0.0 NS						3.2 NS
(b)	Female: Age 4 - 8																
	Same mate	4 - 8	2.09	0.45	248		11	184	53	2.17		31	73	115	16	1.49	

χ^2 test of number young fledged = 0 v 1 v 2 or 3
NS = not significant, * = $P < 0.05$, ** = $P < 0.01$

The reproductive performance of females (age 4 - 8) paired with the same males (age 4 - 8) for at least two years was used to test whether divorce resulted in reduced reproductive success even if the new partner was experienced (Table 1.5). Their reproductive performance was compared with that of divorced older female - older male pairs. The relative date of laying, clutch size and productivity did not differ significantly between these two groups (Table 1.5).

Reproductive performance of kittiwakes in their last year of life

Data presented earlier showed that the reproductive performance of a pair was affected if the male (Tables 1.1 & 1.2) or the female (Table 1.3) was in its last year of life. Few of these birds disappeared during the breeding season under consideration and most disappeared (and presumably died) between September and March of the following year.

Pairs (male age and female age = 1 - 12) in which both members survived to the next breeding season laid earlier than those in which both members died (mean difference = 2.0 days), or only the female died (mean difference = 1.7 days), before the next breeding season commenced (Table 1.6). Similarly, the clutch size was significantly reduced if both members of the pair died, or only the female died, before the next breeding season commenced. Pairs in which both members survived to breed in the following year fledged significantly more young (mean = 1.39) than pairs in which one (female died = 1.23, male died = 1.21) or both members of the pair (mean = 0.98) were in their last year of life (Table 1.6). On average, productivity was reduced by 12% if one member of the pair was in the last year of life and by 29% if both members were in their last year of life. A high proportion (25 - 35%) of the pairs in which one or both members of the pair were in their last year of life failed to fledge any young (Table 1.6). Of the pairs which fledged young, 53% ± 5% ($n = 100$) of the pairs in which both members were in their last year of life fledged only one young. This proportion was significantly higher than in pairs in which both members survived (37% ± 2%, $n = 923$) (no. young fledged 1 v 2 or 3, $\chi^2 = 9.4$, df = 1, $P < 0.01$).

Table 1.6. Reproductive performance of kittiwakes in relation to the survival or death of one or both members of the pair in the next year. Female age and male age = 1 - 12 to control for the decreased survival rate of kittiwakes above the age of 12.

			Relative date of laying			Clutch size				Number young fledged					
	Female	Male	Mean (days)	SE	*n*	1	2	3	Mean	0	1	2	3	Mean	% failed breeding
i	Survive	Survive	1.27	0.24	1180	72	920	188	2.10	195	339	541	43	1.39	17 ± 1
ii	Survive	Die	0.79	0.46	277	24	222	32	2.03	65	76	112	4	1.21	25 ± 3
iii	Die	Survive	-0.47	0.53	254	31	199	25	1.98	63	77	95	12	1.23	26 ± 3
iv	Die	Die	-0.74	0.63	164	21	133	11	1.94	54	53	43	4	0.98	35 ± 4
		i v *ii*	z = 0.9 NS			$\chi^2_2 = 5.2$ NS				$\chi^2_2 = 8.9^*$					
		i v *iii*	z = 3.0^{**}			$\chi^2_2 = 16.0^{***}$				$\chi^2_2 = 10.2^{**}$					
		i v *iv*	z = 3.0^{**}			$\chi^2_2 = 17.7^{***}$				$\chi^2_2 = 35.1^{***}$					

NS = not significant, $^* = P < 0.05$, $^{**} = P < 0.01$, $^{***} = P < 0.001$

When female age was taken into account (Table 1.7), the relative date of laying of females, up to the age of 12, was consistently later for pairs (male age = 1 - 12) in which both members died, when compared to pairs in which both members survived, and differed significantly for the 2 year old females (mean difference = 5.6 days) (Table 1.7). The small number of females over the age of 12, do not allow precise estimates of reproductive performance of this group of birds, although the data are presented. Pairs in which both members died did not lay significantly smaller clutches than pairs in which both members survived (Table 1.7). However, for all age groups, the mean number of young fledged per pair in their last breeding year was less than for pairs in which both members survived and differed significantly for all but the two year old females.

Table 1.8 shows that, on average, females fledged more young in their penultimate breeding attempt than in their last attempt. The mean number of young fledged was reduced appreciably and significantly for females which died after their fourth breeding year (mean = 1.05), when compared to their penultimate breeding year (mean = 1.51). Of the females which died following their fourth breeding attempt ($n = 43$), 70% ± 7% had lower than average productivity in their final year (i.e. failed or fledged only one chick), compared to 37% ± 7% in their penultimate year ($n = 43$) (no. young fledged, 0 or 1 v 2 or 3: $\chi^2 = 7.9$, df = 1, $P < 0.01$).

Table 1.7. Reproductive performance of kittiwakes this year in relation to whether both members of the pair survived until, or died before, the next breeding season commenced. Data sub-divided by female age. Except for when both members of the pair are over the age of 12, male age of 1 - 12 has been used to control for the decreased survival rate of kittiwakes above the age of 12.

		Relative date of laying				Clutch size					Number young fledged					
Female	Male	Mean (days)	SE	*n*	z	1	2	3	Mean	χ^2_2	0	1	2	3	Mean	χ^2_2
<u>Age 1</u>																
Survive	Survive	-1.12	0.56	270	1.3 NS	33	223	14	1.93	5.4 NS	62	90	104	4	1.19	11.4^{**}
Die	Die	-3.21	1.56	38		10	28	1	1.77		17	15	6	0	0.71	
<u>Age 2</u>																
Survive	Survive	2.38	0.58	193	3.7^{**}	12	152	29	2.09	4.5 NS	31	57	88	5	1.37	3.7 NS
Die	Die	-3.23	1.41	31		4	26	1	1.90		8	10	8	1	1.07	
<u>Age 3-5</u>																
Survive	Survive	1.84	0.38	377	0.0 NS	15	301	61	2.12	5.4 NS	52	102	189	15	1.47	14.0^{***}
Die	Die	1.81	0.90	58		5	49	4	1.98		18	17	18	1	1.04	
<u>Age 6-12</u>																
Survive	Survive	1.90	0.40	340	1.6 NS	12	244	84	2.21	2.5 NS	50	90	160	19	1.46	6.8^{*}
Die	Die	-0.14	1.20	37		2	30	5	2.08		11	11	11	2	1.11	
<u>Age 13-19</u>																
Survive	Survive	0.13	1.01	46	0.0 NS	3	32	11	2.17		10	10	21	2	1.35	
Die	Die	0.14	2.17	14		0	12	2	2.14		6	4	4	0	0.86	

χ^2 test of number young fledged = 0 v 1 v 2 or 3
NS = not significant, $^{*} = P < 0.05$, $^{**} = P < 0.01$, $^{***} = P < 0.001$

Table1.8. Reproductive performance of female kittiwakes in (a) the penultimate year of life and in (b) the last year of life, in relation to female age

		Relative date of laying				Clutch size					Number young fledged					
	Age	Mean (days)	SE	*n*	z	1	2	3	Mean	χ^2_2	0	1	2	3	Mean	χ^2_2
(a)	2	2.24	1.04	55	0.2 NS	1	47	7	2.11	4.4 NS	9	15	27	1	1.38	2.5 NS
(b)	3	2.49	0.91	55		6	45	4	1.96		15	11	22	1	1.18	
(a)	3	3.36	0.96	45	3.0**	3	36	6	2.07	2.6 NS	6	10	26	1	1.51	9.2**
(b)	4	-0.69	0.98	45		7	35	3	1.91		12	18	12	1	1.05	
(a)	4	0.94	1.31	32	0.3 NS	1	27	4	2.09		3	4	19	2	1.71	
(b)	5	1.44	1.43	32		3	25	4	2.03		6	5	20	1	1.50	

χ^2 test of number young fledged = 0 v 1 v 2 or 3
NS = not significant, ** = $P < 0.01$

Discussion

Several studies have examined the causes of divorce in birds, paying particular attention to the relationship between reproductive failure and increased likelihood of divorce in the subsequent season (Coulson 1966; Mills 1973; Brooke 1978a; Harris *et al.* 1987; Ollason & Dunnet 1988; Bradley *et al.* 1990; Weimerskirch 1990). Coulson (1972) suggested that divorce in the kittiwake, which was correlated with breeding failure in the preceding year, was a result of incompatibility within the pair. Divorce tends to be effected through the two birds arriving back at the colony at markedly different times for the next breeding season (Coulson 1972; Coulson & Thomas 1983), the result of which is that the partner which arrives earlier takes a new mate before its previous partner returns.

The technique of examining the performance of individual birds before an event, in addition to the more usual approach of considering whether the event has had a subsequent effect on the bird, has proved to be valuable in gaining a better understanding into the cause and effect relationships which influence productivity. This method has shown that the average breeding performance of female kittiwakes in the year before divorce and in the breeding season following remained unchanged and in both cases was lower than for females which had retained their mate. Thus, the low productivity in the year of taking a new mate is not solely the result of problems associated with a new partnership. This lends support to the suggestions from studies on the great tit that poorer quality individuals have both a poorer breeding success and a lower tendency to retain the same mate (Perrins & McCleery 1985). In effect, the tendency to divorce is therefore a correlate of low breeding success and not a direct effect of it.

Coulson (1968) and Coulson and Porter (1985) showed that considerable variation in the quality of individual kittiwakes was reflected in differences in their survival and reproductive success. A reduced survival rate was associated with low productivity and poorer quality individuals. As the survival rate of kittiwakes in the year following divorce was lower than for those which had retained their mate, the implication is that the birds which had divorced were poorer quality individuals. The fact that a higher proportion of divorced females either failed to fledge young or fledged only one chick, in the year of divorce, than females which retained their mate, also suggests that birds which divorced were of poorer quality. As the quality of the individuals affect the compatibility of the pair, the incidence of divorce is highest in poorer quality birds.

In some cases, divorce was not a direct or simple consequence of breeding failure and incompatibility within the pair, as shown by the fact that some pairs of kittiwakes which had high productivity (fledged 2 or 3 young) divorced in the next year, and some pairs which failed in the previous year retained the pair bond. The implication is that some good quality birds divorced as a result of divorce not being a precise mechanism. For example, young and old female kittiwakes which took a new mate through divorce and would retain the same mate in the following year, showed no difference in their average productivity per pair in the year of divorce, compared to females of comparable age paired with the same mate for at least two years. Similarly, the average reproductive success of divorced, but experienced breeding females which took experienced males as their new mate was immediately as high as that of females of comparable age which had retained their mate. In terms of reproductive performance, these females were not affected by divorce and their above average productivity shows that they were not poorer quality individuals.

As breeding experience increased, the likelihood of divorce reduced, and mate retention increased. Accordingly, amongst older females, the death of the male is more important in causing the break in a pair bond (Coulson & Thomas 1980). Coulson (1972) inferred that repeated breeding with the same mate led to an increased familiarity and co-ordination in breeding activities, which increased reproductive success. The converse of this is that individuals which acquire a new mate have lower reproductive success compared to pairs which retained their mate. Breeding success following divorce was, to some extent, dependent on both male and female age. For example, old females which acquired a new mate which was old had higher than average productivity. Whilst many kittiwakes pair with a mate of the same or similar age (Coulson & Thomas 1983), there was increased variation in the age of the partners following divorce. Due to the lower survival rate of male than of female kittiwakes (Aebischer & Coulson 1990), there was fewer old males in the colony than old females. Hence, it is advantageous for older females to retain their mate as some old females have to mate with young inexperienced males.

Ens *et al.* (1993) challenged the incompatability hypothesis in their work on the oystercatcher, and suggested that divorce may not have occurred because mates were incompatible, but rather because one member of the pair had a better option. The category of divorced birds then included many victims which were not expected to benefit from the divorce. Kittiwakes which divorced were, on average, of poorer quality than individuals which retained their mate, as indicated by their lower productivity and survival rate. Therefore, I believe that for the majority of the birds it is the quality of the individual which is important in determining the incidence of divorce. As divorce was not always a consequence of breeding failure and incompatibility within the pair, detailed behavioural studies of the way in which kittiwakes select new mates are required, for example, in relation to mate choice by individuals of different quality. Whilst I do not challenge the incompatibility hypothesis for the majority of the kittiwakes which divorced, I emphasise both the role of individual quality in determining the compatibility of the pair and the significance of mate age and mate choice on productivity in the year of divorce. Earlier studies on divorce in the kittiwake have not looked at the birds for whom, in terms of reproductive performance with a new mate, divorce has entailed no apparent cost.

Reproductive performance of kittiwakes in their last year of life

As previous studies of age related reproductive performance in birds have suggested that senescence may have reduced the performance of old birds (Newton *et al.* 1981; Reid 1988; Wooller *et al.* 1989; Hamer & Furness 1991), consideration of the breeding performance of kittiwakes in the year before death is informative. On average, productivity was reduced by 12% if one member of the pair was in the last year of life and by 29% if both members died before the next breeding season. This reduction in productivity by females (age 1 - 12), with mates of 1 - 12 years, could not have been as a result of the rise in the mortality rate, indicative of senescence (Wooller *et al.* 1989), which occurs above the age of 12 in the kittiwake (Aebischer & Coulson 1990). Further, it could not have been an effect of age, as the productivity of even one year old females was reduced by 40% if both members of the pair were in their last year of life.

If the birds which died at a young age were of poorer quality than those which were long lived, it would be expected that their productivity would have been no higher in their penultimate breeding attempt. However, on average, females fledged more young in their penultimate breeding attempt than in their last attempt. The low productivity and deterioration in breeding performance, evident in an individuals last breeding year, is indicative of a decline in fitness. Since many of these birds apparently die soon after the end of the previous breeding season, this strongly suggests that many kittiwakes die from a progressive illness, the early effects of which reduces their breeding performance in their last breeding season, rather than from a sudden event, such as predation.

CHAPTER 2

THE INFLUENCE OF FORCED SITE CHANGE ON THE DISPERSAL AND BREEDING OF THE KITTIWAKE

Introduction

Many workers have studied philopatry and its converse, natal dispersal (the movement of juveniles from birth site to first breeding site; Greenwood 1980), in birds and breeding site fidelity and dispersal of birds (the distance moved by individuals between successive breeding sites; Greenwood 1980). Natal dispersal is common among colonial seabirds (e.g. red-billed gull *Larus novaehollandiae scopulinus*, Mills 1973; herring gull *Larus argentatus*, Chabrzyk & Coulson 1976; kittiwake *Rissa tridactyla*, Wooller & Coulson 1977, Coulson & Nève de Mévergnies 1992; Manx shearwater *Puffinus puffinus*, Brooke 1978b). In contrast, seabirds typically return to the same site in consecutive years once they have bred (breeding site fidelity; Oring & Lank 1984) (e.g. common tern *Sterna hirundo*, Austin 1949; kittiwake, Wooller & Coulson 1977, Aebischer & Coulson 1990; guillemot *Uria aalge*, Birkhead 1977; fulmar *Fulmarus glacialis*, Ollason & Dunnet 1978; red-billed gull, Mills 1989).

Although natal dispersal has been shown to occur in the kittiwake (Wooller & Coulson 1977; Coulson & Nève de Mévergnies 1992), movement between colonies was extremely rare once an individual bred (Wooller & Coulson 1977; Aebischer & Coulson 1990). The degree of site fidelity of kittiwakes is such that both sexes exhibit a strong attachment to the nest site of the previous breeding season (Coulson & Thomas 1983). Though this effect is more precise in the male, most females move only a few metres from their nest site of the previous breeding season (Coulson & Thomas 1983). Recently it has been shown that unfaithfulness to the breeding colony was related to disturbance and nest predation at the colony (Coulson & Nève de Mévergnies 1992) and that kittiwakes breeding in an unproductive colony showed much lower breeding site fidelity than birds in a flourishing colony (Danchin & Monnat 1992).

This study is one of few which have examined the movement of birds in response to a forced site change, such as when some, or all of the nesting sites at the breeding site have disappeared. It can be considered to be an experiment where a sample of adult male and female kittiwakes were forced to disperse. As kittiwakes show strong breeding site fidelity and nest site tenacity, movements resulting from this forced site change would be more extreme than movements previously recorded within the colony (Coulson & Thomas 1983; Fairweather & Coulson submitted data; but see Danchin & Monnat 1992).

Methods

The study colony was situated on a warehouse at North Shields, Tyne and Wear, England (Fig. 2.1). Since 1954, virtually all breeding birds in the colony have been marked with a unique combination of coloured leg rings (Porter & Coulson 1987), so were recognisable as individuals. The sex of each bird has been determined by behaviour or by measurement and checked against the sex of the mate.

In 1990, planning permission was granted to convert the warehouse into residential accommodation, subject to a "cliff" being built nearby onto which the kittiwakes could move. This resulted in ledges being constructed on the side of a disused Lifeboat station, at the mouth of the River Tyne, about 1 km from the warehouse (Fig. 2.1). The window ledges, used as nesting sites at the warehouse, were covered with wire mesh before the kittiwakes returned to the colony for the 1991 breeding season, preventing kittiwakes from nesting on the same sites in 1991 as had been used in previous years. From 1991 onwards, the term "**North Shields colony**" refers to the location of the nest sites of the kittiwakes which subsequently bred in the immediate vicinity of the warehouse (i.e. the warehouse roof and the roof of an adjacent building). These sites had not been used as nest sites by kittiwakes prior to 1991.

The colonies at North Shields and Marsden (5 km from North Shields) were visited at least twice a week from February to August, 1991 - 93. The Tynemouth colony (3 km from North Shields) was visited at least twice a week from February to August in 1992 and 1993. Fortnightly visits were made to other kittiwake colonies within a 70 km radius. During visits to the colonies, the identity and location of all colour-ringed kittiwakes present; their mate; date of onset of nest building; date of laying; clutch size; date of fledging and number of young fledged were recorded. Additional observations of the colour-ringed kittiwakes were made at the North Shields Lifeboat station at the fish quay at the mouth of the River Tyne (Fig. 2.1). The fish quay is a loafing area for kittiwakes where they do not engage in nesting activities.

For each year of the study (1991 - 93), only the surviving kittiwakes which had bred at the warehouse colony in 1990 are considered. The surviving adult kittiwakes are divided into three categories in relation to their breeding status in each year of the study:

i. **Breeding birds** - bred or, in a few cases, occupied a nest site until at least the end of the egg-laying period (mid-June).

ii. **Birds attempting to nest** - paired and even began nest building but occupied the nest site for less than 3 weeks.

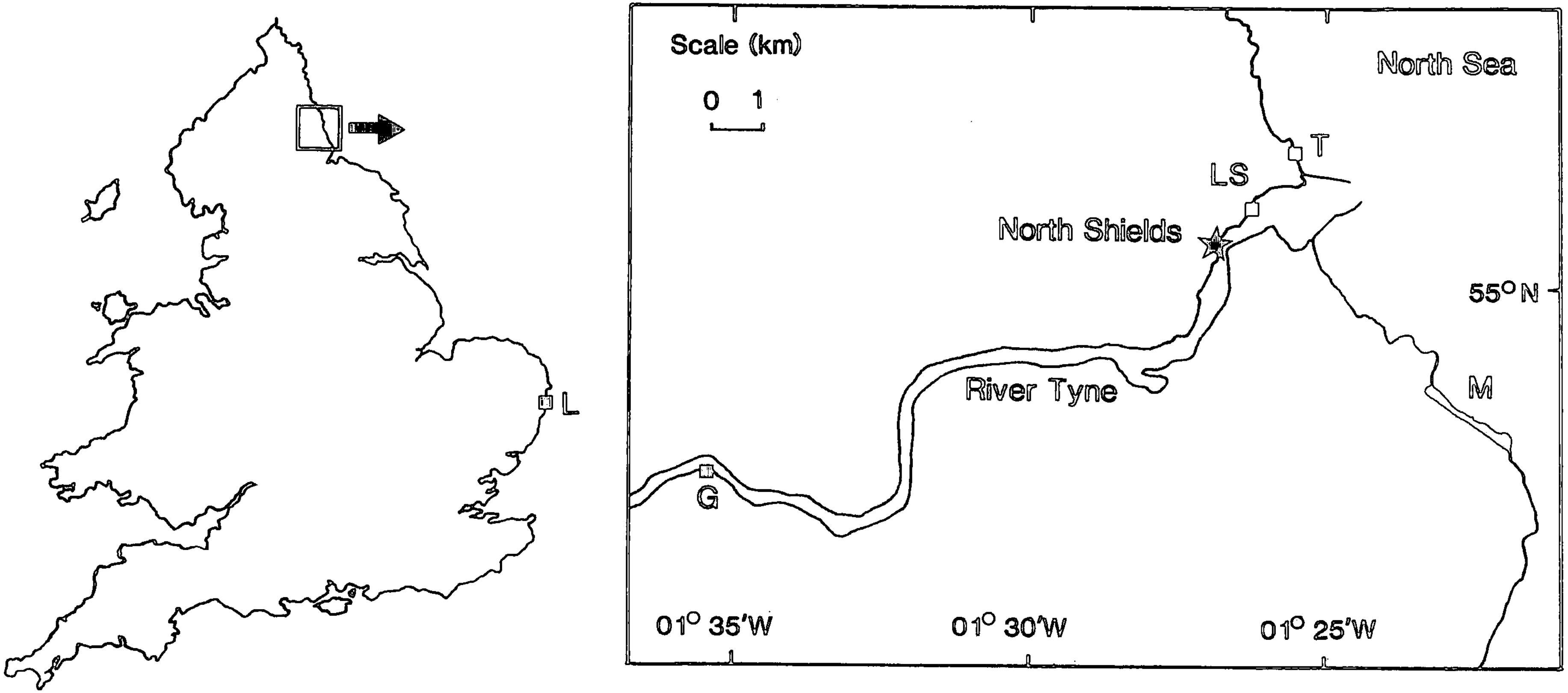
iii. **Birds which did not nest** - were not observed nest building or occupying a nest or nest site. Some, but not all, were seen in pairs.

The survival rate is the proportion of the adult birds which were alive in the summer of the previous breeding season which were seen in the summer of the following breeding season.

In 2 by 2 χ^2 calculations, Yates' correction factor has been used. All means are expressed as ± 1 SE, unless otherwise stated.

Figure 2.1 Map showing the location of colonies where kittiwakes which had bred at the warehouse colony in 1990 were found breeding in the years 1991 - 93.

Key: G = Gateshead; L = Lowestoft; LS = Lifeboat station; M = Marsden; T = Tynemouth.


L
Scale (km)
0 1
North Sea
T
LS
North Shields
55° N
River Tyne
M
G
01° 35'W
01° 30'W
01° 25'W

Results

Annual survival rates, 1990 - 93, of the kittiwakes which had bred at the warehouse colony in 1990

The average annual survival rates for 1990 to 1993 of the kittiwakes which had bred at the warehouse colony in 1990, based on sightings of individually marked birds, are given in Table 2.1. These were all higher than the average annual survival rates of kittiwakes which had bred at the warehouse colony in the previous three years (average annual survival rate 1987 - 90: 74.2 ± 2.1%, *n* = 434, unpublished data) suggesting that most of the surviving birds were located.

Behaviour of the kittiwakes on their return to the colony in 1991

The first kittiwake returned to the North Shields colony on 1 March 1991; the mean date of return was 23 March ± 11.4 days (SD; *n* = 150). The windows used as nesting sites at the warehouse had been covered with wire mesh and, for at least three weeks, the kittiwakes were seen flying up to, and clinging to the mesh in an attempt to gain access to nest sites. As they were unable to return to their original nest sites, most gathered on the gutters, roof and gable ends of the warehouse, the roof of an adjacent building (Ferry Office) and a quayside, 50 m from the warehouse. Some of the kittiwakes formed pairs and at the end of April 1991 birds began to frequent ledges within a disused dry-dock in a shipyard 200 m from the warehouse. By 12 May, 39 of the marked kittiwakes were in this dock, on ledges which were below surrounding ground level. All of these sites had not previously been used as nest sites by kittiwakes.

By 17 May 1991, 29 pairs were involved in nest building on the sloping warehouse roof or gutter, a further 15 pairs were building nests on the Ferry Office roof. Birds brought a small amount of nest material into the dry-dock and 14 of the birds began nest building (birds attempting to nest) but no nests were completed and the site was deserted on 19 May, although it had received little disturbance.

Table 2.1. Average annual survival rates[1] of the kittiwakes which had bred at the warehouse colony in 1990.

Year	No. at risk	No. surviving	Annual survival rate ± SE
1990 - 91	173	150	86.7 ± 2.8
1991 - 92	150	133	88.7 ± 2.8
1992 - 93	133	101	75.9 ± 3.7

---

[1] Based on sightings of individually marked birds

Breeding status in 1991 - 93 of the kittiwakes which had bred at the warehouse colony in 1990

In 1991, the year of the warehouse closure, only 43% (*n* = 150; Table 2.2) of the surviving adult kittiwakes bred at the North Shields colony (i.e. on the warehouse roof and the roof of an adjacent building) or at colonies shown in Table 2.3. An additional 18% (*n* = 150) began nest building but occupied a nest site for less than 3 weeks (Table 2.2). In 1992, 88% (*n* = 133) of the surviving kittiwakes bred and this proportion increased to 92% (*n* = 101) in 1993 (Table 2.2). Twelve of the surviving kittiwakes did not breed in two successive breeding seasons (1991 and 1992 or 1992 and 1993). This behaviour was unusual, as of 70 kittiwakes which had bred at the warehouse colony in 1987 and were still alive in 1990, only one had failed to breed in two successive breeding seasons.

Movement and distribution of the kittiwakes which had bred at the warehouse colony in 1990

Movements in 1991

Non-breeding adult kittiwakes (birds attempting to nest and birds which did not nest) which had bred at the warehouse colony in 1990, began leaving the North Shields colony at the end of April 1991 (Fig. 2.2). The mean date that these non-breeding kittiwakes were last seen at the colony was 3 June ± 31 days (SD; *n* = 85); 43 (51%) left in the 2 week period, 13 - 26 May (Fig. 2.2). In contrast, kittiwakes which bred at the North Shields colony in 1991 left the colony an average of 6 weeks later (19 July ± 19 days (SD), *n* = 54). Thus, the date that individuals were last seen at the North Shields colony in 1991 was dependent on their breeding status.

As egg-laying typically starts in early May and continues into mid June (Coulson 1974), the majority of the birds which left the North Shields colony early in 1991 did so when egg-laying should have been taking place. Many remained at North Shields in 1991 until it was too late to build nests and breed in other colonies. For example, 15 of

Table 2.2. Breeding status of the kittiwakes which had bred at the warehouse colony in 1990 in the years 1991 - 93.

Year	Breeding birds		Birds which attempted to nest[1]		Birds which did not nest		Total
	n	%	*n*	%	*n*	%	
1991	65	43	27	18	58	39	150
1992	117	88	0	0	16	12	133
1993	93	92	2	2	6	6	101

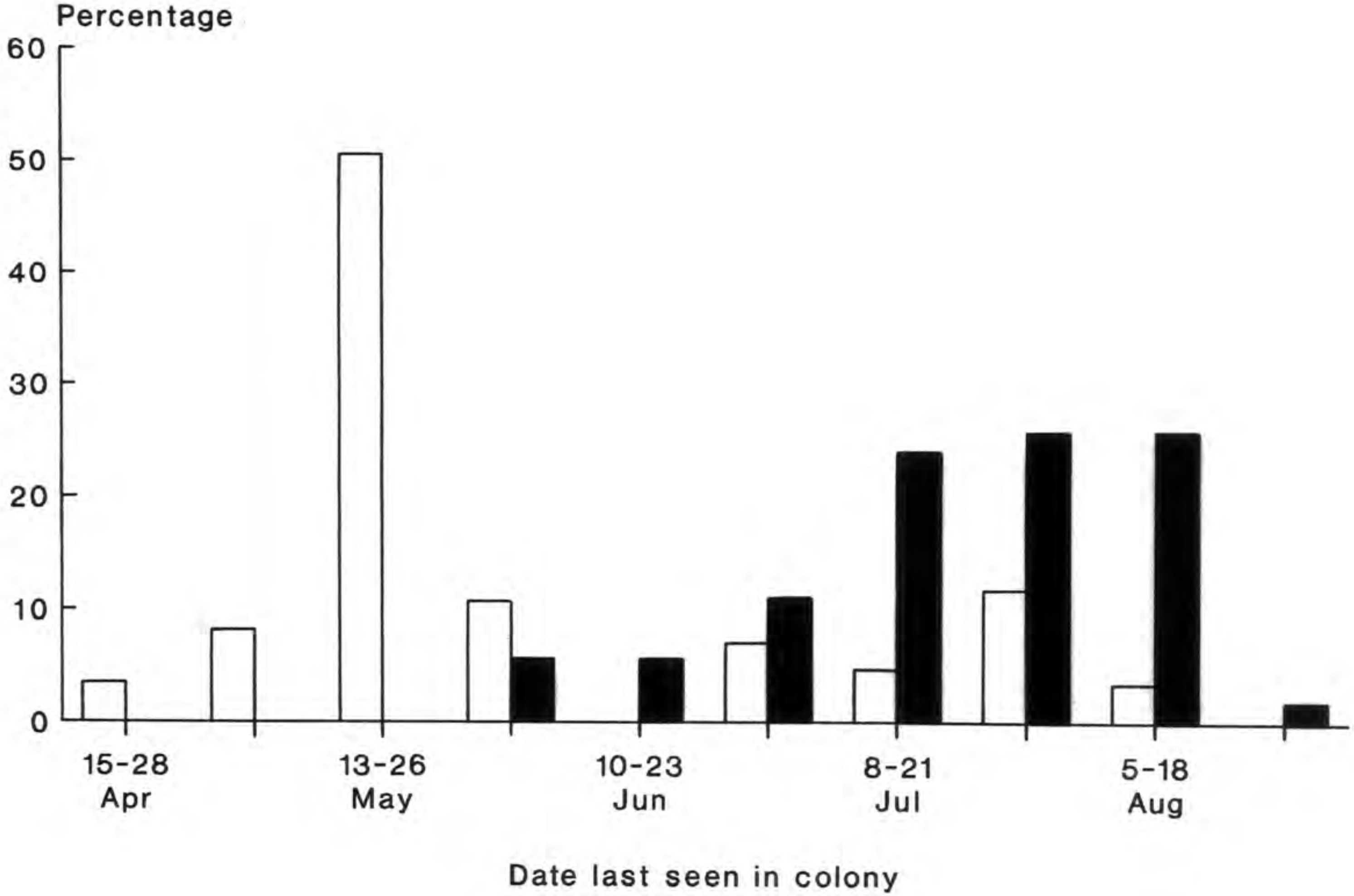
[1] These birds began nest building but occupied a nest site for less than 3 weeks.

Table 2.3. The number of kittiwakes which had bred at the warehouse colony in 1990 located breeding at the warehouse and other colonies in each year of the study, 1991 - 93.

Colony	Distance (km) from North Shields	1991		1992		1993	
		n	%	*n*	%	*n*	%
North Shields warehouse	-	37	57	39	33	31	33
Ferry office	-	17	26	8	7	4	4
Tyne Comm. Quay	1	1	1	0	0	0	0
Lifeboat station	1	0	0	2	2	2	2
Tynemouth	3	0	0	45	38	39	42
Marsden	5	6	9	20	17	15	16
Gateshead	11	3	5	3	3	2	2
Lowestoft	316	1	1	0	0	-	-
Total		65	100	117	100	93	100

Other colonies (and distance (km) from North Shields) which were searched in order to locate the kittiwakes which bred at the warehouse colony in 1990: Seaham Harbour (20 km); Coquet Island (37 km); Hartlepool (40 km); Cullernose (53 km); Dunstanburgh (58 km); Saltburn (58 km); Seahouses (67 km); Staithes (69 km) and the Farne Islands (73 km).

Figure 2.2 Distribution of dates that the kittiwakes which had bred at the warehouse colony in 1990 were last seen in the North Shields colony in 1991, in relation to their breeding status in 1991 (□ = non-breeding; □ = breeding).


Percentage
60
50
40
30
20
10
0
15-28
Apr
13-26
May
10-23
Jun
8-21
Jul
5-18
Aug
Date last seen in colony

the non-breeding birds were first seen at Marsden, Tyne and Wear (Fig. 2.1) on 24 June ± 13 days (SD), an average of 3 months after their arrival at the North Shields colony.

Distribution in 1991

Of 65 (43%) surviving kittiwakes known to breed in 1991, 37 nested on the warehouse roof and 17 nested on the roof of the Ferry Office (Table 2.3), only a few metres from their previous sites. Only 11 (17%) of the surviving kittiwakes known to breed in 1991 did so in other colonies (Table 2.3). These birds had been present at the North Shields colony until 12 May 1991 ± 21 days (SD; $n = 11$), i.e. in common with the non-breeding birds, they spent a period of time at the North Shields colony. The furthest known movement in 1991 was that of a female kittiwake which bred at Lowestoft, 316 km from North Shields (Fig. 2.1 and Table 2.3). No other movements of more than 11 km were recorded.

Of the kittiwakes which attempted to nest in 1991 (Table 2.2), 16 did so on the warehouse roof and the adjacent Ferry Office roof. Three of the birds which had attempted to nest in the dry dock left North Shields and bred in other colonies in 1991 (two bred at Marsden, one bred at Gateshead; Fig. 2.1). In 1991, no kittiwakes from the warehouse colony nested on the ledges at the Lifeboat station, although several unringed birds did so.

Distribution in 1992

An additional 61 of the surviving kittiwakes moved to other colonies to breed in 1992 (i.e. to Marsden and Tynemouth; Tables 2.3 and 2.4). Nine of these birds had been seen at Marsden late in 1991 but had not bred there. Overall, 56% of the surviving kittiwakes which bred in 1992 (and had not bred at a different colony in 1991; Table 2.4) moved to and nested at other colonies (all within 5 km of North Shields) in 1992. A total of 45 of these birds bred at Tynemouth (3 km from North Shields; Fig. 2.1), constituting 42% ($n = 106$) of the kittiwakes which nested there in 1992. Tynemouth had only 13 breeding pairs of kittiwakes in 1991 (Jardine *et al.* 1993) and none of these

Table 2.4. The number of kittiwakes which had bred at the warehouse colony in 1990 which, in each subsequent year of the study, remained at the North Shields colony or moved and bred at other colonies[1]. The proportion of these birds located breeding at North Shields and other colonies is shown in relation to sex.

Year	Sex	North Shields		Other colonies		
		n	%	*n*	%	χ^2_1
1991	Female	25	89	3	11	
	Male	29	78	8	22	0.7 NS
1992	Female	22	45	27	55	
	Male	25	42	34	58	0.0 NS
1993	Female	17	100	0	0	
	Male	18	95	1	5	

[1] Other colonies at which the birds were located breeding are shown in Table 2.3. Data for 1992 and 1993 excludes birds which bred at other colonies in the previous year.

χ^2 test: female v male - North Shields v other colonies. NS = not significant had bred at the warehouse colony in 1990. A further 14 of the kittiwakes bred in a colony of more than 5000 pairs at Marsden, 5 km from North Shields (Fig. 2.1). Although 28 kittiwakes nested on the ledges at the Lifeboat station in 1992 (Fig. 2.1), only two which had bred at the warehouse in 1990 nested there in 1992.

In 1992, the overall proportion of surviving kittiwakes which bred increased to 88% (*n* = 133; Table 2.2) and there was an increased movement of birds to other colonies (Tables 2.3 and 2.4). As a result, the proportion of the kittiwakes which bred at the North Shields colony was reduced from 83% of the marked birds which bred in 1991 (*n* = 65; Table 2.3), to 40% of the surviving kittiwakes which bred in 1992 (*n* = 117; Table 2.3). Although 48 of the kittiwakes which were known to have survived to 1992 had bred at the North Shields colony in 1991, only 26 (54%) of these birds returned to breed there in 1992 (Table 2.5); 18 moved to other colonies and 4 did not breed in 1992. In all, 30% of the 61 kittiwakes which moved to other colonies to breed in 1992 (Table 2.4) had bred at the North Shields colony in 1991, inclusive of two birds from different pairs which fledged young in 1991.

Return to the North Shields colony prior to movement to a different colony in 1992

Of the 61 kittiwakes which moved to and bred at a different colony in 1992 (Table 2.4), only 20% were seen in 1992 at the North Shields colony prior to moving. Hence, an appreciable proportion of the birds which bred in a different colony in 1992 apparently did not first return to the North Shields colony for any length of time before moving. Whether or not birds were seen at the North Shields colony prior to breeding in a different colony in 1992, did not depend on their breeding status in 1991 (bred at the North Shields colony in 1991, 5/18 returned in 1992; did not breed in 1991, 7/43 returned in 1992; $\chi^2 = 0.5$, df = 1, NS).

Distribution in 1993

Three (3%) of the surviving kittiwakes which bred in 1993 were in a different colony to that in which they had nested in 1992. These movements involved; *i*) one bird

Table 2.5. Dispersal and breeding status in 1992 of the 48 surviving kittiwakes which had bred at the warehouse colony in 1990 and in the immediate vicinity of the colony in 1991. Also shown is the dispersal and breeding status in 1993 of 21 kittiwakes which had bred at the warehouse colony in 1990 and in the immediate vicinity for 2 years (1991 and 1992).

	1992				1993			
Colony	Female		Male		Female		Male	
	n	%	*n*	%	*n*	%	*n*	%
North Shields	10	48	16	59	8	89	11	92
Lifeboat station	0	0	1	4	0	0	0	0
Tynemouth	6	28	6	22	0	0	0	0
Marsden	1	5	4	15	0	0	1	8
Non-breeding	4	19	0	0	1	11	0	0
Total	21	100	27	100	9	100	12	100

moving from the North Shields colony to Marsden (Table 2.5), *ii*) one bird moving from Marsden to Tynemouth and *iii*) one bird from Tynemouth returning to the North Shields colony (although it had bred successfully at Tynemouth in 1992). These additional movements suggest that the disturbance in 1991 was still having an effect on some of the kittiwakes two years later as this degree of movement had not been recorded between 1954 and 1990.

Factors potentially influencing breeding status and distribution in 1991 - 93:

Sex

In 1991 and 1993 there was no sex difference in the proportions of adult kittiwakes which were breeding or non-breeding birds (Table 2.6). In 1992, 66 of the males (94%) bred, compared with 51 of the females (81%), a difference which is significant ($\chi^2 = 4.4$, df = 1, $P < 0.05$).

In each year of the study, there was no difference in the proportions of male and female kittiwakes which bred at the North Shields colony or moved to other colonies (Table 2.4). For example, 34 of the males (58%) and 27 of the females (55%) which bred in 1992 and had not bred at other colonies in 1991, nested at colonies within 5 km of North Shields in 1992 (Table 2.4; $\chi^2 = 0.0$, df = 1, NS). Table 2.5 shows the movements in 1992, of male and female kittiwakes which had bred at the North Shields colony in 1991. There was no difference in the proportions of male and female kittiwakes which remained at the colony in 1992 or moved to a different colony ($\chi^2 = 0.1$, df = 1, NS). Thus, there is only one instance of a sex difference in the behaviour of breeding kittiwakes in response to the closure of the warehouse.

Breeding experience

Of the kittiwakes which had bred at the warehouse colony in 1990, the previous breeding experience (i.e. number of breeding years) of those which bred in 1991 (2.8 ± 0.2 years; $n = 65$) did not differ significantly to that of birds which did not breed (3.1 ± 0.2 years; $n = 85$; $z = 1.1$, NS). Similarly, there was no difference in the previous

Table 2.6. Breeding status in 1991 - 93 of the kittiwakes which had bred at the warehouse colony in 1990, in relation to sex.

Year	Sex	Breeding birds		Non-breeding birds[1]		
		n	%	*n*	%	χ^2_1
1991	Female	28	37	47	63	
	Male	37	49	38	51	1.7 NS
1992	Female	51	81	12	19	
	Male	66	94	4	6	4.4*
1993	Female	39	89	5	11	
	Male	54	95	3	5	0.6 NS

[1] Non-breeding birds = birds which attempted to nest and birds which did not nest

χ^2 test: female v male - breeding v non-breeding

NS = not significant, * = $P < 0.05$

breeding experience of birds which bred at the North Shields colony in 1992 (3.8 ± 0.3 years, *n* = 47) and those which moved to and bred at other colonies in 1992 (4.0 ± 0.2 years, *n* = 61; z = 0.3, NS). Therefore, breeding experience did not appear to have an effect on the response of the kittiwakes to the closure of the warehouse.

Productivity of the kittiwakes which had bred at the warehouse colony in 1990

In 1990, the mean number of young fledged per female at the warehouse colony was 1.15 (*n* = 92). Productivity was reduced in 1991 as only 48% of the females which bred fledged one or more young and many did not lay at all (mean number of young fledged per female = 0.74, *n* = 27). When the females which did not breed in 1991 are taken into account, (*n* = 47; Table 2.6), a total of only 20 young were fledged by the 74 surviving adult females in 1991 (mean young per female = 0.27). This low productivity was a direct result of the disturbance to the kittiwakes. In the nearby colony at Marsden, productivity remained high in 1991 (mean number of young fledged per female = 1.16, *n* = 477). In 1992, a mean of 1.16 young were fledged by each surviving female which had bred at the warehouse colony in 1990 (*n* = 51), indicating a return to normal productivity.

Discussion

Whilst many studies have considered the effect of human disturbance on the breeding biology of colonial seabirds (for review see Götmark 1992), few have considered the impact of preventing a colonial breeding species from using its previous breeding site. Kittiwakes are known to be highly faithful to their breeding colony (Coulson & White 1958a; Coulson 1966; Aebischer & Coulson 1990), although a recent study has revealed that the degree of breeding site fidelity in different colonies may be directly related to the level of breeding success (Danchin & Monnat 1992).

A number of options were available to the kittiwakes which had been excluded from their nesting ledges at the warehouse colony in 1991. The simplest option was for the birds to move *en bloc* to another colony or to form a new colony at a suitable site. This did not happen in 1991 and a number of unexpected events occurred.

1. On returning to the colony in early March, the birds stood around on the roof of the warehouse and on a nearby quay for many weeks. Attempts were made to land on their previous nest sites, but these became less frequent as time went by. The kittiwakes behaved as if they expected the site would soon become accessible, as, for example, with ice cover on cliff faces adjacent to tidewater glaciers in the Arctic (Irons 1988). It was two months later (beginning of May; the start of the egg-laying period) that the first bird which had bred at the warehouse in 1990 was seen in a different colony.

2. The majority (57%) of the adult kittiwakes which lost their nest sites did not breed in 1991. Non-breeding affected all age classes equally and was very much greater than the age related non-breeding at the warehouse in previous years, which only affected 6% of the males and 10% of the females during their life spans (Wooller & Coulson 1977).

3. Of the birds which bred in 1991, 83% built nests within a few metres of their previous nest sites, either on the roof and guttering of the warehouse or a similar position on an adjacent building. A small group took up sites within a disused dry-dock,

200 m away, but these deserted before much nest building had taken place. In all, only 11 birds bred in other colonies in 1991.

4. No kittiwakes from the warehouse colony nested on the ledges put up at the Lifeboat station in 1991, although several unringed birds nested there.

5. The female kittiwake which moved to Lowestoft had been seen, with a ringed partner, near the North Shields warehouse on 17 May 1991. Therefore, its long distance move must have been both sudden and rapid to allow it to pair with another male, nest-build and lay by mid-June. It is evident that few, if any other birds made such long distance moves as the annual adult survival rate of the birds based on sightings between 1990 and 1991 and again between 1991 and 1992 was high, which is indicative that most of the birds were located.

6. Many of the adults apparently gave up attempting to breed in 1991 and left the North Shields area at the end of May, at a time when most other kittiwakes in the area had built nests and were completing egg-laying. This was at least two months earlier than their usual departure from the colony. It is evident that most of these birds did not visit other colonies in 1991 and only 18 were seen at colonies further afield.

The situation in 1992 and 1993 was somewhat different.

1. Non-breeding was reduced from 57% in 1991 to 12% in 1992 and 8% in 1993. Twelve of the adults did not breed in two successive breeding seasons.

2. A further 61 of the surviving kittiwakes nested at other colonies within 5 km of the North Shields colony in 1992. Despite adult males being less likely to move nest site than females (Coulson & Thomas 1980), there was no difference in the proportion of male and female kittiwakes which bred at the North Shields colony or moved and bred at other colonies in 1992. Although most of the birds which moved had not bred in 1991, 30% had found new sites and bred at the North Shields colony in 1991 (i.e. on the warehouse roof and the roof of an adjacent building). The fact that birds moved to a different colony after breeding in 1991 shows that the disturbance to the warehouse was

still affecting the kittiwakes in 1992. As some of the birds which moved had visited, but not bred in, other colonies in 1991, it is evident that they had been prospecting, a behaviour more typically associated with kittiwakes which have not bred previously (Porter 1988).

3. Although the Lifeboat station and Tyne Commission Quay were the nearest colonies to the warehouse, only two ringed kittiwakes moved there to breed in 1992. The majority of the birds which moved in 1992 bred at Tynemouth and Marsden, 3 km and 5 km from North Shields respectively. Seventy four percent of the birds which moved to and bred at other colonies in 1992 joined a very small colony at Tynemouth, constituting 42% of the birds which nested there in 1992. In contrast, birds which moved to Marsden were scattered amongst the extensive colony of 5000 pairs.

4. It is apparent that the disturbance in 1991 was still having an effect on the kittiwakes two years later, as three of the surviving kittiwakes which bred in 1993 were in a different colony to that in which they had nested in 1992.

The covering of the nesting ledges at the warehouse colony before the start of the 1991 breeding season had a marked effect on the behaviour and breeding biology of the kittiwakes. As the majority of the birds did not move to other colonies to breed until 1992, the response to the unavailability of the nest sites was not as expected. Further, the kittiwakes which eventually moved to other colonies did not choose the two nearest colonies to North Shields but mainly moved to two colonies 3 km and 5 km away. In 1992, there was a movement of a substantial group of kittiwakes to one particular colony (Tynemouth), clearly indicating a social consensus amongst many of the birds, although other birds did not behave as a group and nested in a scattered fashion in other local colonies. Even in 1993, minor and atypical differences were found, such as one bird moving from the North Shields colony to Marsden and two birds moving colony for a second time; an event which had never happened in the previous 37 years of the colony's history. The attempt to "transfer" the birds to the ledges on the Lifeboat station essentially failed, although surprisingly, other, unringed kittiwakes colonised the site immediately.

As a result of the extensive non-breeding in 1991, only 13 of the females which had bred at the warehouse colony in 1990, fledged young in 1991 and productivity was 77% lower than in 1990 (mean number of young fledged per female in 1991 = 0.27). Therefore, a direct effect of the forced site change was low reproductive output. As many of the birds failed to breed in one season and a small proportion missed two breeding seasons, there was a potential reduction in lifetime reproductive success for all but a few of the kittiwakes.

Endpiece: The warehouse has not been converted to flats for human accommodation as the firm involved in the development encountered financial difficulties. Some of the netting covering the ledges on one side of the building has been removed and some kittiwakes now breed on the original nest sites.

CHAPTER 3

MATE RETENTION IN THE KITTIWAKE AND THE SIGNIFICANCE OF NEST SITE TENACITY

Introduction

Breeding site fidelity (the tendency to return to the same breeding site in consecutive years, Oring & Lank 1984) is typical of many species of seabird, for example, common tern *Sterna hirundo* (Austin 1949), kittiwake (Coulson & White 1958a; Aebischer & Coulson 1990), common guillemot *Uria aalge* (Birkhead 1977), puffin *Fratercula arctica* (Harris & Wanless 1991) and shag *Phalacrocorax aristotelis* (Aebischer, Potts & Coulson in press). Associated with intense breeding site fidelity is a high incidence of between year mate fidelity, as exhibited by kittiwakes (Coulson 1972), Buller's mollymawk *Diomedea bulleri* (Richdale & Warham 1973), fulmars *Fulmarus glacialis* (Ollason & Dunnet 1978) and South Polar skuas *Catharacta maccormicki* (Ainley, Ribic & Wood 1990).

The high degree of breeding site fidelity shown by some species of bird has been suggested as an important or even sole factor in promoting mate fidelity (Allan 1962; Soikkeli 1967; Holmes 1971; Rowley 1983). For example, retention of the same mate is largely or totally dependent on nest site tenacity in the Leach's storm-petrel *Oceanodroma leucorhoa* and birds which move site invariably change mates (Morse & Kress 1984). In the Caspian tern *Sterna caspia*, 92% of the pairs changed mate when the previous year's nest sites were covered by high water levels, and the terns were forced to change their nest sites (Cuthbert 1985). Few studies have shown that other factors are involved in the retention of the same mate. Individuals which retain the same mate probably do so because enhanced reproductive success is a product of increasing familiarity and coordination within an established pair bond (Coulson 1972; Brooke 1978a; Chardine 1987).

Breeding site fidelity of the kittiwake is such that the male normally nests on its original site, or within a few metres of it, in subsequent years (Coulson & Thomas 1983). Whilst mate fidelity in kittiwakes increased with tenacity to the nest site (Coulson 1972), it has been suggested that the reforming of pair bonds within the colony after several months apart relied more on individual vocal recognition than on nest site tenacity (Wooller 1978). The great majority of kittiwakes at North Shields, Tyne and Wear, England which retained the same mate also used the same nest site. However, there are sufficient cases of pairs using a different site to that used in the previous year to consider whether the reforming of pairs occurs by chance or by some other means, such as individual recognition (Wooller 1978).

At the start of the 1991 breeding season, kittiwakes were prevented from returning to their nest sites on window ledges at the warehouse colony as a result of re-development of the building. Of the surviving birds which had bred at the warehouse in 1990, 57% did not breed in 1991. Of those which bred in 1991, 83% nested on the warehouse roof and the roof of an adjacent building (sites which had not previously been used by nesting kittiwakes) and 17% moved to other colonies. In 1992, 88% of the surviving kittiwakes bred. Fifty six percent of those which bred in 1992 and had not previously moved to a different colony to breed, moved to colonies within 5 km of the warehouse (Fairweather & Coulson submitted data).

The exclusion of kittiwakes from the window ledges at the warehouse in 1991 has produced information on mate retention in a situation where nest site tenacity can not be a factor involved. Whilst many studies have examined mate retention in relation to nest site tenacity, few have had the opportunity to study mate retention in an "experimental" situation where some or all of the birds are unable to return to their previous breeding sites. If repeated pairing in the kittiwake arises as a result of birds returning to the same nest site each year, birds which are prevented from returning to their nest site should have a reduced probability of reforming the pair bond at the beginning of the breeding season.

Methods

The study colony was situated on a warehouse at North Shields, Tyne and Wear, England. Since 1954, virtually all breeding kittiwakes in the colony have been marked with a unique combination of coloured leg rings (Porter & Coulson 1987) and so are recognisable as individuals. The sex of each bird has been determined by behaviour or by measurement and checked against the sex of the mate. Kittiwakes nested on window ledges on all four sides of the building with two pairs of birds nesting adjacently on the majority of the ledges. Birds which did not retain their nest site of the previous breeding season usually made the least possible movement to new sites within the colony, i.e. to an adjacent nest on the same ledge. A proportion moved further from the previous site, but remained within the colony (Table 3.2). Prior to 1991, the movement of breeding adults from North Shields to other colonies was virtually non-existent (Aebischer & Coulson 1990, c.f. Danchin & Monnat 1992).

There is no evidence to suggest that kittiwakes form pairs away from the colony, or feed as a pair, or that members of the pair remain together after the adults desert the colony at the end of the breeding season each year. Kittiwakes which return to the colony at the start of a new breeding season can either retain the same mate as they had in the previous breeding season (**same mate**) or change mate. Change of mate is evident at the beginning of the breeding season when nest sites are re-occupied and occurs when both members of the pair return to the colony but select different mates (**divorce**) or when one member of the pair dies before the breeding season commences (**mate death**). Over the period of study (1954 - 90), 73% of kittiwakes which could retain the same mate as the previous breeding season did so (Fairweather & Coulson submitted data).

In 1990, planning permission was granted to convert the warehouse into residential accommodation. The window ledges were covered with wire mesh before the birds returned to the colony for the 1991 breeding season, preventing kittiwakes from nesting on the same sites in 1991 as they had used in 1990. The term "**North Shields colony**" refers to the location of the nest sites of kittiwakes which subsequently bred in the immediate vicinity of the warehouse (i.e. the warehouse roof and the roof of an adjacent building).

The colonies at North Shields and Marsden (5 km from North Shields) were visited at least twice a week from February to August, 1991 - 93. The Tynemouth colony (3 km from North Shields) was visited at least twice a week from February to August, 1992 - 93. Fortnightly visits were made to other kittiwake colonies within a 70 km radius of North Shields. During visits to colonies, the identity and location of all colour-ringed kittiwakes present, their mate, date of onset of nest building, date of laying, clutch size, date of fledging and number of young fledged were recorded.

For each year of the subsequent study (1991 - 93), only the surviving kittiwakes which had bred at the warehouse colony in 1990 are considered. The surviving adult kittiwakes are divided into two categories in relation to their breeding status in each year of this study (1991 - 93):

i. **Breeding birds** - bred or, in a few cases, occupied a nest site until at least the end of the egg-laying period (mid-June).

ii. **Non-breeding birds** - adults which did not breed in the particular breeding season. Some began nest building but occupied the nest site for less than three weeks and others did not occupy a nest site. Some, but not all, were seen in pairs, an association which was maintained for several days.

During the subsequent study, the proportion of birds exhibiting mate retention is calculated only for those birds in which both members of the previous pair survived from one breeding season to the next and so were potentially able to reform the same pair, regardless of whether they both returned to the same colony. Mates of birds who had died in the intervening year are excluded throughout this paper. For analysis of mate retention of non-breeding adult individuals, only those which formed pairs in the season under consideration are included.

In 2 by 2 χ^2 calculations, Yates' correction has been used. All means are presented as mean ± SE, unless otherwise stated.

Results

Factors influencing mate retention at the warehouse colony, 1954 - 90:

Nest site tenacity

Data from the warehouse colony (1954 - 90) were analysed in relation to mate retention (for kittiwakes in which both members of the pair had survived and returned to the colony) and nest site tenacity (Table 3.1). Most kittiwakes which could have retained their mate of the previous breeding season used the same nest site (female: 71%, 904/1273; male: 81%, 1044/1296). Of the kittiwakes which returned to the same nest site, 92% of females (n = 904) and 80% of males (n = 1044) also retained their mate, whereas 73% of females (n = 369) and 60% of males (n = 252) which changed nest site divorced (Table 3.1). Females were more likely to change nest site after a divorce than males ($\chi^2 = 101$, df = 1, $P < 0.001$). The majority of birds which changed nest site also divorced, but 100 pairs of kittiwakes which changed nest site and retained the pair-bond of the previous breeding season are of particular interest and are discussed below (Table 3.1).

Movements within the colony

Table 3.2 shows the mate retention of kittiwakes which changed nest sites at the warehouse colony, in relation to their movement from the previous nest site. Whilst 92% of females and 80% of males which retained the same nest site also retained their mate (Table 3.1), a significantly smaller proportion of the birds which moved to an adjacent nest site on the same ledge (movement = 0.3 m) did so (Table 2); 43% of females (n = 30) and 54% of males (n = 24) (female: $\chi^2 = 77.7$, df = 1, $P < 0.001$; male: $\chi^2 = 8.1$, df = 1, $P < 0.01$). The reduced mate retention of kittiwakes which moved to a different ledge on the same window (movement = 0.7 m) (female: 31%, n = 29; male: 35%, n = 26), did not differ from that of birds which moved to an adjacent nest site on the same ledge (female: $\chi^2 = 0.5$, df = 1, NS; male: $\chi^2 = 1.2$, df = 1, NS), or from those which moved greater distances (Table 3.2).

Table 3.1. Pair status[1] of male and female kittiwakes at the warehouse colony, in relation to nest site tenacity. Data for all years, 1954 - 90.

	Site faithful		Change site	
	n	%	*n*	%
<u>Male</u>				
Same mate	835	80.0	100	39.7
Divorce	209	20.0	152	60.3
Total	1044	100	252	100
<u>Female</u>				
Same mate	835	92.4	100	27.1
Divorce	69	7.6	269	72.9
Total	904	100	369	100

The number of divorced females (*n* = 338) is less than the number of divorced males (*n* = 361). The discrepancy results from intermittent breeding when both members of the pair returned to the colony but only one bred. Only the bird which bred was considered to have divorced.

[1] Birds whose mate had died since the previous breeding season are excluded.

Table 3.2. Movements within the warehouse colony by adult male and female kittiwakes which changed nest site and could retain their mate. Data for all years, 1954 - 90.

	Same window:														
	Adjacent nest		Different ledge		Adjacent window		> 1 window		1 floor		> 1 floor		Different side		Total
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
<u>Male</u>															
Same mate	13	54	9	35	23	44	11	32	31	35	7	44	6	55	100
Total[1]	24	100	26	100	52	100	34	100	89	100	16	100	11	100	252
<u>Female</u>															
Same mate	13	43	9	31	23	30	11	21	31	24	7	23	6	33	100
Total	30	100	29	100	77	100	53	100	131	100	31	100	18	100	369

[1] The difference between same mate and total is the number which divorced

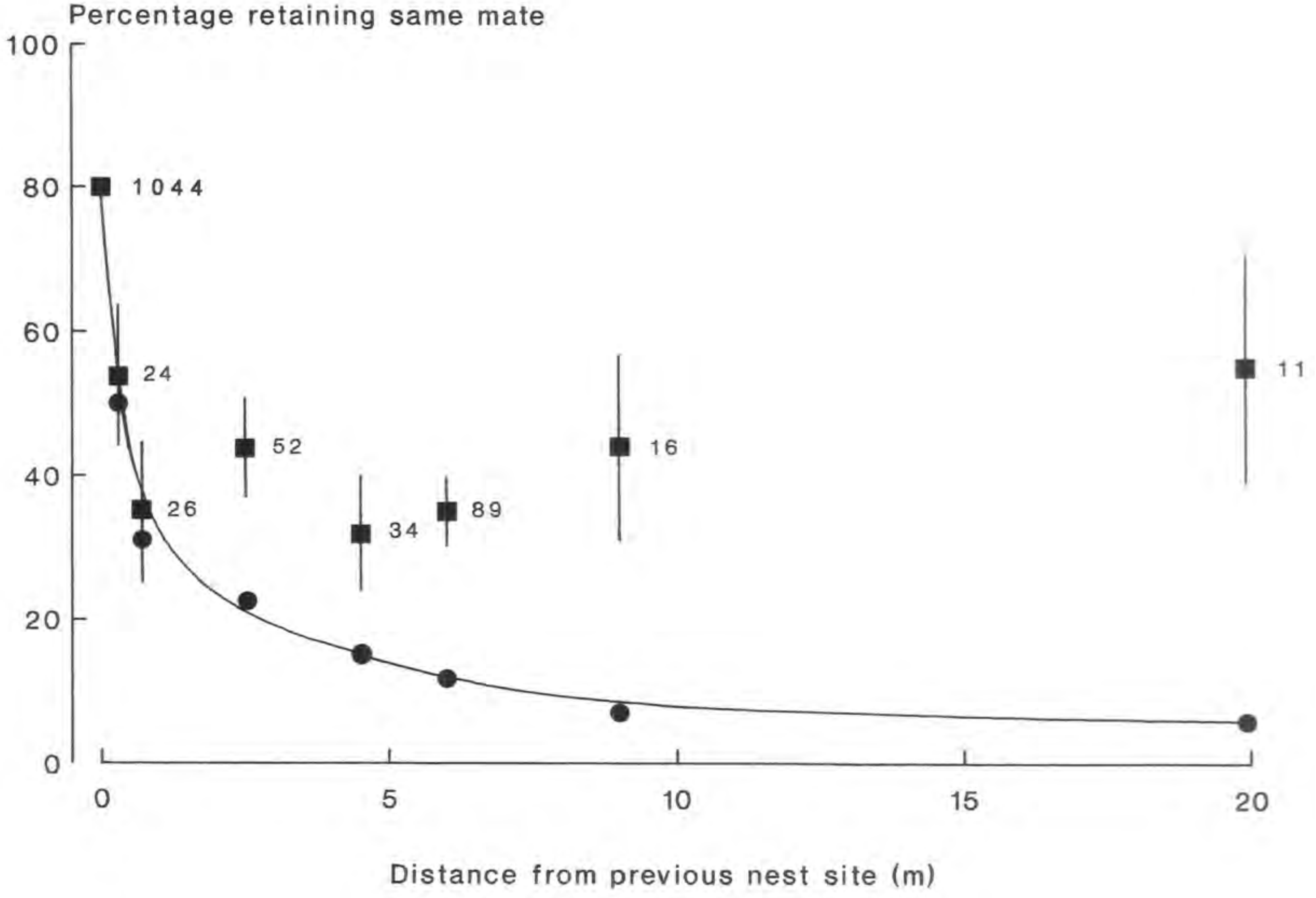
The majority of birds which changed nest site and could retain their mate remained on the same side of the building (Table 3.2). The most frequent movement was to the floor above or below the previous nest site (1 floor: female: 36%, 131/369; male: 35%, 89/252). Of the kittiwakes which changed nest site and could retain their mate, only 5% of the females (18/369) and 4% of the males (11/252) moved to a different side of the building.

Distance moved within the colony

If mate retention was dependent on nest site tenacity, the probability that birds would retain their mate of the previous breeding season by chance on a different site would decrease with the increasing number of other nest sites available at progressively greater distances moved. The model in Figure 3.1 shows the probability of male kittiwakes retaining their mate by chance in relation to the distance moved from the previous nest site (i.e. the number of males which changed nest site divided by the number of females on nest sites within the area between the previous and new nest site).

The extent of mate retention by male kittiwakes which changed nest site, in relation to the distance moved from the previous nest site, is shown in Figure 3.1. Mate retention of birds which moved further than 0.3 m from the previous nest site did not decrease significantly with distance and at distances greater than 0.7 m was consistently and appreciably higher than that predicted by the model. For example, the probability of kittiwakes retaining their mate by chance after moving 9 m (i.e. > 1 floor of the building) was only 7%, though 44% ± 13% did so ($n = 16$). In contrast to the model, mate retention averaged 38% (87/228) at distances greater than 0.3 m from the previous nest site and did not change significantly with increasing distance. This suggests that pairs which moved nest site within the warehouse colony reformed the pair by a mechanism other than chance.

Figure 3.1 Mate retention (± SE) of male kittiwakes at the warehouse colony, in relation to the distance moved from the previous nest site (▤). The model (●) shows the probability of males retaining their mate by chance, in relation to the distance moved from the previous nest site. Numbers for each point are sample sizes.


Percentage retaining same mate
100
80
60
40
20
0
1044
24
26
52
34
89
16
11
0
5
10
15
20
Distance from previous nest site (m)

Mate retention of the surviving kittiwakes which had bred at the warehouse colony in 1990

In 1990, the year preceding warehouse closure, 72% of both male and female kittiwakes which could retain the same mate as the previous year did so (*n* = 50 pairs). Mate fidelity of the surviving kittiwakes which bred on a different site in 1991 was high (female: 73%, *n* = 22; male: 60%, *n* = 30), as was that of birds which formed pairs in 1991 but did not breed (Table 3.3). In 1992, only 41% of females (*n* = 39) and 42% of males (*n* = 36) which bred retained their mate of the previous year. Mate retention of the breeding birds increased to a more typical level in 1993 when many retained the site used in 1992.

Mate retention in relation to breeding site fidelity

Table 3.4 shows the mate retention of the surviving kittiwakes which had bred at the warehouse colony in 1990, in relation to the colony in which they bred in the following years. In 1991, 76% of females (*n* = 21) and 78% of males (*n* = 23) which returned to the immediate colony area to breed retained their mate of the previous year. Two pairs which did not breed in 1991 moved to Marsden (5 km from North Shields) and retained their pair-bond of the previous breeding season, despite some 5000 pairs nesting in the colony. In 1992 and 1993, mate retention of the breeding birds did not differ significantly, in relation to whether the birds bred at the North Shields colony or at colonies within 11 km of North Shields (Table 3.4).

Mate fidelity of the kittiwakes which bred at the North Shields colony and colonies within 5 km of North Shields in 1992 (i.e. Tynemouth and Marsden) was analysed with respect to their breeding status in 1991 and, where applicable, the colony in which they bred in 1991 (Table 3.5). Eight of the 19 females (42%) and seven of the 23 males (30%) which moved to Tynemouth or Marsden to breed in 1992 retained their mate of the previous breeding season.

Table 3.3. Mate retention of male and female kittiwakes which had bred at the warehouse colony in 1990, in relation to their breeding status in 1991 - 93.

		Breeding status[2]					
		Breeding birds			Non-breeding birds which formed pairs		
Year	Sex	Potential mate retention	Actual mate retention	%	Potential mate retention	Actual mate retention	%
1991[1]	Male	30	18	60	22	13	59
	Female	22	16	73	24	15	63
1992	Male	36	15	42	0	0	0
	Female	39	16	41	0	0	0
1993	Male	29	20	69	1	1	100
	Female	29	21	72	1	1	100

[1] Kittiwakes prevented from nesting at the warehouse. [2] The categories of breeding and non-breeding birds in 1992 and 1993 include birds which bred in the previous year and birds which did not breed in the previous year but had established a pair bond and could retain their mate in the next breeding season.
Potential mate retention considers birds which could retain the mate they had in the previous year i.e. both members of the pair survived, whilst actual mate retention considers the number of these birds which did so. The potential mate retention of male and female kittiwakes is not equal as the data represent the potential mate retention of individuals which had bred at the warehouse in 1990. A mate is not represented in the category "potential mate retention" if it had not bred at the warehouse in 1990.

Table 3.4. Mate retention of male and female kittiwakes which had bred at the warehouse colony in 1990, in relation to whether the birds bred at the North Shields colony or at colonies within 11 km of North Shields. Data for 1991 - 93.

		Breeding birds						
		North Shields			Local colonies			
Year	Sex	Potential mate retention	Actual mate retention	%	Potential mate retention	Actual mate retention	%	χ^2_1
1991	Male	23	18	78	7	0	0	-
	Female	21	16	76	1	0	0	-
1992	Male	12	7	58	24	8	33	1.2 NS
	Female	19	7	37	20	9	45	0.0 NS
1993	Male	12	6	50	16	13	81	1.8 NS
	Female	13	8	62	15	12	80	0.4 NS

χ^2 test = North Shields v local colonies

NS = not significant

Table 3.5. Mate retention of male and female kittiwakes which bred at the North Shields colony or at colonies within 5 km of North Shields in 1992, in relation to their breeding status and, where applicable, the colony in which they bred in 1991.

1991			Breeding birds in 1992								
			North Shields			Tynemouth			Marsden		
Status	Colony	Sex	Potential mate retention	Actual mate retention	%	Potential mate retention	Actual mate retention	%	Potential mate retention	Actual mate retention	%
Breeding	North Shields	Male	8	7	88	4	1	25	3	0	0
		Female	9	6	67	6	1	17	0	0	0
Non-breeding	-	Male	4	0	0	10	4	40	6	2	33
		Female	10	1	10	11	5	45	2	2	100
Breeding	Marsden	Male	-	-	-	-	-	-	1	1	100
		Female	-	-	-	-	-	-	1	1	100

Factors influencing mate retention:

Breeding status in the previous season

Of the breeding kittiwakes (both sexes) which could have retained their mate in 1992 (*n* = 75; Table 3.3), 43 had formed pairs in 1991 but did not breed (Table 3.5). In 1992, mate retention of these birds was low; 35% of females (*n* = 23) and 30% of males (*n* = 20). Similarly, mate retention of birds which had bred at North Shields or Marsden in 1991 was low in 1992; 50% of females (*n* = 16) and 56% of males (*n*= 16). Thus, mate retention of the birds which bred in 1992 did not depend on their breeding status in 1991 (female: $\chi^2 = 0.4$, df = 1, NS; male: $\chi^2 = 1.6$, df = 1, NS).

Breeding failure

Of the kittiwakes which could retain their mate at the warehouse colony (1954 - 90), 13% of males (*n* = 998) and 12% of females (*n* = 854) which were nest site faithful had failed to fledge any young in the previous season (Table 3.6). In contrast, the proportion of birds which had failed and changed site was three times as high; male 37% (*n* = 231), female 33% (*n* = 351).

Of the 17 kittiwakes which bred at the North Shields colony in 1991 and 1992, and could have retained their mate in 1992 (female: *n* = 9; male: *n* = 8; Table 3.5), none of the males and only 11% of the females had failed in 1991. All of these birds which retained their mate in 1992 (female: 67%, *n* = 9; male: 88%, *n* = 8; Table 3.6) had bred successfully in 1991. In contrast, few birds which bred at the North Shields colony in 1991 and then dispersed to breed in 1992, retained their mate in 1992 (female: 17%, *n* = 6; male: 14%, *n* = 7; Table 3.5). All of these females (*n* = 6) and 86% (*n* = 7) of the males which could have retained their mate in 1992 had failed in 1991.

Of 14 birds (both sexes) which were present, but did not breed, in 1991 and then bred at the North Shields colony in 1992, only one retained its mate of the previous year (Table 3.5). The previous mates of six of these birds moved to local colonies to breed in 1992, and a further three did not breed in 1992.

Table 3.6. Nest site tenacity of male and female kittiwakes at the warehouse colony, in relation to pair status and breeding success or failure in the previous breeding season. Data for all years, 1954 - 90.

	Site faithful			Change site			
	No. failed	No. successful	% fail	No. failed	No. successful	% fail	χ^2_1
Male							
Same mate	92	697	12	36	55	40	48.9^{***}
Divorce	36	173	17	49	91	35	13.4^{***}
Total	128	870	13	85	146	37	73.6^{***}
Female							
Same mate	92	697	12	36	55	40	48.9^{***}
Divorce	14	51	22	71	179	28	0.9 NS
Total	106	748	12	117	234	33	70.8^{***}

χ^2 test = site faithful v change site

NS = not significant, *** = $P < 0.001$

Discussion

The importance of nest site tenacity to mate retention

Many studies of the effect of mate change in seabirds have shown that repeated breeding attempts with the same mate increase reproductive success (Coulson 1972; Mills 1973; Davis 1976; Brooke 1978a; Ollason & Dunnet 1988; Bradley *et al.* 1990). Previous studies of birds have examined the importance of breeding site fidelity and nest site tenacity to the maintenance of the pair-bond (Allan 1962; Soikkeli 1967; Holmes 1971; Coulson 1972; Coulson & Thomas 1983; Rowley 1983; Morse & Kress 1984; Cuthbert 1985; Aebischer *et al.* in press) and have suggested that individuals may retain the same nest site in order to increase the probability of the pair-bond reforming at the start of the next breeding season.

Mate fidelity in kittiwakes does not arise solely from nest site tenacity, as birds which did not have access to nest sites of the previous breeding season still retained their mate of the previous year. For example, in the first year of the warehouse closure (1991), 76% of female kittiwakes and 78% of males which returned to the immediate colony area to breed retained their mate. Birds which formed pairs in 1991 but did not breed, also exhibited a high incidence of mate retention. This study also demonstrated that birds which moved greater distances to a new nest site, i.e. to another colony, could still retain their mate. Two pairs which moved to Marsden in 1991 retained their pair-bond of the previous breeding season and in 1992, 42% of females and 30% of males which moved to Marsden or Tynemouth to breed retained their mate.

At the warehouse colony (1954 - 90) there was no evidence as to whether the pair-bond could be maintained if movements between colonies were involved as, over this period, the movement of breeding adults from North Shields to other colonies was virtually non-existent (Aebischer & Coulson 1990). As 92% of females and 80% of males which retained the nest site of the previous breeding season also retained their mate, the importance of nest site tenacity to the maintenance of the pair-bond at the warehouse colony was demonstrated. However, if mate retention is only dependent on both birds returning to the same nest site, the probability of birds retaining their mate by chance would decrease with the distance moved from the previous nest site. Although the majority of birds which changed their nest site had divorced (or their partner had died), an analysis of the data demonstrated that kittiwakes could change their nest site yet still retain their mate of the previous year. Mate retention decreased sharply if birds moved only 0.3 m to a nest site immediately adjacent to the previous site, but, in contrast to the model, did not show a further significant decrease when the distance moved was greater. Hence, within the warehouse colony, birds could move the maximum distance to a new nest site and retain their mate of the previous breeding season. However, these site changes only involved movements within a relatively small colony of 80 - 100 pairs.

The subsequent study (1991 - 93) has shown that kittiwakes could move to another colony but still retain their mate of the previous breeding season. The reforming of these pairs could occurr by two mechanisms. Individuals could have returned briefly to the North Shields colony and reformed the pair prior to moving. In 1992, however, only one of the relevant birds was seen at the North Shields colony prior to moving. Alternatively, individuals could have moved to another colony independently of their mate, and reformed the pair at the colony after they moved. The latter would require that birds are able to recognise their previous mate once at another colony (Wooller 1978). If individual recognition is an important factor involved in the reforming of the pair-bond, it is of significance that birds which moved to Marsden (5 km from North Shields) retained their mate, as this was a colony of more than 5000 pairs of kittiwakes. Although we can only speculate as to the way in which these pairs reformed, it is evident that whilst breeding site fidelity may often be important, pairs could reform independently of nest site tenacity.

Factors influencing mate retention

In 1992, mate retention of the breeding birds at the North Shields colony and local colonies was lower than at any time since the study began (Fairweather & Coulson submitted data). Mate retention increased to more typical levels in 1993 when most of the birds remained in the colonies in which they bred in 1992 (Fairweather & Coulson submitted data). Divorce has been associated with reproductive failure in the previous year (Coulson 1966; Coulson 1972) and early departure from the colony has been shown to increase the likelihood of divorce in the following year (Coulson & Thomas 1983). Therefore, it would be expected that mate fidelity of the breeding birds in 1992 would depend on the breeding status of these individuals in 1991. Birds which did not breed in 1991 did leave the colony early (Fairweather & Coulson submitted data), and, as would be expected from their reproductive failure and early departure, their mate retention in 1992 was low.

The low incidence of mate retention of kittiwakes which bred at the North Shields colony in 1991 and dispersed to local colonies to breed in 1992 further reduced the extent of mate fidelity in 1992. Only one of these birds which could retain their mate in 1992 had bred successfully in 1991, whereas 89% of females and all males which remained at the North Shields colony had bred successfully. As shown by the data from the warehouse colony (1954 - 90), site change was more frequent following breeding failure. Associated with breeding failure is an increased likelihood of divorce. Hence, a low incidence of mate retention would be expected for these birds as most which moved to local colonies to breed in 1992 had failed in 1991.

It has been suggested that many seabirds are strongly site-faithful because the costs of changing colony are high (Birkhead & Furness 1985). This study has shown that kittiwakes can move to a new colony and still retain their mate of the previous breeding season, which has important implications for lifetime reproductive success. Kittiwakes which retain their mate from the previous year typically fledge more young than birds which change mate (Coulson 1966; Coulson & Thomas 1980; Fairweather & Coulson submitted data). In terms of lifetime reproductive success, forced site change should not impose such a great cost on kittiwakes which move to a new colony and retain their mate of the previous breeding season as on birds which move but do not retain their mate.

CHAPTER 4

THE EFFECT OF NEST POSITION ON THE REPRODUCTIVE PERFORMANCE OF THE KITTIWAKE

Introduction

Since Darling (1938) suggested that colonial breeding enhanced the reproductive performance of the individual through social stimulation, many studies have analysed the reproductive performance of colonial seabirds in relation to their breeding density and position in the colony (Coulson 1968; 1971; Tenaza 1971; Nettleship 1972; Parsons 1976; Birkhead 1977; Nelson 1978a; Potts, Coulson & Deans 1980; Ryder & Ryder 1981; Furness 1984; Jehl 1994). Most seabird species require social stimulation from other pairs in order to breed, though the amount of stimulation which individuals receive depends on the density of the breeding birds, the proximity to other nesting pairs and the size of the colony (Coulson & White 1960; Coulson 1971; Nelson 1978a; 1978b; Coulson & Dixon 1979; Coulson 1985). The consequence of social stimulation is the completion of reproductive development and the initiation of egg-laying at a time which tends to maximise the number of young which survive to recruit into the breeding population (Nelson 1978a; Coulson 1985). Social stimulation serves to advance the date of laying, hence, early nesting and the spread of breeding is related to the maximum density the birds achieve in any part of the colony (Coulson & White 1960; Nelson 1978a; Coulson 1985).

In colonial species, high productivity is generally associated with nesting at high density, such as in the centre of a colony (Coulson 1968; Birkhead 1977; Harris 1980), although for some species increased nest density is associated with decreased reproductive performance (Parsons 1976; Butler & Trivelpiece 1981; Gaston, Chapdelaine & Noble 1983; Møller 1987; Hill 1988; Kilpi 1989). For the kittiwake *Rissa tridactyla* the difference in productivity between the centre and edge of a colony was influenced by the quality of the birds (Coulson 1968; Porter & Coulson 1987), whilst for some seabird species predation was important in determining productivity (Adelie penguin *Pygoscelis adeliae*, Tenaza 1971; guillemot *Uria aalge*, Birkhead 1977). The position in which a kittiwake nests in a colony can be considered as a measure of its individual quality as birds are segregated on the basis of their ability to attain nest sites in the favoured and thus most dense areas (Coulson 1968; Porter & Coulson 1987). For example, kittiwake recruits which nested in the centre of the colony were heavier than those which nested on the edge of the colony (Porter & Coulson 1987).

Breeding experience has a marked effect on the breeding of seabirds. In general, an increase in experience results in earlier laying and higher productivity (e.g. kittiwake, Coulson & White 1958a; red-billed gull *Larus novaehollandiae*, Mills 1973; Arctic tern *Sterna paradisaea*, Coulson & Horobin 1976; common tern *Sterna hirundo*, Nisbet, Winchell & Heise 1984). Various parameters affect the date of laying of individual kittiwakes, including breeding experience and the stability of the pair bond (Coulson & White 1958a; Coulson 1966; Coulson & Thomas 1980; Fairweather & Coulson submitted data). Date of laying had a significant effect upon clutch size (Coulson & White 1961), although certain females tended to lay the same number of eggs in different years (Coulson & Thomas 1985a). The number of chicks fledged per pair increased with the breeding experience of the female parent, reaching a peak amongst birds which had bred for two years previously (Thomas 1983).

This study considers the effect on reproductive performance of nest position in the colony and the proximity to other nesting kittiwakes. Whilst this effect has been studied in relation to whether pairs nested on the same window as another pair or alone on a window at the warehouse colony, North Shields, Tyne and Wear, England (Porter 1990), I considered pairs which either nested adjacent to another pair on the same window ledge or nested alone on a window ledge. By taking account of position in the colony and breeding experience, an assessment of the importance of social stimulation can be made. The conclusions, relating to the effect of position in the colony on productivity, are tested by comparison with a cliff colony at Marsden, Tyne and Wear, England.

Methods

The kittiwake colony at North Shields, Tyne and Wear, England has been studied since its establishment in 1949, when four pairs of kittiwakes nested on the south face of the building. Since 1954, virtually all kittiwakes breeding in the colony have been marked with unique combinations of coloured rings. Since peaking in 1965 at 104 breeding pairs, about 80 pairs have bred at the warehouse colony each year. The colony was divided into two areas, "**centre**" and "**edge**", where the centre was defined as the area occupied when the colony was half its maximum size (Coulson 1971). At the centre of the colony the density of nesting birds was highest (Porter 1990).

Kittiwakes nested on window ledges on all four sides of the building. The majority of the pairs nested on the top three floors of the south and west sides. Breeding birds tended to nest on their original site or within a few metres of it in subsequent years (Coulson & Thomas 1983; Fairweather & Coulson submitted data). Extra ledges were added to the centre of the colony in 1962 and more were added in 1983 (Porter 1990). There was up to three identical ledges within one window frame and each ledge could be occupied by one or two pairs of nesting kittiwakes; one pair could nest **alone** on a ledge or two pairs could nest **together** on the same ledge. Two pairs which nested on the same ledge had less than one nest width (c. 30 cm) between the edges of the nests and, as a result, were within pecking distance of each other (Porter 1990). Pairs which nested alone on a ledge were unable to see the behavioural interactions which occurred within and between the pairs which nested on the surrounding ledges. Up to 4 pairs could nest in a row on the door of the warehouse (3 or 4 pairs nested in a row on 17 occasions over the period of study and accounted for 59 pairs of kittiwakes). These pairs could not be included in the above categories of alone or together and were excluded from the analysis

Data collected since 1954 include details of nest location, members of each pair, date that the first egg of the clutch was laid, clutch size, hatching success and the number of chicks fledged per pair. The mean date of laying (1954 - 90) was 19 May ± 9.0 days (SD; *n* = 2655). The earliest mean date of laying for any one year was 14 May in 1984, the latest was 25 May in 1982. To exclude small annual variations, the relative date of laying has been used in the calculations. The relative date of laying is the deviation of the laying date of a pair from the mean for the colony in that year. Positive figures indicate the number of days before the mean date that the pair laid, whilst negative figures indicate the number of days after the mean.

Pairs were classified according to the breeding experience of the individuals within the pair:

Established breeders - both birds had bred previously, but may not have bred together before.

Intermediate breeders - one of the pair with no known breeding experience and one with previous breeding experience.

Recruits - pairs in which neither bird was known to have bred before.

The "age" of the bird in this chapter is presented as the number of breeding years (i.e. breeding experience). Most kittiwakes breed for the first time when 3 - 4 years old (Wooller & Coulson 1977; Porter & Coulson 1987). Therefore, "age" underestimates true age by 3 or 4 years.

The analysis only considers pairs in the above categories which either nested adjacent to another pair (i.e. together) or alone on a ledge. The detailed study of the effect of proximity to other nesting pairs concentrates on the pairs of established breeders as they constituted 60% of the breeding pairs over the study period (*n* = 2422 pairs). As such, this large sample can be sub-divided in order to examine the relative date of laying of pairs which nested alone or together on a ledge in relation to year, age of the members of the pair and nest position in the colony relative to that of other kittiwakes (Fig. 4.2, Tables 4.10 & 4.11).

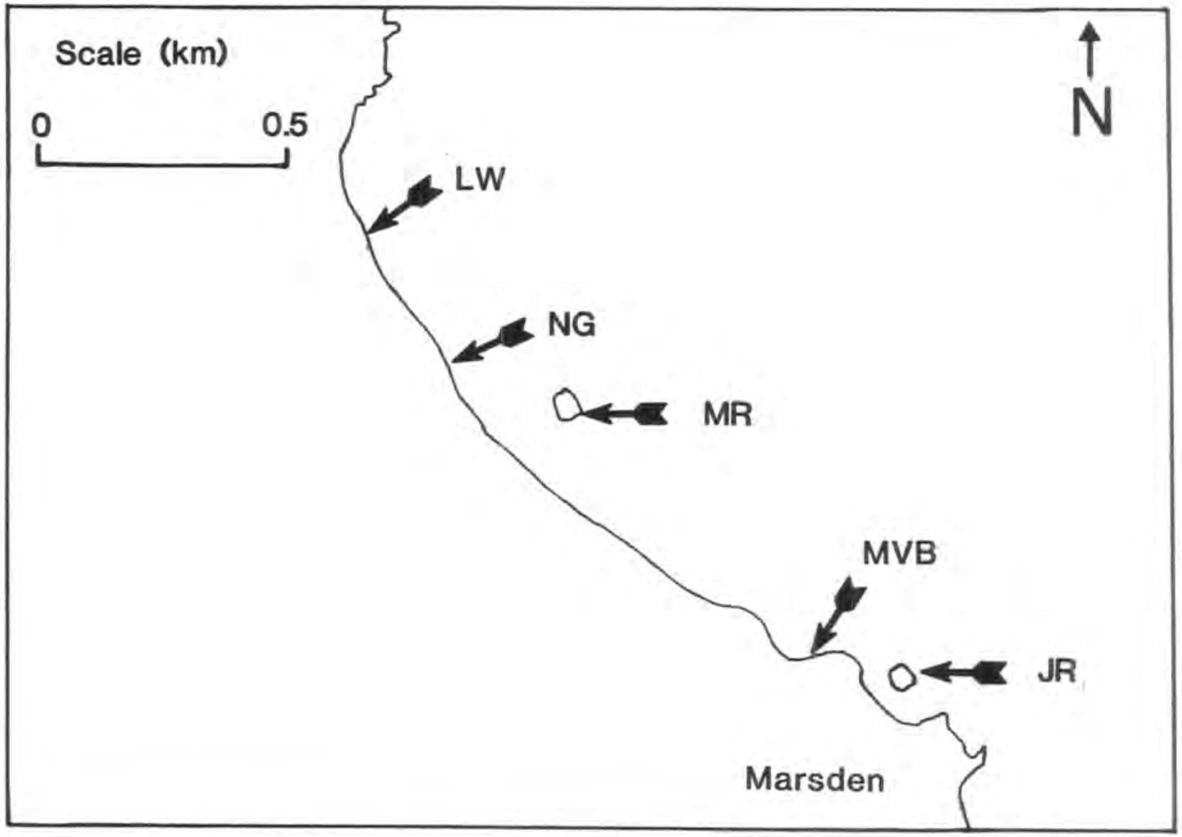
A three-way analysis of variance was used to examine the effects of pair status, nest position in the colony and proximity to other nesting pairs on the relative date of laying (dependent variable). This allowed the effects of each variable to be examined independently of all the other variables and also allowed examination of the interactions of the variables.

The conclusions, relating to the effect of position in the colony and proximity to other nesting pairs on productivity at North Shields, were tested by comparison with kittiwakes nesting at Marsden, Tyne and Wear, England. The Marsden colony was usually visited three times each week during June, July and August (1991 - 93). As the individual quality and breeding performance of kittiwakes differs in relation to their nest position in the colony (Coulson 1968; Porter & Coulson 1987), two areas of the Marsden colony were selected for detailed study: **centre** - the study area was in the centre of the colony (North of Grotto; Fig. 4.1 & Appendix); **edge** - the study area was at the periphery of the colony (Marsden Village Bay; Fig. 4.1 & Appendix). As at North Shields, the two areas differed in relation to the density of the nesting pairs: centre - the density of the nesting pairs was high; edge - the density was low.

The two areas of the cliff were photographed and the nests were numbered on the photographs. The nests chosen for study at Marsden were comparable, in terms of their proximity to other nests, to the nests at North Shields. Therefore, pairs which nested **alone** at Marsden had more than one nest width between the edge of their nest and the edge of the nearest nest. Two pairs which nested **together** had less than one nest width between the edges of the nests and the pairs were within pecking distance of each other. Three or more pairs which nested in a group (i.e. with less than one nest width or no space between the surrounding nests) are not included in the analysis.

On each visit the number of chicks present in each nest was recorded. The following number of nests were studied: 1991, centre 367, edge 110; 1992, centre 342,

Figure 4.1 Map showing the location of the study areas at Marsden, Tyne and Wear, England. Key: LW = Lot's Wife; NG = North of Grotto; MR = Marsden Rock; MVB = Marsden Village Bay; JR = Jack Rock. The kittiwake colony extended from north of LW to JR. North Grotto = "centre" and Marsden Village Bay = "edge".



Scale (km)
0
0.5
N
LW
NG
MR
MVB
JR
Marsden

edge 105; 1993, centre 337, edge 93. In 1992 and 1993, the same nest sites were studied as in the preceding year, with the exception of a few which had been destroyed since the previous breeding season or which were not attended by a pair prior to the incubation period.

The mean age at fledging at North Shields was 42.7 days, with minimum periods of 32 - 34 days (Coulson & White 1958b). The fledging date at Marsden was considered to be the first date that a chick of 32 days or older was absent from the nest. The age of the chicks were estimated on each visit using a description of the stages of development of a kittiwake chick (Maunder & Threlfall 1972). If a chick less than 32 days old disappeared from the nest it was presumed to have died.

Unless otherwise stated, all means are expressed ± 1 SE. For 2 by 2 χ^2 tests Yates' correction factor was employed.

Results

North Shields: 1954 - 90

Factors influencing the reproductive performance of kittiwakes at the warehouse colony:

Nest position in the colony

Pairs of kittiwakes which nested at the centre of the warehouse colony laid significantly earlier than pairs at the edge (mean difference = 2.7 ± 0.3 days; Table 4.1). At the centre of the colony, pairs laid, on average, larger clutches and fledged more young per pair than pairs at the edge (Table 4.1). Whilst 21% ± 1% of pairs at the centre of the colony failed to fledge any young (n = 1114), 29% ± 1% of pairs at the edge of the colony failed (n = 1150). The proportion of pairs which failed at the edge of the colony was appreciably and significantly higher than at the centre (fail v fledge; $\chi^2 = 20.1$, df = 1, $P < 0.001$).

The breeding experience of the pair

Table 4.2 shows the reproductive performance of kittiwakes in relation to the breeding experience of the pair. The breeding experience of the pair significantly affected their date of laying as established breeders laid, on average, 1.7 ± 0.4 days earlier than intermediate breeders and 5.7 ± 0.5 days earlier than recruits. Established breeders also showed less variation in their date of laying than the intermediate breeders and recruits, as shown by the smaller standard deviation. Further, established breeders laid larger clutches and fledged significantly more young per pair than the intermediate breeders and recruits.

Table 4.1. Reproductive performance of kittiwakes which nested at the centre and edge of the warehouse colony. Data for all years, 1954 - 90.

	Relative date of laying				Clutch size					Number of young fledged					
	Mean	SD	*n*	z	1	2	3	Mean	χ^2_2	0	1	2	3	Mean	χ^2_2
Centre	1.22	8.32	1172	8.0**	105	903	164	2.05	12.4***	229	347	498	40	1.31	22.2***
Edge	-1.45	8.30	1250		143	991	124	1.98		331	346	442	31	1.15	

χ^2 test of number of young fledged = 0 v 1 v 2 or 3

** = $P < 0.01$, *** = $P < 0.001$

Table 4.2. Reproductive performance of kittiwakes at the warehouse colony in relation to the breeding experience of the pair. Data for all years, 1954 - 90.

	Relative date of laying			Clutch size				Number of young fledged				
Experience	Mean	SD	*n*	1	2	3	Mean	0	1	2	3	Mean
i. Established	1.34	7.24	1449	88	1117	245	2.11	261	403	636	61	1.37
ii. Intermediate	-0.32	8.62	477	45	399	33	1.97	105	148	175	7	1.19
iii. Recruits	-4.37	9.86	496	115	378	10	1.79	194	142	129	3	0.87
								No. fledged: 0 v 1 v 2 or 3				
i v *ii*	z = 3.8**			$\chi^2_2 = 32.7$***				$\chi^2_2 = 12.0$**				
i v *iii*	z = 11.9**			$\chi^2_2 = 165.1$***				$\chi^2_2 = 110.2$***				
ii v *iii*	z = 6.9**			$\chi^2_2 = 42.8$***				$\chi^2_2 = 33.4$***				

** = $P < 0.01$, *** = $P < 0.001$

Proximity to other nesting pairs

Pairs of kittiwakes which nested together on a ledge laid significantly earlier than pairs which nested alone on a ledge (mean difference = 2.1 ± 0.3 days; Table 4.3). The mean clutch size per pair did not differ in relation to the proximity to other nesting pairs but the productivity of pairs which nested alone on a ledge was significantly reduced (Table 4.3). A significantly higher proportion of the pairs which nested alone on a ledge failed to fledge any young (alone: 27% ± 1% failed; together: 16% ± 1% failed; $\chi^2 = 39.3$, df = 1, $P < 0.001$). Therefore, the proximity to other nesting pairs influenced the reproductive performance of the kittiwakes.

A three-way analysis of variance was performed to examine the relationship between the relative date of laying (dependent variable) of kittiwakes and the breeding experience of the pair, the position in the colony and the proximity to other nesting pairs (Table 4.4). The overall model was significant and explained 11% of the variation (F = 26.0, df = 11, 2410, $P < 0.001$). Breeding experience, position and proximity to other nesting pairs were all significant effects. Although the model was significant, it only explained a small proportion of the variation. Studies at this colony have shown that other factors, particularly individual variation, account for a high proportion of the unexplained variance (Coulson & Thomas 1985a). Table 4.4 also shows the 2-way interactions and the significant interactions are discussed below.

Two-way interactions:

Nest position in the colony × the breeding experience of the pair

Significant differences in the relative date of laying in relation to whether pairs nested at the centre or edge of the colony were shown for the established and intermediate breeders (Table 4.5). At the centre of the colony, established and intermediate breeders laid significantly earlier than at the edge (mean difference = 3.0 ±

Table 4.3. Reproductive performance of kittiwakes at the warehouse colony in relation to their proximity to other nesting pairs. Data for all years, 1954 - 90.

	Relative date of laying				Clutch size					Number of young fledged					
	Mean	SD	*n*	z	1	2	3	Mean	χ^2_2	0	1	2	3	Mean	χ^2_2
Together	0.87	7.61	1239	6.2**	124	952	166	2.03	5.6 NS	165	364	487	43	1.39	39.9***
Alone	-1.23	9.01	1183		124	942	122	2.00		295	329	453	28	1.19	

χ^2 test of number of young fledged = 0 v 1 v 2 or 3

NS = not significant, ** = $P < 0.01$, *** = $P < 0.001$

Table 4.4. The results of a three-way analysis of variance to examine the relationship between the relative date of laying of kittiwakes (dependent variable) and the breeding experience of the pair, position in the colony (centre/edge) and proximity to other nesting pairs (alone/together). Data for 1954 - 90. The overall model explains 11% of the variation (F = 26.0, df = 11, 2410, $P < 0.001$).

Source of variation	Sum of squares	df	F	*P*
Main effects				
Experience	10166.0	2	79.9	< 0.001
Position	2559.4	1	40.2	< 0.001
Proximity	879.8	1	13.8	< 0.001
2-way interactions				
Experience × position	497.0	2	3.9	< 0.02
Experience × proximity	997.9	2	7.8	< 0.001
Position × proximity	13.5	1	0.2	NS

The 3-way interaction was not significant; F = 1.7, df = 2

Table 4.5. The relative date of laying of pairs of kittiwakes at the centre and edge of the warehouse colony, in relation to the breeding experience of the pair. Data for all years, 1954 - 90.

	Relative date of laying						
	Centre			Edge			
Experience	Mean	SD	*n*	Mean	SD	*n*	z
Established	2.76	6.81	766	-0.26	7.38	683	8.0^{**}
Intermediate	1.13	8.59	198	-1.35	8.50	279	3.1^{**}
Recruits	-4.34	10.48	208	-4.40	9.42	288	0.1 NS

NS = not significant, ** = $P < 0.01$

0.4 days and 2.5 ± 0.8 days respectively). In contrast, the relative date of laying of recruits did not differ in relation to their position in the colony.

The breeding experience of the pair × the proximity to other nesting pairs

The relative date of laying in relation to whether pairs nested adjacent to another pair or alone on a ledge also differed significantly for the established and intermediate breeders (Table 4.6). Both established and intermediate breeders laid significantly earlier if they nested adjacent to another pair than if they nested alone (mean difference = 2.2 ± 0.4 days and 2.7 ± 0.8 days respectively). In contrast, recruits which nested adjacent to another pair did not lay earlier than recruits which nested alone. For all three groups, pairs which nested alone on a ledge showed less variation in their date of laying than pairs which nested adjacent to another pair (as indicated by the smaller standard deviation).

Three-way interaction:

Nest position in the colony × the breeding experience of the pair × the proximity to other nesting pairs

The three way analysis of variance performed in order to examine the factors influencing the relative date of laying did not show a significant 3-way interaction (Table 4.4). However, the relative date of laying in relation to the breeding experience of the pair, nest position in the colony and proximity to other nesting pairs is of interest and is shown in Table 4.7. Established breeders which nested adjacent to another pair laid significantly earlier than established breeders which nested alone on a ledge, at both the centre and edge of the colony (mean difference: centre 1.7 ± 0.5 days, edge 1.7 ± 0.6 days). Intermediate breeders laid significantly earlier if they nested adjacent to another pair at the centre of the colony (mean difference = 3.1 ± 1.2 days) but did not lay significantly earlier at the edge of the colony. The mean date of laying of the recruits at the centre and edge of the colony was not advanced by nesting adjacent to another pair.

Table 4.6. The relative date of laying of pairs of kittiwakes in relation to the breeding experience of the pair and proximity to other nesting pairs. Data for all years, 1954 - 90.

	Relative date of laying						
	Together			Alone			
Experience	Mean	SD	*n*	Mean	SD	*n*	z
Established	2.29	7.32	811	0.12	6.96	638	5.7**
Intermediate	1.12	9.56	225	-1.61	7.47	252	3.4**
Recruits	-5.10	11.71	203	-3.86	8.33	293	1.3 NS

NS = not significant, ** = $P < 0.01$

Table 4.7. The relative date of laying of pairs of kittiwakes at the centre and edge of the warehouse colony, in relation to the breeding experience of the pair and the proximity to other nesting pairs. Data for all years, 1954 - 90.

		Relative date of laying							
		Centre				Edge			
Experience	Proximity	Mean	SD	*n*	z	Mean	SD	*n*	z
Established	Together	3.37	6.91	490	3.4^{**}	0.65	7.63	321	3.0^{**}
	Alone	1.68	6.51	276		-1.06	7.08	362	
Intermediate	Together	2.55	9.34	108	2.6^{**}	-0.19	9.61	117	1.9 NS
	Alone	-0.57	7.30	90		-2.19	7.53	162	
Recruits	Together	-5.60	11.74	112	1.9 NS	-4.49	11.71	91	0.1 NS
	Alone	-2.86	8.60	96		-4.35	8.18	197	

NS = not significant, $^{**} = P < 0.01$, $^{***} = P < 0.001$

In contrast to the established and intermediate breeders, recruits which nested adjacent to another pair at the centre of the colony did not lay earlier than recruits which nested alone (adjacent = 2.7 ± 1.4 days later than recruits which nested alone).

Two further three-way ANOVAs with clutch size and fledging success as the dependent variables were performed to examine the influence of the breeding experience of the pair, nest position in the colony and proximity to other nesting pairs. No significant 2-way or 3-way interactions were produced. However, as the mean number of young fledged per pair at the edge of the colony differed in relation to the proximity of other nesting pairs (Table 4.8), the productivity in relation to the breeding experience of the pairs is of interest (Table 4.9). At the edge of the colony, 49% ± 4% of recruits which nested alone failed to fledge any young (*n* = 180), whilst a significantly smaller proportion, 34% ± 5%, which nested adjacent to another pair failed (*n* = 86) (fail v fledge; $\chi^2 = 4.8$, df = 1, $P < 0.05$).

Factors influencing the proportion of pairs which nested together or alone on a ledge:

Nest position in the colony

At the centre of the colony 61% ± 1% of the pairs (*n* = 1172) nested adjacent to another pair whereas at the edge of the colony only 42% ± 1% of the pairs (*n* = 1250) nested adjacent to another pair. Therefore, the proportion of pairs which nested together or alone on a ledge differed in relation to whether pairs nested at the centre or edge of the colony.

The breeding experience of the pair

The proportion of pairs which nested adjacent to another pair or alone on a ledge was compared in relation to the breeding experience of the pairs. Fifty six percent (± 1%) of the established breeders nested adjacent to another pair (*n* = 1449), compared to 47% ± 2% of the intermediate breeders (*n* = 477) and 41% ± 2% of the recruits

Table 4.8. The number of young fledged by pairs of kittiwakes at the centre and edge of the warehouse colony, in relation to proximity to other nesting pairs. Data for all years, 1954 - 90.

	Number of young fledged													
	Centre							Edge						
	0	1	2	3	Mean	% failed breeding	χ^2_2	0	1	2	3	Mean	% failed breeding	χ^2_2
Together	142	206	292	27	1.31	21 ± 2	0.5 NS	123	158	195	16	1.21	25 ± 2	6.1*
Alone	87	141	206	13	1.32	19 ± 2		208	188	247	15	1.10	32 ± 2	

χ^2 test of number young fledged = together v alone: 0 v 1 v 2 or 3

NS = not significant, * = $P < 0.05$

Table 4.9. The number of young fledged by pairs of kittiwakes at the centre and edge of the warehouse colony, in relation to the breeding experience of the pair and the proximity to other nesting pairs. Data for all years, 1954 - 90.

		Number of young fledged											
		Centre						Edge					
Experience	Proximity	0	1	2	3	Mean	χ^2_2	0	1	2	3	Mean	χ^2_2
Established	Together	78	131	228	26	1.44	0.7 NS	66	89	129	12	1.29	0.8 NS
	Alone	40	74	145	10	1.46		77	109	134	13	1.25	
Intermediate	Together	17	39	40	0	1.24	0.2 NS	28	37	43	2	1.17	1.4 NS
	Alone	17	33	31	3	1.24		43	39	61	2	1.15	
Recruits	Together	47	36	24	1	0.81	3.3 NS	29	32	23	2	0.98	7.9*
	Alone	30	34	30	0	1.00		88	40	52	0	0.80	

χ^2 test of number young fledged = together v alone: 0 v 1 v 2 or 3

NS = not significant, * = $P < 0.05$

($n = 496$). The proportion of established breeders which nested adjacent to another pair was significantly greater than the proportion of intermediate breeders or recruits which nested adjacent to another pair (adjacent v alone: established breeders v intermediate breeders, $\chi^2 = 10.8$, df = 1, $P < 0.001$; established breeders v recruits, $\chi^2 = 32.9$, df = 1, $P < 0.001$). No significant difference was shown between the proportion of intermediate breeders and recruits which nested adjacent to another pair (adjacent v alone: $\chi^2 = 3.6$, df = 1, NS). Therefore, the proportion of pairs which nested together or alone on a ledge also differed in relation to the breeding experience of the pairs.

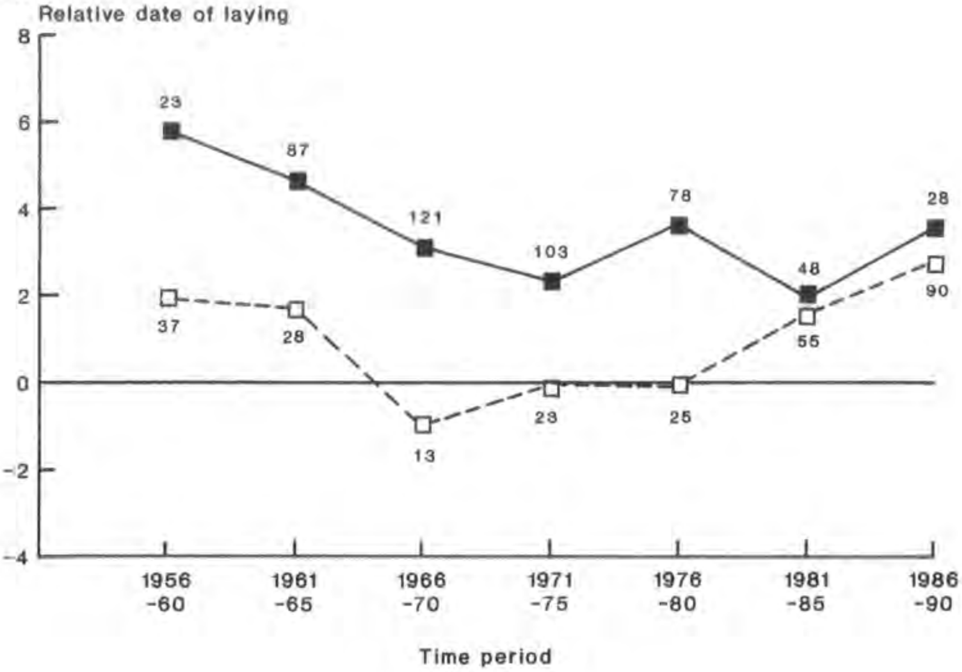
The relative date of laying of established breeders which nested alone or adjacent to another pair in relation to:

Year

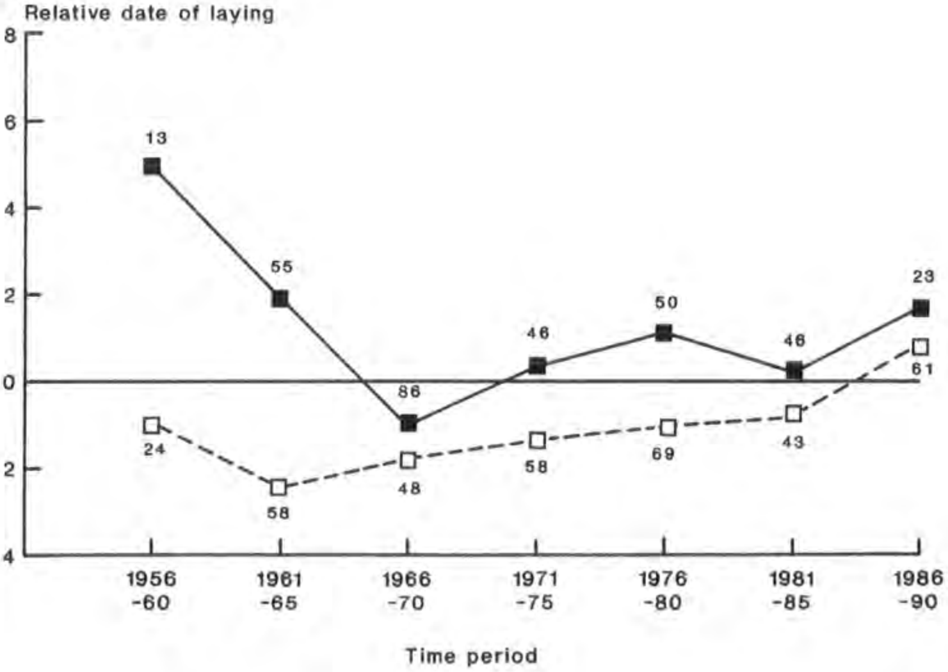
As described in the methods, this part of the study concentrates on the established breeders and examines their relative date of laying in relation to the proximity to other nesting pairs in detail. To establish whether pairs which nested adjacent to another pair laid earlier throughout the period of study than pairs which nested alone on a ledge, the relative date of laying of the established breeders was considered in relation to year (1956 - 90). To allow for the effect of position in the colony (Table 4.1), the analysis was performed in relation to whether pairs nested at the centre or edge of the colony. Figure 4.2. shows the relative date of laying of established breeders which nested at the centre or edge of the warehouse colony, in relation to the proximity to other nesting pairs and the year group (the data were divided into seven groups of years). In all seven time periods, established breeders which nested adjacent to another pair laid earlier than established breeders which nested alone, at both the centre and edge of the colony. Therefore, established breeders which nested adjacent to another pair laid consistently earlier throughout the study period.

Figure 4.2 The relative date of laying of established pairs of kittiwakes in relation to nest position in the warehouse colony (Fig. 4.2a: centre; Fig. 4.2b: edge), year and proximity to other nesting pairs (▤ = adjacent to another pair; □ = alone). Data pooled in 5-year time periods. Numbers for each point are sample sizes. The relative date of laying is the deviation of the laying date from the mean for the colony in that year. Positive figures indicate the number of days before the mean date that the pair laid, whilst negative figures indicate the number of days after the mean.

a.


Relative date of laying
8
6
4
2
0
-2
-4
23
87
121
103
78
48
28
37
28
13
23
25
55
90
1956 -60
1961 -65
1966 -70
1971 -75
1976 -80
1981 -85
1986 -90
Time period

b.


Relative date of laying
8
6
4
2
0
-2
-4
13
55
86
46
50
46
23
24
58
48
58
69
43
61
1956 -60
1961 -65
1966 -70
1971 -75
1976 -80
1981 -85
1986 -90
Time period

Nest position in the colony relative to that of other kittiwakes

As sites differ in quality with regard to their position in the colony relative to other birds (Coulson 1971), this analysis considers the date of laying after controlling for the position in the colony relative to other birds. Twenty seven windows, which included centre and edge sites in the colony, on which established breeders had nested were investigated individually (Table 4.10). Table 4.10 shows the average number of days difference in the relative date of laying between established breeders which nested adjacent to another pair and those which nested alone, for each of the 27 windows. The advanced date of laying of established breeders which nested adjacent to another pair was shown for centre and edge sites and for all four sides of the building (Table 4.10).

As shown on Table 4.7, established breeders which nested adjacent to another pair laid significantly earlier than established breeders which nested alone on a ledge, at both the centre and edge of the colony (mean difference: centre 1.7 ± 0.5 days, edge 1.7 ± 0.6 days). As the mean difference in the date of laying did not differ between the centre and edge of the colony, the results for the centre and edge in Table 4.10 were grouped for analysis. Established breeders which nested adjacent to another pair laid earlier on 20 of the 27 windows than established breeders which nested alone on a ledge and laid later on only seven of the windows (sign test, $P < 0.05$). Therefore, the earlier date of laying of pairs which nested adjacent to another pair (Table 4.7) did not arise as a result of the nest position in the colony relative to that of other kittiwakes.

Age of individuals within the pair

Table 4.11 shows the relative date of laying of established breeders at the centre of the colony, in relation to the age of both members of the pair and the proximity to other nesting pairs. For established breeders of all age-groups, the relative date of laying was earlier for pairs which nested adjacent to another pair than for those which nested alone on a ledge. Young female-young male pairs (female and male age = 2 or 3 years) which nested adjacent to another pair laid significantly earlier than pairs of the same age which

Table 4.10. The mean difference (days) in the relative date of laying between established pairs of kittiwakes which nested adjacent to another pair and those which nested alone on a ledge for 27 windows[1] at the centre or edge of the warehouse colony. Data for all years, 1954 -90. Positive figures indicate the number of days that pairs which nested adjacent to another pair laid earlier than pairs which nested alone.

Centre						Edge			
Site[2]	Mean difference (days)	Site	Mean difference (days)	Site	Mean difference (days)	Site	Mean difference (days)	Site	Mean difference (days)
E1A	6.6	S2C	3.6	W1F	-2.5	S3A	3.4	W2E	-0.7
E1B	4.2	W1A	2.8	W2A	0.1	S3C	2.6	W3B	0.4
S1A	3.4	W1B	0.1	W2B	2.9	S4B	1.0	N1A	5.7
S1C	4.8	W1C	-3.9	W2C	1.1	W1I	3.3	N1B	0.6
S2A	2.4	W1D	1.4			W1J	-2.2	N2A	3.7
S2B	-0.3	W1E	-1.2			W2D	-0.8		

[1] Only includes windows on which the number of established pairs which nested alone or adjacent to another pair was 5 or more

[2] Each site code represents one window at the warehouse, e g. E1A: East face, floor 1, window A

Table 4.11. The relative date of laying of established pairs of kittiwakes at the centre of the warehouse colony, in relation to female and male age and proximity to other nesting pairs. Data for all years, 1954 - 90.

		Relative date of laying						
		Together			Alone			
Female age	Male age	Mean	SD	*n*	Mean	SD	*n*	z
2 - 3	2 - 3	4.15	6.52	92	0.98	7.88	89	3.0^{**}
	≥ 4	4.06	7.45	50	2.08	4.08	37	1.6 NS
≥ 4	2 - 3	2.00	7.02	78	1.44	7.08	34	0.4 NS
	≥ 4	3.36	6.89	270	2.16	5.78	116	1.8 NS

NS = not significant, ** = $P < 0.01$

nested alone on a ledge (mean difference = 3.2 ± 1.1 days). Therefore, early laying by established breeders which nested adjacent to another pair was not a result of an age difference between pairs which nested together or alone.

Comparison of the factors influencing productivity at North Shields and Marsden:

The conclusions relating to the effect of position in the colony and proximity to other nesting pairs on the productivity of kittiwakes at North Shields, were tested by comparison with kittiwakes nesting at Marsden.

Nest position in the colony

Table 4.12 shows the productivity of kittiwakes which nested at the centre and edge of the Marsden colony (1991 - 93). Productivity differed significantly between the centre and edge of the colony; pairs at the centre fledged 24% more young than pairs which nested at the edge. At the edge of the colony 33% ± 3% of pairs failed to fledge any young (*n* = 308), compared to only 20% ± 1% at the centre (*n* = 754) (fail v fledge; $\chi^2 = 19.4$, df = 1, $P < 0.001$). This is a similar effect to that shown at North Shields (1954 - 90; Table 4.1) where a significantly higher proportion of the pairs failed to fledge any young at the edge of the colony (edge: 29% ± 1% failed, *n* = 1150; centre: 21% ± 1% failed, *n* = 1114). Therefore, the productivity in both colonies differed in relation to the nest position in the colony.

The influence of nest position in the colony and proximity to other nesting pairs

The mean number of young fledged per pair at Marsden did not differ significantly between pairs with respect to nest position in the colony and proximity to other nesting pairs (Table 4.13). Although the mean number of young fledged was lowest for pairs which nested alone at the edge of the colony, the proportion of pairs which failed to fledge any young did not differ significantly between pairs which nested together or alone at the edge of the colony (failed: edge-alone, 36% ± 3%, *n* = 233; edge-together, 25% ± 5%, *n* = 75; fail v fledge, $\chi^2 = 2.3$, df = 1, NS). However, a

Table 4.12. Productivity of kittiwakes at the centre and edge of the Marsden colony. Data for 1991 - 93.

	Number of young fledged						
	0	1	2	3	Mean	% failed breeding	χ^2_2
Centre	152	302	285	15	1.22	20 ± 1	20.8^{***}
Edge	102	111	95	0	0.98	33 ± 3	

χ^2 test of number of young fledged: 0 v 1 v 2 or 3

$^{***} = P < 0.001$

Table 4.13. The number of young fledged by pairs of kittiwakes at the centre and edge of the Marsden colony, in relation to proximity to other nesting pairs. Data for 1991 - 93.

	Number of young fledged													
	Centre							Edge						
	0	1	2	3	Mean	% failed breeding	χ^2_2	0	1	2	3	Mean	% failed breeding	χ^2_2
Together	47	89	72	4	1.16	22 ± 3	2.0 NS	19	31	25	0	1.08	25 ± 5	2.8 NS
Alone	105	213	213	11	1.24	19 ± 2		83	80	70	0	0.94	36 ± 3	

χ^2 test of number young fledged = together v alone: 0 v 1 v 2 or 3

NS = not significant

comparison of the four categories (centre-alone, centre-together, edge-alone, edge-together) for homogeneity of failure or success showed a highly significant heterogeneity (fail v fledge, $\chi^2 = 24.1$, df = 3, $P < 0.001$). Clearly one (or more) of the groups was behaving differently from the rest. By far the greatest contribution to the heterogeneity came from the category of edge-alone ($\chi^2 = 17.6$, df = 1, $P < 0.001$) and this category differed significantly from the rest. The evidence suggests that success at the edge of the colony was significantly lower if the pair did not have an immediate neighbour.

A comparison of the four categories at North Shields (Table 4.8) for homogeneity of failure or success also showed a highly significant heterogeneity (fail v fledge; $\chi^2 = 27.7$, df = 3, $P < 0.001$). As at Marsden, the greatest contribution to the heterogeneity came from the category of edge-alone ($\chi^2 = 16.6$, df = 1, $P < 0.001$). Therefore, productivity at the edge of both colonies was significantly lower if pairs nested alone whilst no such effect was evident for pairs which nested alone in the centre of the colonies.

Discussion

The effect of nest position in the colony and proximity to other nesting pairs on productivity at North Shields and Marsden.

Several studies of colonial nesting seabirds have shown that the nest position in the colony influences reproductive performance (Coulson 1968, 1971; Tenaza 1971; Nettleship 1972; Parsons 1976; Birkhead 1977; Nelson 1978a; Potts *et al.* 1980; Ryder & Ryder 1981; Furness 1984). A comparison of the productivity of kittiwakes at North Shields and Marsden showed that productivity varied according to whether pairs nested at the centre or edge of the colonies. Pairs which nested in the centre of both colonies fledged significantly more young than those at the edge, where the density of the breeding pairs was lower and the proportion of breeding failures was higher. At North Shields, the productivity of pairs nesting at the centre and edge of the colony was influenced by the quality of individuals and therefore pairs (Coulson 1968; Porter & Coulson 1987). Although some studies of colonial nesting seabirds have shown a high incidence of predation at the edge of the colony (Tenaza 1971; Birkhead 1977), predation and disturbance at the warehouse colony (Coulson 1988) and Marsden were minimal.

The productivity of kittiwakes in both colonies was further influenced by the proximity to other nesting pairs. In both colonies, pairs which nested alone on a ledge at the edge of the colony had the lowest productivity, whilst at the centre, productivity was not influenced by the proximity to other nesting pairs. At North Shields, the difference in productivity between pairs which nested together or alone was modified by the breeding experience of the pairs. For example, although no significant difference was shown for the established and intermediate breeders, recruits which nested adjacent to another pair at the edge of the colony fledged significantly more young than recruits which nested alone on a ledge. The importance of social stimulation to recruits has been discussed by Nelson (1978a), who suggested that in areas where social stimulation is high, the reproductive physiology of young breeders is probably stimulated and the tendency to spend time at the nest is increased. Hence, the productivity of young, inexperienced breeders is increased. Similarly, when competition for nest sites is less intense and the overall density of breeding kittiwakes is low, as at the edge of a colony, it is advantageous for kittiwake recruits to nest in close proximity to other pairs in order to maximise the social stimulation which they receive. Although the influence of breeding experience could not be taken into account at Marsden, as the birds were not marked, the factors which influenced productivity at North Shields, i.e. position in the colony and proximity to other nesting pairs, were shown to effect productivity at Marsden.

The influence of social stimulation on the date of laying

It has been suggested that social stimulation has a role in stimulating reproductive development and advancing the date of laying of seabirds (Nelson 1978a; Coulson 1985). At North Shields, the relative date of laying of the kittiwakes was influenced by the breeding experience of the pair, the nest position in the colony and the proximity of the nearest pair. For example, at the centre of the colony, where the density of nesting birds was high, established and intermediate breeders which nested adjacent to another pair laid earlier than pairs which nested alone. In contrast, recruits which nested adjacent to other pairs in the centre of the colony did not lay earlier than those which nested alone. This was due to aggression by nesting birds when recruits tried to gain access to a site immediately adjacent to one already occupied (Porter 1990). As a result, sites adjacent to other pairs were available to recruits later in the season than unoccupied ledges and only 41% ± 2% of the recruits nested adjacent to another pair, compared to 56% ± 1% of the established breeders.

Although all sites at the warehouse had the same physical characteristics, they differed in quality with regard to their position in the colony relative to other birds (Coulson 1971). By controlling for the effect of nest position in the colony relative to that of other birds, it was shown that the difference in the relative date of laying of established breeders (between pairs which nested adjacent to another pair or alone) did not arise due to the position of the nest in the colony. The implication is that, compared to pairs which nested alone on a ledge, established breeders which nested adjacent to another pair differed in age, individual quality or in the amount of social stimulation they received as a result of their proximity to other nesting pairs.

As breeding experience has a marked effect on the timing of breeding of seabirds (Coulson & White 1958a; Mills 1973; Coulson & Horobin 1976; Nisbet *et al.* 1984), the relative date of laying of pairs of kittiwakes which nested adjacent to another pair at the centre of the colony was compared to that of pairs of the same age which nested alone at the centre. Young female - young male pairs (age 2 or 3) which nested adjacent to another pair laid significantly earlier than pairs which nested alone. Therefore, early laying by pairs which nested together was not a result of an age difference between pairs which nested together or alone. In a similar analysis, Nelson (1978b) compared experienced pairs of gannets *Sula bassana* from a group subject to relatively little stimulation (i.e. an isolated group) with birds from a large group, in order to show that social stimulation was important. Gannets subject to relatively little stimulation bred later and had a greater spread of laying. Hence, both studies infer that social stimulation is important in advancing the date of laying. However, whilst the breeding success of Gannets with similar breeding experience does not differ between the centre and edge of a colony (Nelson 1978a), and therefore gannets are probably not segregated in relation to individual quality, effects arising from differences in the quality of individuals and therefore pairs must be considered for the kittiwake. Whilst kittiwakes nesting in the centre of the warehouse colony are of higher quality than those nesting at the edge (Coulson 1968; Porter & Coulson 1987), it is not known whether birds which nested together are of higher quality than those which nested alone. Therefore, the earlier laying date of pairs which nested together could either have been a result of social stimulation advancing the laying date or due to better quality individuals laying earlier than other pairs. The latter implies that high quality pairs tend to choose nests adjacent to other pairs.

When additional ledges were added to the centre of the colony in 1962 and again in 1983, the proportion of pairs which nested together reduced as pairs with at least one bird breeding for the first time nested alone on the extra ledges (Porter & Coulson 1987). Before and after the addition of extra ledges, the proportion of pairs which nested together increased as the size of the colony increased (Porter & Coulson 1987). The implication is that pairs of kittiwakes prefer to nest alone on a ledge and will only double up on a ledge when lack of space forces them to do so. The fact that few pairs nested together on a ledge when the colony was small (Porter & Coulson 1987) is evidence that good quality pairs would not preferentially compete for space on an occupied site in the centre of the colony when access to empty ledges in the centre was available. This is further supported by the fact that whilst 61% ± 1% of the pairs nested together at the centre of the colony, only 42% ± 1% of the pairs nested together at the edge of the colony where the density of nesting pairs was lower. Therefore, whilst kittiwakes differ in individual quality, there is no reason to suggest that the average quality of pairs which nested together was higher than that of pairs which nested alone.

Previous studies of kittiwakes have associated high productivity with high quality individuals (Coulson 1968; Coulson & Thomas 1985a; Coulson & Porter 1985). Therefore, if pairs which nested together were of higher quality than those which nested alone, a difference in the average productivity per pair nesting together or alone would have been expected. Whilst the relative date of laying of established and intermediate pairs which nested adjacent to another pair at the centre of the colony was earlier than for pairs which nested alone at the centre, this was not reflected in an increased clutch size or productivity. Therefore, it is more likely that social stimulation, rather than a difference in individual quality, served to advance the date of laying of pairs which nested together. Hence, the advanced date of laying of pairs which nested together on a ledge arose as a result of the close proximity of the pairs, which increased the amount of social stimulation both pairs received.

In some seabird species, the post fledging survival of early hatched chicks is higher than that of late hatched chicks (Perrins 1966; Burger 1972; Nisbet & Drury 1972; Jarvis 1974; Parsons, Chabrzyk & Duncan 1976; Nelson 1978a; Harris, Halley & Wanless 1992; Spear & Nur 1994). Hence, the advantage of social stimulation is earlier laying which increases post-fledging survival and subsequent recruitment to the breeding population. Therefore, although the majority of pairs of kittiwakes which nested together did not fledge more young than pairs which nested alone, their earlier laying may result in higher lifetime reproductive success if their young have a higher post-fledging survival and thus survive to breed.

CHAPTER 5

ATTENDANCE OF ADULT KITTIWAKES AT NESTS DURING CHICK-REARING

Introduction

In recent years, partial or total breeding failure has occurred at a number of seabird colonies in Britain and elsewhere in northern Europe (Barrett & Runde 1980; Barrett *et al.* 1987; Heubeck 1988; Monaghan *et al.* 1989; Harris & Wanless 1990; Hamer, Furness & Caldow 1991). Breeding failure of kittiwakes *Rissa tridactyla* has been recorded at colonies in Shetland, the east coast of Scotland and as far north as Norway (Barrett & Runde 1980; Harris & Wanless 1990; Danchin 1992; Hamer *et al.* 1993).

During the breeding season, sandeels *Ammodytes* spp. and clupeids (members of the herring family) are important foods of adult kittiwakes and their chicks in Britain (Pearson 1968; Galbraith 1983; Coulson & Thomas 1985b; Harris & Wanless 1990). However, sandeel stocks around Shetland have declined for several years (Kunzlik 1989). The breeding failure of kittiwakes in Shetland and at other colonies, has been associated with the decrease in food availability, which resulted in an increased time spent foraging by the adults and, consequently, lower attendance at the nest site (Barrett & Runde 1980; Wanless & Harris 1989; Harris & Wanless 1990; Murphy, Springer & Roseneau 1991; Danchin 1992; Hamer *et al.* 1993; Roberts & Hatch 1993).

Kittiwakes rarely leave eggs and young chicks unattended (Barrett 1978; Coulson & Wooller 1984; Coulson & Johnson 1993; Hamer *et al.* 1993). Despite this, considerable variation has been shown in the attendance of adults at the nest during the later chick-rearing period (Barrett & Runde 1980; Galbraith 1983; Coulson & Wooller 1984; Wanless & Harris 1989; Coulson & Johnson 1993). Attendance by adult kittiwakes decreased as chicks increased in age (Wanless & Harris 1989; Coulson &

Johnson 1993; Roberts & Hatch 1993) and differed in relation to brood size (Wanless & Harris 1989; Coulson & Johnson 1993). It was suggested that chick neglect is directly related to increased energy requirements as broods of two were more than twice as likely to be left unattended as single chicks (Wanless & Harris 1989). However, for chicks which hatched late in the season, another study showed virtually no difference in attendance of adults at broods of one and two (Coulson & Johnson 1993). This suggests that brood size *per se* may not be the factor causing the effect and that quality of the individual parents may be important (Coulson & Porter 1985).

Many studies consider low attendance by adult kittiwakes to be an indicator of food shortage. However, a large range of variation occurs in the attendance of individual pairs in the same year without food shortage, suggesting differences in the quality of individual adults and pairs (Coulson & Porter 1985; Coulson and Johnson 1993). Further, few studies have considered adult attendance in relation to the age of the chicks, date of hatching and brood size, hence, there is need for caution before concluding that parental attendance is invariably an indicator of food availability (Coulson & Johnson 1993).

With the exception of studies at North Shields, Tyne and Wear, England, (Coulson & Wooller 1984; Coulson & Johnson 1993), attendance patterns at kittiwake colonies in England have not been monitored. This paper examines the attendance and productivity of kittiwakes breeding at Marsden, in northeast England, between 1991 - 93. The attendance of adults is considered in relation to the date of hatching, chick age, brood size and in relation to individual pairs of adult kittiwakes.

Methods

The study was carried out at Marsden, Tyne and Wear, England in a colony of about 5000 breeding pairs of kittiwakes. As the individual quality and breeding performance of kittiwakes differs in relation to nest position in the colony (Coulson 1968; Porter & Coulson 1987), two areas of the colony were selected for a detailed study of parental attendance in 1991 - 93: **centre** - the study site was in the centre of the colony; **edge** - the study site was at the periphery of the colony. The two areas were photographed (Appendix) and the nests were numbered on the photographs. The following number of nests were studied: 1991: centre 367, edge 110; 1992: centre 342, edge 105; 1993: centre 337, edge 93. In 1992 and 1993, the same nests were studied as in 1991, with the exception of a few which had disappeared since the previous breeding season or which were not attended by a pair prior to the incubation period.

The colony was usually visited three times each week during June, July and August. The majority of the nests were viewed from the beach (using a telescope with a x20 - 60 zoom lens) so hatching success could not be measured as the eggs were not visible. The number of chicks present, their stage of development and the number of adult kittiwakes present at each nest were recorded on each visit. At North Shields, Tyne and Wear, the mean fledging age was 42.7 days with minimum periods of 32 - 34 days (Coulson & White 1958b). The fledging date at Marsden was considered to be the first date that a chick of 32 days or older was absent from the nest, although it is appreciated that fledged chicks may return to the nest site (Coulson & White 1958b). The age of the chicks were estimated on each visit using a description of the stages of development (Maunder & Threlfall 1972). If a chick of less than 32 days was absent from the nest it was presumed to have died.

Kittiwakes typically lay in early May to mid-June (Coulson 1974) and incubation lasts for about 27 days (Coulson & White 1958b). Adult attendance was monitored during the following chick-rearing periods: 29 June - 9 August 1991; 6 July - 6 August 1992; 7 June - 6 August 1993. The study at Marsden was primarily to determine the productivity of birds nesting at the centre and edge of the colony and the study of adult attendance was secondary. As a result, observations of adult attendance in 1991 and 1992 did not commence until June or early July when the monitoring of the number of chicks present in each nest commenced. In 1992, chick hatching dates were recorded from 10 June. Coulson and Johnson (1993) showed that chicks were left alone overnight more frequently than during the day. The observations at Marsden were made between 1000 h and 1800 h to prevent bias in the results arising from the overnight absences of adult kittiwakes.

The attendance of adult kittiwakes is considered during the chick-rearing period, i.e. until the fledging of the individual chicks. During each visit to the colony the number of broods of one, two and three chicks that were a) unattended by an adult and b) had one or two adults present were recorded. As only 1 - 4% of the nests with broods attended by an adult kittiwake had both adults in attendance, no distinction was made in the analysis between broods attended by one or two adults. Although non-breeding adult kittiwakes may occupy a nest with chicks which are not their own (Cadiou, Monnat & Danchin 1994), these visitors were usually identified by their behaviour and were therefore excluded from the analysis. The paper only considers adult attendance at nests with chicks. The spot observation data on attendance for each visit to the colony are presented as the proportion of nests with broods which had at least one adult kittiwake in attendance; I have described this definition as **parental attendance**. For analysis of the variation of attendance between individual pairs, the data are presented as the percentage attendance of adult kittiwakes at each nest with a brood during the chick rearing stage ($n \geq 10$ observations at each nest). As only 3% of the broods had three chicks, they were included with broods of two for the analysis of parental attendance.

Studies of kittiwakes have shown differences in the quality of individuals nesting at the centre and edge of a colony (Coulson 1968; Porter & Coulson 1987). The average parental attendance of kittiwakes at the centre and edge of this colony did not differ significantly within years, although productivity was significantly lower at the edge of the colony (Chapter 4). Only birds nesting at the centre of the colony are considered in the detailed analysis of parental attendance to avoid effects arising from additional variables.

Unless otherwise stated, all means are expressed ± 1 SE. For 2 by 2 χ^2 tests, Yates' correction factor was employed.

Results

Parental attendance: 1991 - 93

The mean date of fledging of kittiwake chicks in the study areas at Marsden differed by an average of only five days between the three years at the centre of the colony and by four days at the edge of the colony (Table 5.1). Therefore, a comparison of the parental attendance of adult kittiwakes over the same time period in each year of the study is possible (Table 5.2). Table 5.2 shows the proportion of observations during comparable time periods (1991 - 93) when nests with broods had at least one adult kittiwake in attendance, divided into nests at the centre and edge of the Marsden colony. In each year, the average parental attendance did not differ significantly between the centre and edge of the colony. The average parental attendance was high in 1991 and 1993; nests with broods were attended by an adult for 93% of the observations in 1991 (6 July - 7 August, number of nest-days (n) = 1771) and for 76% of the observations in 1993 (5 July - 6 August, n = 2138). During a comparable time period in 1992, nests with broods had an adult in attendance for an average of only 51% of the observations (6 July - 6 August, n = 1990).

Parental attendance in relation to calendar date

Figure 5.1 shows the proportion of nests with broods which had at least one adult kittiwake in attendance, in relation to calendar date and year. The average parental attendance showed a marked decrease from the third week in July in all three years. In 1991 and 1993, the average parental attendance exceeded 90% of the observations until the third week in July. In 1992, the average parental attendance was low at an earlier date in the season than in 1993. For example, on 6 July 1992, parental attendance was only 69% ± 3% (n = 288), whilst on a similar date in 1993 (7 July) parental attendance was 94% ± 2% (n = 263).

Table 5.1. The mean date of fledging of kittiwake chicks at the centre and edge of the Marsden colony in relation to year, 1991 - 93.

	1991		1992		1993	
	Mean fledging date (± SD days)	*n*	Mean fledging date (± SD days)	*n*	Mean fledging date (± SD days)	*n*
Centre	28 July ± 5.9	300	23 July ± 6.3	282	26 July ± 6.8	226
Edge	29 July ± 5.7	68	25 July ± 5.7	69	27 July ± 7.4	65

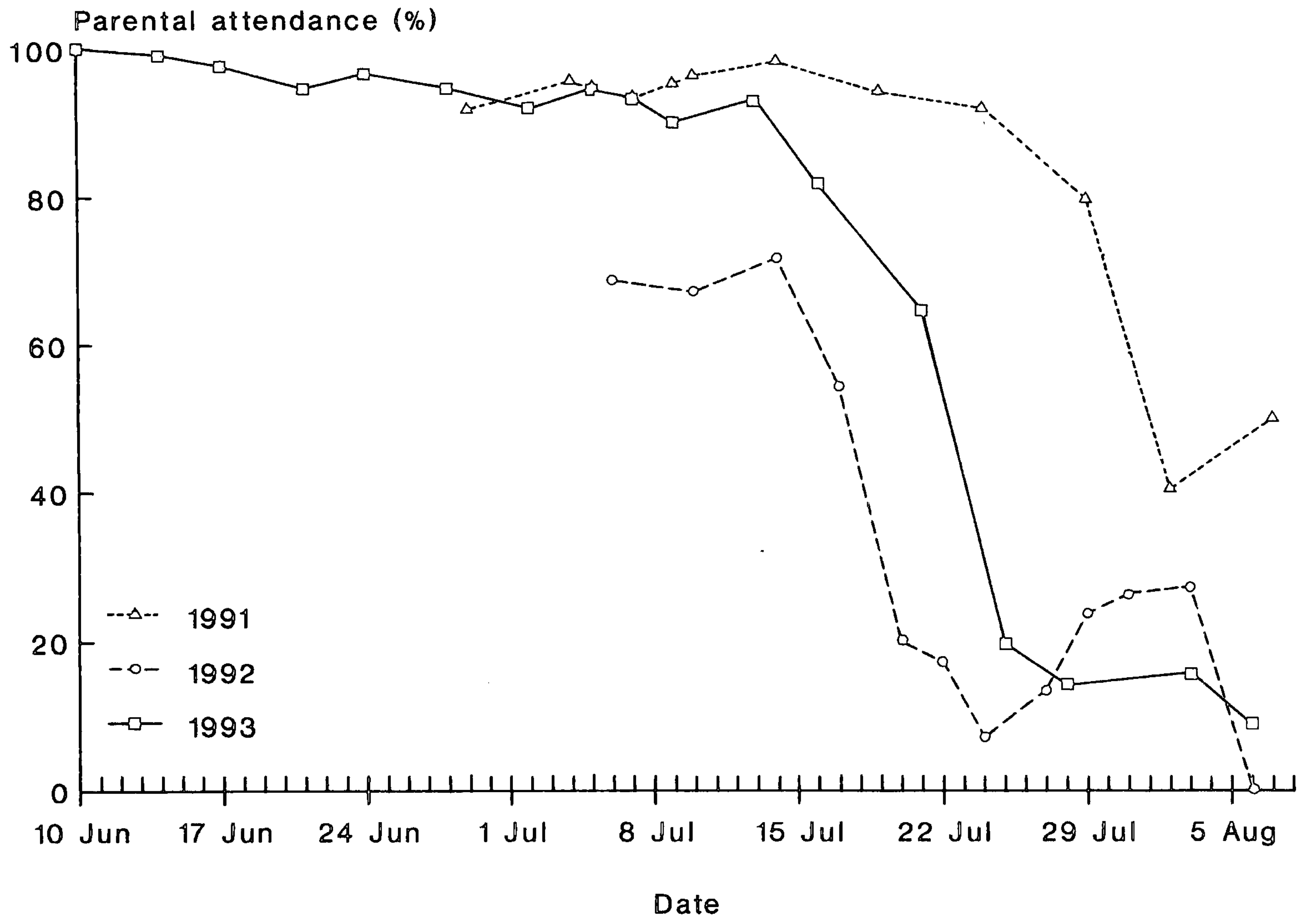
Table 5.2. The proportion of observations during the chick-rearing period at Marsden when nests with broods had at least one adult kittiwake in attendance. Data for the centre and edge of the colony and for comparable time periods, 1991 - 93[1].

	1991		1992		1993	
	% nests attended (± SE)	*n*	% nests attended (± SE)	*n*	% nests attended (± SE)	*n*
Centre	92.5 ± 0.7	1406	50.0 ± 1.3	1553	75.6 ± 1.0	1737
Edge	92.8 ± 1.3	365	54.8 ± 2.7	347	76.1 ± .12	401
Total	92.5 ± 0.6	1771	50.9 ± 1.1	1900	75.7 ± 0.9	2138

χ^2 test: centre v edge = not significant for each year

[1] Time periods: 6 July - 7 August 1991; 5 July - 6 August 1992; 6 July - 6 August 1993

Figure 5.1 The proportion of nests with broods which had at least one adult kittiwake in attendance, in relation to calendar date and year (1991 - 93).


Parental attendance (%)
100
80
60
40
20
0
10 Jun
17 Jun
24 Jun
1 Jul
8 Jul
15 Jul
22 Jul
29 Jul
5 Aug
Date
1991
1992
1993

Factors affecting parental attendance in 1992 and 1993:

Chick age

The average parental attendance in relation to chick age is shown in Figure 5.2. In 1992 and 1993, parental attendance decreased progressively as the chicks increased in age. The average parental attendance in 1992 declined from 74% ± 5% for chicks 11 - 15 days old ($n = 74$) to 13% ± 4% for chicks 41 - 45 days old ($n = 69$). Young chicks of 1 - 15 days were almost constantly attended in 1993 (96% ± 1%, $n = 1239$) but parental attendance declined to 27% ± 5% ($n = 82$) for chicks 41 - 45 days old. However, the analysis does not take account of the date of hatching and this is discussed below.

A comparison of the average parental attendance of chicks of the same age-group in 1992 and 1993 showed that chicks 11 - 25 days old were attended for a significantly smaller proportion of the observations in 1992 than in 1993 (1992: 71% ± 2%, $n = 469$; 1993: 93% ± 1% $n = 1175$; $\chi^2 = 143$, df = 1, $P < 0.001$). Similarly, older chicks (26 - 40 days) were attended less frequently in 1992 than in 1993 (1992: 43% ± 2%, $n = 801$; 1993: 68% ± 2%, $n = 803$; $\chi^2 = 93.9$, df = 1, $P < 0.001$). Hence, for chicks of a comparative age, the average parental attendance in 1992 was lower than in 1993, although again, the analysis does not take account of the date of hatching.

Date of hatching

Figure 5.3 shows the age of the chicks in 1992 and 1993 when the average parental attendance of chicks which hatched on each of the dates shown first became less than 70%. In 1992, chicks which hatched early in the season on 13 June were attended for less than 70% of the observations for the first time on 11 July, when 28 days old (number of nests with chicks (n) = 32). Chicks which hatched late in the season (26 June 1992) were attended for less than 70% of the observations for the first time on 15 July, when 19 days old ($n = 19$). The age at which chicks were attended for less than 70% of the observations for the first time in 1992 differed in relation to the date of hatching ($r_7 = -0.72$, $P < 0.05$). Similarly, in 1993, chicks which hatched early

Figure 5.2 The average attendance (± SE) of adult kittiwakes at the nest during chick rearing, in relation to chick age in 1992 (●) and 1993 (■). The numbers for each point are the number of nest-days.

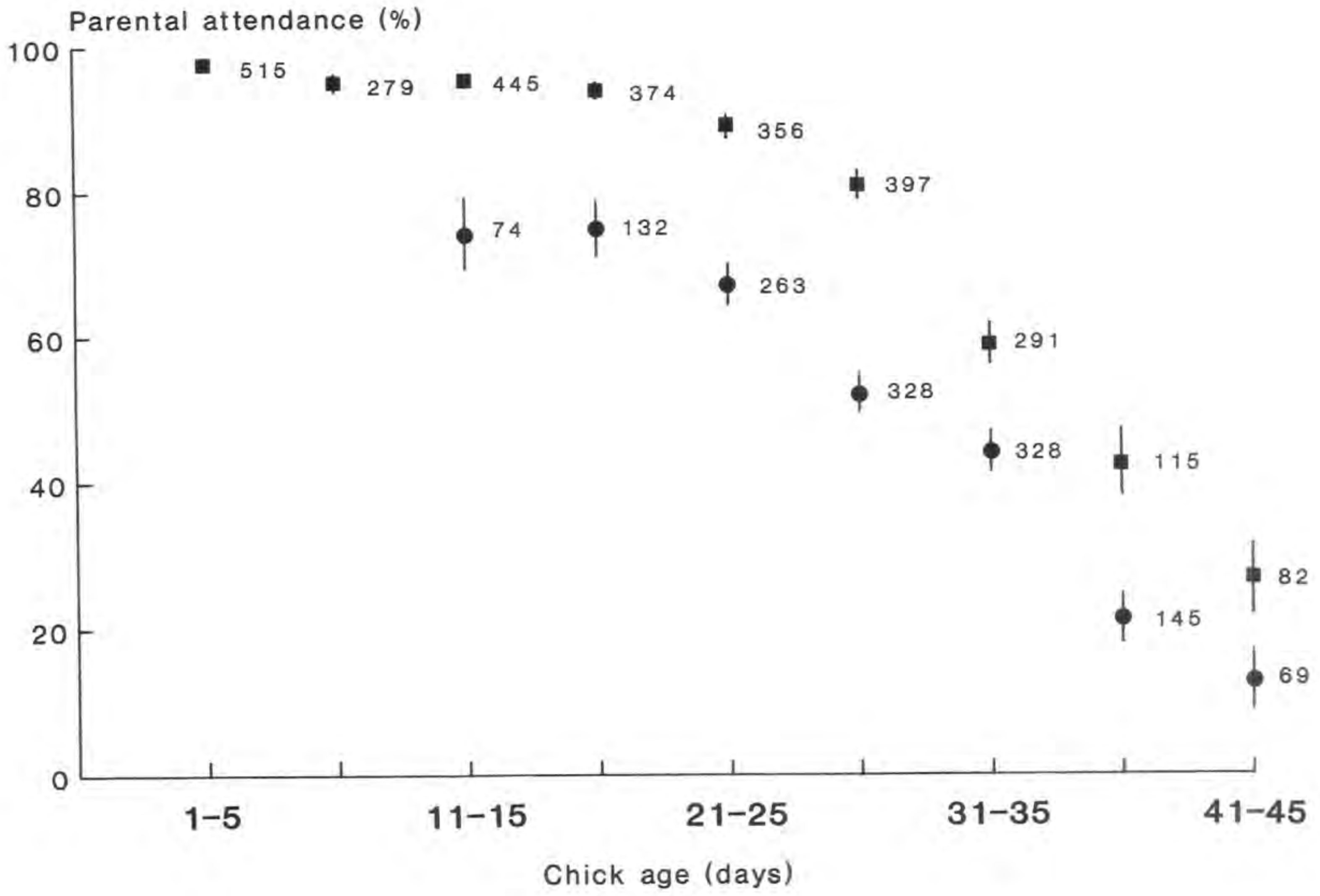
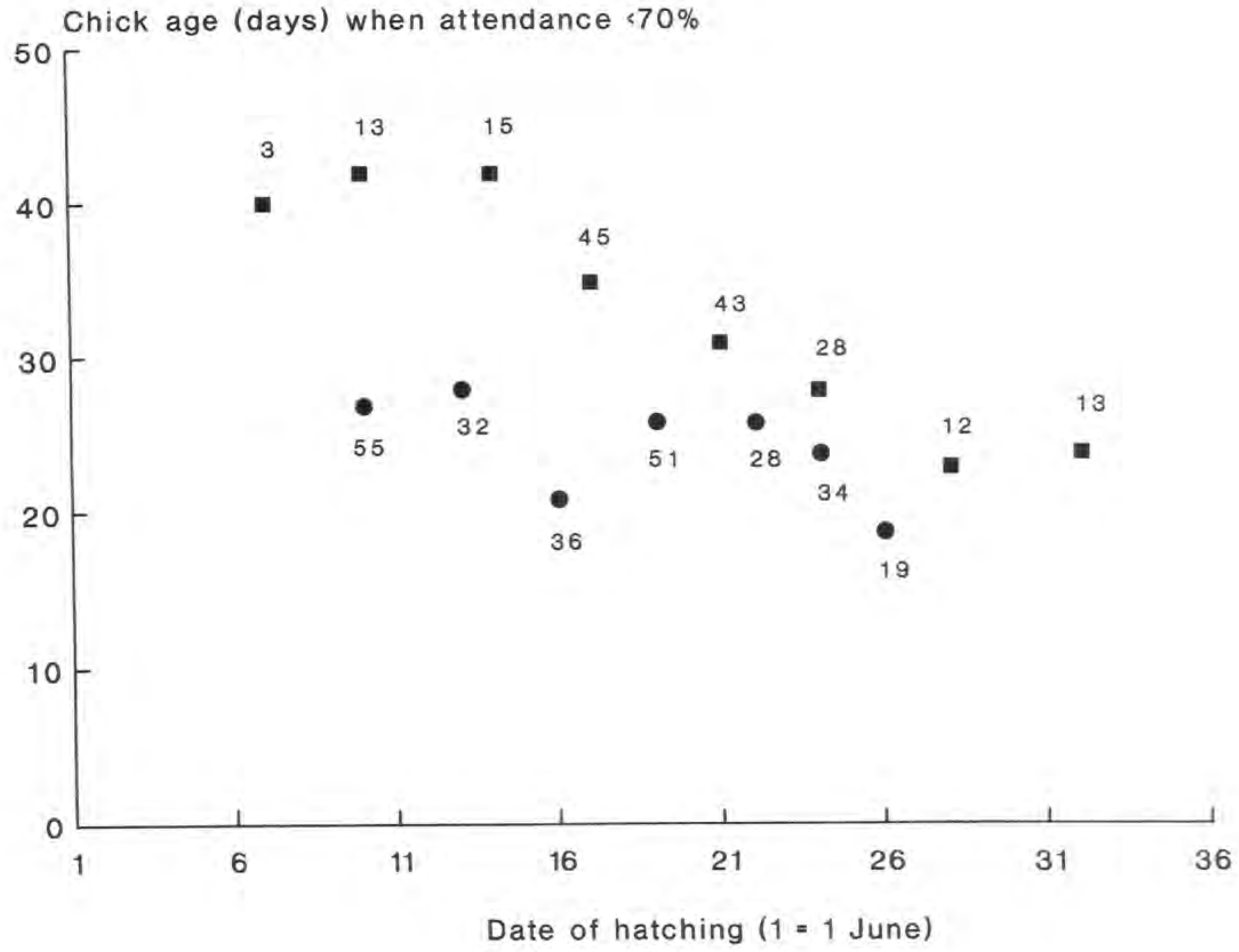

Parental attendance (%)
100
80
60
40
20
0
515
279
445
374
356
397
74
132
263
328
291
328
115
145
82
69
1-5
11-15
21-25
31-35
41-45
Chick age (days)

Figure 5.3 The age of the kittiwake chicks when the average parental attendance of chicks which hatched on each of the dates shown first became less than 70%. Data for 1992 (●) and 1993 (■). The numbers for each point are the number of nests with chicks.


Chick age (days) when attendance ‹70%
50
40
30
20
10
0
1
6
11
16
21
26
31
36
Date of hatching (1 = 1 June)
3
13
15
45
43
28
12
13
55
32
36
51
28
34
19

in the season were attended for at least 70% of the observations for longer than those which hatched later in the season ($r_s = -0.89, P < 0.01$). For example, chicks which hatched on 10 June 1993 were attended for less than 70% of the observations for the first time on 22 July, when 42 days old ($n = 13$), whilst chicks which hatched on 24 June 1993 were attended for less than 70% of the observations for the first time on 22 July, when only 28 days old ($n = 28$).

Chicks which hatched on 10 June were 27 days old ($n = 55$) in 1992 when, for the first time, they were attended for less than 70% of the observations. This is in marked contrast to chicks of comparable age in 1993, which were not attended for less than 70% of the observations until 42 days old ($n = 13$). For late hatched chicks, there was less difference between years in the age at which they were first attended for less than 70% of the observations (hatched 24 June: 1992; 24 days old, $n = 34$, 1993; 28 days old, $n = 28$).

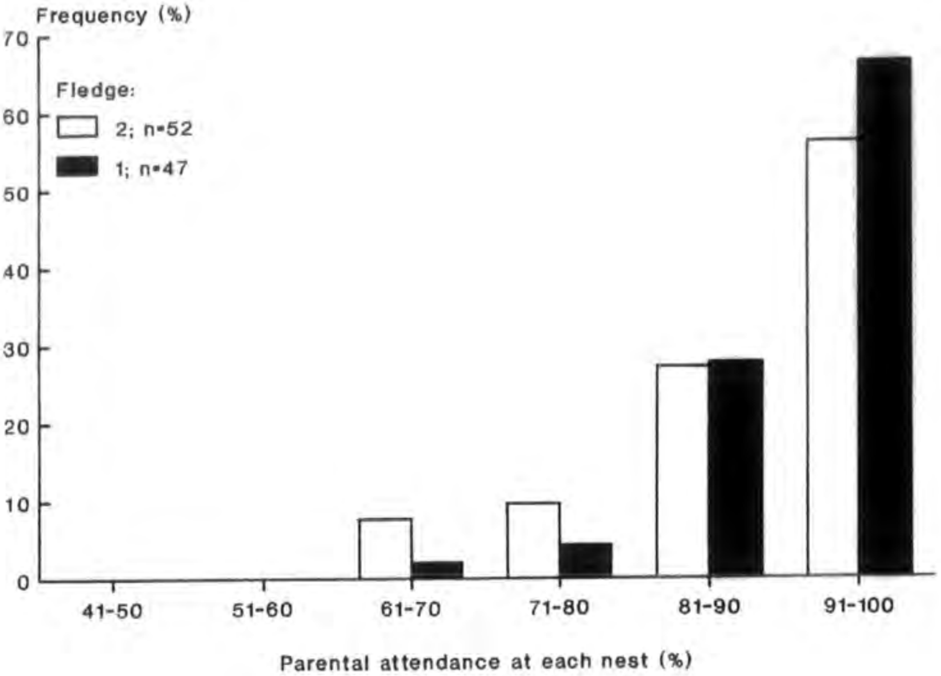
Variation in individual pairs

The average parental attendance by one or more adults at individual nests in 1993, in relation to the date of hatching and number of young fledged is shown in Figure 5.4. The data are presented as the percentage attendance of adult kittiwakes at each nest with a brood during the chick rearing stage (for each nest $n \geq 10$ observations). The average parental attendance of chicks which hatched early in the season (7 - 14 June 1993, nests with chicks (n) = 99; Fig. 5.4a) was 90%; chicks were always attended on more than 60% of the observations. In contrast, the parental attendance of chicks which hatched later in the season (21 June - 2 July, $n = 87$; Fig. 5.4b) averaged 79% and was more variable; 13% of the nests were each attended on only 41 - 60% of the observations. Of the chicks which hatched early in the season, 88% were attended on more than 80% of the observations ($n = 99$), compared to only 46% of the chicks which hatched later in the season ($n = 87$) ($\chi^2 = 35.6$, df = 1, $P < 0.001$).

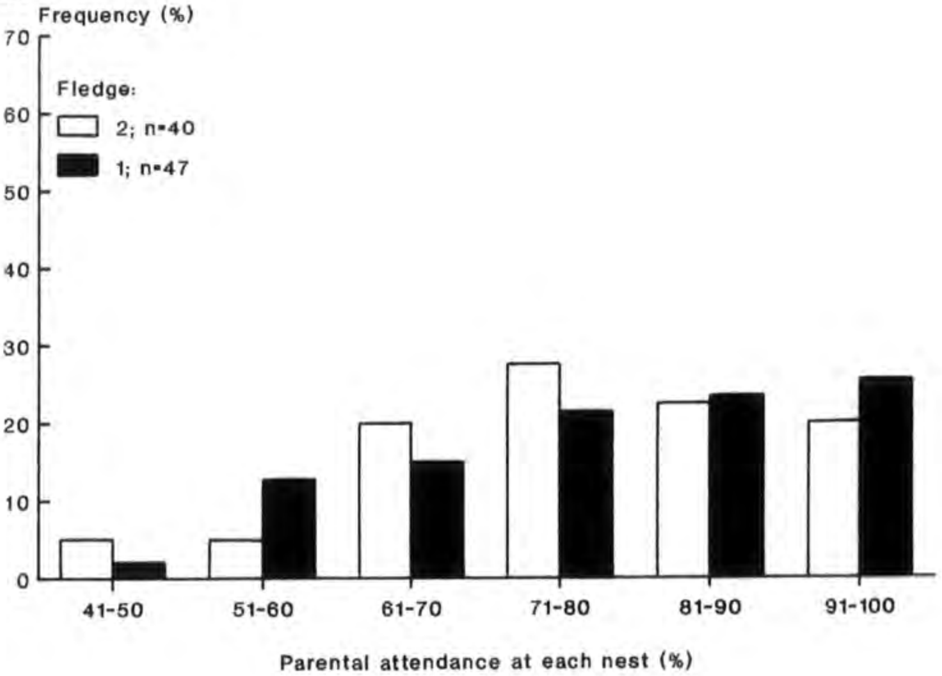
Of pairs which fledged one chick, 94% of the early breeders were in attendance on more than 80% of the observations ($n = 47$), compared to only 49% of the late breeders

Figure 5.4 The average attendance of adult kittiwakes at individual nests with broods during chick rearing (for each nest $n \geq 10$ observations), in relation to the date of hatching and number of young fledged. Date of hatching: 7 - 14 June 1993 (Fig. 5.4a); 21 June - 2 July 1993 (Fig. 5.4b).

a.


Frequency (%)
70
60
50
40
30
20
10
0
Fledge:
2; n=52
1; n=47
41-50
51-60
61-70
71-80
81-90
91-100
Parental attendance at each nest (%)

b.


Frequency (%)
70
60
50
40
30
20
10
0
Fledge:
2; n=40
1; n=47
41-50
51-60
61-70
71-80
81-90
91-100
Parental attendance at each nest (%)

(*n* = 47) ($\chi^2 = 20.8$, df = 1, $P < 0.001$). A similar trend was shown for birds which fledged more than one chick (early breeders: 83%, *n* = 52; late breeders: 43%, *n* = 40; $\chi^2 = 14.4$, df = 1, $P < 0.001$). The proportion of early breeders in attendance on more than 80% of the observations was significantly higher for pairs which fledged one chick than more than one chick ($\chi^2 = 16.3$, df = 1, $P < 0.001$) but the difference was not significant for the late breeders ($\chi^2 = 0.2$, df = 1, NS).

Productivity: 1991 - 93

The average productivity of pairs of kittiwakes which either hatched chicks or had been incubating eggs was high in all three years of the study (≥ 1.15 young fledged per pair; Table 5.3). The mean number of young fledged per pair did not differ significantly between 1991 and 1992 (1.24 and 1.26 respectively), but declined significantly to 1.15 in 1993. In 1993, 26 ± 2% of the pairs failed to fledge any young (*n* = 336), compared with 18 ± 2% of the pairs in 1991 and 1992 (*n* = 367 and 342 respectively).

Table 5.3. Productivity of kittiwakes at Marsden in relation to year, 1991 - 93.

	Number of young fledged				Mean	% fail[1]	χ^2_1
	0	1	2	3		(± SE)	
1991	65	158	135	9	1.24	18 ± 2	
							0.3 NS
1992	60	141	133	8	1.26	18 ± 2	
							7.8*
1993	88	117	123	8	1.15	26 ± 2	

[1] To calculate % fail, *n* = the total number of pairs studied which hatched chicks or had been incubating eggs.

χ^2 test of number young fledged = 0 v 1 v 2 or 3.

NS = not significant, * = $P < 0.05$

Discussion

Studies at kittiwake colonies have shown low adult attendance in years when kittiwakes had partial or total breeding failure (Barrett & Runde 1980; Harris & Wanless 1990; Danchin 1992; Hamer *et al.* 1993). In 1992, the average parental attendance of kittiwakes in the northeast of England was only 51%. For chicks of a comparative age, the average parental attendance was lower than in 1993. Further, chicks were left unattended at a younger age in 1992 than in 1993. However, there was no direct or obvious effect on productivity in 1992. This suggests that the adults provided sufficient food for the young by increasing their time away from the nest. The fact that birds were able to increase the time spent foraging, whilst maintaining high productivity, suggests that adults were, to an extent, buffered against extreme feeding conditions (Hamer *et al.* 1993) and were not beyond the limits of their buffering capacity in 1992. Further, although low attendance at the nest by the adults increases the potential risk of chick predation by, for example, herring gulls *Larus argentatus* (Barrett & Runde 1980; Galbraith 1983), the high productivity in 1992 suggests that chick loss due to predation was minimal.

In 1993, productivity was an average of 9% lower than in 1992. Although the average parental attendance was high in 1993 (76% during the time period comparable to that of other years), the attendance rate declined rapidly from the third week in July. The decline in attendance was more marked than that which occurred in July 1991 and implies that seasonal variation in food availability (Hunt & Hunt 1976; Mills 1979) may have been a factor influencing adult attendance near the end of the 1993 breeding season. Interestingly, in 1994, the rapid decline in parental attendance did not occur in July and a high proportion of the adults were still on nests in August after the chicks had fledged (J. C. Coulson). If adults have to increase the time which they spend searching for food, this may impose a stress on the individuals concerned and result in an increase in the adult mortality rate and/or lower fledging success. Previous studies have considered the stress on adult birds, such as that brought about by food shortage, in relation to life history theory (Hamer *et al.* 1991).

The costs of increased competition for food may be borne entirely by offspring, or may be shared between offspring and their parents (Birkhead & Furness 1985). If adults were stressed in relation to food supply during the breeding season this could have an effect on the young outside of the breeding season. For example, it was shown that post-fledging survival in the herring gull (Parsons, Chabrzyk & Duncan 1976), Manx shearwater *Puffinus puffinus* (Perrins, Harris & Britton 1973) and great skua *Catharacta skua* (Hamer *et al.* 1991) could be related to conditions at the colony during the breeding season.

Although productivity in this study was not reduced in 1992, the post-fledging survival of the kittiwakes in that year is not known. Factors which reduce the post-fledging survival of the kittiwake lower the lifetime reproductive success of the adults concerned and subsequently alter the population dynamics of the species. Porter and Coulson (1987) gave evidence for the existence of a pool of potential recruits, which were young kittiwakes which had not bred previously. The size of this non-breeding pool serves as the first indicator of a decline in the well-being of a kittiwake population as it declines several years before the breeding population declines (Porter & Coulson 1987). Kittiwakes delay breeding until 3 or 4 years old (Wooller & Coulson 1977; Porter & Coulson 1987). Therefore, whilst the number of kittiwakes breeding at colonies on the east coast of England has continued to increase in recent years (Lloyd, Tasker & Partridge 1991), only time will show whether low post-fledging survival will reduce the number of kittiwakes which recruit into the breeding population.

Factors influencing parental attendance

This study and that of Coulson and Johnson (1993), have shown that even in years when the average parental attendance of kittiwakes is high, as in 1993, large differences in frequency of attendance are shown by individual pairs with broods. Whilst 88% of the early breeding pairs were in attendance for more than 80% of the observations in 1993, this varied in relation to brood size, resulting in broods of two being attended less than broods of one. Amongst the late breeders there was greater variation in parental attendance (41 - 100%) but no effect of brood size. The low parental attendance by late breeders, compared to that of the early breeders, suggests either a difference in their age and/or individual quality (Coulson & White 1958a; Coulson & Porter 1985; Coulson & Johnson 1993) or an effect of a seasonal decline in food availability, which has been shown to influence the breeding performance of seabirds (Hunt & Hunt 1976; Mills 1979). Parental attendance by late breeders in 1993 was, on average, low and variable, although 46% of the broods were still attended for more than 80% of the observations. Evidence for differences between early and late breeders, due either to age and/or quality or food availability in 1993 were further substantiated, as chicks which hatched late in the season were attended for less than 70% of the observations for the first time at a younger age than those which hatched early in the season. As the study area contained few colour-ringed birds it is not possible to consider the effects of individual quality and age on parental attendance. However, the study shows the importance of considering chick age, brood size, date of hatching and parental age and/or quality in studies of attendance, as even in years when the average parental attendance is high, variability will occur in response to these factors.

GENERAL DISCUSSION

The colonial organisation of a species is determined by the environmental and social factors which influence the behaviour of the individual (e.g. food supply, predation, recruitment and nesting density; see Wittenberger & Hunt 1985). This study investigated factors which influence the colonial organisation of the kittiwake and subsequently influence the breeding biology and lifetime reproductive success of an individual. Recent research has considered the movement of breeding and non-breeding birds between colonies in relation to environmental conditions and has considered the factors which may influence the movement of individuals (Danchin 1992; Forbes & Kaiser 1994; Danchin & Boulinier in press). However, few studies have been able to study in detail the response of individuals to changes in their physical and/or social environment. Therefore, this study was carried out from a unique position - that of detailed prior knowledge of the behaviour and ecology of the study species.

Recent research has indicated that the attendance of adult seabirds at the nest during the chick-rearing period may be related to local environmental conditions, in particular to the availability of food (Barrett & Runde 1980; Wanless & Harris 1989; Harris & Wanless 1990; Murphy, Springer & Roseneau 1991; Danchin 1992; Hamer *et al.* 1993; Roberts & Hatch 1993). As was evident in this study, adults may be able to increase their time away from the nest in order to provide sufficient food for themselves and their offspring. However, periods of poor feeding which are prolonged or encompass one or more breeding seasons, as occurred in Shetland (Heubeck 1988; Danchin 1992), may impose a stress on the individuals concerned and be expected to result in an increase in the adult mortality rate and/or lower fledging success (Birkhead & Furness 1985; Hamer, Furness & Caldow 1991).

Whilst the movement of non-breeding birds between colonies is common (Chabrzyk & Coulson 1976; Porter 1988; Ainley, Ribic & Wood 1990; Klomp & Furness 1990), seabirds typically return to the same site in consecutive years once they have bred (Birkhead 1977; Nelson 1978b; Ollason & Dunnet 1978; Harris 1984; Mills 1989; Aebischer & Coulson 1990; c.f. Coulson & Nève de Mévergnies 1992; Danchin & Monnat 1992). However, it has been suggested that it may be advantageous for adult breeding birds which encounter unfavourable environmental conditions during the breeding season (eg. tick infestation, Danchin & Monnat 1992; decreased food availability, see above) to move to and breed at a different colony in the following year (Danchin & Boulinier in press). In the study at Marsden, it is believed that food availability influenced the behaviour of the breeding birds but the average productivity was reduced in only one year of the study. However, a recent study of kittiwakes has shown a movement of breeding birds from an area of low productivity in a colony to sites in a neighbouring colony which was more productive in the previous year (Danchin & Monnat 1992). Therefore, situations resulting from overfishing and unpredictable food supplies may be expected to influence the population dynamics of the species if infidelity to the colony and low recruitment result. In this case, studies of adult attendance and productivity at seabird colonies have value and relevance in providing information in a "before and after" situation. Further, such studies may serve as indicators of changes in environmental conditions (Montevecchi 1993).

In the case of individuals which move to a new breeding site, it has been predicted and demonstrated that the new breeding site should have been visited in the year prior to moving in order to assess the suitability of the area for breeding (Forbes & Kaiser 1994; Cadiou, Monnat & Danchin 1994). Movements of breeding birds are predicted to occur when their individual reproductive success and that of their neighbours is low and other areas are seen to have high productivity. In this way, information can be gained about reproductive opportunities from the presence of conspecifics. For such a mechanism to work, the presence of other individuals must provide information about the resource(s) being sought (eg. abundant food, safe place to nest; Darling 1938; Burger & Shisler 1980; Brown, Stutchbury & Walsh 1990; Kharitonev & Siegel-Causey 1990). The adaptive value of this behavioural mechanism may be that it leads to preferential recruitment in the most favourable breeding sites at a given time (Cadiou *et al.* 1994).

Although a movement of breeding kittiwakes has been shown to occur between colonies under certain conditions (Danchin & Monnat 1992), only this study and one other (Morse & Kress 1984) has had the opportunity to study the behaviour of birds unable to return to their previous breeding sites because of a forced site change. Whilst nest sites may be inaccessible due to natural causes, for example, cliff erosion, snow and ice cover etc., the birds involved are usually able to nest close to their original nest sites. For example, cliff erosion often forms new nesting sites and the influence of snow and ice may serve only to delay the onset of breeding (Belopol`skii 1961; Morris & Chardine 1985; Irons 1988). The situation at North Shields in 1991 was unique in that kittiwakes were unable to gain access to their previous nest sites at any time in the season. Therefore, it was a similar situation to that faced by animals whose breeding sites are lost as a result of habitat loss such as that caused by land use change or flooding.

In 1991, kittiwakes were prevented from returning to their previous nest sites at the warehouse colony in North Shields. This forced site change occurred within a colony where breeding site fidelity and nest site tenacity were exhibited by the adults and the average productivity was high (Wooller & Coulson 1977; Aebischer & Coulson 1990; Coulson & Thomas 1983, 1985b). Despite the detailed studies which have been carried out on the behaviour and ecology of seabirds and other colonial species, no information was available on the response of individuals to a forced site change which involved all of the individuals in a colony. As the closure of the window ledges at North Shields occurred prior to the kittiwakes returning to the colony for the breeding season, there had been no opportunity for the adults to assess other potential breeding colonies in the previous year (Cadiou *et al.* 1994). Therefore, this unique situation resulted in unexpected and unusual responses by the birds. In this case, the response to unfavourable conditions was a high level of non-breeding and low average productivity by the birds which did breed. As the North Shields kittiwakes had no choice in the matter of whether to move to a new nest site, the situation differed from that shown by Danchin and Monnat (1992) when kittiwakes moved in response to poor conditions in the previous year. However, the study resulted in a unique and detailed study of the responses of birds to a unpredictable situation.

One of the reasons thought to be important in the evolution of breeding site fidelity and mate retention (Allan 1962; Soikkeli 1967; Holmes 1971; Rowley 1983) is that birds which change their mate typically fledge less young than birds which retain their mate (Coulson 1966; Mills 1972; Davis 1976; Perrins & McCleery 1895; Bradley *et al.* 1990; Weimerskirch 1990). As only one other study has had the opportunity to study the movement of birds in response to a forced site change (Morse & Kress 1984), it was unknown as to whether birds could move to a different colony with their mate. Whilst the study of Leach's storm-petrels (Morse & Kress 1984) showed that birds could move to a new site within the colony and retain their mate, birds which moved greater distances could not be located. Therefore, whilst previous studies have predicted that birds should move to a new site in response to unfavourable conditions (Gratto, Morrison & Cooke 1985; Thompson & Hale 1989; Danchin & Monnat 1992; Danchin & Boulinier in press), it had been assumed that mate change would result (Ens, Safriel & Harris 1993). Hence, it has been assumed that one of the costs construed by birds which moved to another colony would be a loss of their previous mate (Birkhead & Furness 1985). However, as kittiwakes can move to another colony and retain their mate, the evidence from this study suggests that the most serious consequences of a forced site change may arise from the unpredictability of the situation to the individuals concerned and from the resulting non-breeding which serves to influence lifetime reproductive success.

As a consequence of the study of the movement of birds between colonies, a model for the evolution of coloniality has been suggested (Danchin & Boulinier in press). This suggests that coloniality may evolve and be maintained as birds move from areas of poor productivity to areas of high productivity. This is further enhanced as individuals try to breed as close as possible to the conspecifics which they used as indicators of the local environmental quality, in order to benefit from the same environmental conditions (Danchin & Boulinier in press). However, whilst the mechanisms behind the movements of birds to new breeding sites have been considered, there are problems associated with attaining a nest site in an established colony. For example, owners of sites act aggressively towards newcomers, as shown at North Shields when recruits attempted to gain access to a site immediately adjacent to one already occupied (Porter 1990). Therefore, the advantage to an individual bird is not always directly obvious. For example, whilst the date of laying of pairs which nested adjacent to another pair was shown to be earlier than that of pairs which nested alone on a ledge, the average productivity was not higher. However, early laying and the subsequent fledging of the young early in the season, may result in a higher proportion of young surviving to recruit into a breeding population (Perrins 1966; Burger 1972; Nisbet & Drury 1972; Jarvis 1974; Parsons, Chabrzyk & Duncan 1976; Nelson 1978a; Harris, Halley & Wanless 1992; Spear & Nur 1994).

Whilst nesting adjacent to another pair may confer an advantage due to social stimulation (Nelson 1978a; Coulson 1985), it is obvious that in natural situations there will be areas of differing density in a colony, determined by the nesting substrate (e.g. it is physically impossible to build a nest on some areas of a cliff face, Brown *et al.* 1990). Further, date of arrival at the colony and aggression by established breeders will influence the ease of access onto a new site (Porter 1990). Although it may be advantageous for a pair to nest immediately adjacent to another pair, not all pairs do so as disadvantages may also be incurred. This may explain the aggression shown by established breeders towards recruits as, for example, their productivity may be reduced due to lack of space on the nesting ledge for the young. As suggested by Nelson (1978a), social stimulation may be more important to recruits than established breeders. Hence, inexperienced birds which persevere and establish a site adjacent to another pair may gain more of an advantage from the nesting position than the pair which were already nesting on the ledge.

Whilst it may be advantageous for birds to move to and breed in more productive areas (Danchin & Monnat 1992), the actual benefit of the move to the individual can only be assessed after the breeding attempt in the new breeding site. In other words, whilst an assessment of a potential breeding site can be made in terms of productivity, etc., the actual factors which will affect the reproductive performance of the individual can only be determined when the bird has moved into the colony to breed. Therefore, I believe that the move to a new colony will not always be a positive move for the birds concerned as, whilst birds may attain a nest site, the influence of individual quality, social stimulation and their position in the colony relative to that of other birds will play an important role in determining their reproductive performance. As such, it is of interest that some of the kittiwakes from central areas of the warehouse colony tended to form groups of nests at Tynemouth. This may have conferred an advantage to the birds concerned, arising from familiarity with the birds nesting adjacent to them.

The importance of this study lies in the analyses which could be performed as a result of the detailed long term study of kittiwakes. Factors which influence lifetime reproductive success, such as breeding experience, individual quality, survival, and nest position in the colony were considered in relation to social and environmental factors. As such, it should serve to further our understanding of the importance of, and the processes involved in, breeding site fidelity, nest site fidelity and mate retention. In the future, factors resulting in habitat loss, such as global warming and climate change, and on a smaller but no less important scale, pollution and land use change, may exert important effects. For example, the breeding sites of seals and coastal, ground nesting birds are likely to experience considerable change as a result of predicted sea-level rise. Therefore, studies such as this will be important in our prediction and understanding of the response of animals to changes in their environment.

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SUMMARY

1. THE INFLUENCE OF DIVORCE AND IMPENDING DEATH ON THE BREEDING SUCCESS OF THE KITTIWAKE

1. Data from the 37 year study of colour-ringed kittiwakes at North Shields, Tyne and Wear, England, were analysed to investigate whether divorce affects the reproductive performance of all kittiwakes which divorce and to study reproductive performance in an individuals last year of life.

2. Female kittiwakes had lower productivity in the year of divorce (mean number of young fledged = 1.17) than females which retained their mate (mean = 1.44) and also had below average productivity in the preceding year (mean: would divorce = 1.22; would retain same mate = 1.43).

3. The survival rate of kittiwakes in the year following divorce was 5.6 percentage points lower than for those which had retained their mate, and one explanation of this is that the birds which had divorced were poorer quality individuals.

4. Young and old females which took a new mate through divorce and would retain the same mate in the following year, had similar productivity in the year of divorce to females of comparable age paired with the same mate for at least two years.

5. Sixty five percent of divorced females took a young, relatively inexperienced male as their new mate. The average reproductive success of divorced, but experienced breeding females which took experienced males as their new mate was as high as that of females of comparable age which had retained their mate.

6. Productivity was reduced by an average of 12% if one member of a pair was in the last year of life and by 29% if both members of the pair were in their last year of life. On average, females fledged more young in their penultimate breeding attempt than in their last attempt.

7. The study emphasises the importance of mate age and mate choice on productivity in the year of divorce and indicates that factors other than senescence must have affected the reproductive performance of younger individuals in their last breeding year.

2. THE INFLUENCE OF FORCED SITE CHANGE ON THE DISPERSAL AND BREEDING OF THE KITTWAKE

1. The influence of forced site change on the dispersal and breeding of colour-ringed adult kittiwakes from the warehouse colony at North Shields was examined.

2. In 1991 (the first year that kittiwakes were prevented from nesting at the warehouse colony), only 43% of the surviving adult kittiwakes bred. Although they were unable to nest on their original sites, 54 (83%) of these birds bred in the immediate area of the warehouse where they nested on sites which had not previously been used by nesting kittiwakes. Eleven of the birds nested at other colonies in 1991.

3. In 1992, a further 61 of the surviving kittiwakes moved and nested at other colonies within 5 km of the North Shields colony. Nine of these birds had visited these colonies in 1991.

4. It is evident that the disturbance was still having an effect on the kittiwakes in 1992 as only 54% of the surviving birds which had bred at the North Shields colony in 1990 and 1991 returned to breed at the North Shields colony in 1992. Even in 1993, a further three of the kittiwakes bred in different colonies to that in which they had nested in 1992.

5. There was no difference in the proportions of male and female kittiwakes which bred at the North Shields colony or moved to other colonies in each year of the study.

6. The forced site change resulted in extensive non-breeding, low productivity and a potential reduction in lifetime reproductive success for most of the birds involved.

3. MATE RETENTION IN THE KITTIWAKE AND THE SIGNIFICANCE OF NEST SITE TENACITY

1. The study analyses data on mate retention and nest site tenacity of kittiwakes at North Shields (1954 - 90) and examines the effect of a forced change of breeding site on mate retention (1991 - 93).

2. Although kittiwakes in 1991 were prevented from returning to nest sites of the previous breeding season, 73% of females and 60% of males which bred elsewhere retained their mate of the previous breeding season.

3. Of kittiwakes which moved to other colonies in 1992, 42% of breeding females and 30% of males retained their mate of the previous breeding season.

4. Over the period 1954 - 90, 92% of females and 80% of males which used the same nest site in the following year retained their mate but 100 pairs which changed nest site still reformed the pair-bond of the previous breeding season.

5. A model predicted that the probability of retaining the same mate by chance within the warehouse colony should decrease progressively with distance moved from the previous nest site. Mate retention decreased sharply if birds moved 0.3 m to a nest site immediately adjacent to the previous site but, in contrast to the model, did not show a further consistent change or significant decrease with increasing distance.

6. As birds which changed nest site and moved to a different colony still retained their mate, the annual reforming of the same pair can not result solely from nest site tenacity. This implies that birds recognise each other as individuals and possibly move as a pair. Such behaviour has important implications for lifetime reproductive success, as birds which retain their mate from the previous breeding season typically fledge more young than birds which change mate.

4. THE EFFECT OF NEST POSITION ON THE REPRODUCTIVE PERFORMANCE OF THE KITTIWAKE

1. Data from the 37 year study of marked kittiwakes at North Shields were analysed to study the effect of nest position and proximity to other breeding pairs on the reproductive performance. A comparison was made with the productivity of kittiwakes nesting at Marsden, Tyne and Wear, England.

2. Productivity was highest at the centre of both colonies (mean number of young fledged: North Shields, centre 1.31, edge 1.15; Marsden, centre 1.22, edge, 0.98). At the edge, productivity was highest for pairs which nested adjacent to another pair.

3. The date of laying at North Shields was advanced by the breeding experience of the pair and the density of the breeding birds. The proximity of the nearest neighbour pair exerted an effect as both established and intermediate breeders laid significantly earlier if they nested adjacent to another pair (mean difference = 2.2 ± 0.4 days and 2.7 ± 0.8 days respectively). In contrast, recruits which nested adjacent to another pair did not lay earlier than recruits which nested alone.

4. Early laying by pairs which nested adjacent to another pair was not as a result of age differences between pairs which nested together or alone. Further, pairs of kittiwakes which nested together were not higher quality individuals than pairs which nested alone.

5. Therefore, it is suggested that the advanced date of laying of pairs which nested together arose as a result of the close proximity of the pairs, which increased the amount of social stimulation both members of each pair received.

6. Social stimulation results in earlier laying which may potentially increase post-fledging survival and subsequent recruitment to the breeding population.

5. ATTENDANCE OF ADULT KITTIWAKES AT NESTS DURING CHICK-REARING

1. The attendance of adult kittiwakes at the nest during chick-rearing was monitored for three years at Marsden, 1991 - 1993.

2. During comparable periods in 1991 and 1993, 93% and 75% of the broods, respectively, were attended by an adult, compared to only 51% during the same period in 1992.

3. For chicks of a comparative age, parental attendance was lower in 1992 than in 1993. For example, chicks of 11 - 25 days old were attended for 71% ± 2% of the observations in 1992, but for 93% ± 1% of the observations in 1993. However, in both years, parental attendance decreased progressively as the chicks increased in age.

4. Although chicks were unattended at a younger age in 1992 than in 1993, there was no effect on productivity. This suggests that the adults provided sufficient food for the young by increasing their time away from the nest.

5. In 1993, 88% of the early breeding pairs were in attendance for more than 80% of the observations, but this varied in relation to brood size. The late breeders showed greater variation of parental attendance but no effect of brood size. The low parental attendance by late breeders (average parental attendance = 79%), compared to that of the early breeders (90%), suggests either a difference in their age and/or individual quality or an effect of a seasonal decline in food availability.

6. The study shows the importance of considering chick age, brood size, date of hatching and parental age and/or quality in studies of attendance.

APPENDIX

Photographs of the study areas at Marsden, Tyne and Wear, England:

a. the centre of the colony (North of Grotto; Fig. 4.1)

bi & ii. the periphery of the colony (Marsden Village Bay; Fig. 4.1) a

bi

bii