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Hyde, Laila M.

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DIVORCE IN THE KITTIWAKE GULL

Rissa tridactyla

by

Laila M. Hyde

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fulfilment of the requirements
for the degree of
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TABLE OF CONTENTS

Page

3. Analysis of 1990 data.

LIST OF TABLES

Table **CHAPTER 4** **Page**

Table **CHAPTER 4** **Page**

LIST OF FIGURES

Page

CHAPTER 4

LIST OF APPENDICES

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ABSTRACT

Divorce has been observed in many species of bird. Studies have revealed a relationship between divorce and reproductive success. This study was carried out to investigate whether such a relationship exists in the Kittiwake (*Rissa tridactyla*). The aims were to determine when divorce occurs, what causes divorce to occur, what the effects of divorce on reproductive output are and, finally, why birds divorce. It was conducted at a warehouse on the north bank of the River Tyne in North Shields, Tyne & Wear, during the 1990 breeding season. Analysis of a long-term data set spanning thirty three years was also carried out. Divorce does cause a significant reduction in some measures of reproductive output, acting significantly during incubation. Divorce may be due to lower reproductive success in the preceding season, a possible result of incompatibility between individuals.

1 INTRODUCTION

Breeding systems among bird species are varied. Although examples of polygyny and polyandry are found (Craig 1980), the most common is monogamy: one male-one female. This is the most frequently found breeding system amongst sea birds as chick rearing in a marine ecosystem requires investment of resources from both male and female birds (Hunt 1980). Ninety eight percent of seabird species are colonial (Furness & Monaghan 1987) which suggests that benefits are to be gained such as synchrony of breeding (Darling 1938, Coulson & Dixon 1979), though these may be offset by costs such as site competition or chick cannibalism (Parsons 1976, Coulson & Thomas 1985a, Hunt et al. 1986, Kilpi 1989). Population studies of sea birds have shown that colonies are temporally dynamic (fulmars: Dunnett, Ollason & Anderson 1979; kittiwakes: Coulson & Thomas 1985b) and study of species' breeding biology is necessary to distinguish effects of reproduction and population structure from environmental change (Cairns 1987).

The kittiwake gull, *Rissa tridactyla*, is a small, colonially-nesting sea bird. Its breeding range extends from the North Atlantic coasts of America and Europe to the arctic coast of Russia and western North America (Cramp & Simmons 1983). Outside the breeding season it is oceanic whilst during the breeding season the kittiwake nests on rocky ledges on cliffs and on buildings close to the ocean. The nest, constructed of grass and seaweed, has a defined cup into which are laid between 1 and 3 eggs of a blotched, earthy appearance. Incubation is carried out by both sexes (Coulson & Wooller 1984) and eggs hatch 28 days after laying. Chicks remain in the nest for approximately 34 days during which time both parents feed them (Coulson & Thomas 1985a).

Taking fish, marine crustacea and worms, the bird feeds by diving into the ocean or by feeding on the surface. There is evidence that the kittiwake feeds at night, allowing the establishment of a regular pattern of attendance at the nest by both sexes during incubation (Coulson & Wooller 1984).

The size of kittiwake colonies varies (Coulson & Thomas 1985, Porter & Coulson 1987, Wanless & Kinnear 1988) and this has been attributed in part to fluctuations in food supply which have also affected the population dynamics of other seabird species (kittiwakes: Furness 1978, Coulson 1983, McGrath & Walsh 1985, Harris & Wanless 1990; terns: Uttley et al 1989). However, to distinguish between the effects of changing environmental conditions and those of the birds' reproductive biology on survival (Coulson & Dixon 1979, Hunt et al 1986, Aebischer & Coulson 1990) the breeding system of the kittiwake must be understood.

Breeding systems which maximise the number of offspring surviving to successfully reproduce will tend to be favoured by natural selection. Hence, a kittiwake should devote its resources to producing as many viable young as possible. Lack (1954) proposed that clutch size should be maximised to achieve this aim. However, subsequent researchers have indicated that a compromise must be reached: to maximise lifetime reproductive success current fecundity must be balanced against residual reproductive effort (Pianka & Parker 1975, Williams 1966). Hence clutch size should be optimised rather than maximised (Charnov & Krebs 1974). As a long-lived species of bird the kittiwake comes at the 'K' end of the r-k continuum and should allocate resources accordingly (Horn & Rubenstein 1984).

Study of such behaviour has been carried out to determine the various factors affecting reproductive success in the kittiwake (Coulson & Thomas 1988). The number of chicks produced per pair of birds (as a measure of reproductive success) has been found to be related to clutch size; date of egg laying; location of the nest within the colony; age and experience of the parents; and individual variations amongst adult birds (Coulson & Thomas 1978, Coulson & Thomas 1985, Coulson & Porter 1985, Nisbet 1978, Parsons 1970).

There is also evidence that birds actively select mates (Reid 1988) and that choice of mate may influence reproductive success. It has been demonstrated that retaining a mate from one breeding season to the next increases reproductive success (Coulson 1966, Coulson 1972, Coulson & Thomas 1983, Chardine 1987). This raises the questions:
i. what causes mate change? and
ii. what are the effects on reproductive success of such change?
Various seabird species have been shown to retain the same mate (shearwaters: Bradley et al 1990; oystercatchers: Harris et al 1987; Bullers mollymawk: Richdale & Warham 1973; red-billed gull: Mills 1973) though for some this has been shown to be almost solely a function of nest site tenacity (e.g. Leach's storm petrel: Morse & Kress 1984).

Changing mate from one season to the next whilst the previous mate is still alive and present ("divorce") occurs in the kittiwake (Coulson 1966) and in other species of seabird (Red-billed gull: Mills 1973; shearwater: Bradley et al. 1990; fulmar: Ollason & Dunnet 1988; oystercatcher: Harris et al. 1987; Johnson & Ryder 1987). These studies have shown that divorce often occurs after an unsuccessful breeding season (one in which no young are fledged). Coulson & Thomas (1983) suggest that an incompatibility exists between the two birds that divorce. However, on forming a new pairbond the individuals that divorced had a lower breeding success than those that retained their mate to the next breeding season.

If birds behave in a way which optimises breeding success, why does divorce occur? Is it most common between pairs that have bred unsuccessfully, or is it a stochastic process? Can the lowered breeding success following divorce (Coulson & Thomas 1983) be offset by an increase in long-term breeding success? Are there trends in the divorce rate over time in the kittiwake colony? This study aims to answer the above questions and thus to determine the significance of divorce within the population and demographic dynamics of a single kittiwake colony.

The project involves a study of the breeding biology of the kittiwake gulls at a colony in North Shields, Tyne & Wear, for the 1990 season. In addition, an analysis of trends in kittiwake reproduction & population dynamics using a computerised database spanning 30 years is carried out to elucidate these relationships.

2 METHODS

2.1 Study site

The study was carried out at a colony established on a warehouse in North Shields, Tyne & Wear. Since 1949 kittiwakes have been breeding on this building and the colony reached a maximum of 104 pairs in 1965. The lower floors of the warehouse are now used as a workshop; the top floor is unused and the two floors beneath this are used only for storage. The south side of the building overlooks the River Tyne approximately a kilometre from its mouth where its width is about 500m. The north face overlooks a road and the west & east sides overlook a building site and a yard respectively. The kittiwakes use the window ledges on the top three floors of the warehouse as nest sites.

The area which was occupied by birds when the colony was at 50% of its maximum size is called the "centre" of the colony. Nests outside this area are in the "edge" of the colony. A significant difference has been found between the reproductive successes of birds in each of these areas (Coulson & Thomas 1985a). Additional ledges were added to some windows in the centre of the colony in 1962 & 1983.

2.2 Data collection

Since 1954 all birds breeding in the colony have been marked with a unique colour ring combination and a BTO monel ring (see Coulson & Thomas 1985b). Chicks have been given a BTO monel ring also and, since 1972, an engraved, laminated darvic colour ring. Birds are caught from within the building using a wire hook. Unringed birds are assumed to be breeding for the first time as it has been shown that once a bird has bred it will not subsequently breed in another colony (Coulson & Thomas 1983). This also means that the absence of a bird from the colony for more than two years indicates its death.

This study was conducted between May and July 1990, during which period the colony was visited two to three times a week. On each visit all birds' colour ring combinations were noted as were their breeding sites and their mates' colour ring combination. From this, the status of the bird could be ascertained: whether it had retained its mate from the previous season ("same mate / faithful"), its partner had died ("widowed") or its previous partner was present in the colony but paired with a new bird this year ("divorced"). If unringed the bird was assumed to be a first-time breeder and was captured, ringed with a unique colour combination and a BTO Monel ring; sex was determined where possible from body weight, head & bill length and behaviour.

The date on which the first egg was laid was determined by averaging the dates of the two visits between which the egg appeared (an interval of not more than three days). There is a two day interval between the laying of the first and second egg, so if both eggs were present this further indicated the date of laying of the first egg. An additional indicator of the age of an egg is the dirtiness of its shell: first and second (and the occasional third) egg could therefore be distinguished. (The second egg is also generally longer and narrower than the first). Length and breadth measurements of each egg were taken using Vernier callipers (accurate to the nearest mm). The number of eggs per nest was noted, as was the number which successfully hatched. Eggs which did not hatch within five weeks of lay date were removed and opened to determine the cause of hatching failure. Where an embryo was present it was aged using information published by Maunder & Threfall (1972).

Chicks were ringed with a BTO Monel ring and a darvic colour ring engraved with a unique letter and number combination. From the age of seven days chicks were weighed on each visit using a digital balance, as their growth rate from this age is approximately linear (Coulson & Porter 1985). Subsequent weighings were performed at seven day intervals until chicks had reached their asymptotic weight. Chicks surviving to the age of four weeks were counted as having successfully fledged, as death subsequent to this date is unlikely to be through parental negligence.

Analyses were performed on the 1990 data and on the computerised data set using the Statistical Package for the Social Sciences (SPSS.X) (SPSS 1988). Means are expressed ± 1 S.E. The null hypothesis is rejected if probability of occurrence is less than 0.05.

3 ANALYSIS OF 1990 DATA

The following data were collected for the 1990 breeding season:

i) Colour-ring combination of each bird. From this, the mate and status of each breeding female in the colony was calculated (by determining from record cards its partner of the previous year, and the location of that partner in this year).
ii) Number of eggs in each clutch; length and breadth measurements of each egg laid; and date each egg was laid.
iii) The number of chicks successfully hatched from each clutch.
iv) The growth rate of each chick.
v) The number of chicks which successfully fledged from each brood.

The data were analysed to determine whether birds which had divorced since the previous breeding season showed a significant difference in any aspect of their reproductive biology from birds of other statuses in the colony.

3.1 BREEDING STATUS AND AGE STRUCTURE OF BIRDS IN THE COLONY

The total number of breeding pairs was 85, an increase of 9% over the mean colony size of 76 pairs (Section 4.1).

3.1.1 STATUS

The number of birds of each status was calculated for females only (Table 1) (as performed on the computerised data set, Section 4.1). "First-time breeders" had never bred before, though they may have been present at the colony in the previous season (when they would have been termed "prospectors"). With the exception of one bird, birds of all other statuses had been present and breeding in the colony in the previous year: 50% retained their mate from 1989; 13% took a new mate because their old mate did not return (mate assumed dead, status of remaining bird = "widowed"); and 21% divorced, i.e. their mate was present in the colony but paired with another bird. The one female which had bred previously but missed the 1989 breeding season was excluded from all calculations.

Table 1: The number and percentage of females of each status in the colony for the 1990 season.

	First-time breeder	**Retained mate**	**Mate dead**	**Divorced**
Number:	15	40	11	18
Percentage:	18	48	13	21

The percentage of birds which divorced or retained the same mate was recalculated as a percentage of those pairs of which both members returned to the colony. The divorce rate was 30%, slightly higher than previous years (Section 4.1). The percentage of faithful birds was therefore 70%, far higher than would be predicted by the trends in the computerised data set (Section 4.1). The percentage of widowed birds was recalculated as a percentage of all birds which bred in the colony in the previous season, hence could have potentially lost their mate through death. This gave a result of 16% which is comparable with the percentages found in the data set (Section 4.1).

For 1989, the number of birds of each status (Table 2) was significantly different from the numbers found in 1990 (Table 3).

Table 2: The number and percentage of females of each status found in the colony for the 1989 season.

	First-time breeder	**Retained mate**	**Mate dead**	**Divorced**
Number:	41	23	11	11
Percentage:	47	27	13	13

The percentage of birds retaining their mate (out of all pairs which bred in the colony in the previous year) was 68% and the percentage of widowed birds was 24%. These values were not significantly different from those obtained in 1990 (Table 4).

Table 3: Chi-squared test between number of females of each status in colony for years 1989 and 1990.

		First-time breeder	**Retained mate**	**Mate dead**	**Divorced**
Year:	1989	41(28)	23(32)	11(11)	11(14)
	1990	15(28)	40(31)	11(11)	18(14)

$X^2 = 18.33$ df = 3 $P<0.01$

The percentage of first-time breeders in 1989 was 47%, far higher than in 1990. The Chi-squared test was repeated, omitting first-time breeders, and the result was not significant (Table 4).

Table 4: Chi-squared test between number of females of the three statuses listed which were in the colony for years 1989 and 1990.

		Retained mate	**Mate dead**	**Divorced**
Year:	1989	23(25)	11(9)	11(11)
	1990	40(38)	11(13)	18(17)

$X^2 = 1.28$ df = 2 N.S.

Only the proportion of first-time breeders was significantly different between 1989 and 1990.

3.1.2 BREEDING EXPERIENCE

In the 1990 season, the breeding age frequency distribution for the colony (excluding first-time breeders) was calculated (Table 5).

Table 5: Breeding age frequency distribution within each status for 1990 season.

		Breeding experience						
		2	**3**	**4**	**5**	**6**	**>6**	**TOTAL**
Status	Same mate	21	3	5	5	3	3	**40**
	Widowed	5	2	1	2	0	1	**11**
	Divorced	9	2	6	0	1	0	**18**
	TOTAL	**35**	**7**	**12**	**7**	**4**	**4**	

Of the birds faithful to their mate, 54% had bred for two years. For divorced birds, 47% had a breeding age of two: divorce is occurring no more frequently in younger birds (Table 6) than in older birds (c.f. Coulson & Thomas 1983).

Table 6: Status of birds of different breeding experience

		Breeding experience	
		2	**>2**
Status	Same mate	21(20)	19(20)
	Widowed	5(6)	6(6)
	Divorced	9(10)	9(10)

$X^2 = 0.62$ df = 2 N.S.

The proportion of each status in the two age groups was not significantly different: age did not have a significant effect on status in the 1990 season.

3.2 FACTORS AFFECTING EGG LAYING

The number of eggs in a clutch, the volume of the eggs laid and the date on which they are laid differ significantly with the age of a bird (Coulson 1966, Coulson & Thomas 1978, Thomas 1983). These proximate factors have been shown to significantly affect reproductive success (Coulson & Thomas 1988). Hence, to determine whether divorce has a significant effect on reproductive success, its influence on each of the above must be considered.

3.2.1 Number of eggs

A major factor influencing the breeding success of a bird is the number of eggs it can produce (Thomas & Coulson 1988). For the 1990 breeding season the mean number of eggs laid was not significantly different between the four statuses (Table 7).

Table 7: Mean number of eggs laid by each status

Status	Sample size	Mean number of eggs
Faithful	40	1.98 ± 0.05
Divorced	17	2.00 ± 0.11
Widowed	11	2.00 ± 0.14
First-time breeder	12	1.92 ± 0.08

Analysis of Variance performed on the above groups:

Variance	Sum of Squares	df	Mean S.S.	F	Signif.
Within cells	9.89	76	0.13	0.14	0.93
Status	0.86	3	0.02		
Total	10.75	79	0.15		

Any differences in breeding success between the four statuses could not be attributed to a difference in the number of eggs laid as there is no significant difference between the four groups.

3.2.2 Date of laying

The earlier in the season that a pairbond is established, the earlier the eggs will be laid. Birds which re-establish a bond with the mate of the previous year breed earlier than birds which change mate (Coulson & Thomas 1983). For the 1990 season, the first day of May was taken as Day 1. Most eggs were laid in May, but a few clutches commenced in June (hence date of laying was greater than thirty one).

A One-way Analysis of Variance was carried out between the mean date of laying of the four statuses (Table 8).

Table 8: Mean date of egg laying for each status in 1990.

Status	Mean lay date	Sample size
Divorced	15.7 ± 1.27	13
Faithful	16.1 ± 0.48	40
Widowed	16.6 ± 1.25	11
First-time breeder	20.3 ± 1.56	12

Oneway ANOVA performed on the above groups:

Variance	Sum of Squares	df	Mean S.S.	F	Signif.
Between groups	225.3	3	75.1	4.47	0.006
Within groups	1328.3	79	16.8		
Totals	1553.6	82	91.9		

The Analysis of Variance indicates a significant difference between the means of the statuses (significant between groups variance). To determine which groups were significantly different from one another a Scheffe test was carried out. The result showed the mean date of laying for first-time breeders to be significantly later (at the $P<0.05$ level) than the mean for both divorced and faithful birds, but not significantly different from that of widowed birds. Mean date of laying is not significantly different between the three statuses of experienced birds.

3.2.3 Egg volumes

The volume of an egg from which a chick hatches has been shown, for some species of Larid, to influence the chick's survival rate (Parsons 1970, herring gulls). The 1990 data was tested to determine whether there were significant differences between the egg volumes laid by the various groups and to see whether these had an effect on reproductive success.

The mean volume of the first-laid egg (44.8 ± 0.3 cm^3) was significantly larger than the mean volume of the second egg (43.2 ± 0.4 cm^3) for all breeding birds: Paired t-test, $t = 5.0$, $df = 76$, $P<0.001$. This is consistent with previous studies (Thomas 1983) and hence some calculations on egg volume were performed separately for each egg.

a) Effect of Breeding experience

There was no linear relationship between egg volume and the breeding experience of the female. For the first egg laid, $r = 0.17$, df = 73, N.S.; for the mean volume of first and second eggs, $r = 0.13$, df = 73, N.S.

Thomas (1983) showed egg volume to increase with female breeding age in a non-linear fashion. Using Spearman's Rank Correlation (a nonparametric test not requiring normally distributed data or linear relationships), a significant relationship between breeding age and mean egg volume was obtained ($r_s = 0.22$, df = 81, $P<0.05$). Hence, egg volume does increase with age of the females breeding in 1990 but not in a linear manner.

For birds which bred in 1989 and 1990 and produced two egg clutches there was a significant increase in the mean egg volume of both eggs laid from 43.6 ± 0.3 cm^3 to 44.5 ± 0.3 cm^3 (Paired t-test, $t = 2.02$, df = 50, $P<0.05$) (See Appendix C for data and statistics). The increase in age from 1989 to 1990 produced a significant increase in the volume of eggs laid.

b) Effect of Status

To test whether there was a significant difference between the mean volume of eggs laid by females retaining their mate (44.12 ± 0.41) and the mean volume for divorced females (44.06 ± 0.65) a Student t-test was used. The result was not significant ($t = 0.11$, df = 58, N.S.). To control for female breeding age whilst comparing the mean egg volumes of each status,an Analysis of Covariance, using the Unique Sum of Squares (S.S.) method, was performed (Table 9).

Table 9: ANCOVA between mean volume of eggs laid by faithful females and divorced females, with age as the covariate.

Variance	Sum of Squares	df	Mean S.S.	F	Signif.
Within cells	422.4	56	7.54		
Covariate	4.85	1	4.85	0.64	0.43
Between cells variance	0.84	1	0.84	0.11	0.74
Totals	428.09	58	5.69		

The result was not significant: there was no significant difference between the mean egg volume for faithful females and divorced females (Table 9).

c) Effect of date of egg laying

There was no significant relationship between the date of laying of the first egg in a brood and the volume of the egg (Correlation coefficient, $r = 0.01$, $n= 83$, N.S.). However, the volume of the second egg showed a significant negative correlation with lay date ($r = -0.255$, $n= 77$, $P<0.05$). The test was not performed for each status as: i) sample sizes were too small, ii) there was no significant difference between the date of laying for each status (Table 8).

d) Effect of morphology

When each bird is ringed as an adult either prospecting at the colony or breeding for the first time, a measurement of the length of its head plus bill is taken. This measurement was taken to have a proportional relationship to the bird's skeleton and hence to serve as an indicator of body size. It was unfeasible to weigh every breeding female at the time of egg laying, due in part to a high risk of trauma to the incubating bird.

When a correlation was performed between head and bill length and volume of the first egg the result was not significant ($r = 0.10$, $n = 83$, N.S.). This measure of a bird's body size did not explain any variation in the volume of the first egg laid.

3.3 FACTORS AFFECTING HATCHING AND FLEDGING

3.3.1 Hatching success

Hatching success is calculated as the number of chicks hatched/number of eggs laid. It is a measure of the effectiveness of a pair of birds at successfully incubating the eggs in their clutch.

a) Effect of status

To determine whether status had a significant effect on hatching success an Analysis of Variance was performed. Table 10 compares the mean hatching success for each status for 1990.

Table 10: Mean hatching success for each status.

Test of significance performed using Oneway Analysis of Variance.

Status	Mean hatching Success	Sample size
Divorced	0.89 ± 0.08	14
Faithful	0.73 ± 0.06	40
Widowed	0.86 ± 0.10	11
First-time breeder	0.42 ± 0.14	12

Oneway ANOVA performed on the above groups:

Variance	Sum of Squares	df	Mean S.S.	F	Signif.
Between groups	1.75	3	0.58	4.12	0.009
Within groups	10.60	75	0.14		
Totals	12.35	78	0.72		

Scheffe test: Divorced & First-time breeders are significantly different.

There was no significant difference between the hatching success of the three statuses of experienced birds. The only significant difference was between first-time breeders and divorced birds: the latter were 100% more successful at hatching their chicks than the inexperienced birds. The test distinguished between birds that had bred before and those which had not rather than between faithful birds and those which had changed partner.

Number hatched

A test of the difference between the number of eggs successfully hatched per pair for each status was then carried out. It gave a better indication of the ability of the female to produce eggs, not only to hatch those she had already laid. Hence, it served as a better measure of reproductive success. The mean number of chicks hatched by each status was calculated and a test of significance between the values was performed using a Oneway Analysis of Variance (Table 11).

Table 11: Mean number of chicks hatched for each status.

Status	Mean no.chicks hatched	Sample size
Divorced	1.79 ± 0.19	14
Faithful	1.45 ± 0.12	40
Widowed	1.73 ± 0.24	11
First-time breeder	0.83 ± 0.27	12

Oneway ANOVA performed on the above groups:

Variance	Sum of Squares	df	Mean S.S.	F	Signif.
Between groups	6.98	3	2.33	3.75	0.01
Within groups	46.61	75	0.62		
Totals	53.59	78	2.95		

Scheffe test: Divorced & First-time breeders are significantly different.

The mean number of chicks hatched per pair was significantly different only between divorced birds and first-time breeders, as with hatching success.

Divorced birds in the 1990 data set were the most successful status as a few individuals did exceptionally well: only four, three-egg clutches were laid in the whole colony in 1990. Of these, 50% were laid by divorced females (Appendix A).

b) Effect of date of egg laying

Hatching success had a significant and negative correlation with the date on which the first egg was laid ($r = -0.26$, $n=82$, $P<0.01$). Eggs laid later in the season were less likely to hatch than those laid earlier. Status was not controlled for as there was no significant difference between the mean date of egg laying for each status (Table 8).

c) Effect of egg volume

There was no correlation between egg volume and hatching success ($r = -0.02$, $n=84$, N.S.).

Eggs failing to hatch

Eggs which had failed to hatch seven days after the predicted hatching date (i.e. 35 days after being laid) were removed and examined. Identifying the stage of development of each embryo from Maunder & Threfall (1972) enabled an estimate to be made of the age of the embryo when it died (Appendix B). Generally, embryos from clutches laid by first-time breeders died at a later stage in their development than embryos of other statuses. Over 50% of the eggs of faithful birds that did not hatch were not fertilised, so failure to hatch was not due to inadequate incubation. Sample sizes were too small to test statistically.

3.3.2 Chick growth rates

Chick growth rate approximates to a sigmoidal curve. Between body mass of 100g and 300g the mean growth rate of a chick is linear (approx. 15g/day) (Coulson & Porter 1985). During the 1990 season chicks were weighed from about day seven after hatching until chick mass had reached 300g. The aim was to determine whether status of the female had a significant effect on the growth rate of the chick, whilst considering other factors which may also have influenced the chick growth rate.

a) Egg volume

In a study of the herring gull, *Larus argentatus*, Parsons (1970) found a positive correlation between egg volume and chick survival rate. It has been suggested that chick death occurs in the first week after hatching when reserves of yolk within the egg are insufficient to support the chick during establishment of the parent - offspring bond post hatching (herring gulls: Parsons 1970; terns: Nisbet 1978; geese: Rowher & Eisenhauer 1989).
To determine whether the volume of egg from which the chick hatched correlated with its growth rate data from the first chick hatched in a two-chick brood was used. Clutches of first-time breeding birds were not included as the females lay consistently smaller eggs (Thomas 1983). No relationship was found between the volume of the egg and the linear growth rate of the chick ($r = 0.02$, $df = 40$, N.S.). This may be due in part to the fact that the chicks weighed were already over 100g, i.e. they had survived the initial period of parent-chick bond establishment.

b) Number of chicks

Coulson & Porter (1985) discovered that the first and second chicks hatched from a three-chick brood had significantly higher growth rates than either chick in a two-chick brood. In 1990 only two three-chick clutches were laid so comparisons were performed between, and within, two-chick and one-chick broods. A single chick would logically grow more rapidly than either chick in a two-chick brood as its parents could deliver proportionally more food to it.

A student t-test was carried out between the mean growth rate of chicks in a one-chick brood (15.91 ± 1.67 g/day) and the mean growth rate of both chicks in a two-chick brood (12.46 ± 0.84 g/day). First-time breeders were not included in the calculations. The t-value was significant ($t = 2.07$, $df = 46$, $P<0.05$), indicating that the mean growth rate of chicks in a brood of two was slower than that of chicks in a brood of one.

There was not a significant difference between the mean growth rate of the first chick in a two-chick brood (13.39 ± 1.25) and the mean growth rate of a one-chick brood ($t = 1.20$, $df = 46$, N.S.). Hence the significant difference in growth rates for the two clutch sizes lies between the one-chick brood and the second chick in a two-chick brood.

c) Status

To determine whether there was a significant difference between the growth rate of chicks hatched by divorced birds and chicks hatched by faithful birds Student t-tests were carried out on the data (Table 12).

In one-chick broods, the chicks of divorced females had a significantly lower growth rate than the chicks of females with the same mate since 1989. Familiarity with the partner has a significant and positive effect on chick growth rate (Table 12(i)). In two-chick broods there was no significant difference between the growth rate of either chick (Table 12(ii)). However, the sample sizes were too small (divorced birds = 4) and variance too high for a valid statistical comparison.

Table 12: Mean growth rates of chicks of divorced and faithful females.

i) One-chick brood

Status	Mean Growth Rate	Sample size	t value	Signif.
Divorced	9.98 ± 3.71	5		
Faithful	18.33 ± 1.24	9	2.64	<0.025

ii) Two-chick brood

A. Chick 1

Status	Mean Growth Rate	Sample size	t value	Signif.
Divorced	10.20 ± 4.95	4		
Faithful	13.57 ± 1.49	20	0.86	N.S.

B. Chick 2

Status	Mean Growth Rate	Sample size	t value	Signif.
Divorced	12.87 ± 3.56	4		
Faithful	18.33 ± 1.24	20	0.15	N.S.

Mean chick growth rates for divorced and widowed birds were then combined and the t-tests repeated between faithful birds and birds which had changed their mate since 1989 (Table 13). There was no significant difference between the mean growth rates of the one-chick broods in each group (Table 13(i)). This indicates that adding the mean chick growth rates of widowed birds increased the overall mean. However, variance was still high and sample sizes small.

There was no significant difference between the mean growth rates of the first chick of each status (faithful and changed mate) in the two-chick broods (Table 13(ii)). However, the second chick of birds which had changed their mate since 1989 grew significantly more slowly than the second chick of faithful pairs (Table 13(ii)B). Though mate status does not significantly affect the growth rate of the first chick in a two-chick brood it does have a significant effect on the growth rate of the second chick.

Table 13: Mean growth rates of chicks of faithful females and those females with a new mate since 1989.

i) One-chick brood

Status	Mean Growth Rate	Sample size	t value	Signif.
Changed	13.20 ± 3.10	8		
Faithful	18.33 ± 1.24	9	1.54	N.S.

ii) Two-chick brood

A. Chick 1

Status	Mean Growth Rate	Sample size	t value	Signif.
Changed	13.07 ± 2.35	11		
Faithful	13.57 ± 1.49	20	0.19	N.S.

B. Chick 2

Status	Mean Growth Rate	Sample size	t value	Signif.
Changed	8.40 ± 1.94	11		
Faithful	13.25 ± 0.92	20	2.56	<0.02

Variance in the data is high. Chick mass can vary by over 12g depending on whether it has been fed recently. (Chicks sometimes vomited the contents of their stomach when handled. In such cases the bolus was included in the measurement of the chick's mass. The mass of a bolus recorded from a chick of 108g was 12g - over 10% of its body weight, which would have had an effect on the calculated growth rate of 1.7g/day)

3.3.3 Fledging success

Fledging success is calculated as the number of chicks fledged/number of chicks hatched. It is a measure of the effectiveness of the parents at raising the chicks they have hatched.

To determine whether status had a significant effect on fledging success an Analysis of Variance was performed. Table 14 compares the mean fledging success for each status for 1990.

Table 14: Mean fledging success for each status.

Status	Mean fledging Success	Sample size
Divorced	0.71 ± 0.10	14
Faithful	0.69 ± 0.06	40
Widowed	0.83 ± 0.10	11
First-time breeder	0.46 ± 0.14	12

Oneway ANOVA performed on the above groups:

Variance	Sum of Squares	df	Mean S.S.	F	Signif.
Between groups	4.46	3	1.48	2.38	N.S.
Within groups	46.88	75	0.62		
Total	51.34	78	2.10		

No two groups were significantly different at the 0.05 level (Scheffe test).

There was no significant difference between the fledging success of any of the four statuses of birds, unlike the result for hatching success (Table 10).

Number of chicks fledged

A test of the difference between the number of chicks successfully fledged per pair for each status was then carried out. It gave the most representative measure of reproductive success by presenting actual numbers fledged (rather than a proportion of those laid). The mean number of chicks fledged by each status was calculated and a test of significance between the values was performed using a Oneway Analysis of Variance (Table 15).

Table 15: Mean number of chicks fledged for each status.

Status	Mean no.chicks fledged	Sample size
Divorced	1.43 ± 0.23	14
Faithful	1.19 ± 0.12	40
Widowed	1.54 ± 0.20	11
First-time breeder	0.75 ± 0.25	12

Oneway ANOVA performed on the above groups:

Variance	Sum of Squares	df	Mean S.S.	F	Signif.
Between groups	4.46	3	1.49	2.38	N.S.
Within groups	46.88	75	0.63		
Total	51.34	78	2.12		

No two statuses had significantly different means. Hence, there was no significant difference between the mean number of chicks fledged by each of the statuses.

3.3.4 Breeding success

Breeding success is calculated as the number of chicks fledged/number of eggs laid. It indicates the ability of a pair to produce chicks, controlling for clutch size. When a test was carried out between the mean value for each status the result was, once again not significant (Table 16).

Table 16: Mean breeding success for each status.

Status	Mean breeding Success	Sample size
Divorced	0.68 ± 0.10	14
Faithful	0.60 ± 0.06	40
Widowed	0.79 ± 0.10	11
First-time breeder	0.38 ± 0.13	12

Oneway ANOVA performed on the above groups:

Variance	Sum of Squares	df	Mean S.S.	F	Signif.
Between groups	1.08	3	0.36	2.38	N.S.
Within groups	11.31	75	0.15		
Total	12.39	78			

No two groups were significantly different at the 0.05 level. The level of within groups variance was very high, as in other tests of breeding performance against status presented above.

4 ANALYSIS OF LONGTERM DATASET

In this section the computerised data set spanning the years 1954 to 1986 is analysed to investigate effects of pair status on reproductive output and vice versa. The questions addressed are as follows:

I. WHEN DOES DIVORCE OCCUR?
II. WHAT CAUSES DIVORCE? / WHO DIVORCES?
III.WHAT ARE THE EFFECTS ON REPRODUCTIVE OUTPUT OF DIVORCE?

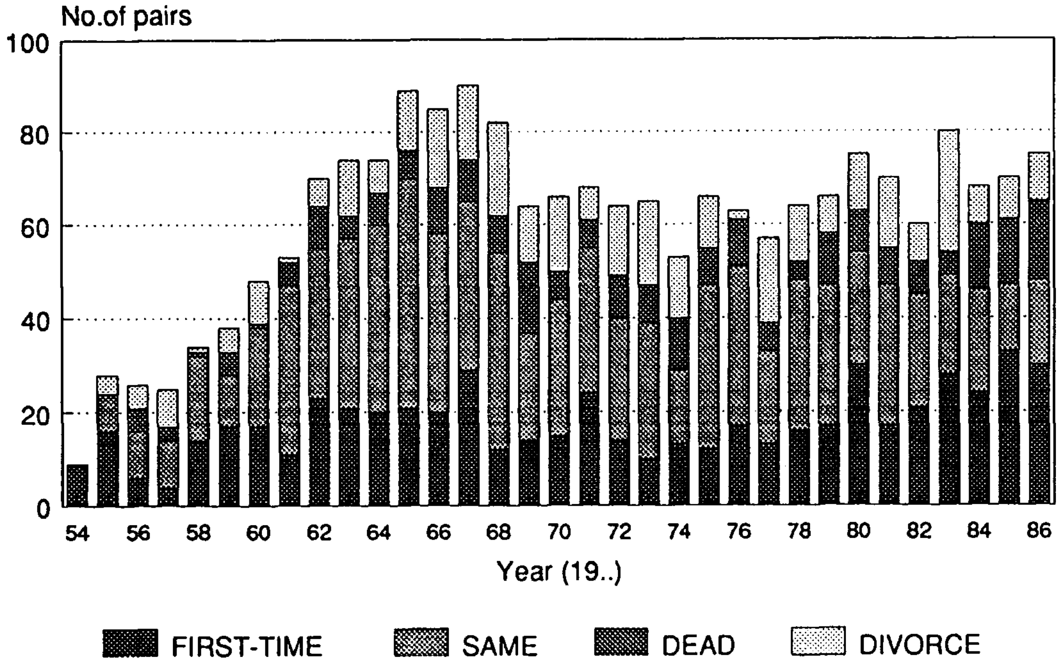
The dataset has been coded such that the status of the female alone is recorded. All calculations, therefore, referring to status are based on the female member of a breeding pair. In analyses of breeding performance this is acceptable as the initial determinant of reproduction is the laying of eggs by the female.

4.1 POPULATION CHANGES & TRENDS IN DIVORCE

The North Shields colony is not a discrete population. Young birds move between it and the nearby colonies of Newcastle (9km distant), Marsden (5km) and Tyneside (3km). However, once a bird has bred at one colony it will not breed elsewhere (Coulson & Wooller 1976). This project studies only those birds that have bred at the colony for at least one season.

Colony size (measured as number of pairs of breeding birds) increased from the time of initial data collection in 1954 until 1965 (Fig.1). The population then declined until 1977 after which it fluctuated about a mean 76

Fig.1: Proportion of each status
in colony for years
1954-1986



pairs (SD=7.2, years=16).

The period from 1956 to 1986 was analysed for population trends; it was chosen as the period over which the colony was large enough to maintain demographic stability.

Subdividing into year groups

To analyse trends in the data set it was divided into five-year periods commencing in 1956. Of the six groups therefore created, the final one contained data from six years (1981-1986). The groups will, however, be referred to as the six, five-year groups and note should be made of the extra year included in the final group.

To test whether there was a significant change in the relative proportions of birds of the statuses faithful (or "same"), widowed & divorced between these groups a Chi-squared test was used (Table 1).

Table 1: Birds of each status in colony for year groups 1 to 6.

i.Numbers of birds

		YEAR GROUP					
		1	**2**	**3**	**4**	**5**	**6**
STATUS:	Faithful	93	168	137	140	129	150
	(EXPCTD)	(67)	(156)	(175)	(143)	(137)	(159)
	Widowed	15	32	48	42	40	65
	(EXPCTD)	(19)	(45)	(51)	(41)	(40)	(46)
	Divorced	28	39	81	64	52	76
	(EXPCTD)	(27)	(63)	(71)	(58)	(56)	(65)

$X^2 = 41.6$ df=10 $P<0.0001$.

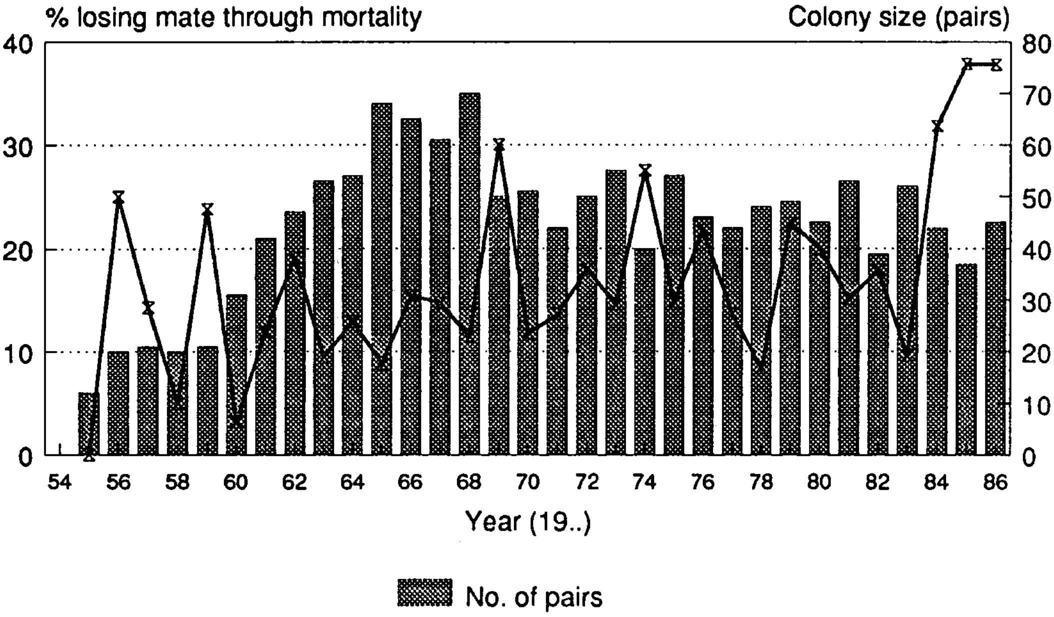
ii.Percentages of each status in each year group

		YEAR GROUP					
		1	2	3	4	5	6
STATUS:	Faithful	62	73	57	56	60	48
	Widowed	13	12	16	17	17	24
	Divorced	25	15	27	27	23	28

The Chi-squared result indicated a significant deviation from the expected between the year-groups. In the first five-year group (1956-1960) the number of birds with the same mate was greater than the expected value. However, by the final period (of six years: 1981-1986) the number retaining the same mate was far lower than the expected. The percent retaining the same mate decreased. The percent of birds widowed followed the opposite trend: initially lower than predicted, by year-group six the number widowed was higher than the expected value. The percentage of birds divorcing fluctuated through the six periods (Table 1); in the final period the number divorcing was greater than the expected value.

To better determine the changing proportions of each status in the colony across time, five-year running means were plotted for the proportion of widowed (Fig.2b), faithful (Fig.3b), and divorced (Fig.4b) birds and regression equations calculated from the actual data (Fig.2a, 3a and 4a). The percentage of each status was calculated as a percentage of all those birds breeding in the colony Each point of the five-year mean included the mean of the two years preceding and the two following that year. Regression equations were calculated on the period 1963 to 1986 for Figures 3a and 4a and on the

Fig.2a: % losing mate through mortality
in colony for years
1954-86



No increase in % losing mate(y)
y=0.18(+/-0.21)x - 14.0(+/-2.5), r=0.18
df=19 N.S.(x=years 0 to 21, ie.1963-83)

Pairs = birds which bred in colony in previous years

Fig.2b: % losing mate through mortality
and five year means

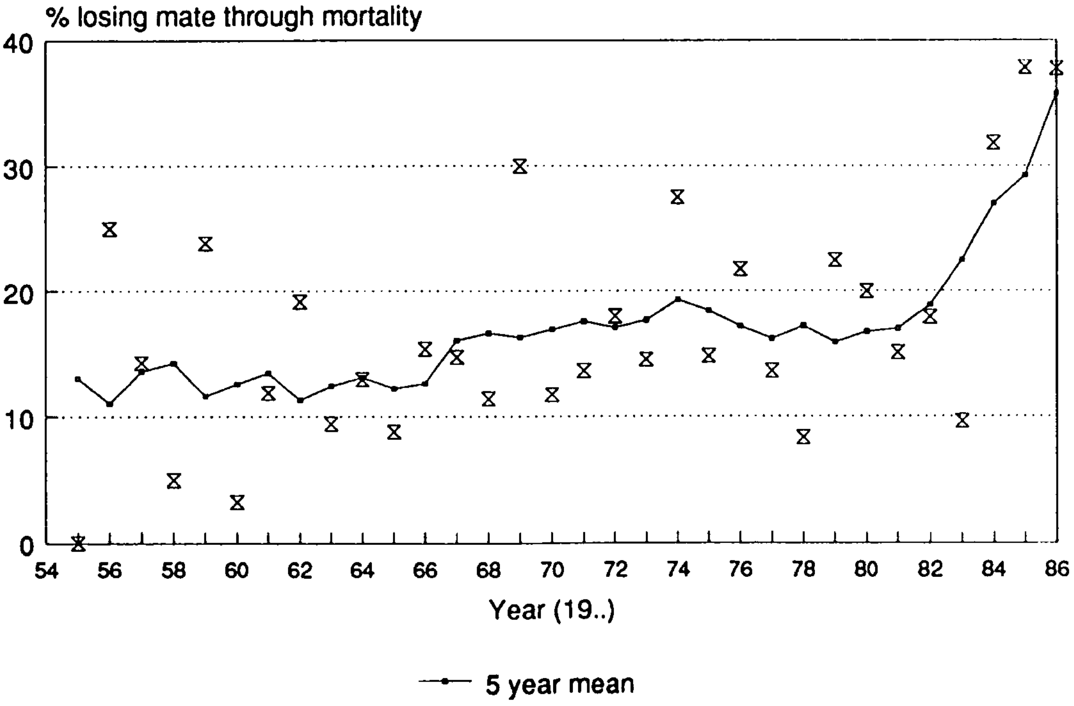
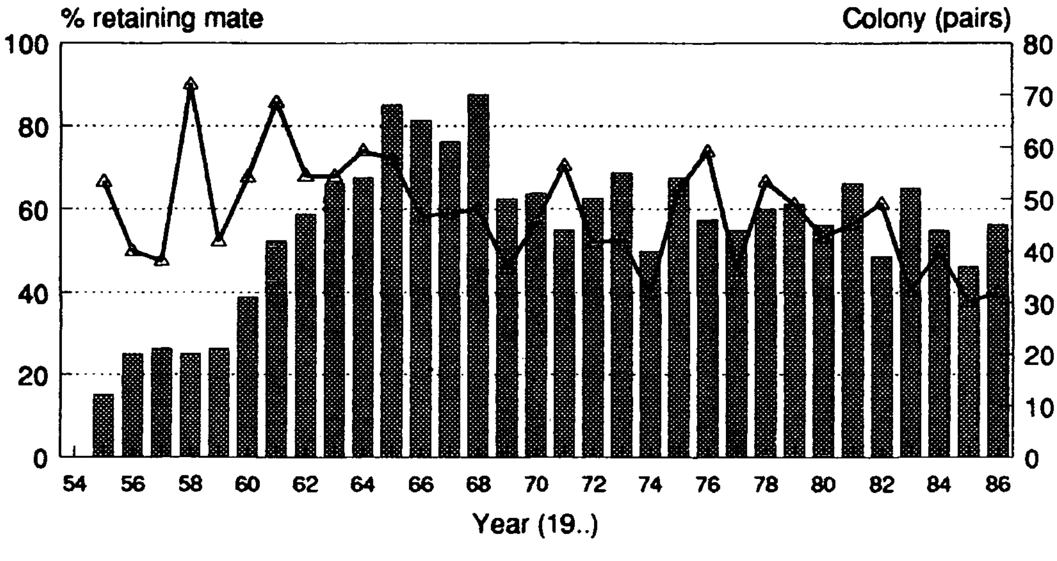


Fig.3a: % birds retaining mate since previous breeding season for years 1954-1986



% retaining mate (y) significantly decreases: y=74.7(+/-4.3)-0.49(+/-0.34)x r=-0.30 df=21 p<0.05(x=yrs 0-22,1963-86)

Where total = birds of status same, dead & divorced

Fig.3b: % birds retaining mate as a five year running mean for 1954-1986

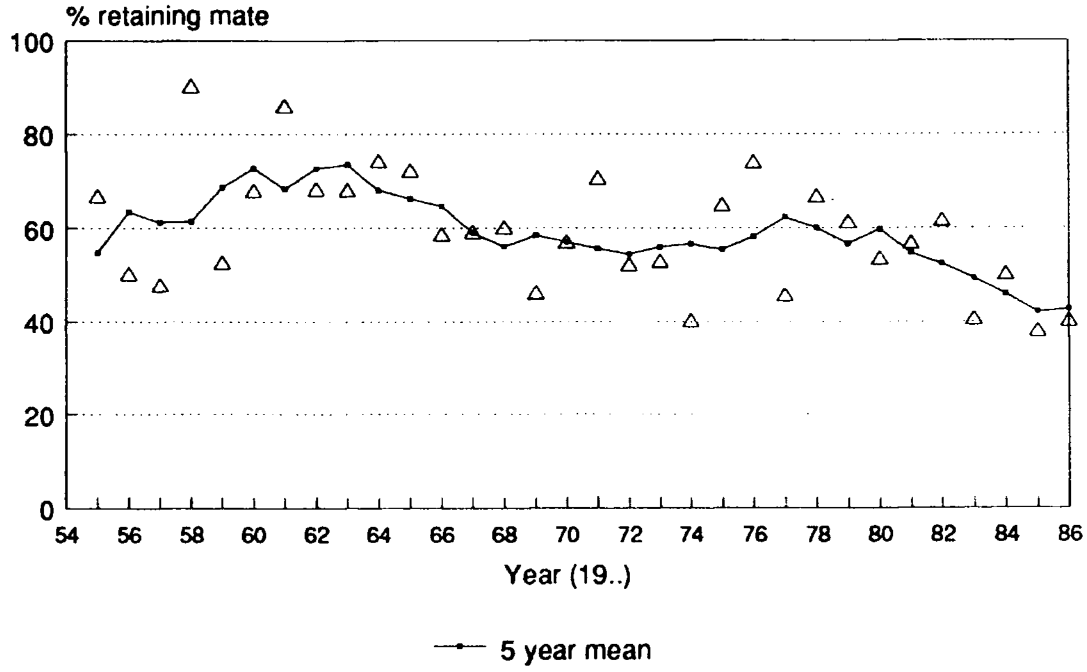
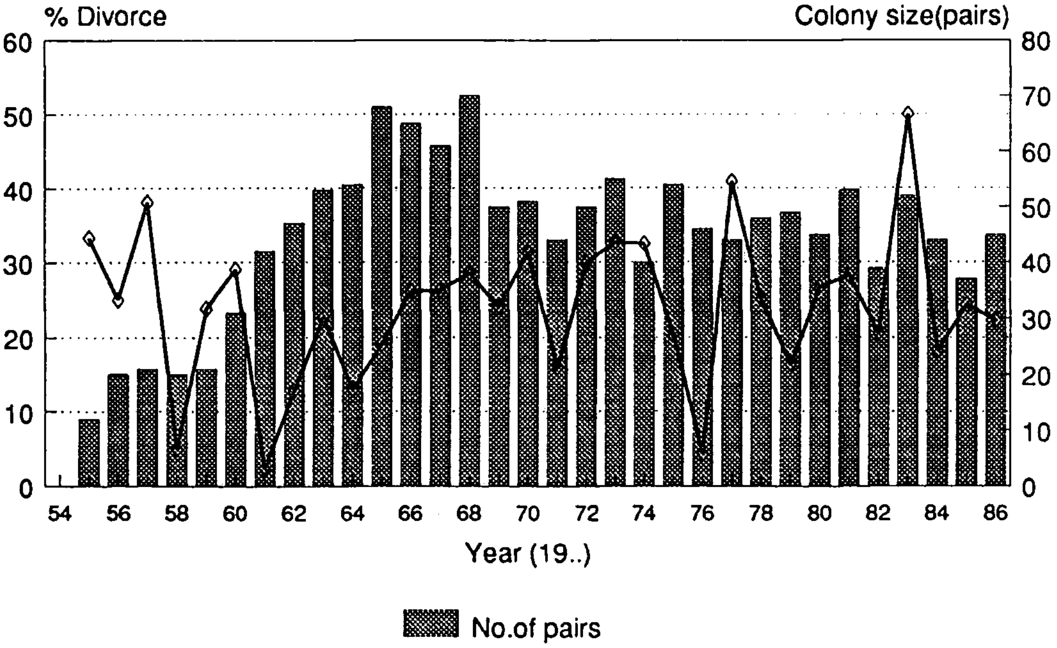


Fig.4a: % of birds divorcing mate of previous season for years 1954-86



% divorcing (y) does not significantly change for years 0-23 (1963-86): y=0.46 (+/-0.34)x +25.4(+/-4.4) r=0.29 df=21 NS

Where no.of pairs= birds of status same, dead & divorced

Fig.4b: % of birds divorcing mate of previous season & 5 year means for 1954-86

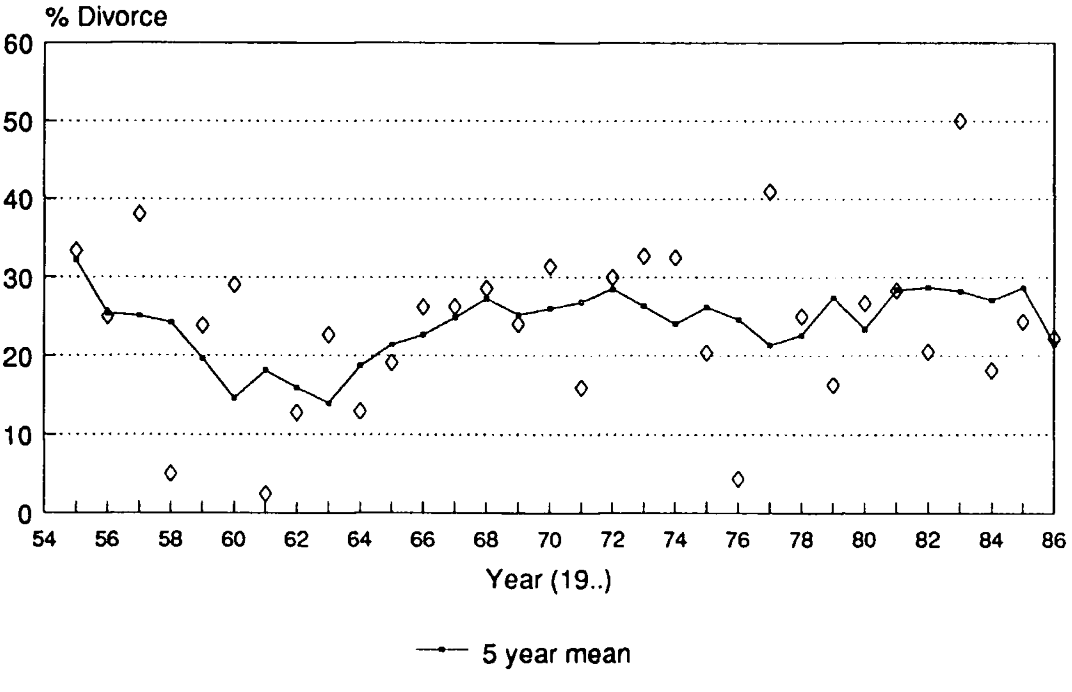
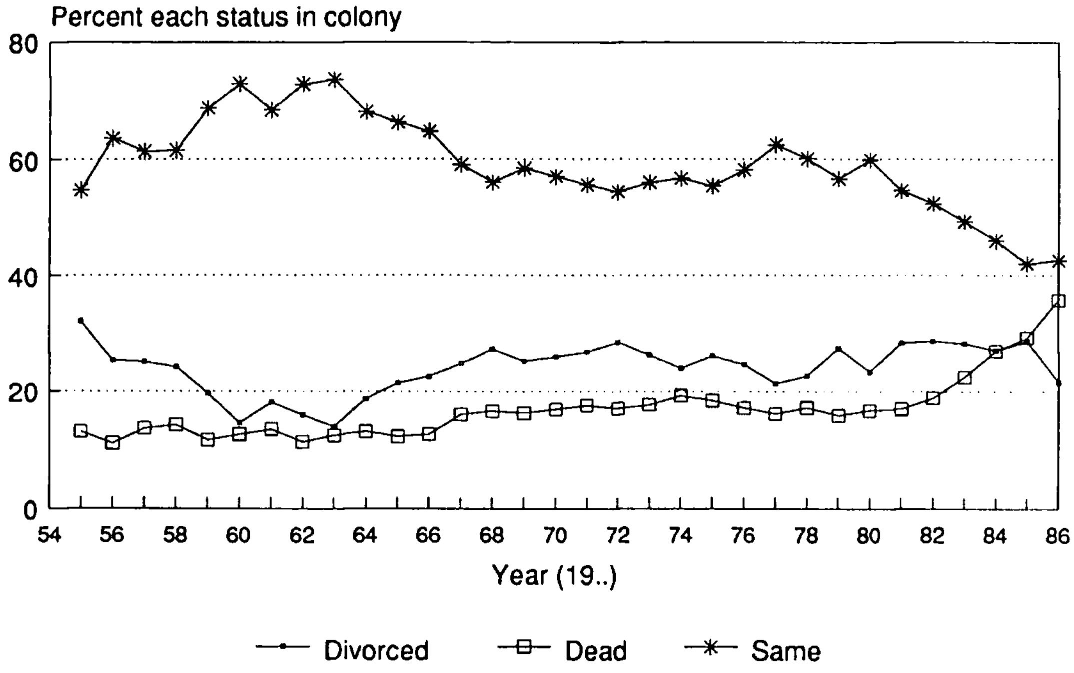


Fig.5 : 5 year running means of % divorcing, retaining mate and losing mate through mortality for years 1955-86



Where colony total = same + divorced + dead only period 1963 to 1983 for Figure 2a. In each test, the first year of the data used was entered as year one.

The percentage of birds in the colony changing partner due to death of the mate of the previous breeding season (status of the remaining bird = widowed) did not significantly increase over the period 1963 to 1983 (Fig.2a). The data from 1984, 1985 and 1986 were excluded as a marked increase in percentage of birds widowed occurred during these years. The five-year mean remained almost constant at 17% until 1966, after which it was approximately 19% until 1983. The mean percent of widowed birds for years 1984-1986 was 35.8% (S.D.= 3.5), a doubling of the rate during the mid 1960's.

The percentage of the colony retaining the same mate from the previous year decreased significantly over the period from 1963 to 1986, reducing by 0.49% per year (Fig.3a). The five-year running mean shows an increase in proportion of faithful birds until 1963. After this the proportion retaining their mate gradually decreased to the end of the dataset, from 68% between 1955 & 1965 to 53% from 1976 to 1986, a reduction of 15%.

There was no significant trend in the percentage of birds divorcing from year to year (Fig.4a). The mean percentage divorcing from 1955 to 1964 was 20.5% whereas from 1965 to 1986 it was 25.6%. However, there was no significant difference between these values (Student's t-test: t=1.326 df=30 N.S.).

4.1.1 Divorce & Mortality

There was no correlation between the number of birds divorcing (calculated as a proportion of those either divorcing or retaining their mate) and the number of birds losing their mate through death (as a proportion of the total number of breeding pairs excluding first-time breeders). This was carried out for the period 1956 to 1965 (ie. the time of initial growth of the colony): r=0.13 df=21 N.S.; and also for the period from 1963 to 1986 (when mean colony size had been reached): r=0.16 df=8 N.S. Increase in the number of widowed birds in the colony (birds which have lost their partner through death) is not accompanied by an increase in the divorce rate.

4.2 MATE CHOICE AND DIVORCE

The dataset was analysed using Chi-squared to establish whether there is a significant difference between the proportion of each status which paired with birds of the other statuses. Females which either divorced, lost their mate through mortality or which had never bred before (firsttime) were tabulated against males of the same three statuses to determine whether a bird of one status preferentially selected a mate of a particular status.

Table 2: Status of mate chosen by each status

		Female			
		1st time	**Widowed**	**Divorced**	
Male	**1st time**:	343(254)	93(127)	78(133)	(EXPECTD)
	Widowed:	57(94)	69(47)	63(49)	
	Divorced:	69(121)	72(61)	104(63)	

$X^2 = 142$ df=4 $p<0.0001$

The result was significant: first-time breeders showed a marked tendency to pair with oneanother so were excluded, and the test repeated (Table 3).

Table 3: Status of mate chosen by widowed & divorced birds; for each sex

i)Numbers

		Female	
		Widowed	**Divorced**
Male	**Widowed**:	69(47)	63(49)
	Divorced:	72(61)	104(63)

X^2= 3.92 (after Yates' correction) df=1 p<0.05

ii)Percentages of females chosen by males

		Female	
		Widowed	**Divorced**
Male	**Widowed**:	52	48
	Divorced:	41	59

Considering males, those which were divorced paired preferentially with divorced females (59%) (Table 3 (ii)); widowed males selected a higher percentage of new mates from females that had also lost their mate (52%). The pairing was significantly different from the expected values. There was no preference by widowed birds to take a new mate from a previously established pair; birds pair preferentially with mates of the same status.

4.3 EFFECT OF REPRODUCTIVE SUCCESS ON DIVORCE

Fledging success (number of chicks fledged/number of chicks hatched per pair) was significantly lower for birds that go on to divorce in the subsequent breeding season than for those which retain their mate (mean fledging success for divorcees= 0.704 ± 0.026, n=275; for those retaining same mate = 0.772 ± 0.014, n=743; t=2.32, df=448, P<0.025). Breeding success (no. of chicks fledged/no. of eggs laid per pair) was not significantly different between birds which went on to divorce and between those which retained the same matein the following breeding season (divorcees= 0.604 ± 0.018, same mate=0.663 ± 0.017, t=1.85, df=1016, N.S.).

A major factor influencing divorce is failure to fledge any chicks in the previous season (Coulson 1966), rather than loss of a proportion of the brood. The dataset was subdivided into birds which failed to fledge chicks and birds which successfully raised one or more chicks; a Chi-squared test was performed between the number of birds in each category which divorced and those which retained the same mate in the following breeding season:

Table 4: Number of birds of each status which either failed or fledged chicks for years 1954-1986

i.Numbers

		Number fledged in previous year:		
		0	**>0**	
Status	Same:	126(140)	617(603)	(EXPCTD)
	Divorced:	66(52)	209(223)	

X^2= 6.05 (After Yates' correction), df=1, P<0.025

ii.Percentage of birds failing or fledging successfully in year prior to divorce or mate retention

		Number fledged in previous year:	
		0	**>0**
Status	Same:	66	75
	Divorced:	34	25

A higher percentage of birds divorced after failing to fledge chicks (34%) than after successfully fledging chicks (25%). Whether or not a bird successfully fledged chicks had a significant effect on mate fidelity: birds successfully fledging chicks are 13% (9/66) more likely to retain the same mate than birds which failed.

Subdividing into year-groups

To investigate whether birds failing to fledge chicks consistently divorce at a higher rate over time than birds which successfully fledged chicks the data were divided into the year-groups used above. Selecting birds which had failed to fledge chicks in the previous breeding season, a Chi-squared test was performed between the number of birds divorcing and the number retaining the same mate in each of the five-year groups (Table 5):

Table 5: Number of birds of status same mate and divorced which failed to fledge chicks in previous season, for year groups 1 to 6

		YEAR GROUP					
		1	**2**	**3**	**4**	**5**	**6**
STATUS:	Same	9	28	37	27	38	15
	(EXPCTD)	(10)	(21)	(33)	(34)	(32)	(24)
	Divorced	5	3	11	22	8	20
	(EXPCTD)	(4)	(10)	(15)	(15)	(14)	(11)

X2=27.8, df=5 p<0.0001

The result is highly significant, indicating that birds which had failed to fledge chicks in the previous year were not divorcing in the same proportion over the year-groups (Fig.6). The percentage of birds retaining their mate was consistently greater than the percentage that divorced for year groups 1-6. The mean divorce rate over the six periods was 31% (± 6%). The divorce rate for birds which had previously failed was highest in the final five year period.

The result for birds which had successfully fledged chicks in the previous breeding season was different (Fig.7). Again, there was a significant difference between the number of birds divorcing and the number remaining together across the six year-groups (Table 6):

Fig.6: % of birds which fail and subsequently divorce or retain mate for six, five-year groups

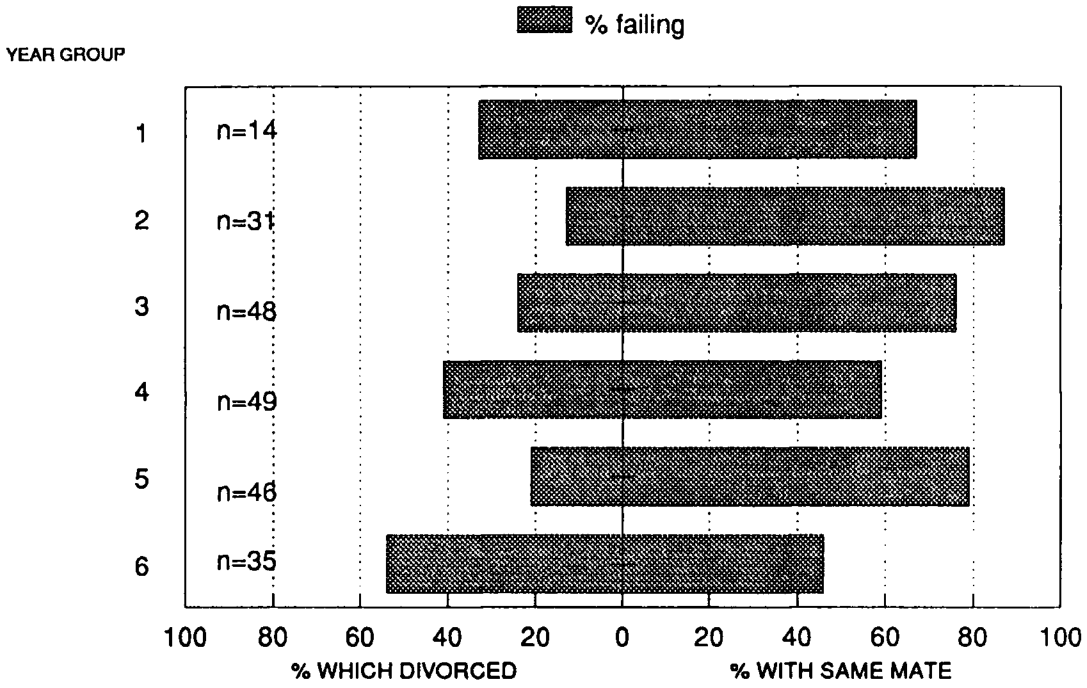


Fig.7: % of birds which fledge chicks & subsequently divorce or retain mate for six, five-year groups

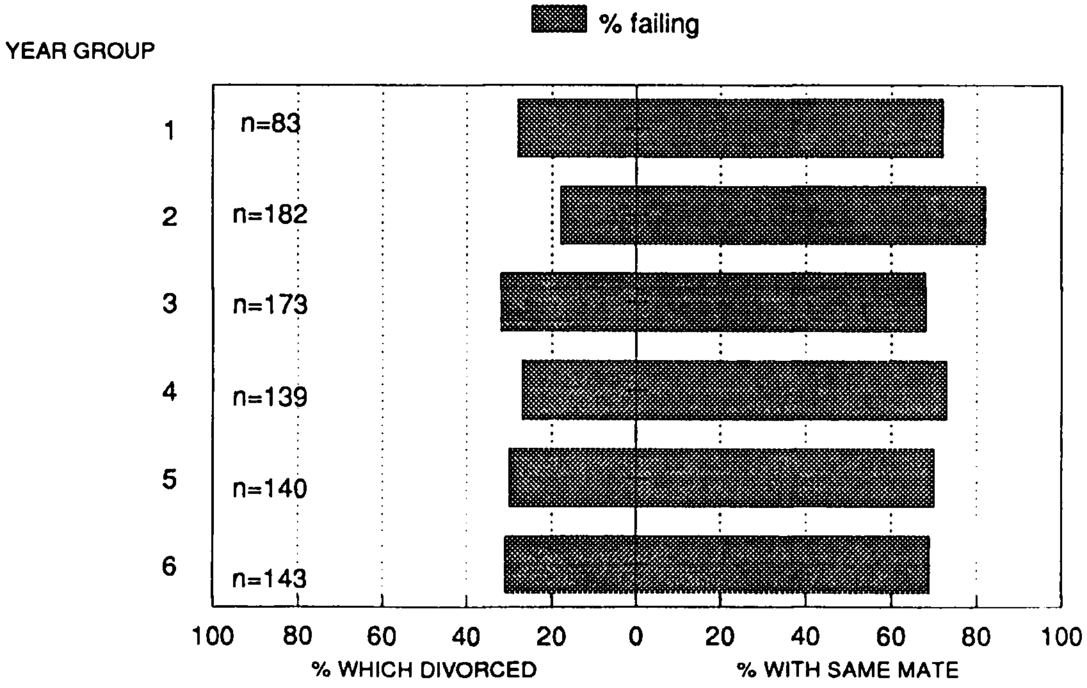


Table 6: Number of birds of status same mate and divorced which successfully fledged chicks in previous breeding season for the six year-groups

		YEAR GROUP					
		1	**2**	**3**	**4**	**5**	**6**
STATUS:	Same	60	149	112	101	97	93
	(EXPCTD)	(59)	(129)	(123)	(99)	(100)	(102)
	Divorced	23	33	61	38	43	50
	(EXPCTD)	(24)	(53)	(50)	(40)	(40)	(41)

X2=16.7 df=5 p<0.005

However, the mean divorce rate for birds which successfully fledged chicks over the six, five-year groups was 28%(± 2%) whereas that for birds which had failed to fledge chicks was 31%(± 6%). The means were not significantly different (t = 0.675, df = 5, N.S.), though birds which had successfully fledged chicks had lower variance in their divorce rate over the six, five-year periods than birds which failed to fledge chicks.

4.4 EFFECT OF DIVORCE ON REPRODUCTIVE SUCCESS

Over the whole dataset divorcees had significantly lower fledging success (mean = 0.664 ± 0.028, n = 295) and breeding success (mean = 0.551 ± 0.024, n = 798) than birds retaining the same mate (mean fledging success=0.753 ± 0.017, breeding success=0.653 ± 0.016):

t-test of fledging success: t=3.22 df=1094 P<0.001;

t-test of breeding success: t=3.7 df=1094 P<0.0001.

To determine whether divorced birds failed to fledge chicks significantly more frequently than faithful birds, a Chi-squared test was performed (Table 7):

Table 7: Number of divorced and faithful birds which either failed or

successfully fledged chicks, for the whole dataset

		No.fledged:		
		0	**> 0**	
<u>Status</u>	Same:	138(160)	638(616)	(EXPCTD)
	Divorced:	86(64)	222(244)	

X^2= 13.2 (After Yates' correction), df=1, P<0.0005

ii.Percentage of each status which either failed or fledged chicks

		No.fledged:	
		0	**> 0**
<u>Status</u>	Same:	18	82
	Divorced:	28	72

The result was significant. Divorced birds did not fail to fledge in the same proportion as did faithful birds: divorced birds failed significantly more than expected

To determine whether divorced birds consistently failed more than faithful birds the data were divided into six, five-year periods and a Chi-squared test performed on the number of birds of each status which failed to fledge chicks (Table 8):

Table 8: Number of divorced or faithful birds which failed to fledge chicks, for year groups 1-6

		YEAR GROUP					
		1	**2**	**3**	**4**	**5**	**6**
STATUS	:Same	7	25	32	26	29	19
	(EXPCTD)	(9)	(19)	(30)	(30)	(28)	(22)
	Divorced	7	6	16	23	17	17
	(EXPCTD)	(5)	(12)	(18)	(19)	(18)	(14)

X^2=8.81 df=5 N.S.

The result was not significant, indicating a constant relationship between the number of divorced birds which failed and the number of faithful birds which failed to fledge chicks. Through time the relative proportion of each status failing has remained constant.

A further test was performed to determine whether the proportion of all divorced birds which failed to fledge chicks was constant over time (Table 9):

Table 9: Number of divorced birds which either fledged chicks or failed to fledge chicks for year-groups 1-6

		YEAR GROUP					
		1	**2**	**3**	**4**	**5**	**6**
NUMBER FLEDGED:	**0**	7	6	16	23	17	17
	(EXPCTD)	(8)	(10)	(20)	(16)	(14)	(18)
	> 0	21	28	56	35	34	48
	(EXPCTD)	(20)	(25)	(52)	(42)	(37)	(47)

X^2=7.88 df=5 N.S.

The number of divorced birds which failed to fledge chicks was not significantly different from the expected values over the six periods. Hence, divorced birds are consistently failing to the same extent over time.

In summary, divorced birds had a significantly lower fledging and breeding success than birds retaining the same mate. Divorced birds failed to fledge chicks significantly more frequently than expected (Table 8); the proportion of divorced birds which failed remained constant over time (Table 9).

4.5 EFFECT OF FLEDGING FAILURE ON DIVORCE & OF DIVORCE ON SUBSEQUENT FLEDGING FAILURE

It has been shown above that birds which go on to divorce have a significantly higher failure rate at chick fledging than birds which go on to retain the same mate in the following season (Section 4.3). Also, birds which divorce fledge significantly fewer chicks than those which have retained the same mate (Section 4.4). To test whether divorce is a mechanism by which reproduction is improved rather than simply a process by which reproductive output is reduced, the following tests were performed.

The dataset was divided into birds which had failed and birds which had successfully fledged chicks in the previous season. The number of birds which divorced or remained together and then fledged chicks or failed to fledge chicks for each of these groups was analysed using Chi-squared (Table 10).

Table 10: Number of chicks fledged for birds of status divorced and same, which i) failed to fledge chicks in previous year, or ii) successfully fledged chicks in previous year

i. failed in previous year:

		Number fledged:		
		0	**> 0**	
<u>Status</u>	Same:	24 (32)	120 (112)	(EXPECTED)
	Divorced:	23 (15)	43 (51)	

X^2= 7.6 (After Yates' correction) df=1 $p<0.006$

ii. successful in previous year:

		Number fledged: 0	>0	
Status	Same:	103 (118)	475 (460)	(EXPECTED)
	Divorced:	62 (47)	165 (181)	

$X^2 = 8.4$ (After Yates' correction) df=1 p<0.004

For birds which had failed to fledge chicks, the proportion that went on to fail again was greater amongst divorced birds (23/66 = 0.34) than amongst birds which retained the same mate (24/144 = 0.17). Divorced birds failed to fledge chicks twice as often as faithful birds; there was no reproductive advantage to divorcing after having failed to produce chicks (Table 10(i)).

The same was true after successfully fledging chicks: divorced birds failed to fledge chicks significantly more frequently (62/227 = 0.27) than did faithful birds (103/578 = 0.18) (Table 10(ii)).

However, considering divorced birds only, there was no significant difference between the number which failed to fledge chicks after failing in the previous year and the number which successfully fledged chicks after failing (Table 11). i.e. Probability of divorced birds failing to fledge chicks this year is not affected by whether or not they failed to fledge chicks last year.

Table 11: The number of divorced birds which either failed to produce chicks or successfully fledged chicks after failing or fledging chicks in the previous year

		Number fledged this year: 0	>0	
No.fledged in previous year	0	23(23)	56(56)	(EXPECTED)
	>0	58(59)	147(147)	

$X^2 = 0.000$ df=1 N.S.

Fig.8: % of birds which fail and
subsequently divorce or retain mate
for six, five-year groups

Includes % of the total which fail again in following season

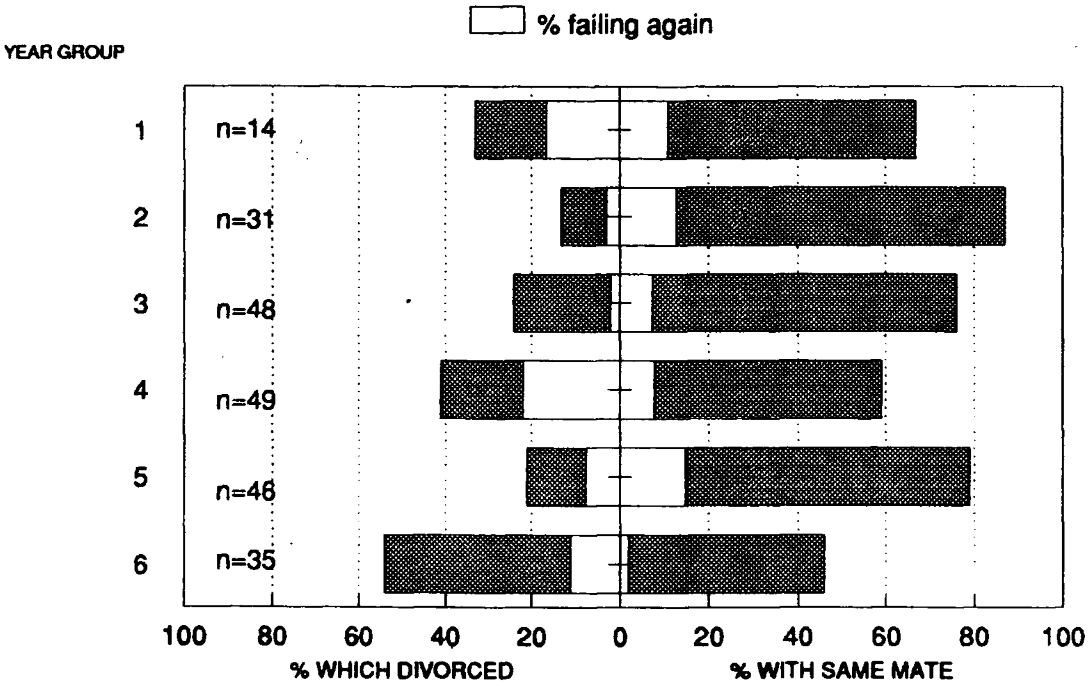
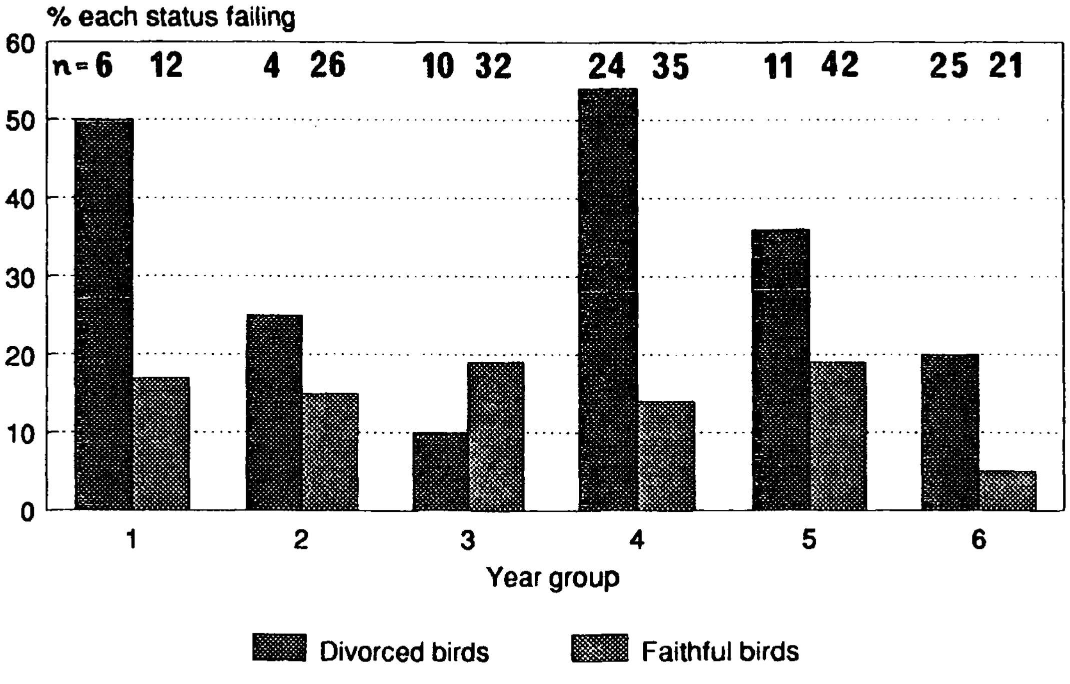


Fig.9: % of birds failing to fledge
chicks after failing in previous year
for year groups 1 to 6



Subdividing into year-groups

To determine whether there was a significant trend with time in the proportion of birds which failed then went on to divorce then fail again, the data set was subdivided as previously into six groups.

Chi-squared tests (as Table 10) within groups were not significant and sample sizes were too small to carry out Chi-squared tests between the six groups. However, Figure 8 shows the proportion of all birds which failed and went on to divorce or stay together. It includes the proportion of all birds which failed again. Figure 9 indicates that, of birds which failed in the preceding season, divorced birds fail more frequently than faithful birds. However, sample sizes were too small to test this.

4.6 EFFECTS OF DIVORCE ON CHICK MORTALITY

Breeding success (no.chicks fledged/no.eggs laid) is significantly lower for birds that have divorced since the previous breeding season than for those that have retained the same mate (Section 4.4). Clutch size is controlled for in the calculation of breeding success, therefore mortality of chicks must be greater for divorcees than for birds retaining the same mate (rather than the latter simply having a higher breeding success due to a greater number of eggs laid). There are two stages at which prefledging mortality could occur:

i. During incubation : **Mortality 1** =

(no.eggs - no.chicks hatched)/no.eggs

ii.During chick rearing : **Mortality 2** =

(no.chicks hatched - no.chicks fledged)/no.chicks hatched

A comparison of mortality 1 and mortality 2 for divorced birds using a paired t-test shows mortality 1 to be significantly larger than mortality 2. This also occurs for birds retaining their mate.

Table 12: t-test results between birds of each status (same & divorced) and mortality 1 & 2 for those birds

	Same mate	Divorced	Student t	Prob.
Mortality 1	0.26(±0.01)	0.34(±0.02)	2.58	<0.01
Mortality 2	0.10(±0.01)	0.11(±0.02)	0.44	n.s.
Paired t:	9.7	7.51		
Prob. :	<0.0001	<0.0001		

A student t-test was performed to determine whether mortality 1 for divorced birds differs significantly from mortality 1 for faithful birds (Table 12). Whilst mortality 1 is significantly larger for divorcees, there is no significant difference between mortality 2 for each status. Divorced birds are losing significantly more eggs during incubation than are faithful birds. However, divorced birds are not losing significantly more chicks prior to fledging than birds with the same mate.

Birds which have divorced since the previous breeding season are losing significantly more eggs during incubation than those with the same mate.

4.7 EFFECTS OF BREEDING AGE ON DIVORCE

As a bird gets older the probability of changing mate through divorce decreases and the likelihood of changing mate through death of the partner increases (Coulson & Thomas 1985a). The longest-lived female kittiwake in the North Shields colony bred for 19 years whilst the oldest male bred for 18 years. ("Age" is defined as the number of years for which a bird has bred in

As age increases, the proportion of birds of each age which divorce decreases (Fig.10). This trend is similar for birds which had successfully fledged chicks in the previous season and for those which have failed (Fig.11) and the rate of decrease is the same for each:

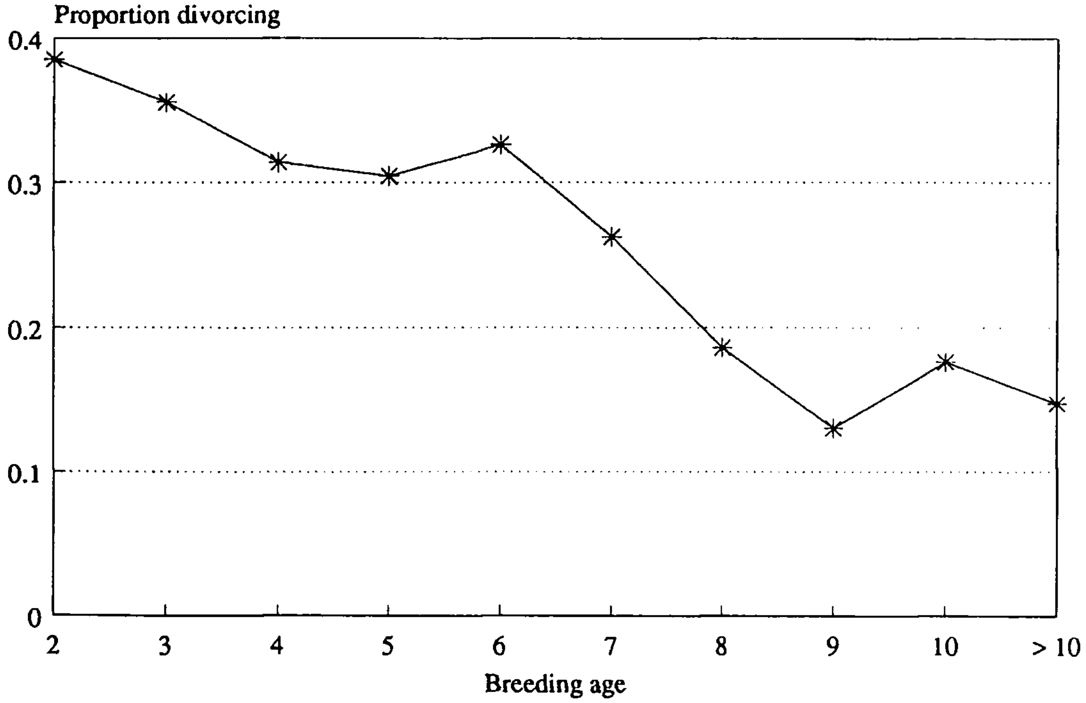
i) proportion of birds divorcing after failing to fledge chicks =
$0.52 - 0.03\ (\pm 0.008)x$ $r = -0.791$, $df=8$, $P<0.01$ (where x=breeding age)

ii) proportion of birds divorcing after successfully fledging chicks =
$0.45 - 0.03\ (\pm 0.004)x$ $r = -0.951$, $df=8$, $P<0.01$

That is, for each year older a bird becomes, the probability of divorcing its mate in any year will decrease by about 3% irrespective of breeding success in the previous year. For each age, the proportion of birds divorcing is higher amongst birds which have failed in the previous season than amongst those which were successful (Fig.11).

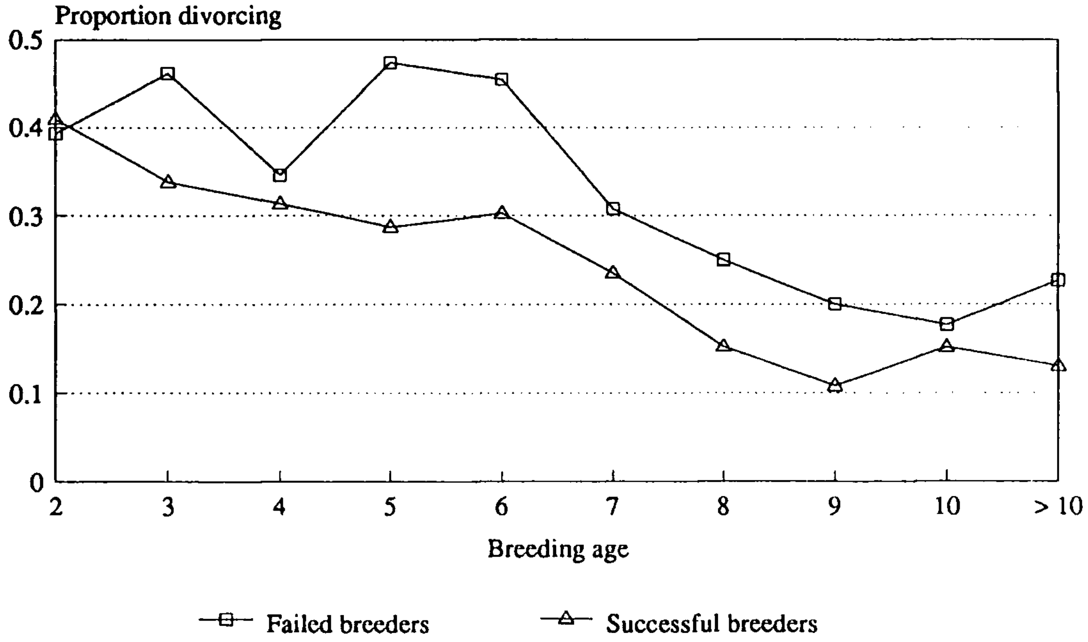
There was a significant difference between the proportion of birds fledging chicks and the proportion failing for each age (Table 13):

Fig.10: Proportion of birds divorcing for each age for years 1954-86



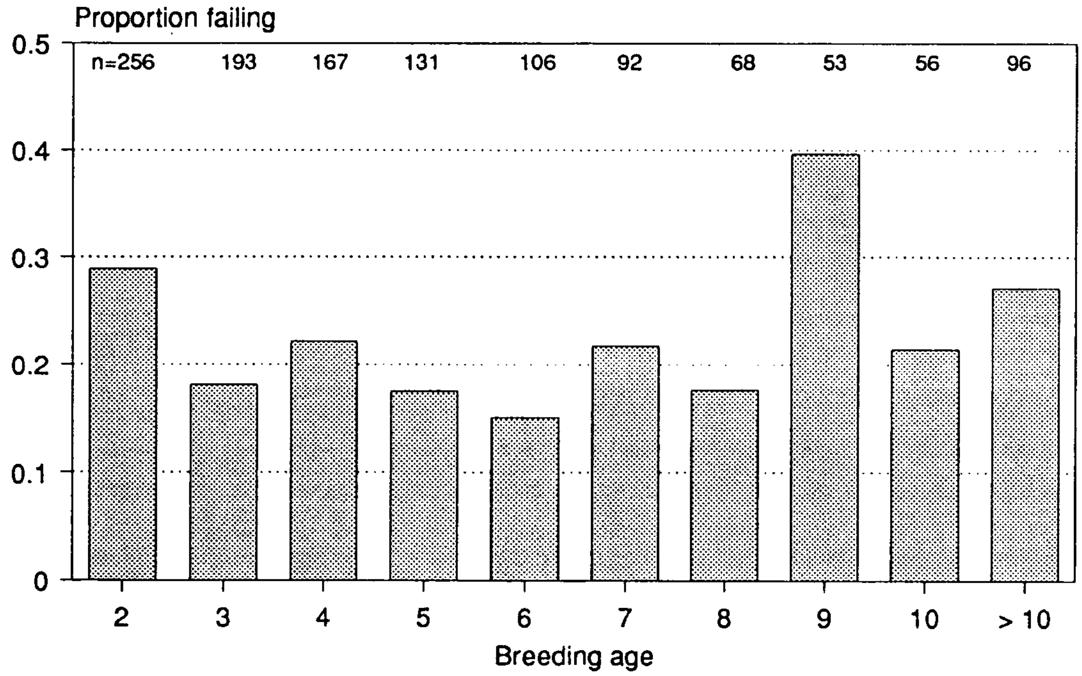
Proportion divorcing calculated as no. divorced/(no.divorced+no.same)

Fig.11: Proportion of birds which divorce after failing or successfully fledging chicks in previous season. Years 1954-86



Proportion divorcing= no.divorcing/ (no.divorcing + no. retaining mate)

Fig.12: Proportion of colony failing
to fledge chicks for age 2 and above
Years 1954-86



Where total colony consists of birds
which bred in previous year

Table 13: Chi-squared test between number of birds which successfully fledge chicks and the number of birds which fail to fledge chicks for ages 2 to 11.

Total sample size comprises birds of status divorced, faithful and widowed.

AGE	NUMBER OF CHICKS FLEDGED		EXPECTED VALUE	
	0	**>0**	**0**	**>0**
2	74	186	58	202
3	35	158	43	150
4	37	130	37	130
5	23	108	29	102
6	16	90	24	82
7	20	82	23	79
8	12	56	15	53
9	21	32	12	41
10	12	44	13	44
11	26	70	22	75

$X^2 = 24.17$ df=9 $P<0.01$

Of birds that had previously bred in the colony, the proportion which failed to fledge chicks showed a minimum at age six (fig.12).

A stepwise multiple regression was performed on the proportion of birds of each age in each calendar year which failed to fledge chicks; both age and $(\text{age})^2$ were entered as the independent variables. A regression equation was obtained in which a higher percentage of the variation in the dependent variable, the proportion of birds failing, was explained by the $(\text{age})^2$ term (4%) than was explained by the linear function, age (a further 2%):

The proportion of birds failing to fledge chicks =

$0.003(\pm 0.001)x^2 - 0.052(\pm 0.011)x + 0.04$

($F=4.62$, $T=2.25$, $P<0.05$, $r^2=0.06$)

This indicates that the $(\text{age})^2$ term is more important in explaining the variation in the proportion of birds failing to fledge chicks than the linear term. However, the percentage of variation in the proportion of birds failing to hatch chicks actually explained by the variables age^2 and age is, in total, only 6% of the variation in the data.

Two independent regressions were carried out, forcing the independent variable (either age or age^2), to obtain two separate equations and to determine the percentage of variation explained by each. For the linear variable, age, the regression was not significant:

$y = 0.003(\pm 0.003)x + 0.21$, ($F=0.75$, $T=0.87$, $P>0.05$) $r^2=0.001$

For the age^2 term the regression was significant:

$y = 0.004(\pm 0.002)x^2 + 0.21$, ($F=4.62$, $T=2.15$, $p<0.05$) $r^2=0.04$

The proportion of birds which divorce in any year decreases with the age of the bird. This proportion remains constantly higher for birds which failed to fledge chicks in the previous season than for those which successfully fledged one or more chicks.

5 DISCUSSION

This study looks at the breeding biology of the kittiwake with specific reference to the effects of divorce, the change of mate when the partner of the previous season is present in the colony, on reproductive success. The questions posed at the beginning of Chapter 4 will now be considered.

Divorce occurs at the same rate for the duration of the computerised data set (32 years). In 1966 the divorce rate was 25% and in 1990 the rate was 30%. It has been suggested that divorce rate is higher for birds which have failed to fledge chicks than for those which successfully fledged chicks in the previous breeding season (Coulson 1966, Coulson & Thomas 1983). The percentage of birds which failed to fledge chicks has not significantly increased over time (Fig. 6). Consistent with this, divorce rate has not significantly increased either. The proportion of birds retaining the same mate has decreased significantly (Fig.3b) between 1963 and 1986 whilst the percentage of birds widowed did not significantly increase until 1984 (Fig.2).

Previous work by Coulson & Thomas (1980, 1985b) has suggested that, as mortality rate in the colony increased, the divorce rate of remaining birds had also increased: birds losing their mate of the previous year through death were taking as a new mate a bird whose partner of the previous season was present in the colony. Calculations on the data set do not include birds where both members of a pair have died since the previous breeding season. Both birds are absent so will not affect the birds which do return to breed.

Hence, the percentage of widowed birds does not reflect the overall mortality in the population, but is relevant to the status of remaining birds. An increase in proportion of widowed birds within the colony could potentially disrupt pairbonds of other birds present. However, the proportion of widowed birds does not correlate with the proportion of birds divorcing. An analysis of where birds of each status take a mate from shows that birds pair preferentially with birds of the same status. Even if the proportion of widowed birds does significantly increase, there may be no increase in divorce rate as the widowed birds are most likely to pair with one another.

Fledging success is significantly lower for birds which go on to divorce (0.704) than for those which retain the same mate (0.772). This would suggest that losing chicks makes a pair more likely to divorce. Coulson & Thomas (1983) found a correlation between failure to fledge chicks and divorce rate, and Coulson discovered in an earlier work (1966) that divorce rate was 50% after failure but only 17% after a successful breeding attempt. Other examples of higher divorce rate following breeding failure have been found (fulmar: Ollason & Dunnet 1978; short tailed shearwater: Bradley et al. 1990; oystercatchers: Harris et al. 1987). However, in a detailed study of the breeding biology of the Great Tit, Perrins & McCleery (1985) discovered that, although divorcing birds had smaller clutches in the season prior to divorce, they did not fledge significantly fewer chicks than faithful birds.

The mean percentage of kittiwakes divorcing after failing to fledge chicks (28%) is not significantly different from the mean divorce rate of birds which successfully fledge chicks (31%) for the data set. It is not correct to say that failure to fledge chicks is a major cause of divorce as the actual number of birds retaining their mate after failing to fledge chicks is far higher than the number divorcing. Rather, it seems that divorce occurs at an approximately constant rate in the population.

Divorce may result from a behavioural incompatibility between individuals (Coulson & Wooller 1984) as witnessed in other species of monogamous higher animal, e.g. birds: in short-tailed shearwaters, Bradley et al.(1990) discovered that impending divorcees were absent significantly more often during the bond than faithful birds, in mammals: humans change partner due to incompatibility. One member of the pair may be a "poor parent", probably during the incubation stage (Coulson & Wooller 1984), hence its partner leaves. The poor quality individual will go on to reproduce in the following year and may have a lower breeding success than better quality birds which have retained their mate. Thomas & Coulson (1988) have shown that better quality birds breed for longer than poor quality birds, which explains why, as birds get older, the proportion divorcing decreases: the birds most likely to divorce have dropped out of the breeding population.

Divorce decreases with the breeding age of a bird (Fig.10; also Coulson & Thomas 1985a), the rate of decrease being the same irrespective of whether the bird failed to fledge chicks or not in the previous season (Fig.11). The proportion of failed breeders which divorced was not significantly higher than the proportion of successful breeders as age increased. When all birds which had previously bred were considered, the proportion which failed to fledge chicks did not increase linearly with age. Instead, the proportion failing was at a minimum at age six and increased again thereafter (Fig.12). The trend was slight, explaining only 6% of the variation in the proportion failing, but was significant. As overall breeding success increases with age until the age of ten, (Coulson & Thomas 1985a), the indication is that the proportion of older birds that are not failing have a higher mean breeding success than younger birds. This is consistent with the findings of Coulson & Thomas (1980), that older birds fledge more offspring.

Divorced birds have a significantly lower fledging and breeding success than faithful birds. If a bird divorces after failing to fledge chicks it is more likely to fail again than if it keeps the same mate. Even if a bird has not failed and divorces, it is will have a significantly higher probability of failing to fledge chicks than if it had stayed with its previous mate. So why divorce?

The 1990 study was conducted to look more closely at ways in which divorce affects reproductive output. Reproductive success increases with age of the bird (Coulson & Thomas 1985a) and divorce decreases with age, hence age distribution within each status group was first calculated. In fact it was similar for divorced and faithful birds. As 50% of all three-egg clutches (total = 4 clutches) were laid by divorced birds, some comparisons of reproductive output were not significant where one may have expected divorcees to be less successful. Birds laying three-egg clutches are significantly more successful than birds laying smaller clutches (Coulson & Porter 1985). This supports Lack's hypothesis (1954) that clutch size should maximise number of young surviving to breed. Pianka & Parker (1975) hypothesized that to maximise total lifetime reproductive success, current fecundity must be balanced against residual reproductive effort; Charnov & Krebs (1974) suggested that adult mortality increases with clutch size, so that the clutch size maximising fitness is smaller than the most productive size. Therefore, young birds should not lay large clutches even if they can, as they should optimise lifetime reproductive success rather than maximising the year's reproductive output. Thomas & Coulson (1988) showed that birds with the highest lifetime reproductive success were those which bred for the greatest number of years.

The mean number of eggs laid was not significantly different between statuses. First time breeders did not lay significantly fewer eggs than older birds as may have been predicted (Pianka & Parker 1975). Experienced birds laid their eggs significantly earlier than first-time breeders, probably due to the fact that the latter arrive at the colony significantly later than experienced birds (Coulson & Thomas 1983) and take longer to establish the pairbond.

Hatching success is dependent on a number of factors: egg volume (Thomas 1983), more efficient incubation (Coulson & Wooller 1984) or to higher fertility rate/more effective copulation behaviour (Chardine 1987). The volume of the egg laid increases nonlinearly with the age of the female. Egg volume did not correlate with status. However, up to 79% of the variation in egg volume has been explained by individual female variations (Thomas 1983). The physiology of an individual female is more likely to affect the volume of eggs she lays than the bird to which she is paired. Egg volume does not correlate with hatching success, which indicates that the significantly higher hatching success of experienced birds is as a result of adult age rather than the volume of eggs they produce. Parsons (1970) found a positive correlation between egg volume and chick survival in herring gulls, which he explained in terms of a higher yolk reserve from the larger egg sustaining the chick whilst the parent-chick relationship is established. Thomas (1983) found the same relationship in kittiwakes, though Maunder & Threfall (1972) found no evidence of a delay in chick feeding immediately after hatching to explain the difference in terms of energy reserves in the chick.

Divorced birds hatch significantly more chicks than first-time breeders. Once again, the "high quality" individuals (Coulson & Thomas 1985a) of the status divorced are positively weighting the measures of reproductive success for this status.

The results from the long-term data set show that divorced birds lose significantly more chicks during incubation than do faithful birds. This may be due to the lower copulation rate between newly-formed pairs (Chardine 1987) resulting in lower fertility of the eggs. When unhatched eggs from the 1990 season were examined, however, there was a tendency for first time breeders to have lost embryos at a later stage in their development than other statuses. Failure by birds with a new mate since the previous breeding season to establish a regular pattern of incubation shifts on the nest may lead to higher hatching failure (Coulson & Wooller 1984). If one member of the pair fails to return to relieve the other, the bird on the nest may be forced to leave the eggs. During the initial stages of embryo development the egg temperature does not need to be kept high (Maunder & Threfall 1972). However, in the later stages of development eggs must be kept warmer. First time breeders in

1990 may be losing embryos at this later stage due to irregular attendance at the nest. Also, the first time breeders laid eggs significantly later than experienced birds so may have deserted their clutches due to the lateness of the season, or because birds around them were no longer exhibiting incubation behaviour.

Coulson & Porter (1985) showed that 75% of chicks that hatched died in their first two weeks. Harris & Plumb (1965) discovered that, in Herring Gulls, this mortality was not due to lack of food but rather to exposure. In 1990 differences between statuses in chick survival was not due to differences in egg volume so instead can be attributed to quality of the parental care.

Having survived the initial week, the linear growth rate of chicks (Coulson & Porter 1985) shows no significant correlation with egg volume. Any initial advantage gained from hatching from a larger egg is not perpetuated after the first week.

Birds which successfully hatch only one chick may be poorer parents than pairs with two chicks (Coulson & Thomas 1985a). Hence, any disruptive effect on chick care caused by having a new mate results in a significantly lower growth rate of the chick in a one chick brood. However, birds with two chicks may be better parents (higher quality individuals) so that each chick is better attended to and chick two does not suffer from a lower growth rate. When mean chick growth rates for divorced and widowed birds are grouped, the growth rate of chick two is significantly slower for these birds than for faithful birds. The ineptitude of the birds which have changed mate is apparent only for chick two as the parents are able to adequately attend to chick one.

In Herring gulls, Harris & Plumb (1965) found that adults supplied adequate food for maximum chick growth even in artificially enlarged broods. For the kittiwake, change of mate may result in less frequent feeding visits to

For the kittiwake, change of mate may result in less frequent feeding visits to the nest resulting in lower chick growth rates for chicks which are given less food (presumably the second and less active chick). Food stocks may be more limited for kittiwakes feeding in the North Sea (Harris & Wanless 1990) off the Northumberland coast than they were for Herring gulls feeding off Skokholm Island in the 1960's, hence pair status more significantly affects chick growth rate.

More research is needed to determine the cause of lower chick growth rate of broods in which the parents have changed mate. Attendance at the nest and chick feeding behaviour need further study; also assessment of the abundance of food for the kittiwakes.

The fledging success (proportion of chicks hatched which go on to fledge) is a measure of the success of a pair of birds at chick rearing. The 1990 data showed no significant difference between fledging success for each status. However, the long-term data set shows divorced birds to have a significantly lower fledging success than faithful birds, indicating poorer parental care in feeding or chick protection (Harris & Plumb 1965). Also, divorce has been shown to have a significant negative effect on reproductive success in other species of bird: short-tailed shearwater, Bradley et al. 1990; fulmar, Ollason & Dunnet 1988; Red-billed gull, Mills 1973.

Rather than supporting such findings, the 1990 data have indicated that divorced birds are the most successful status. It is rash to refute the results not only of the whole data set, but also of other researchers in the field, on the strength of a sample size of 18 (total number of divorced birds). Confounding variables in such small sample sizes may obscure existing relationships which only become apparent in large data sets. Up to 33% of the variation found in the reproductive success of the kittiwake can be explained by individual traits (Coulson & Thomas 1985a). Explanations of the trends in the 1990 data have been proposed: it is likely that the presence of "high quality" individuals in the divorced group have caused the greater reproductive success of this status. Otherwise, it could be postulated that divorce did cause a significant increase in reproductive output hence explaining why it has not been selected out of the population.

It would be difficult to explain how a mechanism which causes a lower reproductive success is not selected out of a population. It is possible that divorce has a long-term advantage: only reproductive success in the year following divorce has been examined here. It has been shown that birds breeding with a new mate have a lower reproductive success (short-tailed shearwater, Bradley et al. 1990; fulmar, Ollason & Dunnet 1988; Red-billed gull, Mills 1973). Once familiarity with the mate has been established, reproductive success increases (Bradley et al. 1990). Hence, a bird divorcing because of failure to fledge chicks would not exhibit increased reproductive success immediately. In subsequent years, the advantage gained from changing mate may cause a nett increase in reproductive success over a pair which failed and remained together, perhaps to fail again in subsequent years. It is difficult to compare birds which have divorced with those which have not. Even if divorcing birds do have a lower reproductive success in the long-term, as compared with faithful birds, they may have had a still lower success rate if they had remained with the same bird. Faithful birds are compatible, and hence successful. Divorcing birds are not. It is not possible to test between a bird's reproductive success if it had not divorced and its reproductive success after it did (for the same year, the same set of environmental conditions, the same mate. To investigate this further, thorough studies of individuals' behaviour within a pairbond must be made.

The highest reproductive success is found in birds which breed for the greatest number of years (Thomas & Coulson 1988).

Further study is needed into the mechanism of divorce. It is known that divorced pairs have significantly different return dates to the colony, and that one bird of the pair may temporarily disappear after its initial return. Will the old mate select a new partner if its old partner is present in the colony, and unpaired, at the same time? Is there evidence of incompatibility in incubation or chick rearing behaviour for birds which subsequently divorce? These questions must be thoroughly researched before valid conclusions can be drawn on the cause of divorce in the kittiwake gull.

6 SUMMARY

I. 1990 DATA SET

1. The proportion of each status in the colony was as follows: Divorced: 21%; Faithful: 48%; Widowed: 13%; First-time breeders: 18%. This was significantly different from the 1989 data when: Divorced: 13%; Faithful: 27%; Widowed: 13%; First-time breeders: 47%. Considering only the birds which had bred for more than one season, there was no significant difference between the percentage of each status in each year.

2. The age distribution was similar for each status.

Egg Laying

3. The mean number of eggs laid by each status of bird in the colony was not significantly different.

4. The mean date of egg laying for divorced and faithful birds was significantly earlier than for first time breeders.

Egg Volume

5. Volume of the first egg laid was significantly greater than the volume of the second egg.

6. Egg volume correlated significantly with female breeding age only when a nonparametric test was used (Spearman's rank correlation), indicating nonlinearity.

7. No significant difference between mean egg volumes laid by divorced and faithful birds (age controlled for).

8. Volume of the first egg laid showed no correlation with the date of laying. Volume of the second egg significanly correlated with the date of laying.

9. Volume of the first egg laid did not significantly correlate with the female's head and bill length (a measure of body morphology).

Hatching Success

10. Hatching success was significantly greater for divorced birds than for first time breeding birds (by a factor of 2). Mean number of chicks hatched per pair of birds was significantly greater for divorced birds than for first time breeders.

11. For the first egg in a clutch there was a significant and negative correlation between hatching success and date of egg laying.

12. No significant relationship between hatching success and egg volume.

13. Of the eggs which failed to hatch, those laid by first time breeders contained the most advanced dead embryos.

Chick Growth Rates

14. No significant relationship with egg volume.

15. There was a significant difference between the mean growth rate of chick in a one chick brood and the mean growth rate of both chicks in a two chick brood.

16. No significant difference between mean growth rate of one chick broods and mean growth rate of the first chick in a two chick brood.

17. Considering one chick broods, the mean growth rate of chicks of divorced birds was significantly lower than that of faithful birds.

18. In two chick broods, there was no significant difference in the mean growth rate of the first chick nor of the mean growth rate of the second chick between divorced and faithful birds.

19. When mean growth rates of chicks of divorced and widowed birds were grouped, there was still no significant difference between the mean growth rate of the first chick in a two chick brood. However, the second chick of faithful parents grew significantly faster than the second chick of birds with a new mate.

Fledging Success

20. No significant difference between statuses.

21. No significant difference between the mean number of chicks fledged by each status.

22. Breeding success was not significantly different between statuses.

II. COMPUTERISED DATA SET

Population trends

23. Colony size was maximum in 1965. Since then it has oscillated around 76 pairs. The proportion of faithful birds decreased from then at about 0.49 percent per year. The proportion of divorced birds showed no significant trend. The proportion of widowed birds showed no significant trend until 1983 when there was a significant increase (from 19 percent before 1983 to 36 percent). There was no correlation between divorce and mortality.

Mate Choice

24. First-time breeders, divorced birds and widowed birds all tend to mate with birds of the same status.

Effects of Reproductive Success on Divorce

25. Fledging success was significantly lower for birds which go on to divorce (0.704) than for those which stay together (0.772).

26. Breeding success did not differ significantly between birds which go on to divorce and those birds which stay together.

27. Birds which go on to divorce had failed significantly more than birds which remained together.

28. Of all birds which failed to fledge young, the proportion which divorced did not remain constant over six five-year groups. Of all birds which had successfully fledged young, the proportion which divorced varied also.

Effects of Divorce on Reproductive Success

29. Divorcees had significantly lower fledging success (0.664) than faithful birds (0.753). Divorcees also had significantly lower breeding success (0.551) than faithful birds (0.653).

30. A significantly greater proportion of divorcees than of faithfuls failed to fledge chicks. Over time, the proportion of divorcees to faithfuls which failed remained constant. The proportion of all divorcees which failed also remained constant.

The Effects of Fledging Failure on Divorce and Vice-Versa

31. Of all birds which failed, those that divorced went on to fail again significantly more than those which stayed together.

32. Of all birds which succeeded, those that divorced went on to fail significantly more than those which stayed together.

33. Divorced birds which had failed in the previous year did not fail significantly more than divorced birds which had successfully raised chicks in the past.

Chick Mortality

34. Divorced birds lose significantly more chicks during incubation than do faithful birds.

Age

35. Divorce decreases with breeding age. Whether birds failed to fledge chicks or were successful, the rate of decrease is the same.

36. The proportion of all breeding birds failing to fledge chicks is lowest at age six then increases again.

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APPENDIX A

DATA COLLECTED IN THE 1990 BREEDING SEASON

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
3747	5	2	17	50.0	41.1	54.9	40.9	.	.	2	2	2	18.6	14.6
-2	0	1	17	57.0	39.9	55.2	39.5	.	.	2	2	2	1.6	11.7
14388	5	3	17	57.1	41.6	56.8	41.6	.	.	2	2	2	23.4	14.6
3951	5	2	17	56.9	42.5	55.8	41.7	.	.	2	1	0	17.1	.
14187	5	3	21	57.1	38.6	57.2	38.0	.	.	2	2	2	.	.
3714	5	2	12	55.5	39.1	55.8	39.0	.	.	2	2	2	15.4	8.6
6422	8	4	17	58.6	41.4	57.1	40.1	.	.	2	2	1	9.6	.
3545	8	3	17	55.2	42.8	58.6	41.9	.	.	2	2	1	1.8	.
3720	7	2	12	55.9	40.1	58.9	40.4	.	.	2	2	2	21.7	7.7
14172	8	6	15	55.5	40.4	53.8	39.6	.	.	2	2	1	17.6	.
-2	0	1	19	59.3	39.0	51.8	35.7	.	.	2	0	0	.	.
92957	5	8	16	54.0	42.5	55.8	41.4	.	.	2	2	2	14.6	9.7
14580	0	1	22	59.6	38.0	54.8	37.7	.	.	2	1	1	10.4	.
3634	8	2	19	55.2	39.9	54.3	38.5	.	.	2	2	2	20.3	16.1
3727	7	2	14	59.1	40.0	58.3	40.0	.	.	2	2	2	15.2	1.4
14622	8	4	17	56.4	41.8	55.1	41.6	57.2	40.0	3	3	3	.	.
50858	5	11	18	57.2	41.0	55.8	40.3	.	.	2	1	1	14.9	.
14480	5	4	17	59.3	40.7	56.7	41.5	.	.	2	2	2	14.9	15.1
3965	7	1	27	54.4	40.8	53.8	38.1	.	.	2	2	2	11.5	6.2
14610	0	4	25	56.9	40.9	56.2	40.4	.	.	2	0	0	.	.
3732	5	2	14	52.5	40.1	52.2	40.2	54.8	38.6	3	2	1	.	.
14616	8	4	17	53.6	42.5	44.1	41.4	.	.	2	2	2	.	.
3728	7	2	14	55.0	40.8	56.6	39.7	.	.	2	0	0	.	.
14627	5	4	14	56.5	40.7	55.2	40.5	.	.	2	2	1	13.1	19.1
3733	5	2	17	51.9	41.5	54.1	40.4	.	.	2	2	1	14.6	.
14290	5	6	14	56.6	40.9	53.8	40.5	.	.	2	2	2	18.3	9.7
-2	5	2	15	52.2	40.4	50.5	40.1	.	.	2	2	2	17.7	12.7
3737	5	2	17	54.8	39.1	54.0	40.1	.	.	2	2	0	14.3	14.8
3736	5	8	17	56.8	40.9	55.7	40.5	.	.	2	2	2	17.7	16.5
3723	0	1	14	60.7	41.8	60.7	41.4	.	.	2	2	2	18.5	13.5
-2	2	1	24	56.9	40.0	56.3	39.8	.	.	2	1	1	15.7	.
19764	5	3	22	55.3	41.0	55.2	40.6	.	.	2	1	1	15.7	.
19770	7	3	17	53.9	41.9	54.6	42.1	.	.	2	2	2	17.1	13.4
-2	7	2	17	55.4	40.6	56.2	39.3	.	.	2	1	1	13.8	.
-2	5	1	11	53.6	40.3	54.3	39.9	53.4	38.2	3	0	0	.	.
3966	5	2	15	54.1	41.4	53.0	41.4	.	.	2	2	1	1.2	14.8
3952	8	2	15	54.2	40.0	54.1	39.5	.	.	2	2	2	17.1	15.4
-2	0	1	19	58.9	41.2	58.8	40.2	.	.	2	2	2	15.1	7.1
-2	0	1	26	57.3	41.6	57.4	40.7	.	.	2	2	1	10.4	.
3742	5	2	14	57.4	39.7	55.1	39.0	.	.	2	2	1	.	.
-2	0	1	30	57.0	39.9	52.5	37.9	.	.	2	0	0	.	.
19765	8	3	17	58.6	39.9	55.0	39.6	.	.	2	0	0	.	.
14458	5	4	19	56.0	39.6	.	.	.	.	1	0	0	.	.
3957	5	2	14	51.9	41.1	53.7	40.4	.	.	2	0	0	.	.
-2	0	1	25	55.2	40.8	53.4	39.0	.	.	2	0	0	.	.
14449	5	5	14	53.4	37.9	.	.	.	.	1	0	0	.	.
3710	5	2	14	55.3	42.6	55.9	41.4	.	.	2	0	0	.	.
14475	7	5	19	52.4	40.5	.	.	.	.	1	1	1	14.2	.
3956	8	2	2	54.5	40.4	.	.	.	.	1	1	0	.	.
3750	5	2	14	53.1	41.4	54.3	40.0	.	.	2	2	1	24.5	.
14470	5	5	14	53.5	40.8	55.6	41.0	.	.	2	2	2	16.5	4.8
14615	5	4	15	56.4	42.1	53.8	42.1	.	.	2	2	2	19.7	17.7
91801	7	13	12	52.0	41.1	52.3	39.9	.	.	2	2	2	15.4	1.2
3650	5	2	14	57.5	41.5	57.5	40.8	.	.	2	2	2	15.1	15.1

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
14619	5	4	17	55.5	40.4	55.7	40.1	.	.	2	2	2	1.2	11.1
14325	1	2	14	58.2	40.7	57.5	39.9	.	.	2	1	0	19.7	.
-2	0	1	22	52.9	37.5	58.1	38.6	.	.	2	0	0	.	.
3741	8	2	22	53.6	39.8	56.9	39.5	.	.	2	1	1	.	.
14624	8	4	15	55.1	40.4	54.6	40.0	.	.	2	2	2	1.8	2.3
3749	5	2	22	58.1	40.0	56.7	40.2	.	.	2	0	0	.	.
93000	1	2	14	55.1	41.0	59.4	41.1	57.2	37.7	3	1	1	14.3	.
-2	1	1	20	58.0	39.8	56.5	38.3	.	.	2	2	2	1.4	.8
3739	8	2	.	-.2	-.2	-.2	-.2	.	.	2	2	2	19.1	.
14469	5	5	.	-.2	-.2	-.2	-.2	.	.	2	2	1	.	.
14435	5	5	19	53.0	40.9	54.1	40.6	.	.	2	1	1	23.1	.
-2	0	1	26	56.3	38.4	.	.	.	.	1	0	0	.	.
3707	0	1	12	55.1	39.9	54.6	38.8	.	.	2	1	1	17.4	.
14173	5	6	14	59.0	40.1	55.6	39.8	.	.	2	1	1	.	.
3958	5	2	18	56.8	40.6	54.8	40.0	.	.	2	2	1	16.	10.3
-2	8	.	14	58.9	40.6	57.4	40.8	.	.	2	2	2	16.	17.7
14416	5	5	17	55.7	41.3	57.9	40.8	.	.	2	2	2	16.3	14.9
19757	5	2	22	55.5	42.0	50.9	39.0	.	.	2	.	.	.	.
92681	5	6	19	56.0	41.7	54.6	41.4	.	.	2	2	2	17.4	14.9
19754	7	3	17	54.9	39.0	54.0	38.0	.	.	2	2	1	27.7	.
3649	5	2	12	55.8	39.6	55.6	39.8	.	.	2	2	2	12.6	5.7
3719	5	2	7	54.0	41.7	61.1	40.6	.	.	2	1	1	15.1	.
3807	5	2	17	53.9	38.6	.	.	.	.	1	1	1	.	.
14405	7	5	17	54.2	41.2	67.8	41.0	57.0	40.4	3	3	2	20.3	9.7
3708	8	2	17	59.5	42.6	56.9	41.7	.	.	2	2	1	18.	.
3745	5	2	14	52.6	38.8	55.2	37.5	.	.	2	1	1	19.7	.
3538	5	4	15	55.0	39.8	53.0	40.1	.	.	2	0	0	.	.
14467	7	5	17	54.2	39.0	53.5	38.6	.	.	2	2	2	18.0	14.0
3635	5	3	15	56.4	41.5	53.8	41.5	.	.	2	1	1	20.3	.
3709	5	2	11	56.6	38.8	58.0	37.4	.	.	2	2	2	18.	20.3
-2	2	.	22	57.4	40.0	55.4	39.6	.	.	2	1	0	.	.

KEY

1	Female BTO ring number
2	Status: 5=faithful, 7=widowed, 8=divorced, 0=first-time breeder
3	Female breeding age
4	Date first egg laid
5	Length of first egg
6	Breadth of first egg
7	Length of second egg
8	Breadth of second egg
9	Length of third egg
10	Breadth of third egg
11	Number of eggs laid
12	Number of chicks hatched
13	Number of chicks fledged
14	Growth rate chick 1
15	Growth rate chick 2

APPENDIX B:

UNHATCHED EGGS COLLECTED AND EXAMINED IN THE 1990 BREEDING SEASON

Nest site	Egg contents
I. DIVORCED BIRDS	
N1C	Equiv to 9 day embryo
N2A i	Ruptured yolk. Embryo equiv to 9 day embryo
N2A ii	Large embryo, equiv to 19 day embryo. Ruptured shell.
II. WIDOWED BIRD	
W2Am	Yolky. No embryo.
III. FAITHFUL BIRDS	
S2Am	Yolky. No embryo.
E1C	Black rotten liquid. 9 day embryo rotting.
E1B i	Yolk no embryo.
E1B ii	Yolk no embryo.
W2Et	17 day embryo.
W2G	No embryo
W2Bm	6 day embryo
IV. FIRST-TIME BREEDING BIRDS	
W1C	19 day embryo
S3Ba i	19 day embryo with yolk
S3Ba ii	19 day embryo ,, ,,
W1D	18 day embryo ,, ,,
E1C	17 day embryo ,, ,,

APPENDIX C Volumes of eggs laid by individual females which laid eggs in 1989 and 1990

1	2	3	4	5	6
43.10	46.68	44.89	45.48	40.70	43.09
48.08	47.82	47.95	48.00	44.92	46.46
41.40	40.18	40.79	46.55	41.71	44.13
42.29	41.29	41.79	40.97	38.59	39.78
48.87	44.67	46.77	47.74	45.08	46.41
50.20	51.06	50.63	47.12	42.46	44.79
47.74	47.18	47.46	44.43	42.73	43.58
44.08	41.04	42.56	44.15	44.07	44.11
47.46	46.54	47.00	45.87	44.69	45.28
42.76	39.16	40.96	45.23	44.11	44.67
46.01	45.39	45.70	43.30	42.16	42.73
46.79	44.09	45.44	42.14	42.68	42.41
47.80	47.52	47.66	49.60	43.14	46.37
46.32	44.62	45.47	37.29	37.79	37.54
47.11	44.77	45.94	47.09	47.67	47.38
44.55	43.41	43.98	45.40	43.74	44.57
45.54	44.06	44.80	43.56	43.68	43.62
43.49	42.97	43.23	40.59	42.41	41.50
46.07	42.93	44.50	43.79	42.53	43.16
41.46	39.50	40.48	40.57	39.89	40.23
43.77	41.25	42.51	45.83	45.27	45.55
46.23	44.45	45.34	47.19	45.61	46.40
51.61	50.61	51.11	45.27	43.31	44.29
44.30	43.40	43.85	42.89	40.53	41.71
45.23	44.27	44.75	46.38	43.86	45.12
44.44	42.24	43.34	38.37	42.71	40.54
45.20	44.06	44.63	41.93	41.31	41.62
48.65	46.23	47.44	39.45	38.45	38.95
48.25	46.27	47.26	42.12	41.00	41.56
44.02	40.78	42.40	43.44	42.68	43.06
44.16	36.70	40.43	47.18	44.88	46.03
45.40	41.96	43.68	41.31	41.15	41.23
42.66	42.64	42.65	46.17	45.71	45.94
44.71	39.51	42.11	44.85	40.83	42.84
48.83	46.61	47.72	44.12	43.74	43.93
44.29	42.27	43.28	41.76	41.38	41.57
43.34	45.48	44.41	48.11	41.87	44.99
48.64	46.40	47.52	43.75	47.03	45.39
42.74	40.52	41.63	47.46	45.46	46.46
48.19	46.57	47.38	46.19	44.03	45.11
44.08	43.58	43.83	45.73	40.37	43.05
46.91	44.53	45.72	42.10	43.52	42.81
41.31	43.19	42.25	45.81	46.51	46.16
43.76	42.50	43.13	44.46	44.94	44.70
45.23	44.59	44.91	43.55	42.59	43.07
44.71	40.33	42.52	46.51	46.05	46.28
43.14	43.38	43.26	46.90	47.76	47.33
42.68	40.00	41.34	45.33	45.83	45.58
46.17	42.85	44.51	37.80	37.98	37.89
45.56	42.66	44.11	41.62	41.22	41.42
47.24	46.48	46.86	44.22	42.18	43.20

KEY

1 Volume of egg 1 in 1990
2 Volume of egg 2 in 1990
3 Mean volume both eggs 1990
4 Volume of egg 1 in 1989
5 Volume of egg 2 in 1989
6 Mean volume both eggs 1989

Mean of column 3=44.58 +/- 0.34 Mean difference= 0.95 +/- 0.45
Mean of column 6=43.63 +/- 0.32 t= 2.02 df= 50 P<0.05