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Kittiwake

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KEY FINDINGS

- The Kittiwake is one of the species in the highest category of conservation concern (red-listed) in the UK, with substantial declines in colonies across Scotland, although remaining relatively stable in the North East.
- Identifying reasons for colony decline is critical for conservation, and requires a detailed understanding of how breeding success and mortality vary with age.
- Since the early 20th Century, many new colonies have become established in North-East England. One of these was formed in 1949 at North Shields, nesting on the riverside window ledges of a warehouse 2 km from the mouth of the River Tyne.
- Over nearly a 40-year period, the biology and behaviour of Kittiwakes breeding here for the first time (usually when 3 or 4 years old) were studied.
- Newly-breeding individuals showed poorer breeding success than older birds: they arrived at the colony last, laid later, and had smaller clutches and lower breeding success.
- Fewer young birds retained the same mate and nest site in successive years and had a higher divorce rate than older birds. However, once they had nested for the first time they showed intense faithfulness to the colony in the following years.
- This study shows that Kittiwakes mature slowly, remaining as non-breeders for at least two years after hatching and thereafter only gradually achieve full breeding potential after several years of breeding.

Chris Redfern, Editor

THE BIOLOGY AND BEHAVIOUR OF YOUNG BLACK-LEGGED KITTIWAKES NESTING AT NORTH SHIELDS

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ABSTRACT

An investigation over 28 years was made of the breeding biology and behaviour of Black-legged Kittiwakes Rissa tridactyla *at a colony at North Shields, Tyne and Wear. The paper describes the behaviour and breeding success of individuals breeding for the first time and are compared with more experienced, older birds. Pairs with both individuals breeding for the first time arrived at the colony last and had the lowest breeding success. In the year following their first breeding attempt, first-time breeders suffered a higher mortality rate than older adults, and those which survived to the next breeding season were more likely to change their mate and nesting site than older adults. Differences in the behaviour of the sexes were also investigated.*

INTRODUCTION

The Black-legged Kittiwake *Rissa tridactyla* (hereafter Kittiwake) is a colonial gull which typically nests on inaccessible or difficult to reach sea cliffs. However, an accessible colony became established on a warehouse at North Shields, Tyne and Wear, England, and it offered the unique opportunity to study in detail the biology of identifiable individuals and pairs in successive years, identifying for the first time the effects such as age on the annual arrival time, survival, clutch size, and breeding success. This paper reports on the biology of individual Kittiwakes breeding for the first time and also makes comparisons with individuals which had bred on two or more previous occasions.

History of the colony and study

In 1949, four pairs of Kittiwakes started to nest on the window ledges of the old riverside Brewery Warehouse at North Shields, which was then being used for storage of contents of ships while being repaired by Smith's Dock Ltd. This was the first known occasion Kittiwakes had bred on a building in England and was about two km from the mouth of the River Tyne and the North Sea. The warehouse had four floors above ground level, with the south end of the building on the edge of the river, which was where Kittiwakes first nested. Subsequently, increasing numbers of pairs nested over subsequent years on exterior window ledges on all four sides of the building with the greatest numbers on the south and west sides and typically with one or two pairs building nests on each ledge. In 1970, additional ledges were put half way up the window frames on some of the south and west sides of the building to supply more nesting sites for the expanding colony. These were subsequently and progressively occupied by nesting Kittiwakes in the following years. The building lost numbers of slates from the roof during a storm in 1980 and was not repaired, resulting in rain water leaking into the top floor, eventually causing the wooden beams and flooring to rot. This made access to some of the windows from inside of the building dangerous and limited the data collection from 1988. Smith's Dock sold the warehouse to a property developer, but access to the building and colony continued. Planning approval was granted late in 1990 to convert the building into riverside flats. The windows used by Kittiwakes were covered in netting and the birds were prevented from reaching the sites. Many of the excluded breeders missed breeding in 1991 and, eventually, most of the surviving Kittiwakes moved to a small existing coastal cliff colony two km away at Tynemouth (Fairweather and Coulson, 1995), with the exception of one female that moved over 220 miles (350 km) to nest at Lowestoft in SE England. Although numbers of young Kittiwakes reared at the warehouse had, when mature, moved up-river to breed at the colonies now established on buildings and structures at Gateshead and Newcastle, following Kittiwakes being first reported flying along the river at Newcastle and beyond in the early 1960s (Coulson and Macdonald, 1962), none of the displaced breeders from the warehouse at Smith's Dock moved there to breed, despite intensive searches. During the 37 years of this study at North Shields, no predation on the Kittiwakes, their eggs and young by predatory birds occurred. No Carrion Crows *Corvus corone* or large gulls were seen in or on the edge of the colony throughout and there was only one brief incident involving birds of prey. In one year, a pair of Kestrels *Falco tinnunculus* started to build a nest on one of the ledges, and frequently disturbed six neighbouring pairs of Kittiwakes during a two-week period, and then left the area. Illegal interference with the nesting birds by humans occurred on only two occasions. In one case, eggs were removed from five nests by youths climbing up two exterior rain-water pipes and further attempts were prevented by coating sections of the pipes with adhesive *Sticktite*. On another occasion, two incubating adults were killed by pellets fired from an air rifle. The local police appeared to know who was concerned and prevented further incidents. Nests remained on the ledges each year and their height grew year after year and resulted in three nests collapsing and their contents falling off the ledges. Data on the breeding of the Kittiwakes involved in these events have been excluded from this analysis for the years concerned. Further such losses were prevented by removing nest material which had accumulated over 20 cm high before the start of each breeding season. A more detailed account of the site and Kittiwake colony can be found in the appendix in Coulson (2011).

METHODS

In 1953, permission was granted to me by the management of Smith's Dock to enter their warehouse on a frequent and regular basis to study the nesting Kittiwakes. The building was secure and staffed by two staff who took a delight in the Kittiwakes. The warehouse was also safeguarded by the adjacent security office at the entry to the dock and was staffed day and night for seven days each week.

Fortunately, the hinged window frames opened into the building which meant that they could be opened without damaging the nests on the exterior sill. The birds and nest contents could be observed from inside the building through the glass in the windows. Alternatively, many nesting pairs could be observed simultaneously from ground level from the nearby ferry landing or the adjacent dockyard. Adults were captured for ringing by slowly opening the window by 1 cm and hooking one of the bird's legs with a 30 cm long wire ending in a 'shepherd's crook' and then withdrawing the bird through the briefly more fully-opened window, without disturbing birds on adjacent sills. Having ringed the captured bird, it was released on the opposite side of the building and usually returned immediately to its nest site.

Use of coloured rings to Identifying individuals

The Kittiwakes captured at the warehouse were ringed with a unique combination of three coloured rings and a BTO metal ring. Initially, celluloid colour rings were used but these faded and changed colour within a year. Helpful staff at ICI plastics division supplied me with sheets of DARVIC© colour-fast PVC in a range of different intense colours and which were cut to size and the thermoplastic material was shaped into rings by immersing in boiling water, inserting into a mould and then cooled (Coulson, 1963). These rings did not change colour even after being on individual Kittiwakes for 15 years. These were the first birds marked with Darvic rings and which are now used worldwide.

Methods of sexing the birds have been described in detail (Coulson, 2009) mainly dependent upon observations of mating. Subsequent changing of mates enabled the majority of birds to be sexed, while wing length and head and bill length was used to sex the remaining minority of individuals.

Colony faithfulness of breeding adults

Over a thousand breeding Kittiwakes and a further 1,500 young were colour-ringed during the study at the warehouse and frequent and repeated searches over 30 years were made to detect any of these birds that had moved to breed in colonies between Edinburgh in the north and Bridlington to the south. Seventy-one young reared at the warehouse were found breeding in other colonies, but only two adult birds which had bred at North Shields were located. Surprisingly, these two birds which had bred at North Shields were paired together at a colony 32 miles (51 km) away at Cullernose Point in Northumberland and were among over 300 other pairs of Kittiwakes nesting there; they bred there at the same nest site for five successive years. Even more remarkable was that they had both bred with different mates at the warehouse. The mechanism of how, when and why they paired up and moved is not known.

The result of these searches indicated that once Kittiwakes bred, they showed intense colony faithfulness if not subjected to major disturbance, which is in contrast to the low philopatry that occurred in young birds before they bred (Coulson and Neve de Mevergnies, 1992) and which was more marked in females than in males (Coulson and Coulson, 2008). In this study, it is reasonable to assume that marked breeding birds which were not seen again had died. Since no major disturbances of breeding Kittiwakes is known in the other colonies searched, birds without rings arriving and nesting at the warehouse (along with birds ringed as nestlings), were assumed to be breeding for the first time. The aim was to colour-ring all breeding Kittiwakes nesting in the warehouse colony. This was achieved in the majority of years and about 95% of birds without rings were captured and colour-marked when they nested there for the first time.

The warehouse was usually visited weekly after the first birds returned, (as early as 18 December in one year), to identify the sites occupied by individuals and pairs. More frequent visits in fine weather were made in three years to identify the return dates of all birds which would breed in each of these three years. The identity of the pair, the date of laying the first egg of the clutch, clutch size, number of young hatched and fledged were recorded for each pair throughout the study. During egg laying, visits were made at five-day intervals and more frequently after 25 May when one-egg clutches became more frequent. Date of first egg in the clutch was estimated for two- and three-egg clutches with an error of less than ±1 day. Laying date of single egg clutch were taken as midway between the visit in which the egg was first found and the previous visit, and had a maximum error of ± 2.5 days. Data used in this study were the identity of each pair, the ledge on which they nested, clutch size and the date of laying its first egg, number of young fledged and breeding success for all nests at the warehouse from 1960 to 1987. Accurate date of first return of each individual was collected from 1967 to 1969. Ringing and observations on the nesting birds were made in each year from 1953 to 1990, but those for first seven years have not been included to allow a wide range of known breeding experience of individuals to be available and to avoid a bias in favour of young pairs in the dataset used. Because of less frequent visits to the colony between 1988 and 1990, and problems in reaching some nests, these data have not been used, except for the identity of pairs which were complete until 1990. To reduce bias in recording more cases where the same pairings persisted for few years, the data used for this aspect of the study were restricted to pairs which were formed for the first time by 1980, leaving only two pairs from that time that were still together at the end of the study in 1990.

In this study, adult Kittiwakes were classified by the number of occasions (years) that they had bred and this is a surrogate of age. Based on birds ringed as nestlings, the age at first breeding is variable and on average, males bred for the first time when 4 years old and females almost a year older at 4.7 years (Coulson, 2011). Accordingly, the classification used in this paper of the number of breeding years represents, on average, adult males 3- and females 4-years older than the number of years that they had bred.

During the study, the date of laying of the first egg of first and last clutches in the colony was spread between the extreme dates of 1 May to 15 June and the spread of laying each year was normally distributed or with a slight tail of late laying. The mean date of egg-laying each year is given in Appendix 1 and shows only minor between-year variation. Years with slightly later means were mainly produced by more first-time breeders in the years after more ledges were added to some sills and these attracted more recruits. Calendar dates of laying have been used throughout.

The spread of individual values within a category has been measured by calculating the standard deviation (sd) of the mean. The reliability of mean dates and percentages have been indicated by standard errors (se) and the significance of differences between two sets of data have been determined by calculating the standard error of the difference between the two means, determining *t* and reading *P* (the probability of obtaining the difference by chance) from Tables. Significance of differences in clutch size and numbers of young fledged from nests have been measured by calculating χ^2.

The North Shields Kittiwake colony

The North Shields Kittiwake colony

RESULTS

The annual return to the colony

The date of annual return to the colony of males of pairs averaged 6 days before that of their female partner, but this should not be interpreted as indicating that the females returned later, because the males spent more time defending ownership of their nesting site than females and so had an increased chance of being seen earlier during observations. The early returning birds initially visited the colony during the morning, but within a few days the period of occupation rapidly extended to most of the daylight hours. The colony was deserted overnight until mid-April, with birds often returning each day before dawn. Thereafter, the colony was continuously occupied, although many of the birds about to breed for the first time continued to leave overnight until early May.

There is considerable variation in the dates that individual breeders returned to the warehouse colony and newly arrived individuals were seen over a period of 90 days. During the three years of intensive study, the first nest sites were occupied in January or early February, but a few individuals did not arrive until early May. On average, the older birds that had bred at least four times were the first to arrive, followed by those which had previously bred on two previous occasions and then by birds which had bred once before. Those about to breed for the first time were last to arrive (Fig. 1). Even within age classes, there was considerable variation in the date of arrival (standard deviation of the mean of 7.4 days).

Characteristics of first-time breeding females

There were three categories of first-time breeders. The most numerous were pairs where both members were breeding for the first time (Type 1). The second category (Type 2) included females breeding for the first time, but paired to males who had breed at least once before. The third category (Type 3) included males breeding for the first time, but paired to females that had nested at least once before. Pairs composed of two first-time breeders bred 4 or 5 days later ($P < 0.001$) than where one of the partners had bred before (Types 2 and 3 pairs, Table 1). The clutch size of pairs of inexperienced birds was 8% lower, they reared 32% fewer young and their breeding success was 28% lower than in pairs where one of the members of the pair had bred previously. A first-time nesting Kittiwake breeding with an experienced partner of either sex resulted in earlier laying and a significantly improved breeding performance. These results raised the question of whether the benefit to first-time breeders of an experienced partner increased with the extent of the older bird's past experience.

In the three categories of the effects of increasing breeding experience in one partner (Table 2), neither sex showed further advancement in the laying date, and both sexes appreciably increased the number of young fledged per pair (by 12% in males and 25% in females) as breeding experience increased. Males showed a progressive trend in clutch size with increasing experience, but this was absent in females, while breeding success increased with experience in females, but not in males.

Figure 1. The 10-day periods that Kittiwakes were first seen in the colony in relation to the number of years they will have bred in the coming breeding season. Based on three seasons of frequent observation from 1 February. Dates are the first day of each 10-day period.

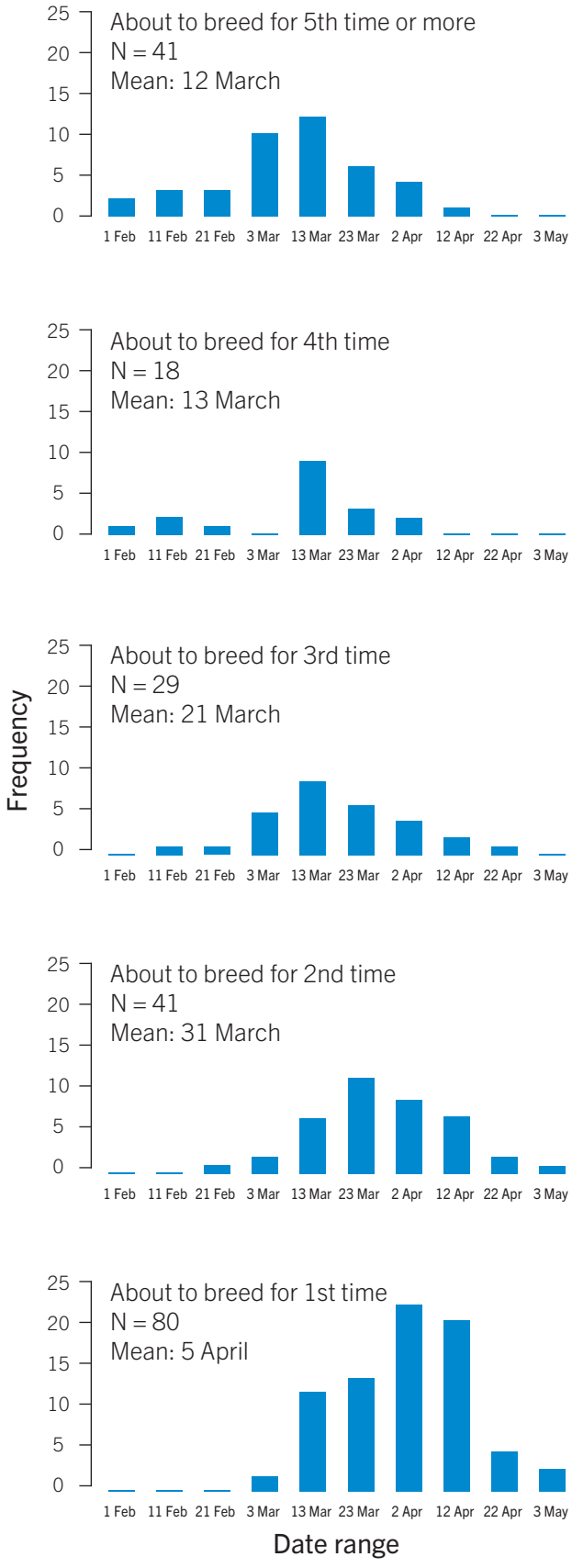

Table 1. *Comparison between the breeding biology in Kittiwakes in which both members of the pair were breeding for the first time (Type 1), where a female was breeding for the first time with a male that had bred previously (Type 2) and where a male was breeding for the first time and was paired with a female that had bred in a previous year (Type 3).*

Pair status	N[1]	Mean first egg date (May ± se)[2]	Mean clutch size	Mean number of young fledged	Mean breeding success[3]
Both breeding for the first time (Type 1)	350	25 ± 0.5	1.79	0.77	43%
Female breeding for first time, male bred before (Type 2)	203	20 ± 0.6	1.96	1.14	58%
Male breeding for first time, female bred before (Type 3)	260	21 ± 0.5	1.95	1.13	58%

[1]N is the number of nests in which eggs were laid.

[2]3% of nests built each year had pairs which failed to lay in them and were excluded as non-breeding birds.

[3]Breeding success is the proportion of young fledged from the eggs laid.

Table 2. *The influence of the partner's sex and previous breeding experience on first-time breeding of Kittiwakes.*

Females breeding for the first time.

Male bred for:	N	First egg date (May ± se)	Clutch size	Young fledged	[1]Breeding success ± se
First time	325	25 ± 0.6	1.79	0.77	42 ± 1.3%
Second time	73	19 ± 1.2	1.92	1.17	61 ± 2.7%
Third time	47	20 ± 1.6	1.97	1.18	60 ± 3.5%
More times	83	17 ± 1.0	2.07	1.31	63 ± 2.6%

Males breeding for the first time.

Female bred for:	N	First egg date (May ± se)	Clutch size	Young fledged	[1]Breeding success ± se
First time	325	25 ± 0.6	1.79	0.77	43 ± 1.3%
Second time	87	21 ± 1.1	1.97	0.99	50 ± 2.7%
Third time	55	19 ± 1.3	1.96	1.21	62 ± 3.2%
More times	118	21 ± 0.8	1.96	1.24	63 ± 2.1%

[1]Breeding success is the proportion of eggs which produced fledged young.

Monogamy and re-laying

The Kittiwake is almost entirely monogamous and only two exceptions were encountered during the study. In both cases, there appeared to be shortage of males at the time and both experienced males paired with similarly experienced females and both laid a clutch. About 8 days later, the males paired with females (which had not bred before) at other sites several meters away and each of the new pairs produced a clutch late in the season. Each male continued to visit the two sites and shared some of the incubation at the two nests even on several days when it overlapped. Once chicks hatched, the males fed young at all four nests and the young fledged successfully at all four nests.

Re-laying was rarely recorded in the colony. When five clutches were stolen early in the season and shortly after laying, all five experienced pairs re-laid after about 10 days. In six cases where the egg(s) of first-time breeding pairs fell from the nest soon after laying, no attempt was made to re-lay.

Individuals breeding only once with same partner

The widely held opinion that many bird species pair for life does not hold for the Kittiwake. Fifty-nine percent of Kittiwakes breeding at the warehouse kept the same partner for only one breeding season. The remaining 41% retained the same mate for two or more years (Table 3) and 1.3% of pairs persisted for over nine years, with one exceptional pair that remained together for 15 consecutive breeding seasons.

The failure to retain the same mate had two causes. Either one of the partners died during the winter or both pair members of the previous year survived and "divorced" by taking a different partner from within the colony. Divorce in the years after individuals bred for the first time declined progressively as their years in which they had bred increased, falling significantly from 48% in first time breeders to 27% in those which had bred for more than three previous breeding seasons (Table 4).

Table 3. *The number of consecutive years that breeding pairs of Kittiwakes remained together. Data have been restricted to pairs which bred for the first time before 1977 to avoid bias in favour of those with fewer years. None of the pairs were still alive in 1989.*

	Number of years															Total cases
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Number of cases	325	113	50	20	18	7	5	5	4	4	0	0	2	0	1	554
Percentage of cases	59%	20%	9%	4%	3%	1%	<1%	<1%	<1%	<1%			<1%		<1%	

Table 4. *The divorce rate of female Kittiwakes in relation to the number of years the birds had previously bred.*

Number of previous years breeding	1	2	3	Over 3	Total
Number of females surviving	195	56	25	33	309
Number divorcing	94	23	10	9	136
% divorcing	48 ± 2%	41 ± 3%	40 ± 5%	27 ± 3%	44 ± 1%

Retaining and changing nest site

Many Kittiwakes nested on the same window sills in successive years, but it was not unusual for others to move to other sills. There was a marked sex difference in the extent to which birds changed their nest site, with females showing much lower site faithfulness (Table 5). Sixty-three percent of first-time breeding females changed their nesting site in the following breeding season and the proportion did not change appreciably with greater breeding experience. Only 33% of first-time breeding males did so and the proportion changing decreased significantly with increasing breeding experience, involving only 19% which had bred more than three times. In a small sample of young birds which were ringed and formed pairs and occupied a site, but did not breed, the individuals only rarely retained the same site in the following year.

Relationship between laying date in Kittiwakes breeding for the first-time and other variables

The possible interactions of laying date, whether they fledged young, their survival or death before the nest breeding season and whether those surviving retained or changed site are explored in Table 6. Successful breeding was the most important factor and was correlated with laying, being about five days earlier than those which failed in their first attempt to breed. The best breeding performances by inexperienced pairs were those which nested early and would survive until the next breeding season when they retain the same nest site and the same mate.

Table 5. *The proportion and standard error of Kittiwakes which retained or changed nesting sites between successive breeding seasons in relation to sex and breeding experience.*

		Previous breeding experience (years)					Total (breeders)
		*0**	1	2	3	0ver 3	
Males	Same site	*3*	58	21	18	55	152
	Changed site	*18*	28	9	6	13	56
	Total	*21*	86	30	24	68	208
	% changed	*86 ± 3%*	33 ± 2%	30 ± 4%	25 ± 4%	19 ± 2%	27 ± 1%
Females	Same site	*0*	28	15	14	44	101
	Changed site	*22*	48	26	19	55	148
	Total	*22*	76	41	33	99	249
	% changed	*100%*	63 ± 3%	63 ± 4%	58 ± 4%	56 ± 2%	59 ± 2%

*A sample of newly arrived and marked birds which were paired on sites, but did not breed until the following year.

Table 6. *The mean date of laying of pairs of first-time breeding Kittiwakes in relation to whether or not they then bred successfully and if they survived or died before the next breeding season.*

	Females		Males	
	N[1]	Mean date May ± SE	N[1]	Mean date May ± SE
Failed breeders				
Died after the first breeding	33	26.8 ± 1.5	33	27.4 ± 1.6
Failed - survived and changed site	49	27.2 ± 1.5	34	28.5 ± 1.9
Failed - survived to breed at same site	25	26.6 ± 1.5	39	25.6 ± 1.8
Successful breeders				
Bred successfully but died after the first breeding	42	22.2 ± 1.4	43	22.4 ± 1.8
Bred successfully, survived, changed site	71	22.9 ± 1.7	38	23.4 ± 1.3
Bred successfully, survived, bred next year at same site	105	17.4 ± 1.1	138	21.8 ± 1.0

[1]Number.

The annual mortality rate in the year following breeding for the first time by male and female Kittiwakes

The individuals in pairs of Kittiwakes which were both breeding for the first time had a mortality rate of 25.3 ± 0.8% in the year following their first attempt at breeding, and this is about six percent higher than for all breeding birds in the colony (Aebischer and Coulson 1990, Coulson and Strowger 1999, Coulson 2011).

Examining this mortality in relation to their sex and whether their first breeding attempt resulted in young fledging or failure (Table 7) showed that there were significantly different mortality rates in both sexes in relation to the success or failure of their breeding attempt, with 31% of both sexes dying, while those which successfully reared at least one chick to fledging experienced only 20% (males) and 19% (females) mortality; these values for the successful breeders being close to that of older breeding birds.

Table 7. *Mortality rate in the year following breeding for the first time by male and female Kittiwakes in relation to whether breeding had been successful or failed to fledge any young.*

	Failed		Successful	
	Males	Females	Males	Females
Number died before next breeding season	33	33	43	42
Number survived to next breeding season	73	74	176	176
Total	106	107	219	218
Percentage mortality	31 ± 2%	31 ± 2%	20 ± 1%	19 ± 1%

DISCUSSION

On average, Kittiwakes breeding for the first time were the last to return to the colony and lay eggs. They laid the smallest clutch sizes, hatched the lowest proportion of the eggs and fledged the fewest young compared to the older year groups in the colony. Having bred, they suffered a higher mortality rate in the following 12 months than experienced (older) breeders, a higher proportion moved to a different nest site in the colony and were more likely to 'divorce' their mates of the previous year. Overall, their ability to breed was poor and they were the only group of breeding Kittiwakes in the colony whose annual production of fledged young (0.77) fell below the value of 0.8 young per breeding pair needed to prevent a decline in the population (Coulson, 2017).

The relatively low breeding success in first time breeders, despite having, on average, laid smaller clutches, was primarily due to their failure to hatch the eggs. Incubation is shared equally between the sexes in the Kittiwake (Coulson and Wooller, 1984) and cases where the eggs were not incubated at all by these inexperienced breeders were recorded, with both members of the pair continuing to visit the nest, but standing on its rim. In the majority of cases failures to hatch the eggs were because incubation ceased before the embryos were fully developed and capable of hatching. Egg(s) which were infertile (eggs open and examined long after incubation period had passed) or fell from the nest because the nest cup was shallow and poorly constructed were an unimportant cause of failure. In contrast to the poor success of incubation, rearing the young by the inexperienced adults was mainly successful and of little importance in determining their low breeding success. However, this is not the case in all Kittiwake colonies and where successful rearing of young was low and a considerable cost to the parents (Golet *et al*., 1998).

In all respects, individuals and pairs of first-time breeders showed considerable variation in their breeding biology and behaviour. For example, only some three-year-old Kittiwakes visited the colony in the year before they nested, while a minority were not seen there until a future year and when they bred for the first time. Some birds in their third year were only seen beyond the edge of the colony, while others occupied potential nesting sites within the colony's limits. Some of the latter formed pairs and a proportion of these brought small amounts of nesting material to the site while others built nests and succeeded in laying eggs (Coulson and Porter, 1987; Porter, 1990; Coulson, 2011).

The dates of first return each year of birds about to breed for the first time showed variation of about 30 days and the dates of the first egg of the clutch was spread over a similar period and difference persisted in the dates of hatching and of the fledging of young. This appreciable individual variation was also evident in all age classes of Kittiwakes and is obviously a characteristic of the species as a whole.

The reason for the poor performance of first-time breeding Kittiwakes is not clear, but it would appear that the development to full maturity and a peak of breeding success is gradual and is spread over more than the first six years of life. It is obvious that this very gradual development is only possible in long lived species. This change in behaviour presumably has a hormonal basis, with more first-time breeders failing to achieve the necessary stimulus for successful breeding evident in older individuals. The first stimulus each year is that which drives the annual return from a pelagic life to inshore areas and to the colony. The timing of this return influences the courtship and display by pairs and determines the date of laying. Coulson (1986, 2011) showed that the seasonal decline in clutch size in the Kittiwakes was directly influenced by the calendar date of laying, detecting this response both in individual females and also between nearby colonies where the start of laying is later than in others.

The cause of the higher mortality rate in first-time breeders than in older Kittiwakes can only be speculated. Perhaps good quality males can select similarly good quality partners (Coulson and Porter, 1987), and this possibility is supported by the earlier pairing and breeding in the successful pairs. Alternatively, some individuals could be suffering from early stages of illness and which led to poor breeding success and later to their subsequent death (Coulson and Fairweather, 2001). At North Shields, few adults died during the breeding season and, presumably, most died while pelagic during the non-breeding part of the year, and where their death failed to produce ringing recoveries, and also explaining the low recovery rate of dead Kittiwakes marked with BTO rings.

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AUTHOR BIOGRAPHY

John's interest in birds was stimulated as a school boy. He achieved a first-class degree in zoology and subsequently a Ph.D. and D.Sc. from Durham University. He became a research fellow, lecturer and then Reader in Ecology there and supervised 57 Ph.D. students, publishing over 160 scientific papers.John maintained research interests in both moorland ecology and colonial breeding in seabirds, with his main work on seabirds involving 37 years of studies on individually marked Kittiwakes breeding at North Shields. He made a study of eiders on Coquet Island, resulting in the first 15 years of protection there while it was colonised by Puffins, Kittiwakes and four species of terns, and has written three books on seabirds, including a monograph on Kittiwakes.

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Appendix 1. *The mean date and standard error of the first egg in the clutches at North Shields for each year 1954 to 1988.*

Year	Date (May ± se)	Year	Date (May ± se)
1954	22 ± 1.6	1972	15 ± 1.0
1955	16 ± 1.5	1973	19 ± 1.0
1956	21 ± 1.3	1974	21 ± 0.9
1957	17 ± 1.2	1975	19 ± 1.1
1958	22 ± 1.3	1976	19 ± 1.0
1959	19 ± 1.2	1977	22 ± 1.0
1960	16 ± 1.3	1978	21 ± 1.1
1961	16 ± 1.2	1979	23 ± 1.0
1962	17 ± 1.2	1980	23 ± 0.9
1963	22 ± .12	1981	19 ± 1.0
1964	18 ± 1.2	1982	24 ± 0.9
1965	18 ± 1.1	1983	19 ± 0.8
1966	18 ± 1.2	1984	14 ± 0.9
1967	16 ± 1.1	1985	21 ± 0.8
1968	20 ± 1.1	1986	21 ± 0.9
1969	22 ± 1.0	1987	21 ± 0.8
1970	17 ± 1.1	1988	20 ± 0.7
1971	15 ± 1.2		

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