Behaviour of kittiwakes during the breeding season: relationships with nest density and breeding success

Nickerson, Michelle

How to cite:

Nickerson, Michelle (2000) *Behaviour of kittiwakes during the breeding season: relationships with nest density and breeding success*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/4412/

Behaviour of kittiwakes during the breeding season: relationships with nest density and breeding success

Michelle Nickerson

Presented in candidature for the degree of Master of Science.
University of Durham, Department of Biological Sciences, 2000.

Acknowledgements

I would like to thank the JNCC for allowing me access to their research facilities on Skomer Island, and the "summer residents" of Skomer who made field work on the island a pleasure. Thanks are also due to my supervisor, Dr Keith Hamer, for his constructive advice and his patience when progress on my thesis was affected by illness. Thanks also to Nick Littlewood and Elizabeth Wilberforce who followed the fledging success of the few late breeders on Skomer, to Dr John Coulson for allowing me access to information on the colour-ringed birds of Tyneside, and to Newcastle University (NSW) for access to library and computer facilities. And particular thanks to Alison Welch, Sue Raven and Louise Revell for their support in Durham, to my sister and mother whose encouragement helped me to persist in spite of increasing debility, and to Philip and Darienne Scanes who willingly provided the vital communication link to Durham.

Contents

Abstract 1

Chapter 1: Introduction 2

Chapter 2: Study sites and methods 7

2.1 Study sites 8

- 2.1.1 Tyneside colony sites 8
  - 2.1.1.1 North Shields Warehouse 8
  - 2.1.1.2 Tynemouth 8
  - 2.1.1.3 Marsden 10
- 2.1.2 Skomer Island sub-colony sites 11

2.2 Fieldwork methods 14

- 2.2.1 Fieldwork at the Tyneside colonies 14
- 2.2.2 Fieldwork at Skomer in 1997 and 1998 16

2.3 Data Analysis 18

Chapter 3: Activity budgets at the nest and temporal variation in behaviour during the breeding season 19

3.1 Introduction 20

- 3.1.1 Behavioural repertoire 21
  - 3.1.1.1 Interactions with conspecifics 21
  - 3.1.1.2 Nest building and maintenance 23
  - 3.1.1.3 Attending eggs and chicks 24
  - 3.1.1.4 Maintenance and resting behaviours 24

3.2 Methods 25

3.3 Results 25

- 3.3.1. Time interacting with conspecifics 25
  - 3.3.1.1 Comparison between successful and unsuccessful nests 30
  - 3.3.1.2 Relative incidence of different aggressive displays during the breeding season 31
  - 3.3.1.3 Aggressive and pairing behaviour of intruders during chick rearing 33

3.3.2 Time spent “inactive” on the nest 33
3.3.3 Maintenance behaviour 36
3.3.4 Nest building and attending to eggs or chicks 37

3.4 Discussion 41

3.4.1 Interactions with conspecifics: aggressive and pairing behaviour 42
3.4.1.1 Pairing behaviour 42
3.4.1.2 Aggressive behaviour 44
3.4.2 Inactive and maintenance behaviours 48
3.4.3 Nest building 50
3.4.4 Attending eggs and chicks 50

3.5 Conclusions 51

Chapter 4. The impact of sub-colony and cluster nesting density on breeding success 52

4.1 Introduction 53

4.2 Methods 57

4.3 Results 57

4.3.1 Nesting density 57
4.3.1.1 Nesting density at Tyneside in 1996 57
4.3.1.2 Nesting density at Skomer in 1997 and 1998 57
4.3.2 Breeding success in relation to nesting density 59
4.3.2.1 Breeding success at Tyneside in 1996 59
4.3.2.1.1 Timing of breeding 59
4.3.2.1.2 Brood size 60
4.3.2.1.3 Fledging success 60
4.3.2.1.4 Nest cluster density and breeding success 61
4.3.2.2 Breeding success at Skomer in 1997 and 1998 64
4.3.2.2.1 Timing of breeding 64
4.3.2.2.2 Clutch size 65
4.3.2.2.3 Brood size 65
4.3.2.2.4 Fledging success 68
4.3.2.2.5 Nest cluster density and breeding success 69

4.4 Discussion 71

4.4.1 Typical or atypical seasons for the colonies in the study 71

4.4.2 Factors affecting breeding success in the Tyneside colonies 72
4.4.3 Factors contributing to the differences in breeding success between Tyneside and Skomer 74
4.4.4 Factors contributing to the differences in breeding success within areas 75
4.4.5 The influence of nest cluster density on breeding success 77
4.4.6 Advantages of high density nesting 79

Chapter 5. Interactions between behaviour, nesting density and breeding success: behaviour as a guide to quality 81

5.1 Introduction 82

5.2 Methods 85

5.3 Results 85

5.3.1 Aggressive behaviour during the pre-laying stage in relation to colony density, nest cluster density and fledging success 85
5.3.1.1 Tyneside in 1996 85
5.3.1.2 Skomer in 1998 87
5.3.2 Aggressive behaviour during incubation at Skomer in 1997 and 1998 in relation to sub-colony density, nest cluster density and fledging success 89
5.3.3 Aggressive behaviour during chick rearing at Skomer in 1997 and 1998 in relation to sub-colony density, nest cluster density and fledging success 91
5.3.3.1 Comparison of nest cluster density between 1997 and 1998 94
5.3.3.2 Proximity of failed nests 95
5.3.4 Pairing behaviour in relation to breeding success, nest cluster density and sub-colony site 96

5.4 Discussion 97

Chapter 6. General Discussion 103

References 108

Abstract

Activity budgets for kittiwakes at the nest site were determined for colonies on Tyneside during the pre-laying period in 1996 and for the Skomer Island colony during the pre-laying period in 1998 and for incubation and chick rearing in 1997 and 1998. The patterns of change in the proportion of time allocated to the behavioural categories considered were consistent across years and colonies. There was considerable flexibility in the time allocated to aggressive behaviour, while the time allocated to pairing behaviour appeared to be fixed within narrow limits.

The impact on breeding success of nesting density at two spatial scales (sub-colony and cluster of nests within 1.5m) was determined. Although there was some association between denser nesting and enhanced breeding success, the relationship was not evident at all sites studied during the three breeding seasons. Variable predation intensity at the level of the sub-colony appeared to be over-riding the expected trend.

Interactions between the time allocated to interactions with conspecifics, nesting density and breeding success were then considered. There were no relationships evident between nesting density or breeding success and the time allocated to pairing behaviour. There were, however, some indications that the time allocated to aggressive behaviour could be related to nesting density and breeding success, but these associations were not apparent during all three breeding seasons.

Chapter 1

Introduction

The kittiwake (*Rissa tridactyla*) is a small gull, with a northern palaearctic distribution. It is an obligate colonial breeder and during summer kittiwakes congregate in cliff colonies, nesting on small and relatively inaccessible ledges. Although nest spacing is in part determined by cliff topography, where possible kittiwakes build evenly spaced nests 30-60 cm apart. Kittiwakes are long-lived, commencing breeding at 3-4 years, and on average breeding 8-9 times. They form monogamous pair-bonds, renewed each breeding season, and are in general faithful to both mate and nest site. Kittiwakes are strictly territorial and both male and female participate in territory defence. Both members of the pair incubate and tend young until chicks reach independence. During the winter they become more pelagic, rarely coming to land, and are regularly found across the whole of the North Atlantic (Cramp and Simmons 1983).

Like many other species of gulls in the second half of this century, kittiwakes have moved into some urban environments, using buildings as substitute cliffs for breeding (Raven 1997). The first recorded instance of kittiwakes nesting on a building in the U.K. occurred at Dunbar, SE Scotland in 1934. This was part of a general habitat expansion as kittiwakes, from being generally restricted to cliffs over 200 foot high, were progressively occupying lower cliffs, some less than 30 foot high (Coulson 1963). Unlike the larger gulls which opportunistically exploit food resources provided by rubbish in the urban environment, kittiwakes have not greatly altered their foraging patterns. Although known to scavenge for fish discards from trawlers, and occasionally seen taking fish waste from processing areas and sewage waste from at least one river (Coulson 1962), kittiwakes principally obtain food from fishing. They generally fly further to feed than other gulls in the UK and have been tracked flying over 40 km from the breeding colony (Hamer et al 1993).

Being conspicuous, colonial and convenient of access, the *Laridae* were selected as objects of study by Tinbergen, one of the founders of field ethology (e.g. Tinbergen 1953, 1958, 1959, 1972). Within this context is Cullen and Tinbergen's qualitative work on kittiwake behaviour, describing the repertoire and context of kittiwake displays and focusing on behavioural adaptations to cliff nesting (Cullen 1957, Tinbergen 1958, 1959). In comparison with members of the *Laridae* nesting at relatively low density on the ground, kittiwakes display behavioural specialisations for high density nesting on cliff ledges relatively free from predation. High density nesting is associated with high levels of aggression, and competition for nest sites in the centre of a kittiwake colony is intense (Coulson and Wooller 1976).

Considerable subsequent work on kittiwakes has focused on factors impacting on breeding success (e.g. Coulson and White 1960, Coulson and Thomas 1984, Coulson and Johnson 1993, Porter 1990). Kittiwake breeding success is affected by age of the individual, breeding experience, timing of breeding, pair status, position in the colony and individual quality (Fairweather 1994). Coulson and co-workers have related position in the colony, in terms of nesting in the "centre" or at the "edge" to the quality of the nesting pair, with only high quality kittiwakes able to occupy sites in the centre. They have also identified quality as the single most important factor determining kittiwake breeding success (Coulson 1968, Coulson and Wooller 1976, Coulson and Thomas 1984, Coulson and Porter 1985, Fairweather 1994).

Much of this information is, however, derived from a single long term study of a warehouse colony at North Shields, Tyneside (e. g. Coulson & White 1960, Coulson 1966, 1968, Thomas 1980, Coulson & Wooller 1984, Coulson & Thomas 1984, Fairweather 1994). Virtually all birds breeding at the warehouse were marked, facilitating the study of individual differences in breeding parameters over time. The colony was observed through its growth phase and during more than two decades of relative stability in numbers, from the late 1960s to 1990. The birds at North Shields appeared, however, to be breeding under near ideal conditions, free from predation, with a low ectoparasite load and largely unaffected by food shortages.

Recent behavioural research has concentrated on kittiwake activity budgets during the breeding season in terms of nest attendance and the duration of time allocated to foraging (Braun and Hunt 1983, Galbraith 1983, Coulson and Wooller 1984, Wanless and Harris 1992, Hamer et al 1993, Cadiou and Monnat 1996, Falk and Møller 1997, Regehr and Montevecchi 1997) while work on kittiwake behaviour at the nest site has focused on behavioural interactions within the colony and the behaviour of prospectors (e.g. Cadiou et al 1994, Danchin 1987, Cadiou 1999). To my knowledge there has been no attempt to determine the activity budget of the kittiwake at the nest site during all stages of the breeding season. The pattern of time allocated to each behaviour would be expected to influence breeding success, as has been shown in studies on geese (e.g. Astrom 1993, Eberhardt et al 1989). The activity budget reflects the energetic and behavioural needs and restrictions for individuals during the breeding season and there may be differences in activity budgets between kittiwake colonies and between breeding season.

Differential breeding success among kittiwakes has, therefore, been associated with nesting density, individual quality and the quality of the pair bond. Both quality and nesting density have also been associated with high aggression levels, while increased time allocated to pairing displays has been recorded for new, and potentially poorly coordinated pairs, in comparison to established pairs (Chardine 1983). To my knowledge, however, there has been no attempt to quantify these relationships by looking at the percentage of time allocated to aggressive or pairing displays in relation to nesting density and subsequent breeding success.

This thesis is, therefore, an initial attempt to quantify the links between nesting density, behaviour at the nest site and breeding success. Chapter 1 provides a brief overview of previous research on kittiwake behaviour and breeding ecology, while chapter 2 outlines fieldwork methodology. In chapter 3 activity budgets for kittiwakes at the nest site are considered, using data from the pre-laying stage at colonies in urban areas and data for all stages of the breeding season from a colony in a more natural situation. Chapter 4 examines the links between breeding success and nesting density at two spatial scales, the level of the sub-colony and that of clusters of nests within a 1.5m radius. The differences between kittiwake colonies in urban and more natural areas are also considered. Chapter 5 examines whether differences in time allocated to aggressive and pairing behaviours at different stages in the breeding season may be related to nesting density and breeding success. Finally, Chapter 6 is an overview of the work in the thesis.

Chapter 2.

Study Sites and Methods

2.1 Study sites

2.1.1 Tyneside colony sites

2.1.1.1 North Shields warehouse

The North Shields colony on a warehouse facing the Tyne River (Figure 1a) has been the subject of a long term study by J. C. Coulson and co-workers. Their study commenced shortly after kittiwakes colonised the building in 1949, and continued until 1991 when the birds were excluded from the window ledge nest sites and the population dispersed. Most birds moved to existing, nearby colonies at Tynemouth, Marsden and other buildings on the River Tyne (Porter 1985; Fairweather 1994). Some of these birds returned to breed at the warehouse 3-4 years later, when the wire mesh excluding them deteriorated. During the study, most breeding adults were given combinations of 3 colour rings, enabling individuals to be identified. From the 1970s all chicks produced at the colony were ringed with a single colour ring, with an alpha-numeric identifier inscribed in a contrasting colour. In 1965 the colony was at its maximum size, with 106 breeding pairs (Porter 1985).

In 1996 only 17 pairs of kittiwakes bred on the riverside face of the building, all of which were included in this study. Approximately 10 pairs bred on the roofs of nearby buildings. Among the 17 pairs monitored in 1996, 8 individuals had been ringed at the North Shields colony as breeding adults and 8 had been ringed as chicks. 16 of the 17 pairs were located in the old "centre" of the colony. It should, however, be noted that choice of window ledge in 1996 was restricted as the screening on some windows remained intact. Although at least one pair of herring gulls (*Larus argentatus*) bred in 1996 on the roof of the warehouse, no predation has ever been recorded at this colony.

2.1.1.2 Tynemouth

This was a small (circa 80 breeding pairs) colony on the cliffs at Tynemouth (Figure 1a), of which 65 nests were included in the study. Kittiwakes have bred at this crumbling limestone and mud cliff since 1957 (Coulson 1963). In the section of colony monitored

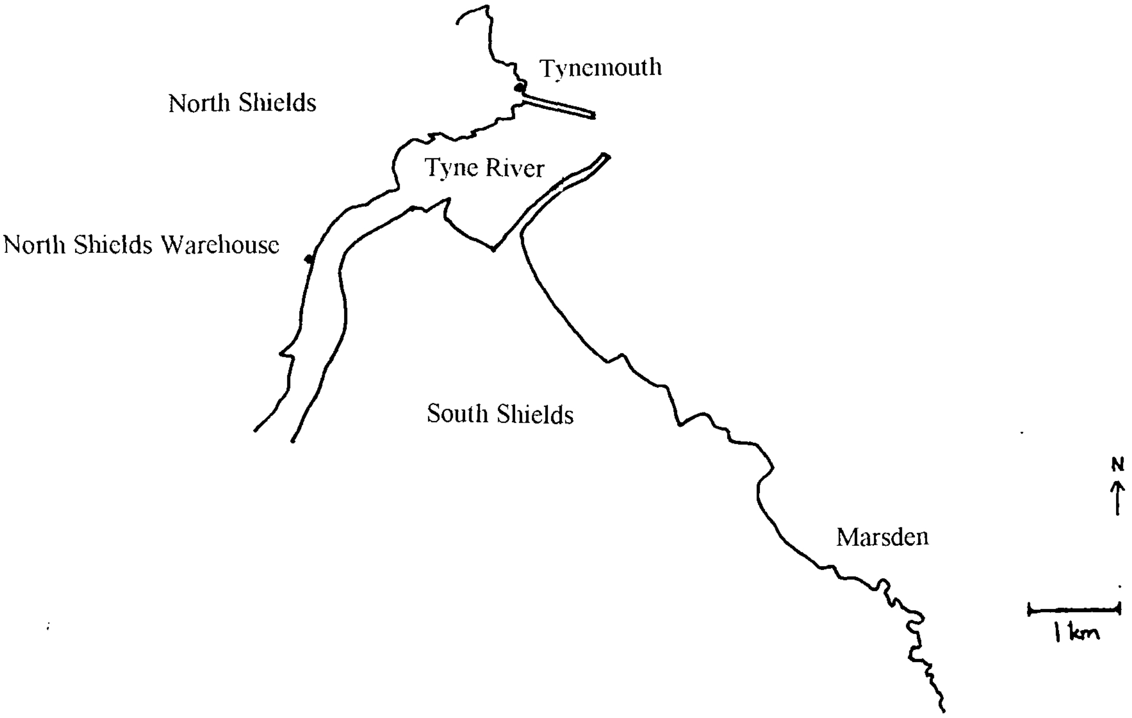

Figure 1a. Location of the study colonies on Tyneside.

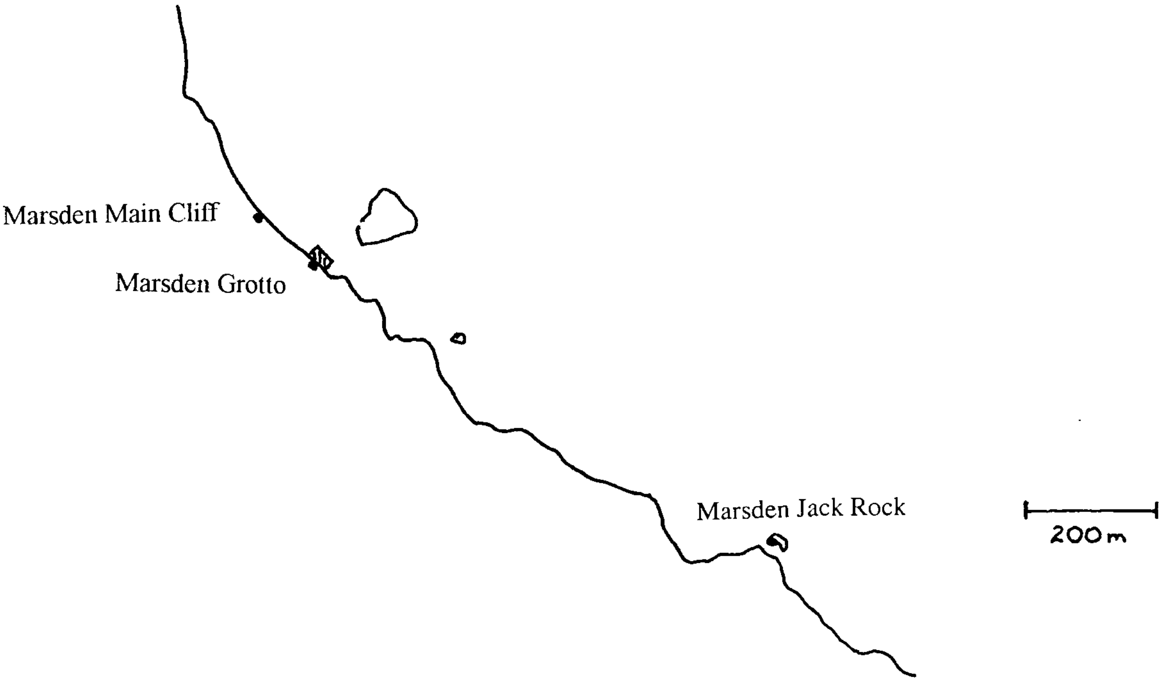

Figure 1b. Location of the sub-colony sites in the Marsden colony.

during this study there were 18 birds ringed as adults (17 at the North Shields colony and one from the nearby Marsden colony) and 8 ringed as chicks either at North Shields or Marsden. No large gulls bred on or above the cliffs. No predation was observed at the colony in 1996. Fulmars (*Fulmarus glacialis*) also breed on the cliffs at Tynemouth.

2.1.1.3 Marsden

Kittiwakes recolonised Marsden Rock in 1930, following abandonment of the colony after intense persecution last century (Figure 1a). From a small group on the seaward side of Marsden Rock, the colony expanded rapidly and in 1996 there were approximately 5,000 pairs breeding in the colony, spread over a few miles of coastline. As at Tynemouth, the cliffs are crumbling mud and limestone and the nest-sites are largely inaccessible, with the exception of the area above the beach-side pub "The Grotto". Ringing of adults and chicks has taken place here in most years since 1990 (Strowger 1993).

In 1996 behavioural observations were undertaken at a small section (53 pairs) above the “Grotto” hotel at the Marsden colony. Two other sites within the Marsden colony were monitored for breeding success: 105 pairs in a densely occupied area (Marsden Main Cliff) which was part of the core area occupied when the colony expanded from Marsden Rock to the mainland and located a few hundred metres north of the Marsden Grotto site; and 76 pairs nesting on the landward side of Jack Rock, around a mile and a half to the south (Figure 1b).

The density of breeding varied enormously at Marsden. The area above the Grotto was very sparsely occupied in comparison to the densely packed site monitored on the main cliff and the intermediate density of the other monitoring site on Jack Rock.

At the grotto site in 1996 there were 56 birds ringed as adults (one at the North Shields colony; the rest at the grotto) and 3 birds ringed as chicks. There were no ringed birds breeding at the Main Cliff or Jack Rock sites. Herring gulls and fulmars bred near the kittiwakes at Marsden.

All three colony sites on Tyneside were located within urban areas

2.1.2 Skomer Island sub-colony sites

Skomer Island is a National Nature Reserve in S.W. Wales managed by the Dyfed Wildlife Trust, and one of the most important seabird breeding sites in southern Britain. Kittiwakes, guillemots *(Uria aalge),* razorbills (*Alca torda*), fulmars, herring gulls, lesser black-backed gulls (*Larus fuscus*) and great black-backed gulls (*Larus marinus*) breed on the island. Guillemots, razorbills and fulmars are potential nest site competitors with kittiwakes (Coulson 1963), and the three species of large gulls are potential predators of kittiwake young. Three land-based potential predators of kittiwake eggs or chicks, ravens (*Corvus corax*), peregrine falcons (*Falco peregrinus*) and jackdaws (*Corvus monedula*) also breed near the cliffs.

My study sites were on the south eastern cliffs in the area of greatest kittiwake concentration at the Wick, High Cliff (where nesting density was lower) and the cliffs below South Stream (Figure 2). The upper Wick site was a densely settled area located at the landward end of the Wick on the cliff furthest from and facing the sea, and marking the landward end of the kittiwake colony. The cliff at upper Wick was principally crumbling mud, with kittiwakes nesting on slanting lines of rock outcrops. The cliff was unstable and a rockfall dislodged two nests in the study area in summer 1997 and further rock falls removed nest sites during the winter of 1997.

The Lower Wick site was near the midpoint of the cliffs and the midpoint of the kittiwake colony, under a large overhang of rock. Few birds nested on the overhang and kittiwakes and guillemots were clustered below it, immediately above the sea. The erosion lines of the rock-face formed individual pinnacles, each of which was used as a nest site by one pair of kittiwakes. Although few nests, therefore, had neighbours immediately adjacent,

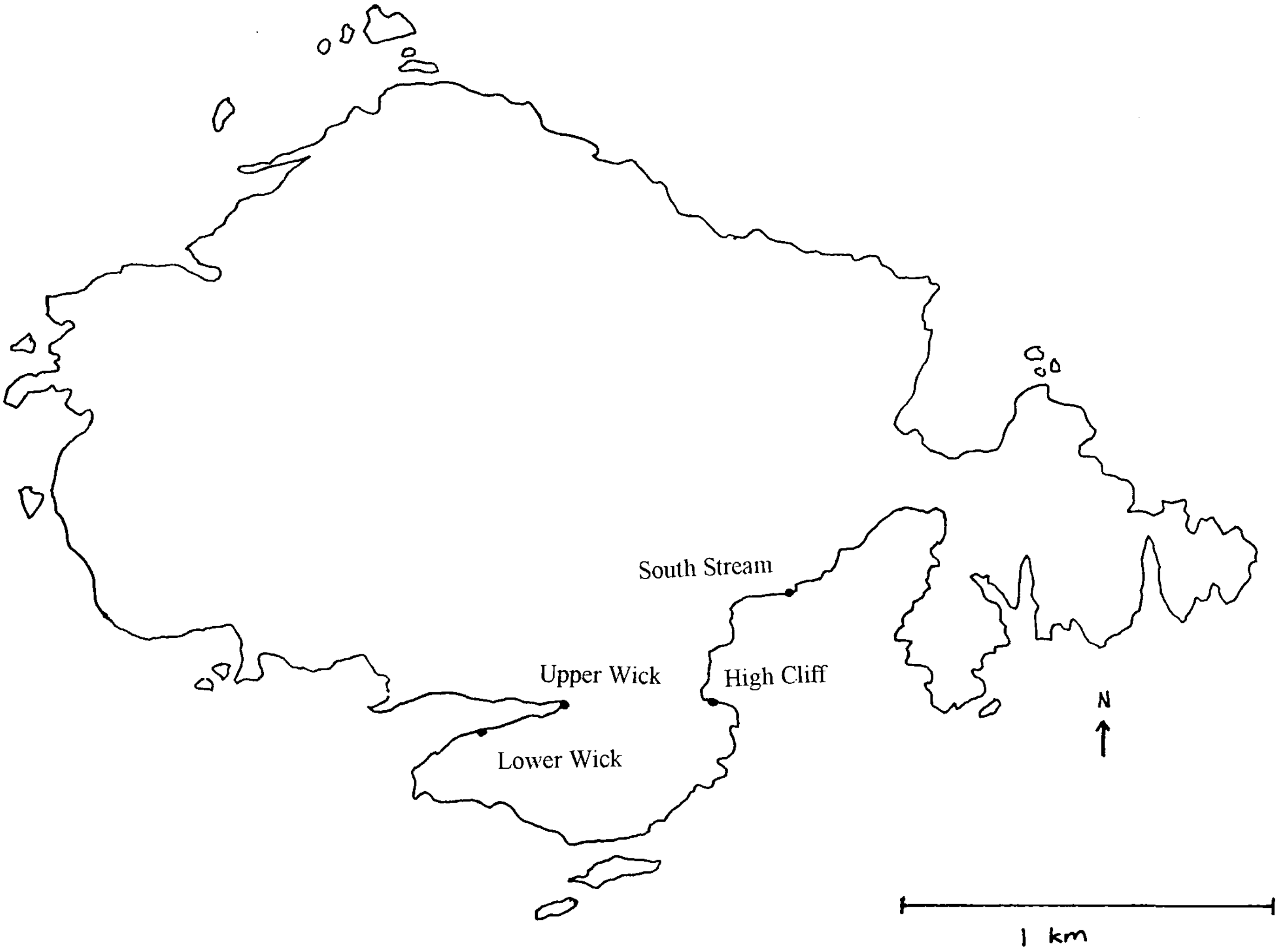

Figure 2. Location of the study sites in the Skomer Island kittiwake colony.

the array of nests formed was of medium density. The site was vulnerable to wave action during southerly gales and six study nests were washed away in 1997 and one nest lost in 1998.

The High Cliff site was located on the eastern side of South Plateau. The cliffs were rock, but not as deeply scarred and ledged as either the Wick or South Stream sites, providing fewer sites suitable for kittiwakes. The area was, therefore, less densely settled. My study group consisted of the scattered birds at the landward end of the cliff. In both years jackdaws frequented the cliff and lesser black-backed gulls bred on the promontory above the cliff. In 1998 a pair of peregrine falcons bred on High Cliff.

South Stream was another dense sub-colony, but the group monitored was on a separate cliff section, at the extreme landward edge and isolated from the main colony. Some ringing has been undertaken at South Stream, principally on the main breeding cliff. Five of the nests in my study site included at least one colour-ringed bird. There was a lesser black-backed gull colony above the South Stream cliffs.

At both High Cliff and South Stream, and to a lesser extent at upper Wick, few birds not belonging to the section, either owning nests or landing to prospect, flew past these sections of the colony. In contrast, in front of the Lower Wick there was a constant coming and going of kittiwakes.

2.2 Fieldwork Methods

2.2.1 Fieldwork at the Tyneside colonies

The Marsden, Tynemouth and North Shields colonies were visited every 2-4 days during the pre-laying period, starting on 21st March 1996 for behaviour observations. The timing of visits varied, the order and time of visit on any day being determined by the tides, as the Tynemouth colony was accessible only at low tide. Observation sessions at the Marsden Grotto and Tynemouth were generally for 2 hours, while observation sessions at the North Shields colony were of one hour's duration.

Data were collected using focal animal sampling (Altmann 1974, Colgan 1978): colour-ringed individuals, or their unringed partners, being watched for 10 minutes and their behaviour noted at one-minute intervals. The behavioural observations were then grouped into six categories:

- aggressive behaviour – choking, bow and moan, fighting, jabbing (Cramp and Simmons 1983);
- pair-bonding behaviour – kittiwaking or greeting, bill flicking, head nodding, courtship feeding, copulating, pre-flight calling (Cramp and Simmons 1983; Daniels et al 1984);
- nest-building – stamping material into the nest, sitting and scraping, arriving with nest material; tucking in pieces of nest material (Cramp and Simmons 1983);
- alert behaviour – standing or sitting on the nest site with head up and eyes open, peering at nest cup, moving around on the nest site;
- non-alert behaviour – standing or sitting on the nest site with head tucked under wing or eyes closed;
- maintenance behaviour – preening, stretching, shaking;

Only complete and clear movements were included in the aggressive, pair-bonding and nest-building classifications. Partial or unclear movements, e.g. if a bird assumed the bowed stance associated with choking but did not proceed with the actions, were included in the alert behaviour category.

On any day, the individuals used as focal animals were those birds whose leg rings were initially observed. The main problem with this methodology was the resultant unequal sampling. If both members of a pair were ringed, or if a nest was in a prominent position from the observers point of view, those nests would be more likely to be sampled frequently. If ringed birds were sitting at the beginning of the observation session, they would not be included on that day. Although no attempt was made to monitor nest site occupation, nests that were more constantly occupied would also be over-represented in the data. Ringed birds and their partners occupied only a small proportion of the nests in the study sub-colony groups, and may not have been representative of all pairs nesting in the group. Behaviour observations were undertaken on 58 nests, and amounted to 377 bird-hours.

From the first day chicks were observed (24th June 1996) the three main sites, North Shields, Tynemouth and Marsden Grotto, were visited at 3-day intervals to determine approximate hatching dates. The Tynemouth and North Shields colonies were usually visited on the same day. The other two Marsden monitoring sites, Main Cliff and Jack Rock, were visited 8 times between 22nd July and 16th August, when the chicks were large enough to be counted quickly. Brood size and the number of young surviving to fledging per well built nest were noted at all sites. Brood sizes at the secondary Marsden sites are underestimated as these sites were not visited until late in chick rearing. Approximate dates of hatching could be noted for most pairs at the three main sites. Chicks were presumed to have died if they disappeared when younger than 33 days and were assumed to have fledged if they disappeared after this age. From observation points below the colonies it was not possible to determine either the exact date of egg laying or the clutch size.

The date of hatching referred to the day on which a chick was first observed in the nest. As Tyneside nests could not be observed from above, these hatching dates are likely to be one or two days later than the actual hatching date, recording when the chick became active, either food begging or defaecating. Visiting the Tyneside colonies at 3 day intervals also introduced an error of up to 2 days in the hatching dates recorded.

Predation of chicks was noted when it occurred at Marsden Grotto during observation sessions, and the presence of dead chicks on nests within the study sites was also noted.

The extent of clustering of nests in the study plots was estimated with the assistance of photographs taken in April 1996. As access to the cliffs for accurate measurement was impossible, the scale was derived from the size of adult kittiwakes in each photograph. The number of active nests within a 1.5m radius of each nest site was used as an index of density.

2.2.2 Fieldwork at Skomer in 1997 and 1998

Fieldwork commenced on 18th May in 1997, after egg laying had begun at some nest sites, and in 1998 fieldwork started on 18th April, before the colony was continuously occupied for the season. Observations were made daily, weather permitting, at all sites. Clutch size (for most nests), brood size, laying date of the first egg (for most nests), hatching date of the first chick and number of chicks fledged per well built nest were recorded. On Skomer Island, vantage points above the colonies allowed chicks to be seen on the first day they were hatched, and sites were visited on all days during the hatching period. In addition, known causes of mortality of eggs or chicks, including incidences of predation of eggs or chicks within the study sites during observation periods as well as instances where adults stopped incubating in spite of the presence of an apparently intact egg in the nest, were noted.

As with the Tyneside sites, clustering of nests in the study plots was estimated with the assistance of photographs taken in June 1997. As access to the cliffs for accurate measurement was impossible, the scale was derived from the size of adult kittiwakes in each photograph.

Behavioural observations were undertaken during incubation and chick-rearing in 1997 and during the pre-laying stage, incubation and chick rearing in 1998 at four sub-colony sites on Skomer Island: South Stream, High Cliff, Upper Wick and Lower Wick. The observation regime was similar to that used in 1996, using focal animal sampling with individual nests being observed for 10 minutes and the presence and behaviour of the birds on site noted at one-minute intervals. The difference in methodology lay in the selection of individuals for behaviour observations. Instead of randomly following ringed individuals, observations were focused on nest sites and all nests in the study plot were observed in the same sequence on each visit, regardless of whether or not birds were present on the nest site. One or two sets of observations were made each day in 1998 and in 1997 until early chick rearing, after which some sites were only sampled on alternate days. Behaviour observations were discontinued at each nest when chicks were known to be able to fly.

In the 1997 breeding season 412 bird hours of observation at 110 nests were made during incubation; 300 bird hours at 79 nests during chick rearing; and 192 birds hours at 47 nests where breeding attempts had failed (a bird hour referring to 60 spot observations). In the 1998 breeding season 1,294 bird hours of observation were made at 100 nests during the pre-laying stage; 432 bird hours at 93 nests during incubation; 383 bird hours at 66 nests during chick rearing; and 230 bird hours at 40 nests were breeding attempts had failed. Observations of behaviour were allocated to breeding stage on the basis of the status of each individual nest, rather than the breeding status of the sub-colony i.e. observations of behaviour of an incubating late breeder would be allocated to the incubation stage, even if the majority of other nests had moved to the chick rearing stage. After the mean laying date, observations of behaviour at well-built nests where no eggs were laid were allocated to the failed nest category. During chick rearing, the behaviour of intruders was recorded separately to nest owners. Intruders were identified by the responses of chicks resident in the nest and the behaviour of neighbouring resident birds.

Behaviour was allocated to seven categories, with the category of attending to the eggs or chicks (turning eggs, feeding or preening chicks) added to the 6 behavioural categories used in 1996 (see above). The nest building category included nest maintenance during incubation. The aggressive behaviour category also included aggressive sitting during incubation and brooding. Aggressive sitting can be equated with the seated phase during Mock Fighting as described by Paludin (1955, in Cramp and Simmons 1983). Two seated birds face each other with neck withdrawn and bill part open or angled obliquely down. This posture frequently alternates with bouts of jabbing.

2.3 Data analysis

The proportion of time allocated to each behaviour, e.g. for the overall activity budget, was derived from the sum of the behavioural observations of each nest in the appropriate category e.g. breeding stage or nesting density. Analysis was undertaken on the percentage data for each individual nest within the appropriate category, arcsine transformed to allow parametric statistics to be used (Fowler, Cohen and Jarvis 1990).

Breeding success and behaviour were examined on two spatial levels, that of the sub-colony or colony site, and that of the number of neighbours within a cluster of 1.5m radius. A nest was allocated to the high density category if it had 4 or more “active” neighbouring nests within 1.5m at the start of the breeding season; and allocated to the low density category if it had fewer than 4 neighbours within 1.5m. The size of the cluster was based on the distance at which kittiwakes respond to the displays of conspecifics; response to displays being infrequent if birds were more than 5 feet away (Coulson & White 1960). I did not attempt to differentiate between pairs nesting in central or peripheral locations within each sub-colony or colony site.

Chapter 3

Activity budgets at the nest and temporal variation in behaviour during the breeding season

3.1 Introduction

As with most species of birds, the behavioural interactions of kittiwakes with conspecifics tend to be in the form of stereotyped displays. The behavioural repertoire of the kittiwake at the nest site has been intensively studied and the context in which most displays are used has been described. The early behavioural studies of Tinbergen and his group adopted a comparative approach to the evolution and function of gull displays (Cullen 1957, Tinbergen 1958, Tinbergen 1960, Tinbergen 1972, Nelson 1967, Danchin and Nelson 1991), while more recent work has focused on the adaptive nature of behaviour, looking for direct effects on reproductive success (Coulson and White 1960, Braun and Hunt 1983, Danchin 1987, Danchin 1988, Porter 1990). Individual pairs should not, however, only be considered in isolation. At the scale of the impact of behaviour within the colony, Danchin (1988) concluded that we "still don't know anything about the exact nature of the social interactions within colonies."

Although kittiwake behaviour has been intensely studied and considerable work has been done on the activity budgets of kittiwakes during the breeding season, in terms of nest attendance and the duration of time allocated to foraging trips (Pearson 1968, Galbraith 1983, Coulson and Wooller 1984, Coulson and Johnson 1993, Wanless and Harris 1992, Hamer et al 1993, Hamer and Turner 1997, Cadiou and Monnat 1996, Falk and Møller 1997, Regehr and Montevecchi 1997), to my knowledge, there has been no attempt to quantify how a kittiwake allocates its time on the nest site during the breeding season. The time and energy allocated to each category of behaviour during the breeding season may be expected to influence breeding success, as has been shown in a number of studies on geese (including Åström 1993, Eberhardt et al 1989). The pattern of time allocated to each behaviour reflects the energetic and behavioural needs and restrictions for an individual in a given situation. At the scale of the colony behavioural time allocation reflects the environmental conditions e.g. feeding conditions and weather, faced by birds at the colony during that season.

The first part of my behavioural study is an examination of the pattern of time allocation in breeding kittiwakes from which to derive activity budgets for behaviour at the nest site during the stages of the breeding season and to determine whether there are consistent changes in time allocation as the breeding season progresses. It should be noted, however, that my results may be applicable only to the colonies studied, and that further studies in different colonies would be needed before definitive activity budgets could be determined.

3.1.1 Behavioural repertoire

3.1.1.1 Interactions with Conspecifics

Among kittiwakes the two contexts for interactions with conspecifics are displays directed toward the partner or potential partner and aggressive or territorial displays directed against other conspecifics. The context in which some displays are used changes as the breeding season progresses.

There are a number of displays and behaviours with which kittiwakes signal varying degrees of aggression. The two most prevalent aggressive displays are "choking" and "bow and moan." The "choking" display is used by males throughout the breeding season to advertise ownership of a nesting territory and to ward off intruders. Early in the breeding season it is also has a role in establishing territory ownership and in attracting a potential mate (Danchin 1987). The "bow and moan" display also signifies ownership of a territory and deters intruders, but does not have the dual role of attracting a mate. Both "choking" and "bow and moan" indicate a moderate level of aggression and may be followed by "jabbing" or fighting if the conflict intensifies. Fighting kittiwakes grip their opponents beak and attempt to twist them from the nest site (Cullen 1957). An intense fight may continue in the water or on the ground below the nest site.

Danchin (1988) suggested that "choking" and "jabbing" denote shorter distance aggression than the "bow and moan " display, which is used in the context of more distant aggression. Both the "bow and moan" display and "choking" are, however, associated with disturbance not directly at the nest site, being used in response to the presence of an intruder near the nest site or in response to the aggressive or "greeting" displays of nearby kittiwakes. Jabbing and fighting are only observed between adjacent birds. Another display used in a short distance aggressive context is the "aggressive sitting stance" of a bird brooding eggs or chicks, directed at an encroaching intruder or neighbour, described by Paludin (1955, in Cramp and Simmons 1983) as part of the mock fighting sequence. Aggressive sitting frequently alternates with "jabbing" or pecking. Kittiwake aggressive displays, therefore, follow a heirarchy of distance from bow and moan at the greatest distance, choking at an intermediate distance and jabbing or aggressive sitting between immediate neighbours.

Behaviours directed to the partner are mutual "kittiwaking" or "greeting"(Tinbergen 1959), pre-flight calling (Daniels et al 1984), courtship feeding and mating. Tinbergen (1958) described kittiwake "greeting" as the functional equivalent of the long call of other gull species. Daniels et al (1984) demonstrated the role of "greeting" in partner recognition and Chardine (1983) concluded that the greeting display functioned to reduce aggression within the pair. The repetition of the greeting ceremony on meeting, therefore, contributes to the maintenance of the pair relationship after initial pair formation. Chardine (1983) also suggested that "greeting" may have the physiological function of stimulating the female to commence ovulation. Daniels et al (1984) described pre-departure calling, which appears to have a role in co-ordinating the activities of the pair. Co-ordination of activities is of particular importance during incubation and early chick rearing, when the presence of at least one parent on the nest is essential.

It has been suggested that among the *Laridae*, courtship feeding may perform the dual functions of reinforcing the pair bond and providing an essential, additional food supply to females during egg production (Brown 1967, Tasker and Mills 1981). Although the primary role of repeated copulation is to ensure the fertilisation of the developing eggs, the fact that kittiwakes begin copulating early in the pre-laying stage, before the nest has been built and before the female is ready for insemination, suggests a possible supplementary role of repeated copulation in reinforcing the pair bond or bringing the female into breeding condition (Chardine 1983). Although uncommon, copulation and courtship feeding have been observed after clutch completion (personal observations).

Extra-pair copulation has not been noted as common in kittiwake colonies (Coulson, pers. comm.), although male interference with copulating pairs has been noted (Chardine 1986). The possibility of extra-pair paternity cannot, however, be ruled out, given the extensive variation observed among different populations and species (Petrie and Kempenaers 1998). Various researchers (e.g. Birkhead et al 1987, Hunter et al 1992) have suggested frequent copulation was a method of paternity assurance, while Villarroel et al (1998) suggested frequent copulation in the American kestrel *(Falco sparverius)* was associated with assessment of mate quality and Petrie (1992) associated frequent copulation with female mate guarding. Although head nodding and bill flicking generally act as preludes to copulation or courtship feeding, they may also occur in isolation and have been observed after the clutch has been completed.

"Choking," "bow and moan" and "greeting" have all been observed as responses to disturbances within the colony. These displays appear "contagious" and may spread across the colony in response to the displaying of a single pair (Coulson and White 1960, Coulson and Dixon 1979).

3.1.1.2 Nest building and maintenance

Kittiwakes follow a set of recognisable behaviour patterns while nest building, alternating between stamping nest material onto the nesting ledge with a motion which appears to be akin to choking, and forming the nest cup by sitting within the partly formed nest and scraping with the feet. Kittiwake nest building bouts are episodic and of limited duration. Collecting nest material has the appearance of a social activity, as many kittiwakes simultaneously collect material from one site. Although the apparent synchrony of collection of nesting material may function as a defence against being vulnerable on the ground (Cullen 1957) it is more probable that, as kittiwakes generally collect material from the nearest available source, a large colony will inevitably form a continuous stream moving between the colony and the source of material during the few weeks of intensive nest building. At the Tyneside and Skomer Island colonies nest-building does not commence in earnest until a week or two before eggs are laid, some weeks after nest site occupation. In contrast, in colonies in the north of the species range colony occupation and nest building may occur simultaneously (Falk and Møller 1997).

3.1.1.3 Attending eggs and chicks

Kittiwake eggs and young chicks are brooded continuously (Coulson and Wooller 1984). The eggs are monitored and turned regularly. Kittiwakes feed their chicks by regurgitation, the chicks taking food from the parents' beak. Feeding bouts usually follow an adult's return from foraging, but feeding may occur at any time during a brooding shift, following solicitation by the chicks (personal observation). Parents spend little time preening their chicks.

3.1.1.4 Maintenance and resting behaviours

At least one member of a pair of kittiwakes remains in attendance at the nest site almost continuously from the time of nest building until the chicks are several weeks old (Coulson and Wooller 1984, Coulson and Johnson 1993). It would, therefore, be expected that a large proportion of a kittiwake's time at the nest site would be allocated to "doing nothing" categories, which include resting and brooding and to maintenance behaviours. The presence of the owner on the nest may act as a passive deterrent to conspecific intruders throughout the breeding season and, during incubation and chick rearing, may also deter predators. There has been considerable work suggesting that birds adjust their vigilance rates according to assessments of current danger and vigilance is also influenced by the size and density of the group or colony (Pöysä 1994, Roberts 1996, Bednekoff and Lima 1998) and this may be reflected in my study in the relative allocation of time to alert and non-alert behaviour. All birds spend considerable time maintaining the integrity of their feathers, which is essential for efficient flight, and amongst water birds such as kittiwakes, for water-proofing and insulation. There is some evidence for social facilitation of preening amongst Larids, with preening frequency increasing among common terns in denser groups on loafing areas (Palestis and Burger 1998)

Kittiwake behaviour away from the nest site, including flying to the feeding grounds and foraging, has been shown to take up a large proportion of a kittiwake's time during the breeding season (Pearson 1968, Galbraith 1983, Coulson and Wooller 1984, Coulson and Johnson 1993, Wanless and Harris 1992, Hamer et al 1993, Hamer and Turner 1997, Cadiou and Monnat 1996, Falk and Møller 1997, Regehr and Montevecchi 1997). The proportion of time spent away from the nest site has not, however, been considered in this study.

3.2 Methods

Methods are described in Chapter 2.

Behaviour data recorded from each nest was grouped by stage of the breeding cycle, the three main categories being pre-laying, incubation and chick rearing. Additional categories covered nests after breeding attempts had failed either during incubation or during chick rearing. These were also combined to form a post all fail category. An additional category, that of intruders on nests sites where chick rearing was in progress, was included when time interacting with conspecifcs was considered.

3.3 Results

3.3.1 Time interacting with conspecifics

During the breeding season kittiwakes allocated only a small percentage of their time on the nest site to interactions with conspecifics. During the period before egg-laying, when nest site ownership was established and pairs formed, kittiwakes spent 2-3% of their time in aggressive displays and 5% of their time in behaviours directed toward the partner. During the pre-laying stage, although the proportion of time allocated to pairing displays was consistent between the Tyneside colonies in 1996 and the Skomer Island colony in 1998 (t-test using arcsine transformed data; $t = -1.63$, 156 d.f., $P = 0.11$), there were significant differences in the proportion of time spent in aggressive displays between the Tyneside colonies in 1996 and the Skomer colony in 1998 ($t = -3.43$, 156 d.f., $P = 0.0001$). Birds in the Skomer colony in 1998 allocated more time to aggressive displays than did birds in the Tyneside colonies (Figure1).

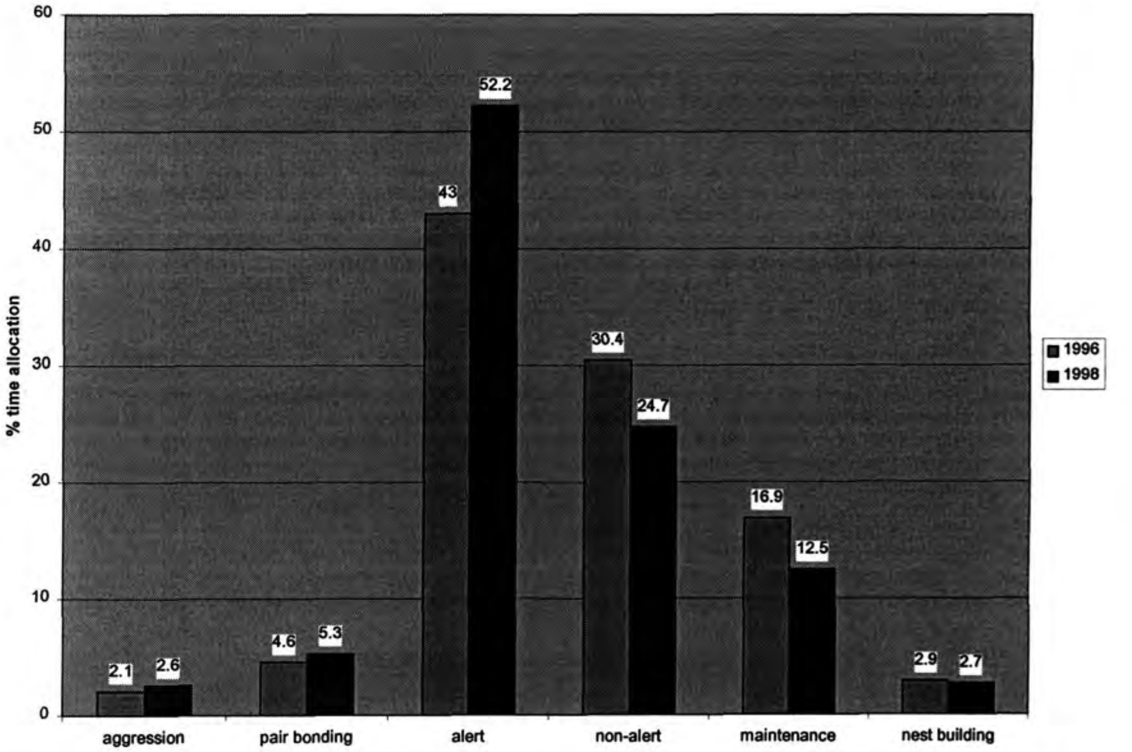

Figure 1. Percentage of time at the nest allocated to six behavioural categories during the pre-laying stage by kittiwakes at the Tyneside colonies in the 1996 breeding season and at the Skomer Island colony in 1998.

On Skomer in 1998, less time was allocated to aggressive and pairing displays during incubation than in the prelaying stage (Figure 2; $t = 14.82$, 191 d.f., $P < 0.0001$) and (Figure 3; $t = 20.86$, 191 d.f., $P < 0.0001$) respectively. No data are available for the prelaying period in 1997.

When the effects of stage of the breeding season and year were separated, there were differences in the amount of time allocated to aggressive displays between the incubation and chick rearing stages, and between the 1997 and 1998 breeding seasons (Two-way ANOVA: stage $F_{1,347} = 157.9$, $P < 0.0001$, no significant interactions; year $F_{1,347} = 13.7$, $P < 0.0001$, two-way interactions $F_{1,347} = 21.3$,$P < 0.0001$). In both years, aggression levels during chick rearing were higher than during incubation (Figure 2). During chick rearing, however, aggression levels were higher during the 1997 breeding season, than during the 1998 season while there were no differences in aggression levels during incubation between the 1997 and 1998 breeding seasons, accounting for the interaction between the tested variables (Figure 2; $t = -0.75$, 201 d.f., $P = 0.45$).

When the effects of stage of the breeding season and year were separated , there were no differences in the amount of time allocated to pairing behaviours among the incubation and chick rearing stages during the 1997 and 1998 breeding seasons (Figure 3: Two-way ANOVA: stage $F_{1,347} = 0.15$, $P = 0.70$; year $F_{1,347} = 0.92$, $P = 0.34$, no significant interactions).

Although the proportion of time spent in aggressive behaviour during chick rearing was small, a pattern was discernible during this period. In both 1997 and 1998, aggression levels were very low during the first two weeks of chick rearing, and increased as chick rearing progressed (Figure 4). In 1997 aggression levels increased throughout chick rearing, being highest after the minimum fledging date of 33 days. The differences between weeks were significant ($F = 12.91$, 5 d.f., $P < 0.0001$), and a Tukey-HSD test indicated that aggression levels during the first two weeks of chick rearing were lower than during weeks 3, 4, 5 and the period after minimum fledging age. In 1998, there were again significant differences among weeks in the proportion of time allocated to

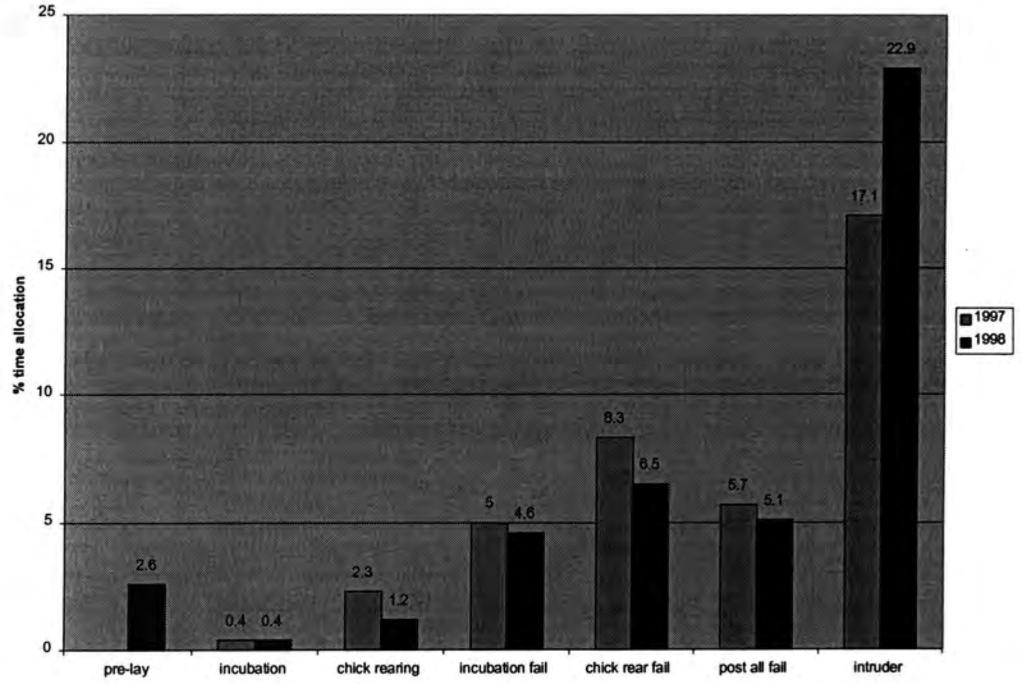

Figure 2. Changes in the percentage of time allocated to aggressive behaviour by kittiwakes in the Skomer Island colony in the 1997 and 1998 breeding season.

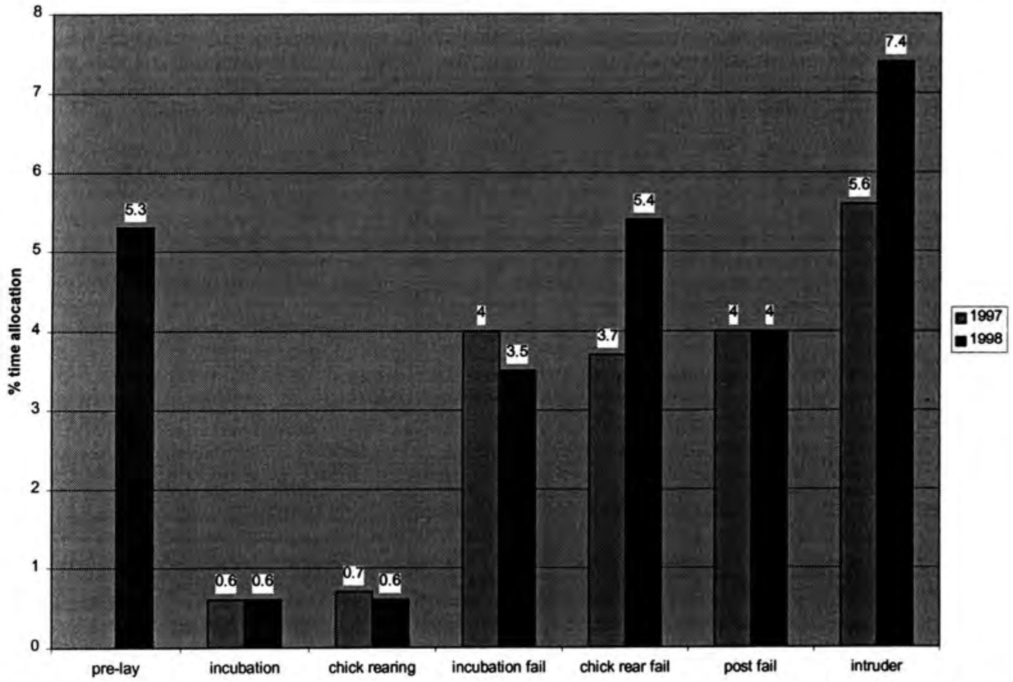

Figure 3. Changes in the percentage of time allocated to pairing behaviours by kittiwakes in the Skomer Island colony in the 1997 and 1998 breeding seasons.

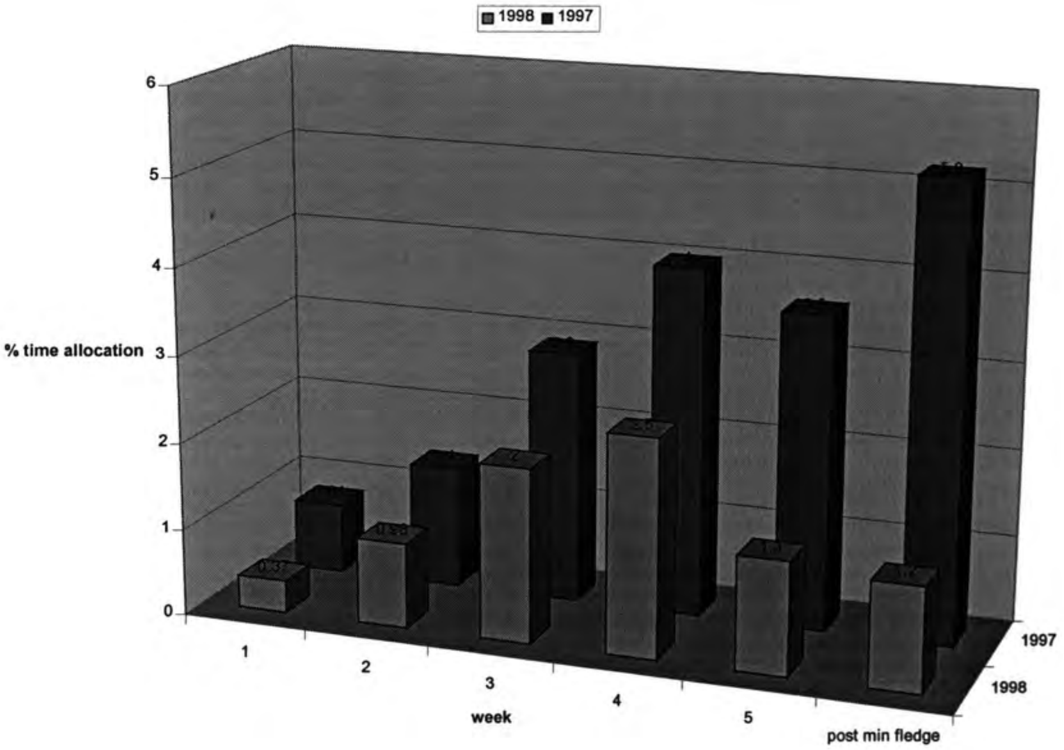

Figure 4. Percentage of time on the nest site allocated to aggressive behaviour during each week of chick rearing and after the minimum fledging age of 33 days in the kittiwake colony on Skomer Island in the 1997 and 1998 breeding seasons.

aggressive displays ($F = 11.04$, 5 d.f., $P < 0.0001$). In this year a Tukey-HSD test indicated that aggression levels during weeks 3 and 4 were significantly higher than during the initial 2 weeks and the latter stages of chick rearing. In 1998, therefore, levels of aggression peaked during the 3rd and 4th weeks of chick rearing.

3.3.1.1 Comparison between successful and unsuccessful nests

At nests where breeding attempts failed during incubation the proportion of time allocated to aggressive and pairing displays increased after breeding failure, and these differences were consistent between the 1997 and 1998 breeding seasons (Aggressive behaviour Figure 2: Two-way ANOVA stage: $F_{1,259} = 362.6$, $P < 0.001$; year $F_{1,259} = 0.01$, $P = 0.92$, no significant interactions; Pairing behaviour Figure 3: Two-way ANOVA: stage $F_{1,259} = 135.3$, $P < 0.001$, year $F_{1,259} = 0.36$, $P = 0.55$, no significant interactions). At nests where breeding attempts failed during chick rearing the proportion of time allocated to aggressive and pairing displays also increased after breeding failure, and the differences in levels of pairing behaviour were consistent between the 1997 and 1998 breeding seasons (Aggressive behaviour Figure 2: Two-way ANOVA: stage $F_{1,174} = 107.8$, $P < 0.001$; year $F_{1,174} = 3.09$, $P = 0.081$, two-way interactions $F_{1,174} = 3.72$, $P = 0.056$; Pairing behaviour Figure 3; Two-way ANOVA: stage $F_{1,174} = 61.7$, $P < 0.001$, year $F_{1,174} = 0.02$, $P = 0.9$; no significant interactions). When aggressive behaviour was considered, however, interaction between the two variables approached significance, as lower levels of aggression during chick rearing in 1998 increased the magnitude of change in aggression levels after failure during that breeding season (Figure 2).

The second highest levels of aggression were recorded at nests after failure of the breeding attempt. In 1998 aggression levels at all failed nests were significantly higher than levels of aggression during the pre-laying stage (Figure 2; $t = -5.20$, 139 d.f., $P < 0.0001$). In contrast, in 1998 the proportion of time allocated to pairing displays by birds on failed nests, was lower than the time allocated to pairing during the pre-laying stage (Figure 3; $t = 3.69$, 139 d.f., $P < 0.0001$).

When the effects of the stage at which failure occurred and year were separated, there were differences in the time allocated to aggressive behaviour at nests after failure during incubation compared with nests where failure occurred during chick rearing, but no differences between the 1997 and 1998 breeding seasons (Figure 2; Two-way ANOVA; stage $F_{1,86} = 7.08$, $P = 0.009$; year $F_{1,86} = 0.017$, $P = 0.9$, no significant interactions). Levels of aggression were higher at nests which failed during chick rearing. When the effects of stage at which failure occurred and year were separated, there were no differences in time spent in pairing behaviour between nests after failure during incubation or chick rearing, or between years (Figure 3; Two-way ANOVA: stage $F_{1,86} = 0.046$, $P = 0.83$; year $F_{1,86} = 0.007$, $P = 0.93$; no significant interactions).

3.3.1.2 Relative incidence of different aggressive displays during the breeding season

There were differences between Tyneside in 1996 and Skomer in 1998 in the relative incidences of the choking ($t = 4.19$, 63 d.f., $P < 0.001$) and the bow and moan displays ($t = -4.93$, 72 d.f., $P < 0.001$) while there was no difference in the relative incidence of jabbing ($t = -0.79$, 63 d.f., $P = 0.43$). The incidence of choking behaviour was higher and bow and moan displays less frequent on Tyneside in 1996 (Figure 5).

During the 1998 breeding season there were changes between the pre-laying and incubation stages in the relative incidences of the choking display ($t = 10.06$, 47 d.f., $P < 0.0001$), bow and moan display ($t = 7.27$, 137 d.f., $P < 0.001$) and jabbing ($t = -6.55$, 41 d.f., $P < 0.0001$). The relative incidence of choking and bow and moan displays decreased, while there was an increase in jabbing once incubation commenced (Figure 6).

When the effects of stage and year were separated, there were differences in the incidence of choking (Two-way ANOVA: stage $F_{1,208} = 147.0$, $P < 0.0001$; year $F_{1,208} = 0.50$, $P = 0.48$; no significant interactions), bow and moan (Two-way ANOVA: $F_{1,208} = 7.28$, $P = 0.008$; year $F_{1,208} = 0.64$, $P = 0.43$; no significant interactions) and jabbing (Two-way ANOVA: stage $F_{1,208} = 107.2$, $P < 0.0001$; year $F_{1,208} = 2.60$, $P = 0.11$; no significant interactions) displays between incubation and chick rearing, and these changes

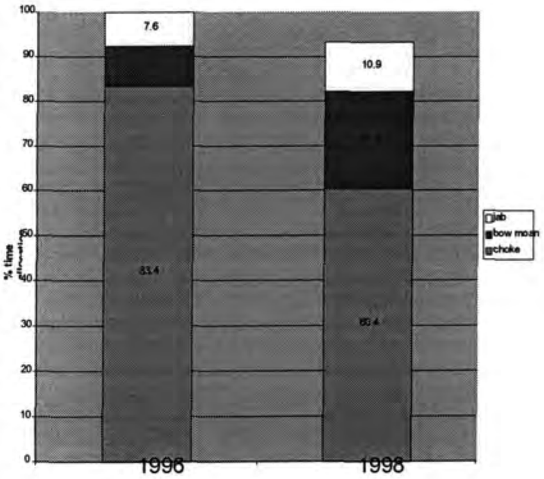

Figure 5. Relative incidence of aggressive displays during the pre-laying period at Tyneside in 1996 and at Skomer in 1998.

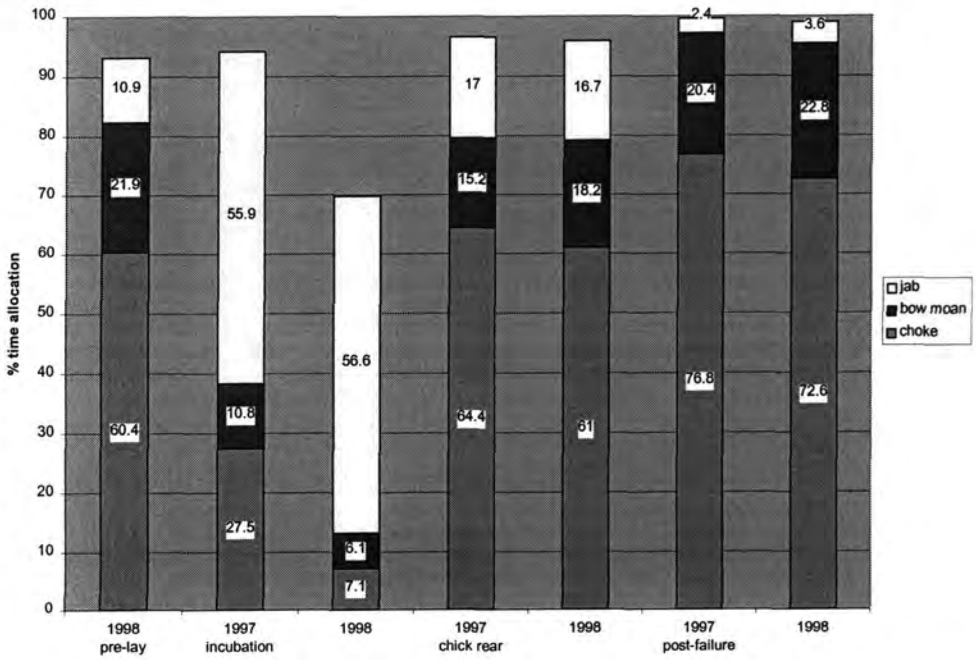

Figure 6. Relative incidence of aggressive displays during all stages of the breeding season at Skomer in 1997 and 1998.

were consistent between years (Figure 6). The relative incidence of choking and bow and moan displays increased, while the incidence of jabbing decreased once chicks hatched.

When aggressive behaviour during the pre-laying stage was compared with behaviour at nests after all breeding failures in the 1998 breeding season, there were differences in the relative incidence of choking ($t = -3.60$, 143 d.f., $P < 0.0001$) and jabbing ($t = 3.84$, 143 d.f., $P < 0.0001$), but no differences in the incidence of bow and moan displays ($t = 0.50$, 143 d.f., $P = 0.62$). In comparison to the pre-laying stage, there was a relatively higher incidence of choking and lower incidence of jabbing after breeding failure (Figure 6). At nests after breeding failure, there was consistency between the 1997 and 1998 breeding seasons in the relative incidences of choking ($t = 1.12$, 94 d.f., $P = 0.27$), bow and moan ($t = -0.71$, 94 d.f., $P = 0.48$) and jabbing ($t = -1.51$, 94 d.f., $P = 0.13$).

3.3.1.3 Aggressive and pairing behaviour of intruders on nests during chick rearing

Intruders on occupied nests during chick rearing allocated the highest percentage of time to aggressive behaviour of all categories observed. When the effects of status and year were separated, intruders allocated significantly more time to aggressive behaviour than residents, and this difference was consistent between years (Figure 2, Two-way ANOVA: status $F_{1,239} = 250.4$, $P < 0.0001$; year $F_{1,239} = 0.93$, $P = 0.34$; two-way interactions $F_{1,239} = 10.03$, $P = 0.002$). There were, however, significant interactions between the two variables, as aggressive behaviour of residents was lower in the 1998 breeding season.

When the effects of status and year were separated, intruders also allocated more time to pairing behaviour than residents during chick rearing, and this difference was consistent between years (Figure 3, Two-way ANOVA: status $F_{1,239} = 11.23$, $P = 0.001$; year $F_{1,239} = 0.011$, $P = 0.92$, no significant interactions).

3.3.2 Time spent “inactive” on the nest

The largest proportion of a kittiwake’s time on the nest site during all stages of the breeding season was allocated to either alert or non-alert behaviour. These two categories accounted for 73-77% of time spent at the nest during the pre-laying season, 90-91% of time spent on the nest during incubation and 80-82% during chick rearing, (Figures 1, 7 & 8). During incubation and early chick rearing, time spent in alert or non-alert behaviour roughly equated with time spent incubating or brooding.

During the pre-laying stage, birds in the Tyneside colonies in 1996 spent less time in alert behaviour than birds in the Skomer colonies in 1998 (Figure 1; $t = -4.51$, 156 d.f., $P < 0.0001$), while there was no difference in the amount of time spent in non-alert behaviour (Figure 1; $t = 0.65$, 156 d.f., $P = 0.52$).

Between the pre-laying and incubation stages in the Skomer colony in 1998, there was an increase in the proportion of time allocated to alert behaviour (Figure 7; $t = -7.12$, 191 d.f., $P < 0.0001$), while there was no difference in the time spent non-alert on the nest (Figure 8; $t = - 0.49$, 191 d.f., $P = 0.62$).

When the effects of stage of the breeding season and year were separated, there were no changes in the amount of time allocated to alert behaviour between incubation and chick rearing to minimum fledging, but there were differences between the 1997 and 1998 breeding seasons (Figure 7; Two-way ANOVA: stage $F_{1,347} = 0.10$, $P = 0.75$; year $F_{1,347} = 18.05$, $P < 0.0001$; no significant interactions). Kittiwakes allocated more time to alert behaviour during both incubation and chick rearing in the 1998 breeding season. When the effects of stage and year were separated, there were significant changes in the amount of time allocated to non-alert behaviour between incubation and chick rearing and between the 1997 and 1998 breeding seasons (Figure 8; Two-way ANOVA: stage = $F_{1,347} = 20.6$, $P < 0.0001$; year $F_{1,347} = 11.57$,$P = 0.001$; no significant interactions). More time was allocated to non-alert behaviour during incubation than during chick rearing in both years, and more time was allocated to non-alert behaviour during both stages in the 1997 breeding season.

There were no consistent patterns in change of alert and non-alert behaviour at nests where breeding attempts had failed. There were no changes in the time allocated to alert behaviour among incubating pairs and at nests where breeding attempts failed during

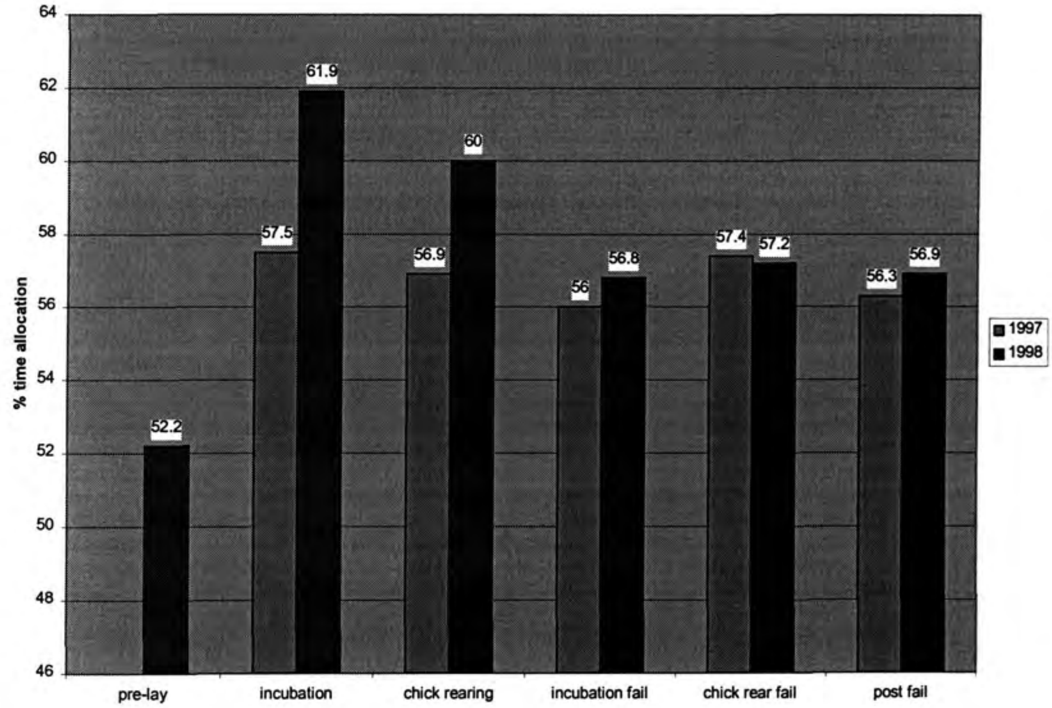

Figure 7. Changes in the percentage of time allocated to alert behaviour by kittiwakes at Skomer in 1997 and 1998.

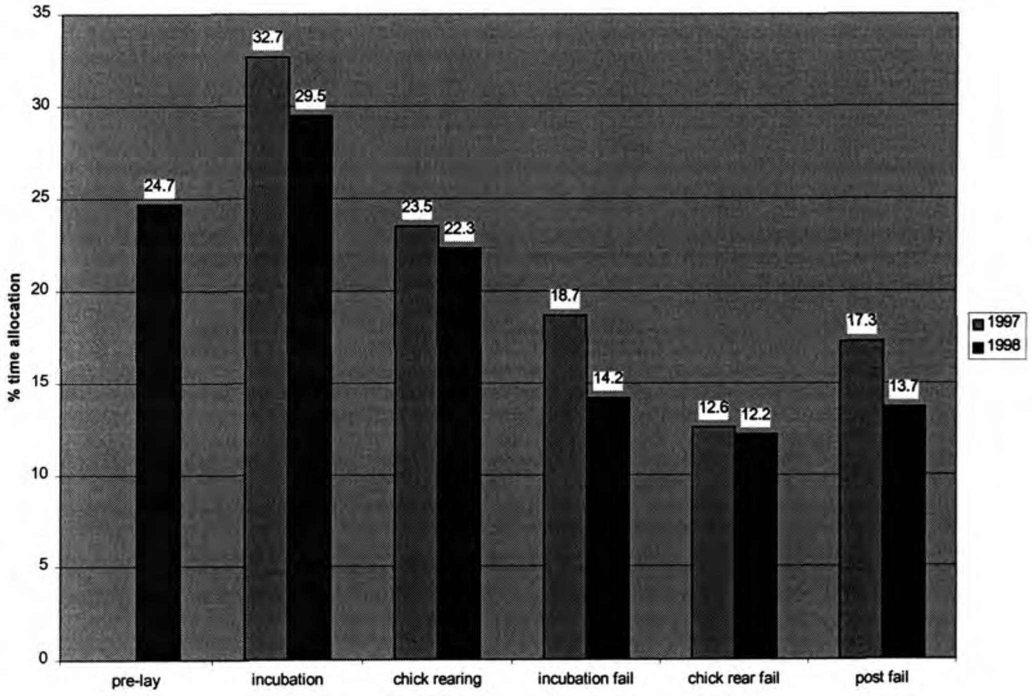

Figure 8. Changes in the percentage of time allocated to non-alert behaviours by kittiwakes at Skomer in1997 and 1998.

incubation during the 1997 and 1998 breeding seasons (Figure 7; Two-way ANOVA: stage $F_{1,259} = 1.82$, $P = 0.18$; year $F_{1,259} = 0.89$, $P = 0.35$; two-way interactions $F_{1,259} = 4.37$, $P = 0.038$). There were, however, significant interactions between the two variables as more time was allocated to alert behaviour during incubation in 1998 (Figure 7). There were significant changes in the time allocated to non-alert behaviour after failure during incubation, and differences in non-alert behaviour between years (Figure 8; Two-way ANOVA: stage $F_{1,259} = 35.9$, $P < 0.0001$; year $F_{1,259} = 3.87$, $P = 0.05$; no significant interactions). There was a decrease in the time allocated to non-alert behaviour after incubation failure in both years, and less time was spent in non-alert behaviour during both stages in 1998 relative to the 1997 breeding season.

When failure during chick rearing was considered, there were significant differences in the time allocated to alert behaviour between years, and the difference between birds rearing chicks and at nests where the breeding attempt failed approached significance (Figure 7; Two-way ANOVA: stage $F_{1,174} = 3.49$, $P = 0.064$; year $F_{1,174} = 4.36$, $P = 0.038$; no significant interactions). More time was allocated to alert behaviour during chick rearing in 1998 than in 1997, and after failure during chick rearing the time allocated to alert behaviour increased in 1997 and decreased in 1998. When the time allocated to non-alert behaviour was considered, there were changes between stages and consistency between years. The time allocated to non-alert behaviour decreased after failure during chick rearing in both breeding seasons (Figure 8; Two-way ANOVA: stage $F_{1,174} = 32.87$, $P < 0.0001$; year $F_{1,174} = 2.23$, $P = 0.14$; no significant interactions).

3.3.3 Maintenance behaviour

The third largest allocation of time was to maintenance behaviour, 17% and 13% during the pre-laying stages on Tyneside and Skomer respectively. During the pre-laying stage, birds in the Tyneside colonies in 1996 allocated more time to maintenance behaviour than did birds in the Skomer colony in 1998 (Figure 1; $t = 3.91$, 156 d.f., $P < 0.0001$).

In the Skomer colony in 1998 there was a significant change in the amount of time allocated to maintenance behaviour between the pre-laying and incubation stages, decreasing from 13% to 3% (Figure 9; $t = 18.87$, 191 d.f., $P < 0.0001$).

When the effects of stage and breeding season were separated, the proportion of time allocated to maintenance increased between incubation and chick rearing stages, while remaining consistent between years (Figure 9; Two-way ANOVA: stage $F_{1,347} = 358.26$, $P < 0.0001$; year $F_{1,347} = 1.94$, $P = 0.17$, no significant interactions).

After failure during incubation, the time allocated to maintenance behaviour increased in both the 1997 and 1998 breeding seasons, and there were differences in the allocation of time to maintenance behaviour before and after incubation failure between years (Figure 9; Two-way ANOVA: stage $F_{1,259} = 400.65$, $P < 0.0001$; year $F_{1,259} = 4.61$, $P = 0.033$, two-way interactions $F_{1,259} = 20.78$, $P < 0.0001$). More time was allocated to preening at nests post incubation failure in the 1998 breeding season. The time allocated to maintenance behaviour increased after failure during chick rearing in both breeding seasons, and a trend for differences at both stages between years approached significance (Figure 9; Two-way ANOVA: stage $F_{1,179} = 4.26$, $P = 0.041$; year $F_{1,179} = 2.79$, $P = 0.097$; no significant interactions).

3.3.4 Nest building and attending to eggs or chicks

Birds on nest sites spent a small proportion of their time in nest building and nest maintenance, only 2-3% during pre-laying and incubation (Figures 1 & 10). During the pre-laying stage, the amount of time allocated to nest-building was consistent between the Tyneside colonies in 1996 and the Skomer colony in 1998 (Figure 1; $t = -0.11$, 156 d.f., $P = 0.91$).

In the Skomer colonies in 1998, there was no difference between the amount of time allocated to building behaviour at the nest site during the pre-laying stage and the amount of time spent maintaining the integrity of the nest during incubation (Figure 10; $t = 0.88$,

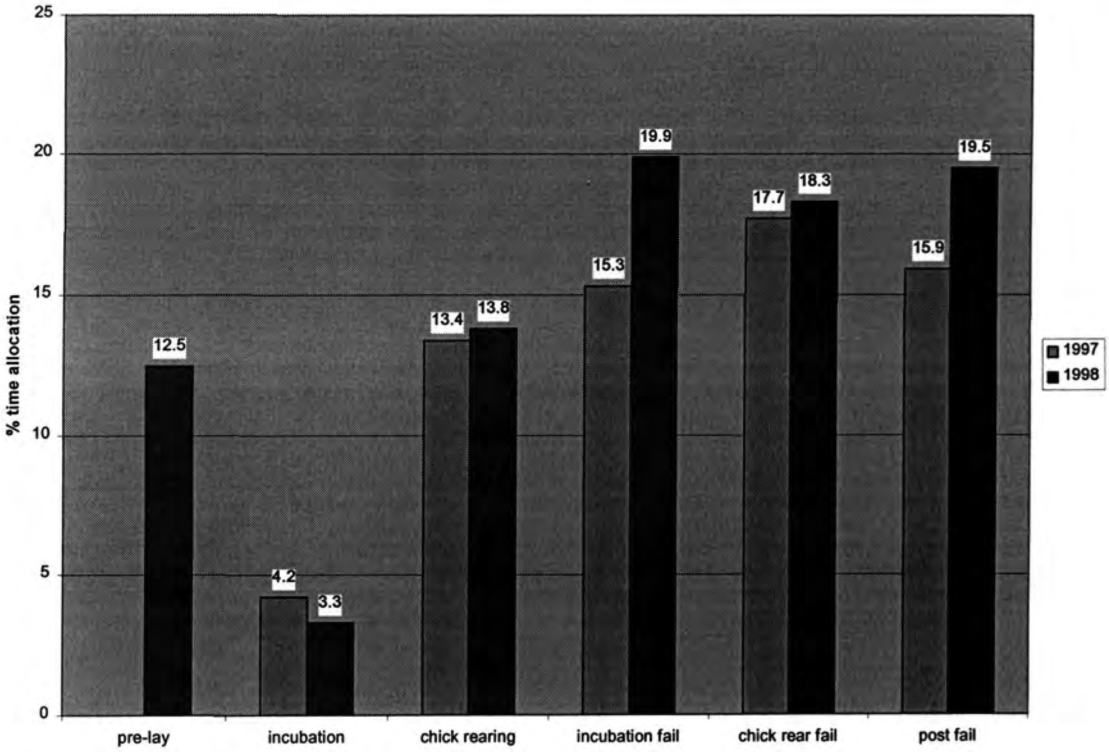

Figure 9. Changes in the percentage of time allocated to maintenance behaviour by kittiwakes at Skomer in1997 and 1998.

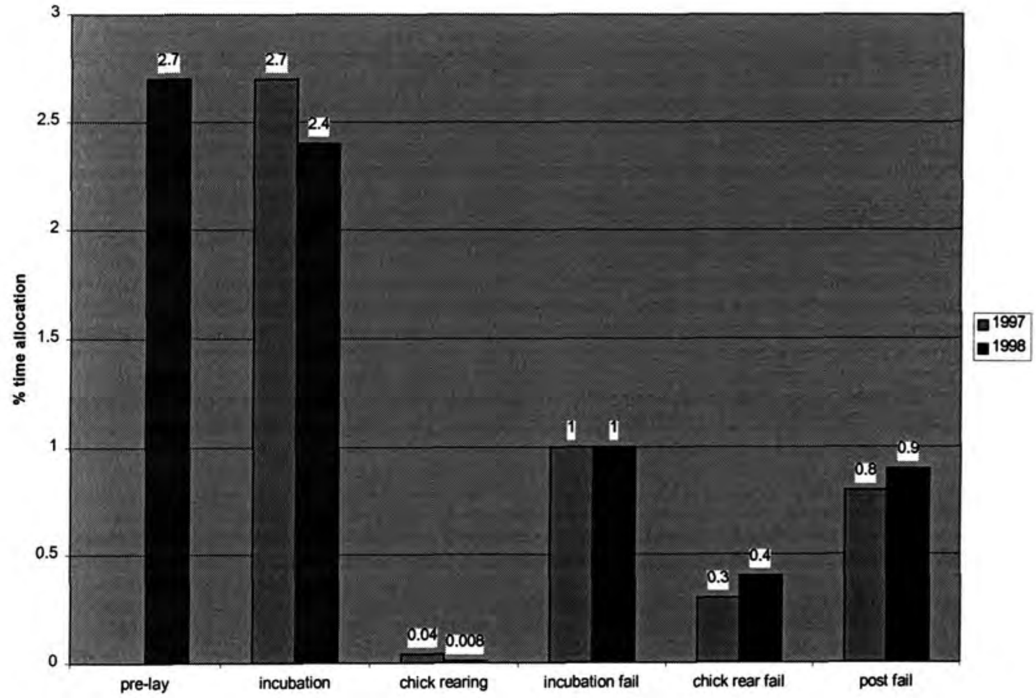

Figure 10. Changes in the percentage of time allocated to nest building and nest maintenance behaviours by kittiwakes at Skomer in 1997 and 1998.

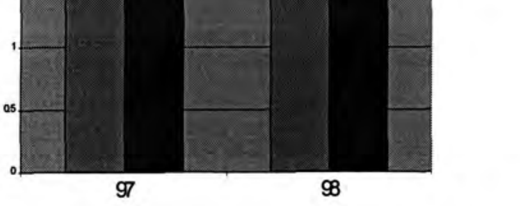

Figure 11. The time allocated to turning eggs during incubation and feeding or preening chicks during chick rearing by kittiwakes at Skomer in 1997 and 1998.

191 d.f., $P = 0.38$). No attempt was made, however, to determine the time allocated to collecting and bringing material to the nest site during the period when nests were built.

When the effects of stage and year were separated, there was a decrease in the time allocated to nest building and maintenance, effectively to nothing, after chicks hatched, while there was consistency between years during these stages (Figure 10; Two-way ANOVA: stage $F_{1,347} = 506.1$, $P < 0.0001$; year $F_{1,347} = 0.03$, $P = 0.86$, no significant interactions).

During incubation there were no differences between the 1997 and 1998 breeding seasons in the amount of time allocated to turning eggs (Figure 11; $t = -0.32$, 201 d.f., $P = 0.75$). During chick rearing, birds in the Skomer colony spent more time feeding or preening chicks in 1997 than in 1998 (Figure 11; $t = 2.74$, 143 d.f., $P = 0.007$). If there was a minimum amount of time adults must allocate to preening or feeding each chick, more time allocated to these behaviours may have reflected a higher mean number of chicks per active nest. There were, however, no differences between years in the number of chicks hatched (Mann Whiney U test $Z = -0.084$, $P = 0.93$) or the number of chicks fledged ($Z = -0.46$, $P = 0.64$) per nest where a breeding attempt was still in progress (Table 1) i.e. the birds whose behaviour was included in the chick-rearing category were feeding approximately the same number of chicks per feeding bout in both years.

Table 1. Mean number of chicks hatched and chicks fledged per nest where a breeding attempt was still in progress at the time of hatching and fledging respectively, at Skomer in 1997 and 1998

	No. active nests	No. chicks hatching	No. active nests	No. chicks fledging
1997	80	1.65	62	1.44
1998	66	1.65	52	1.38

3.4 Discussion

The patterns of change in the proportion of time allocated to seven behavioural categories at each stage of the breeding season were consistent across years and colonies, suggesting that my observation regime provided an adequate representation of a kittiwake nest site activity budget. In summary, throughout the breeding season, most of a kittiwake's time on the nest site was allocated to the categories of "inactive behaviours" and only a small proportion of time was allocated to behavioural interactions with conspecifics. During the period before laying, relatively more time was allocated to interactions, both aggressive and pairing, and most aggressive interactions were in the form of displays denoting aggression at some distance (i.e. choking and bow and moan displays). The time allocated to these behaviours dropped almost to nothing during incubation and the nature of aggressive interactions changed, with a higher frequency of jabbing, i.e. short distance aggression, relative to the time allocated to displays denoting aggression at greater distances. During chick rearing, although there was no further change in the incidence of pairing displays, there was a progressive increase in the time allocated to aggressive displays and the relative frequency of jabbing decreased. At nest sites where breeding attempts had failed, relatively large amounts of time were allocated to both pairing and aggressive displays. The highest levels of aggression and relatively high levels of pairing behaviour were recorded for intruders on nests during chick rearing. The time allocated to maintenance behaviours was consistently high, second in time allocation only to inactive behaviours, except during incubation, where a significant reduction in the time allocated to maintenance behaviour was observed. Kittiwakes allocated the same overall proportion of time to maintaining the integrity of the nest during incubation, as was allocated to building behaviours at the nest site prior to egg-laying. After eggs hatched virtually no time was spent on nest maintenance.

There were, however, some differences in the proportions of time allocated to the various behavioural categories between years and colonies, most notably more time allocated to aggressive displays during the pre-laying stage in the Skomer colony than in the Tyneside colonies; and more time allocated to aggressive displays during chick rearing in the Skomer colony in the 1997 breeding season than in the 1998 season.

3.4.1 Interactions with conspecifics: aggressive and pairing behaviour

3.4.1.1 Pairing behaviour

Although only a small proportion of time was spent in pairing activities there were clear patterns of change in the time allocated to these activities as the breeding season progressed. As expected, relatively high levels of pairing behaviours were recorded during the pre-laying stage, when pair-bonds were established and fertilisation of the egg took place. Interactions within the pair were reduced almost to nothing when incubation commenced and remained at very low levels throughout incubation and chick rearing. Several factors would have contributed to the decrease in the proportion of time allocated to pairing behaviours. Once incubation commenced courtship feeding and mating, two behaviours included in the pairing display category, were observed very infrequently. The reduction of time spent on the nest with the partner once eggs were laid would also have reduced the opportunities for within pair displays (Coulson and Johnson 1993). A third factor which may have contributed to the decrease in the proportion of time allocated to pairing displays may be that the presence of eggs or chicks inhibited these behaviours.

After loss of eggs or chicks, birds in reproductive condition appeared to revert to behaviours associated with an earlier stage of the breeding cycle, with an increase in the proportions of time allocated to both pairing and aggressive displays and in some cases replacement clutches were laid. The time allocated to pairing displays at failed nests was, however, lower than that recorded during the pre-laying stage. I suggest that the failed pair may have continued to be present on the site and, as an existing pair, would not need to allocate time to re-establish the bond. Without being able to identify individuals I could not, however, be certain that the same birds were involved in the second breeding attempt. Although Cadiou et al (1994) have demonstrated an advantage for prospectors in occupying a nest site, as far as I know, there has been no evidence to suggest that incipient pair bonds between prospectors increases the likelihood of pairing in the following season. Higher levels of pairing displays among intruders during chick rearing suggests that there may be some advantage to practising pairing.

All forms of display are energetically more expensive than resting behaviour, with courtship feeding being particularly energy-demanding for males. Once the roles of these behaviours have been fulfilled, in terms of the pair bond being established for the season and a fertilised egg being produced, there is no need for these behaviours to persist, nor does there appear to be a need for both members of the pair to be together on the nest site. It would appear that very low levels of pairing displays are needed to maintain the smooth working of the pair bond between kittiwakes during incubation and chick rearing. The observed decrease in the amount of time allocated to pairing displays after egg-laying would, therefore, be partly a construct of the observation regime, but would also reflect a genuine decrease.

There appeared to be very little flexibility in the allocation of time to pairing behaviours at all stages of the breeding season as the proportions of time spent in pairing behaviours at each stage of the breeding cycle were consistent between colonies (Tyneside and Skomer) and between observation years. I suggest the level of allocation of time to pairing displays needed to form a viable pair may be a species characteristic, not varying greatly among colonies. There may be a minimum amount of pairing behaviour needed to establish a pair bond, bring the pair into breeding condition and ensure fertilisation of eggs. It would, however, be interesting to see if there are difference in colonies in the north of the species range, where pre-laying activities are temporally compressed (Falk and Møller 1997). Although Chardine (1983) found associations between the time spent in pairing displays and the age and longevity of the pair bond, I suggest that the observed proportion of time allocated to pairing displays in the Tyneside and Skomer colonies represented the average amount of time kittiwakes in a mature colony must allocate to pairing and mating to ensure a successful breeding attempt. More time may be allocated to pairing in a newly established colony, where a greater percentage of breeding pairs would be expected to be breeding together for the first time. There may also be bigger differences at a colony during adverse environmental conditions such as poor food supply. There was also consistency between years at nests after failure in the allocation of time to pairing between the different classes of failed birds.

3.4.1.2 Aggressive behaviour

As with pairing displays, a relatively high proportion of time was allocated to aggressive displays during the pre-laying stage, when nest sites and pair-bonds were being established for the season. As would be expected from previous work on the ritualisation of aggression to reduce the risk of injury, most aggression was expressed in the form of the ritualised displays, choking, bow and moan and jabbing, while fighting was relatively rare (Krebs and Davies 1981, Stamp Dawkins 1986).

At this stage of the season there would be some overlap in context between pairing and aggressive displays (Danchin 1987). Choking, bow and moan, included as aggressive displays, and greeting, included as a pairing display, have all been observed as responses to disturbances within the colony and at times appear "contagious," spreading across the colony in response to the displaying of a single bird or pair (Coulson and White 1962, Coulson and Dixon 1979). As the three displays appeared to some extent to be used interchangeably, I suggest that "greeting," like "choking," may also function to advertise a pair's presence on and ownership of territory.

Once pairs began to incubate eggs there was a significant decrease in the amount of time allocated to aggressive displays. I suggest that the presence of eggs in the nest strongly inhibited aggressive display as displaying or fighting would entail an interruption to incubation and risk the egg being dislodged from the nest or taken be a predator. The decrease in time allocated to overt aggressive displays need not, however, necessarily be associated with a decrease in aggressive tendencies, as evidenced by more frequent resort to aggression between neighbours, jabbing and aggressive sitting. It would be interesting to determine whether the incidence of non-breeders visiting the colony falls when most birds have commenced incubation. I suggest that after incubation commences an

intruding bird would have very little chance of dislodging a breeding pair, so there would be little benefit continuing to visit the colony to contend for a site.
Cadiou et al (1994) have studied the changes in numbers of prospectors visiting colonies during chick rearing, but I am not aware of work on prospectors during the earlier stages of the breeding season. Without marked breeding birds it was not, however, possible to distinguish between breeders and non-breeders at these stages.

After chicks hatched, the time allocated to aggressive displays increased, and the relative frequency of vigorous displays denoting distance aggression increased while jabbing decreased. The presence of chicks evidently did not have the same strong inhibitory effect on aggressive display as eggs. Kittiwake chicks actively cling to the nest and can move to avoid a displaying adult. Increasing levels of aggression during chick rearing have been reported for other gull species, attributable at least in part to the increasing mobility of chicks and a corresponding increase in territory border clashes (e.g. Pierotti 1981, Burger and Gochfeld 1996). Kittiwake chicks do not, however, move from the nest site until they fledge and will not, therefore, contribute to increasing aggression between territory holders.

As chick rearing proceeded, increasing numbers of failed nests and the aggressive displays associated with the presence of prospectors on these nest sites would have provided greater stimulus for aggressive display on neighbouring sites where chicks were still being raised. In this context the term "prospector" included birds whose breeding attempt in this season had failed and birds which had not attempted to breed in this year. After the chick has achieved thermal independence, at around 8 days, constant adult attendance at the nest site ceases (Coulson and Johnson 1993, Barrett and Runde 1980, Galbraith 1983, Wanless and Harris 1992). The presence of unattended, but obviously successful, nests has been shown to attract prospectors, further increasing the likelihood of aggressive displaying by neighbouring site owners. The presence of prospectors peaks in the second half of chick rearing, when the information relating to breeding success in the colony is most accurate (Cadiou et al 1994, Cadiou 1999) and prospectors are known to preferentially recruit to nests where they have "squatted" in the previous season

(Cadiou and Monnat 1996). Given the breeding advantages conferred on kittiwakes by mate and nest site fidelity (Coulson and Thomas 1984) it is in the interests of owners to ensure that squatters are discouraged hence the high levels of aggression. If the presence of prospectors contributed to the increasing levels of aggression during chick rearing, there may be a difference in aggression levels at nests with or without failed neighbours and this will be considered in chapter 5.

There was, however, an unexpected decrease in aggression levels in the latter stages of chick rearing in 1998 which may be related to the location of failed nests. Although the cluster density of the nests where chicks hatched and fledged was the same in both years (see chapter 4), a concentration of failed nests in one section of the upper Wick site, and the consequent virtual abandonment of half the site may have reduced the numbers of prospectors attracted. Cadiou (1999) observed prospecting activity was lower in areas of poor breeding success. It is also possible that the frequent observations of hunting peregrines at all sub-colony sites during the 1998 breeding season reduced the incidence of prospecting.

There were consistent increases in the proportion of time allocated to aggressive displays at nests where breeding attempts had failed, with birds on failed nests allocating more time to aggressive interactions, in particular to the choking and bow and moan displays, in comparison to birds during the pre-laying stage. Differences in aggression levels between nests where breeding attempts failed during incubation relative to nests which failed during chick rearing demonstrated the greater flexibility in time allocation to aggressive behaviour, relative to the consistent level of pairing behaviour observed after breeding failure.

Several factors may have contributed to the increase in interactions between conspecifics at failed nest sites. If the presence of eggs or chicks acted to inhibit aggressive or pairing behaviour, their removal may release these behaviours among birds still in breeding condition. Higher levels of aggression and pairing displays on failed nest sites may also be associated with non-owner birds attempting to claim the nest site, especially in the later stages of chick rearing when the presence of prospectors peaks. The time allocated to aggressive behaviours at failed nests was higher than that recorded for aggression during the pre-laying stage. I suggest competition on failed nest sites may be more open, as the failed breeders may not defend their nests as assiduously as successful breeders reclaiming their sites at the beginning of the season. It has been established (Danchin et al 1998, Danchin and Monnat 1992) that failed breeders were more likely than successful breeders to change nest site, and even change colony, in the following breeding season.

Concentration of aggressive interactions on the small number of failed sites, in comparison to the situation at the start of the breeding season when ownership of all sites was disputed, may partly explain the high levels of aggression post-failure, relative to the aggression levels during the pre-laying stage. Although time spent in aggressive displays tended to rise during chick rearing, presumably at least partly in response to the presence of prospectors, it did not reach the high levels associated with post failure nests, because the presence of successfully breeding owners would discourage intruders.

Although the pattern of change in aggression levels was consistent, there were differences in the proportions of time allocated to aggressive behaviour between colony areas (Tyneside and Skomer) and between breeding seasons in the Skomer Island colony. The differences in aggression levels during chick rearing between seasons have already been considered. During the pre-laying period more time was allocated to aggressive behaviour in the Skomer Island colony in 1998 than in the Tyneside colonies in 1996. If more successful birds were more aggressive, the opposite would be expected, as breeding success on Tyneside was higher than breeding success on Skomer (see chapter 4). The difference may, however, be accounted for by differences in nest cluster density between the two areas, with the larger allocation of time to aggression on Skomer being a consequence of denser nesting clusters (see chapter 5). Also in 1996 all behaviour recorded was for site owners only, identified by colour rings, whereas in 1998 during pre-laying I could not distinguish between site owners for that season or intruders. Without behavioural observations from Tyneside of nesting sites of equivalent density to the

Skomer colony sites, I cannot dismiss the possibility that the differences may be attributed to other factors at the two colony locations.

3.4.2 Inactive and maintenance behaviours

Most of the time spent on the nest during all stages of the breeding season was allocated to the inactive categories. Maintenance activities were given next priority in terms of time allocation, as would be expected given the importance of maintaining plumage in peak, waterproof condition. My results provided no evidence for social facilitation of preening among kittiwakes on nest sites, as during the pre-laying period birds nesting at low density at the Tyneside colonies (see chapter 4) allocated more time to preening than birds nesting at higher densities at Skomer in 1998.

Time on the nest apparently doing nothing, sleeping or preening cannot, however, be dismissed as not related to the breeding attempt. During the pre-laying stage, while nesting territories were being established the presence of a territory owner on site would prevent territory seekers from attempting to occupy the site, a form of passive defence complementing the active defence of aggressive displays (Tinbergen 1958). During incubation and chick rearing, time spent apparently inactive on the site would play a triple role: defence of the nest site; defence of eggs or chicks; and, most importantly, incubation or brooding of eggs and young. Kittiwakes are more assiduous in nest attendance than other gulls, with attendance of at least one adult exceeding 99.7% (Coulson and Wooller 1984). The greater proportion of time allocated to alert behaviour in the Skomer Island colony in 1998 than in the Tyneside colonies in 1996 does not appear to be related to differences in density between sites, a situation observed by a number of researchers (e.g. Pöysä 1994, Roberts 1996, Bednekoff and Lima 1998). I suggest it may be the result of differences in predator pressure to be considered further in chapter 4.

Although I was confident distinguishing when a bird was performing a positive action, and attributing that action to a behavioural category, I was less assured that there was a functional difference between the alert and non-alert categories. The increase in the proportion of time allocated to alert behaviour, but not in non-alert behaviour, once incubation commenced and continued high levels of alert behaviour during chick rearing may, however, have reflected an increase in vigilance associated with guarding and caring for eggs and chicks. If there was no functional difference between alert and non-alert behaviour I would have expected that during incubation there would be an increase in the time allocated to both of these behavioural categories, compensating for the decreases in time allocated to pairing, aggression and maintenance. During chick rearing although there was a decrease in non-alert behaviour, presumably reflecting the increases in aggressive and maintenance activities, alert behaviour remained at the same high level as during incubation.

During incubation and chick rearing in the Skomer Island colony, the allocation of more time to alert and less time to non-alert behaviours in 1998 in comparison to 1997 may be related to the higher incidence of egg predation by great black-backed gulls at the Upper Wick site and the presence of peregrine falcons breeding at High Cliff. Both of these species constitute a threat to adult kittiwakes as well as their young. As I did not attempt to quantify the presence of predators, noting only the few occasions on which eggs and chicks were taken from nest sites under observation, I can only record an impression that the presence of peregrines breeding at the High Cliff site in 1998 resulted in more frequent observations of peregrines at all sites in 1998 than had occurred in 1997.

There was no consistency in the inactive categories of behaviour at nests where breeding attempts had failed. I suggest the amount of time allocated to inactive behaviours directly reflected attendance at the site by the failed residents and prospectors, a subject not dealt with in this study. Two categories of behaviour, nest building or maintenance and caring for eggs or chicks, were absent after failure so a compensating increase in the proportion of time allocated to inactive behaviours would be expected.

Only a small proportion of time was allocated to maintenance behaviour during incubation, relative to all other stages of successful or failed breeding attempts. I suggest that egg chilling or disturbance may be associated with extended bouts of preening.

Although unquantified, my impression was that incubating kittiwakes usually made preening movements while sitting, whereas preening movements were otherwise generally made while standing. I suggest that the demands of incubation are incompatible with adequate preening, and most preening at this stage occurs away from the nest. The increase in maintenance activities on the nest site during chick rearing may reflect the greater demands for food associated with feeding chicks, resulting in less time away from the nest being available for preening.

3.4.3 Nest building

Although only a small proportion of time was spent in activities related to nest building and nest maintenance, there was a clear pattern in time allocation as the breeding season progressed. Consistency between years and colony areas in the amount of time allocated to "on-site" nest building before eggs were laid suggests there was a fixed amount of time needed to construct a viable nest. As much time was spent on nest maintenance during incubation, as had been allocated to on site nest building activities during the pre-laying stage. Once the chicks hatched, however, virtually no nest maintenance behaviour was observed. Maintaining the integrity of the nest would be vital during incubation as, if the nest structure began to break down, eggs would easily be lost. Once eggs have hatched, the chicks cling to the nest ledge so it would no longer be imperative to maintain the nest. As the chicks grew, it would be an advantage to allow the nest to degrade, as the nest cup would not provide adequate space for the growing brood.

3.4.4 Attending eggs and chicks

Although kittiwakes allocated little time to overt care of eggs or chicks, most time on the nest during incubation and the first half of chick rearing would be occupied in brooding young. The time allocated to turning eggs was consistent between years, but the time spent feeding young differed between breeding seasons. As a feeding bout would be likely to occupy more time the more chicks to be fed, a possible explanation for less time to be allocated to chick feeding during the 1998 breeding season would be the smaller number of chicks fledged during 1998 (see chap 5). This was not, however, the case as the difference in overall breeding success between years resulted from young fledging from fewer nests, rather than fewer young fledging from the same number of active nests at the end of the breeding season.

3.5 Conclusions

Overall there was consistency in the patterns of change in time allocated to the various behavioural categories, in spite of differences in the actual proportions of time allocated to some behaviours at some stages of the breeding season. While pairing behaviour appeared to be fixed within narrow limits, there was more flexibility in the allocation of time to aggressive behaviours, enabling pairs to respond to specific environmental circumstances, chiefly the density of nesting and the intensity of intruders in the latter stages of chick rearing. The differences in observed behaviour should also be taken as a warning that considerably more observational time, over a number of seasons and colonies, would be needed before an activity budget for kittiwakes at the nest site could be confidently derived.

Chapter 4.

The impact of sub-colony and cluster nesting density on breeding success

4.1 Introduction

A considerable amount of work has been done to determine how breeding success of colonially-nesting birds is influenced by nest site location within a colony. Much of this work has focused on differences between pairs nesting in the centre and on the edges of a colony. Many studies (including Coulson and White 1961, Coulson 1968, Balda and Bateman (1972 cited in Brunton 1997), Brown and Bomberger Brown (1987), Kruuk (1964 cited in Brunton 1997) and Spear 1993) have found that birds breeding in the centre of a colony were more successful. For instance, kittiwakes that nested in the "centre" of a colony in N E England laid earlier, laid larger clutches and fledged more chicks and those on the "edge" of the colony (Coulson 1968; Coulson and Thomas 1984, Fairweather 1994). However other studies have found no difference between pairs in the centre and on the edge (van Vessem and Draulans 1986; Berg et al 1992) and Brunton (1997) found that edge nesting least terns *(Sterna antillarum)* were more successful than centre nesting birds. Moreover Bunin and Boates (1994) found that in some years arctic terns *(S. paradisaea)* in the central area of the colony experienced greater breeding success, while in other years birds at the edge of the colony were more successful, and manipulation studies implied that better quality birds were nesting preferentially on the periphery of the colony.

Different researchers have used different definitions for "centre" and "edge" and this has contributed to the range of results from different studies. For example, Brunton (1997) defined "edge" as a band three nests wide around the perimeter of the colony: a definition reflecting direct access to nests by predators approaching on the ground. In contrast, the "centre" of the North Shields colony was defined as the area occupied when the colony was half its maximum size. This area included parts of two faces of the building that birds were nesting on and birds at the physical edge of the colony (Thomas 1980). Pairs were artificially divided into clusters; i.e. all pairs in one window were relatively isolated from other windows. By installing additional ledges on some centre windows, researchers effectively created two potential nest cluster densities (Porter 1985) and this may have contributed to or exaggerated the differences between centre and edge nests.

Also by defining the centre of the colony in terms of time of occupation it is possible that there was a preponderance of older, experienced birds in the centre of the colony, while younger birds may have been occupying sites on the periphery. This may also have exaggerated the differences between centre and edge, because many studies of birds have shown a positive relationship between breeding success and breeding experience, at least for the first few breeding seasons (Coulson and Thomas 1984, Clutton-Brock 1988).

Many of the above studies specifically associated "central" nesting with higher density nesting, and peripheral nesting with lower density nesting, although in the case of the kittiwake study described above no attempt was made to quantify the difference in nesting density. Research into the centre/edge dichotomy has, therefore, overlapped with work on effects of variation in local density within small parts of colonies. This research has indicated that nesting at high density confers a selective advantage, particularly in terms of defence from predators and/or social stimulation promoting early or synchronous breeding (e.g. Coulson and White 1960, Nelson 1967, Lack 1968, Birkhead, 1977, Harris 1980, Falk and Møller 1997, Brown and Bomberger Brown 2000). However, between species, high colony density is generally associated with low vulnerability to predation. It has been suggested (Lack 1954 cited in Coulson and White 1960, Clode 1993) that only those species which are relatively invulnerable to predation, either because of the size or aggression of the species, or the selection of inaccessible locations, can form colonies for breeding. Although arguing that nesting more densely confers an advantage in terms of predation when only relatively invulnerable species can nest densely may seem contradictory, even a very slight advantage will result in selection for birds prepared to nest in closer proximity to their neighbours.

Between these two extremes of scale (i.e. species variation and local density) is variation between colonies or areas of a large colony within a species, and less information is available on the relationships between breeding success and breeding density at this scale. In this chapter I shall examine breeding success in relation to nest density at two spatial scales: clusters of nests within a 1.5m radius and at the scale of the small colony or sub-colony, with particular reference to the impact of predation.

As most data on the impact of nest density on reproductive success of kittiwakes were derived from a single colony, the North Shields colony studied by Coulson and co-workers, consideration must be given to whether this colony is representative of the species. Subsequent work (e.g. Danchin and Monnat 1992, Boulinier and Danchin 1996) has shown that the North Shields colony may not be representative of the majority of kittiwake colonies, with life histories being atypical in many ways.

The breeding success of kittiwakes at North Shields was consistently high, when compared to other regions monitored in the UK. At the North Shields colony high fledging success, relative to hatching success, led to the conclusion that inadequacy of care during incubation was the primary cause of breeding failure in kittiwakes (Coulson & Wooller 1984). In contrast Harris and Wanless (1990) found that most kittiwake breeding failures at North Sea colonies occurred during chick-rearing, rather than during incubation.

No predation was observed in more than 30 years of breeding and behavioural observations at North Shields, although there have been some instances of kittiwakes at the North Shields colony being shot (Coulson, pers. comm.). Most other studies have recorded predation on kittiwakes (e.g. Jacobsen and Erikstad 1995; Galbraith 1983; Andersson 1976; Barett & Runde 1980; Falk and Møller 1997, Cadiou 1999). Moreover, in a survey of 54 samples in 26 locations, only the two colonies on buildings, the North Shields warehouse and Baltic Flour Mills, Gateshead, were not infested with the common kittiwake ectoparasite *Ixodes uriae* (Boulinier and Danchin 1996). Cliff colonies of similar age to the two building colonies were included in the sample, so it was unlikely that the absence of ectoparasites could be related to the more recent colonisation of buildings.

During the study at North Shields, no kittiwakes having bred once at the colony ever left to breed at another colony, leading to categorical statements about absolute colony fidelity (Fairweather 1994). Subsequent work on colonies at Cap Sizun, Brittany, has shown that breeding kittiwakes will change colonies after breeding failure, particularly when surrounded by failing birds (Danchin and Monnat 1992). The absolute site fidelity at North Shields was, therefore, likely to have been a reflection of the unusually favourable conditions prevailing in that colony during the period of the study.

Kittiwakes at North Shields were able to raise artificially enlarged broods, with 4 pairs able to fledge (underweight) broods of 4 young (Coulson (pers comm., cited in Lack 1966). The maximum natural number in a brood is 3. In contrast Jacobsen and Erikstad (1995) found that no kittiwake pair could raise an enlarged brood (adding one chick to broods of 2) and that the females of pairs raising enlarged broods experienced higher mortality in the subsequent winter.

Coulson and Wooller (1984) suggested the long-term hatching success of 67% and fledging success of 87% recorded for the North Shields warehouse colony, may represent the breeding potential of kittiwakes breeding in ideal conditions.

Studies undertaken by Coulson and co-workers at the large Tyneside colony centred on Marsden Rock (Coulson and White 1960, Strowger 1993), may also not be typical of the majority of kittiwake colonies, because the cliffs at Marsden are also situated in an urban area and seem, like the North Shields Warehouse, to be subject to little predation pressure. Kittiwakes do not seem to be disturbed by human activity in the vicinity of their colonies.

In the light of the above discussion, this chapter examines breeding success at three kittiwake colonies within the Tyneside conurbation, differing in local nest density and predation pressure, then replicates the comparison using colonies in a more natural setting on Skomer Island, Wales. Timing of breeding and colony-wide breeding success were recorded to determine whether or not the breeding seasons monitored during this study were typical of the colonies under study, and whether they can be considered to be representative of kittiwake colonies in general.

4.2 Methods

Methods are described in detail in chapter 2.

4.3 Results

4.3.1 Nesting density

4.3.1.1 Nesting density at Tyneside in 1996

The main study plots on Tyneside were not densely settled (Table 1) but there were significant differences in nest density among the three colonies, when the number of nests within a radius of 1.5m from each nest was considered (Kruskal-Wallis One way ANOVA, Chi-square = 7.13, 2 d.f. P = 0.028). A Tukey HSD test indicated that the extent of nest clustering at Tynemouth was significantly greater than at Marsden Grotto (Table 1).

Table 1. Nest density at study sub-colonies on Tyneside, based on the number of neighbouring nests within a radius of 1.5m from each nest.

	n	Neighbours within 1.5 m		
		Mean	Std Dev	Max
Tynemouth	64	2.64	1.53	5
North Shields	17	2.12	1.41	4
Marsden Grotto	53	1.89	1.49	5

4.3.1.2 Nesting density at Skomer in 1997 and 1998

In comparison to the Tyneside study plots, the Skomer sites showed a greater range of nest densities (Tables 2 and 3). In 1997 there were significant differences among colony sites (Kruskal-Wallis One-way ANOVA, Chi-square = 71.75, 3 d.f. $P < 0.0001$). A Tukey HSD test indicated the Lower Wick site was significantly more clustered than the South Stream and High Cliff sites, and that the Upper Wick site was significantly more clustered than the other three sites.

Table 2. Nest density within sub-colonies on Skomer Island in 1997, based on the number of neighbouring nests within a radius of 1.5m from each nest.

	n	Neighbours within 1.5m		
		Mean	Std Dev	Max
Upper Wick	37	6.08	1.97	10
Lower Wick	33	4.06	1.46	6
High Cliff	31	1.90	1.04	4
South Stream	20	1.75	1.52	5

Some nest sites used in 1997 were not occupied in 1998, but the general pattern of clustering between the sub-colonies remained the same between years, with similar differences between sites in 1998 (Table 3; Kruskal Wallis One-way ANOVA, Chi-square = 51.67, 3 d.f., $P < 0.0001$) and no significant differences between years in nest density at any sub-colony (Table 4).

Table 3. Nest density at sub-colonies on Skomer Island in 1998

	n	Neighbours within 1.5 m		
		Mean	Std Dev	Max
Upper Wick	29	5.69	1.89	9
Lower Wick	32	4.34	1.47	7
South Stream	15	2.13	1.88	6
High Cliff	25	1.84	1.03	4

Table 4. Mann Whitney U test statistics indicating there were no differences between 1997 and 1998 in nest densities at sub-colonies on Skomer Island.

	U	P
Upper Wick	459	0.31
Lower Wick	471	0.44
South Stream	135	0.62
High Cliff	363	0.68

4.3.2 Breeding success in relation to colony density

4.3.2.1 Breeding success at Tyneside in 1996

4.3.2.1.1 Timing of breeding

There was a significant difference in hatching dates among the Tyneside colonies (Kruskal Wallis One-way ANOVA, Chi-square = 20.5, $P < 0.001$). A Tukey HSD test indicated that the mean hatching date for the Tynemouth colony was significantly later than the hatching date for Marsden Grotto (Table 5). Part of this difference may, however, be attributed to the observation regime, as Marsden Grotto was visited one day before Tynemouth and North Shields during the hatching period. At Tynemouth, the latest-hatching chicks were on nest sites where adults had been subject to disturbance from fulmars.

There was a high degree of breeding synchrony, measured as the standard deviation of the hatching date, within colony sites on Tyneside (Table 5). It should be noted, however, that the observation regime will have exaggerated the synchrony within sites to some extent.

There were no significant differences in hatching dates among pairs that fledged different numbers of young (i.e. 0,1 or 2 young; Kruskal Wallis One-way ANOVA, Chi-square = 2.33, 2 d.f., $P = 0.31$).

Table 5. Hatching dates at kittiwake colonies on Tyneside in 1996

	n	Mean	S. D.
Marsden Grotto	48	29/6	4.83
North Shields	13	30/6	3.33
Tynemouth	56	2/7	4.84
All Tyneside	117	30/6	4.68

4.3.2.1.2 Brood size

There were no significant differences in brood size among the three colonies on Tyneside in 1996 (G = 1.18, 4 d.f., $P > 0.05$) (Table 6).

Table 6. Brood size, in terms of the number of chicks hatched per well built nest, and the number of chicks fledged per nest from Tyneside kittiwake colonies in 1996.

Site	Brood size			No. Fledging		
	n	Mean	S.E.	n	Mean	S.E.
Marsden Grotto	53	1.58	0.09	53	0.94	0.12
Tynemouth	66	1.62	0.08	66	1.55	0.08
North Shields	17	1.47	0.19	17	1.41	0.19
Marsden Jack Rock	76	1.53	0.07	76	1.38	0.07
Marsden Main Cliff	105	1.49	0.07	105	1.36	0.07
All Tyneside	317	1.54	0.67	317	1.34	0.73

4.3.2.1.3 Fledging success

In contrast to brood size there were significant differences among colonies in the number of chicks fledged per well built nest (G = 18.08, 4 d.f., $P < 0.01$) with fewest chicks fledged per nest at Marsden Grotto (Table 6).

With the exception of Marsden Grotto, over 90% of chicks that hatched survived to fledge and the fledging success at these four sites (Tynemouth, North Shields, Jack Rock and Marsden Main Cliff) did not differ from the optimum breeding potential of 87% recorded by Coulson and Wooller 1987 ($X^2 = 2.12$, 3 d.f. $P > 0.05$). At these sites most breeding failures occurred before or during incubation (Table 7). The lower fledging success at Marsden Grotto probably reflected the intensity of predation pressure during chick rearing at that site. During periods of observation in 1996, four chicks in the Marsden Grotto study area were taken by herring gulls during periods when the chicks were left unattended at the nest. Although herring gulls were occasionally observed flying to the roof of the Grotto Hotel with kittiwake chicks taken from other parts of the colony, predation pressure seemed to be most intense at the study site, where wide nesting ledges allowed easy access by herring gulls. Only one pair of herring gulls appeared to be preying upon kittiwake chicks and their nest was immediately above the study site.

Table 7. Fledging success of kittiwakes at Tyneside colonies in 1996

	n	% Fledge
Marsden Grotto	48	59.5
Tynemouth	60	95.3
North Shields	14	96.0
Marsden Jack Rock	71	90.5
Marsden Main Cliff	94	91.7
All (except Grotto)	239	92.6

* % fledging success is the % of chicks that survived to fledge.

In the Tyneside area in 1996 there was an unusually high mortality of kittiwakes late in the breeding season. An estimated 2000 kittiwakes died in the area, and at least one ringed bird from the study site was recovered dead before the end of the breeding season (Coulson, pers comm.). This mass mortality has been attributed to an unknown toxin. All three colonies studied appeared to be affected, as dead adults were observed at all sites. The mass mortality may have caused the death of the 2 chicks observed dead on nests at Main Cliff and Jack Rock, either through ingesting the toxin directly from the parents, or through starvation following the loss of parents. Another observed cause of breeding failure was interference from fulmars, which caused three pairs to desert well-built nests before laying at Tynemouth.

4.3.2.1.4 Nest cluster density and breeding success

At the three main study sites in the Tyneside colonies in 1996 there were significant differences in the number of chicks fledged per well built nest between pairs in high and low density clusters (Table 8; $G = 6.16$, 2 d.f., $P < 0.05$). Pairs nesting in high density clusters fledged more chicks than pairs in low density clusters. There were, however, no differences in the number of chicks hatched per well built nest (G = 5.04, 2 d.f., P > 0.05), nor in hatching date (Mann Whitney, U = 1177.5, n = 117, P = 0.33) between pairs nesting in high and low density clusters (Table 8).

Table 8 . Timing of breeding and breeding success of pairs nesting in high and low density clusters in the Tyneside colonies in 1996.

Cluster Density	Hatching Date			Brood Size			No. Fledging		
	n	mean	S.E.	n	mean	S.E.	n	mean	S.E.
High	31	45.1	0.64	35	1.69	0.11	35	1.54*	0.13
Low	86	44.8	0.54	99	1.57	0.07	99	1.21*	0.08

*Denotes significant difference.

As there were relatively few nests in the high density category, a further analysis was undertaken testing for differences among nests with between 0 to 5 neighbours within 1.5m, in the number of chicks fledged per well built nest. There were significant differences in fledging success among nests with different numbers of neighbouring nests (Kruskal-Wallis One-way AOV, Chi square = 17.41, 5 d.f., P = 0.0038). A Tukey HSD test indicated that pairs with no neighbours within 1.5m fledged fewer young that pairs with 2, 3, 4 or 5 neighbours (Table 9). There was also a significant difference in the number of chicks hatched per well built nest among nests with different numbers of neighbours within 1.5m (KW One-way AOV, Chi square = 11.77, 5 d.f., P = 0.038). A Tukey HSD test indicated pairs with no neighbours within 1.5m hatched fewer chicks than pairs with 2 neighbours.

As there was a significant difference in both breeding success and nest cluster density between Marsden Grotto and the other sites, I performed a two way analysis of fledging and hatching success between the two categories of cluster density and sub-colonies of different density, i.e. Marsden Grotto versus the combined results for Tynemouth and North Shields. There was a difference in fledging success associated with nest cluster density, independent of the density of the sub-colony, and there was also a difference in fledging success associated with sub-colony (Two-way ANOVA, cluster density $F_{1,133} = 4.69$, $P = 0.032$; colony density $F_{1,133} = 8.99$, $P = 0.003$, no significant interactions). Pairs in high density clusters fledged more chicks per nest than pairs in low density clusters, and pairs at the denser sub-colonies of Tynemouth and North Shields fledged more chicks than pairs at the Marsden Grotto colony (Table 10).

Table 9. Hatching and fledging success of pairs nesting in the Tyneside colonies in 1996, categorised by no. of neighbouring nests within 1.5.

No. neighbours	Brood Size			No. Fledging		
	n	mean	S.E.	n	mean	S.E.
0	24	1.17	0.18	24	0.71	0.18
1	19	1.68	0.11	19	1.21	0.18
2	30	1.77	0.09	30	1.37	0.14
3	26	1.62	0.11	26	1.5	0.11
4	27	1.63	0.14	27	1.48	0.15
5	8	1.87	0.13	8	1.75	0.16

Table 10. Hatching and fledging success of nests in high and low density clusters at colonies with differing nest density (low density - Marsden Grotto; high density - Tynemouth and North Shields) in 1996.

	Marsden Grotto						Tynemouth and North Shields					
Cluster Density	Low			High			Low			High		
	n	mean	S.E.	n	mean	S.E.	n	mean	S.E.	n	mean	S.E.
No. Chicks	42	1.6	0.10	11	1.6	0.20	57	1.6	0.09	24	1.7	0.14
No. Fledge	42	0.8	0.13	11	1.4	0.24	57	1.5	0.09	24	1.6	0.15

4.3.2.2 Breeding success at Skomer in 1997 and 1998

4.3.2.2.1 Timing of breeding

On Skomer Island the mean laying date for kittiwakes was significantly earlier in 1997 than in 1998 (Table 11; Mann Whitney, U = 1636, $P < 0.0001$) and this led to a similar difference in hatching dates between years (Mann Whitney, U = 882, $P < 0.0001$). In both 1997 and 1998 there were no differences among sub-colony sites on Skomer Island in laying date (1997 Kruskal Wallis One-way ANOVA, Chi-square = 6.36, 3 d.f., P = 0.095; 1998 Kruskal Wallis One-way ANOVA, Chi-square = 1.83, 3 d.f., P = 0.61) or hatching date (1997 Chi-square = 5.14, 3 d.f., P = 0.16; 1998 Chi-square = 2.85, 3 d.f., P = 0.42).

On Skomer Island there was a high degree of synchrony in laying and hatching dates within colonies, taken as the standard deviation of laying and hatching dates (Table 11). In the Skomer Island colonies, in both years, the less clustered sites showed a greater spread in laying and hatching dates. The very synchronised hatching at the Upper Wick in 1998 can be explained by the small number of nest sites from which any chicks were hatched.

In the Skomer sub-colonies in 1997 there were significant differences in the laying date (Mann Whitney, U = 914, n = 110, P = 0.0005) and hatching date (Mann Whitney, U = 303, n = 80, P = 0.003) between pairs that successfully fledged chicks and those that failed to fledge any chicks. Successful pairs laid and hatched earlier than unsuccessful pairs. This relationship was not, however, apparent in 1998, when there were no differences in laying date (Mann Whitney U = 894.5, n = 93, P = 0.18) or hatching date (U = 314.5, n = 66, P = 0.30) between pairs that successfully fledged young and those that failed. The difference between breeding seasons was probably attributable to the loss of many early laid clutches at the Upper Wick in 1998 (see section on Fledging Success).

Table 11. Laying and hatching dates for sub-colonies on Skomer Island in 1997 and 1998.

		Laying Date			Hatching Date		
		n	mean	S. D.	n	mean	S. D.
1997	South Stream	18	26/5	7.64	14	25/6	8.12
	High Cliff	28	27/5	6.25	18	24/6	6.23
	Upper Wick	32	24/5	2.94*	25	20/6	3.09
	Lower Wick	32	25/5	5.20	23	20/6	4.26
	All Skomer	**110**	**25/5**	**5.58**	**80**	**22/6**	**5.58**
1998	South Stream	14	2/6	6.35	11	27/6	4.57
	High Cliff	24	2/6	4.83	18	29/6	4.58
	Upper Wick	25	31/5	3.08	10	28/6	1.75
	Lower Wick	30	1/6	3.94	27	28/6	3.85
	All Skomer	**93**	**1/6**	**4.39**	**66**	**28/6**	**3.96**

*Eggs present at some nests on the first day of observation, so this figure underestimates the spread of laying dates.

4.3.2.2.2 Clutch size

The mean clutch sizes in the Skomer sub-colonies in 1997 and 1998 were 1.72 and 1.69 eggs respectively (Table 12). Among the sub-colony sites (South Stream, High Cliff, Upper Wick and Lower Wick) there were no significant differences in clutch size in either year (1997 – $G = 13.7$, 9 d.f., $P > 0.05$; 1998 – $G = 6.08$, 6 d.f., $P > 0.05$). There were no differences in clutch sizes between years, grouping all the sub-colonies ($G = 5.46$, 3 d.f., $P > 0.05$).

4.3.2.2.3 Brood size

Taking all Skomer Island sub-colonies together, there were no differences in the brood size between 1997 and 1998 ($G = 0.12$, 2 d.f., $P > 0.05$). In 1997 there were no significant differences in the number of chicks hatched per well built nest among sub-colony sites ($G = 2.14$, 6 d.f., $P > 0.05$). There were, however, significant differences in brood size among colony sites on Skomer in 1998 (G = 26.14, 6 d.f., $P < 0.05$). There were fewer chicks hatched per nest at the Upper Wick than at the Lower Wick. (Table 12).

Table 12. Clutch size, brood size and the number of chicks surviving to fledging age in the Skomer Island sub-colonies in 1997 and 1998. Brood size and no. fledging are based on number of chicks and fledglings per well built nests. Clutch size is calculated only from the clutches where eggs could be counted accurately, not from all well built nests.

Year	Site	Clutch Size			No. Chicks			No.Fledging		
		no. nests	Mean	S.E..	no. nests	Mean	S.E.	no. nests	Mean	S.E
1997	South Stream	10	1.60	0.27	19	1.16	0.19	20	0.55	0.17
	High Cliff	20	1.70	0.16	29	0.94	0.16	31	0.71	0.15
	Upper Wick	37	1.70	0.12	37	1.14	0.15	37	0.81	0.14
	Lower Wick	32	1.78	0.10	31	1.26	0.15	33	0.79	0.14
	All Skomer	99	1.72	0.07	116	1.14	0.08	121	0.74	0.07
1998	South Stream	13	1.85	0.15	15	1.27	0.23	15	0.93	0.22
	High Cliff	20	1.75	0.12	24	1.25	0.17	25	0.32	0.11
	Upper Wick	25	1.56	0.14	29	0.66	0.17	29	0.59	0.59
	Lower Wick	32	1.69	0.10	31	1.32	0.13	32	1.03	0.11
	All Skomer	90	1.69	0.06	99	1.10	0.09	101	0.71	0.08

- Re-lays were not included in the calculation of clutch size or brood size.

In 1997 there were no differences among sub-colonies in percentage hatching success, when hatching success for the sub-colonies were compared with the overall hatching success (Table 13; $X^2 = 0.1.9$, 3 d.f., $P > 0.05$). In 1998, the percentage hatching success at the Upper Wick sub-colony was significantly lower than the other three sites (Table 13; $X^2 = 8.97$, 3 d.f., $P < 0.05$). The hatching success at all sub-colonies in 1997 ($X^2 = 2.74$, 3 d.f., $P > 0.05$) and at all sub-colonies except for Upper Wick ($X^2 = 2.42$, 2 d.f., $P > 0.05$) did not differ from the optimum of 67% recorded by Coulson and Wooller (1984).

Table 13. Percentage hatching and fledging success at Skomer in 1997 and 1998

Year		n	% Hatch*	n	% Fledge
1997	South Stream	8	56.3	15	47.8
	High Cliff	17	58.8	18	75.9
	Upper Wick	32	66.7	25	71.4
	Lower Wick	31	68.4	24	65.0
	All sites	88	64.7	82	66.4
1998	South Stream	12	75	11	74
	High Cliff	19	71.4	18	23.3
	Upper Wick	22	48.7	10	89.5
	Lower Wick	30	75.9	27	80.5
	All sites	83	67.8	66	65.1

*% hatching success refers to the number of chicks hatched from a known number of eggs, and similarly % fledging success is the number of chicks which hatched then survived to fledge.

In both years, the incubation failures at the Upper Wick can probably be mainly attributed to great black-backed gull predation. In 1997, a great black-backed gull was observed to land on peripheral nests within the study site from which all eggs had been taken. At the approach of the large gull all incubating kittiwakes left their nests. In 1998 a great black-backed gull was observed taking an egg from a study site nest during an observation period, and was frequently observed landing on nests from which all eggs had disappeared. In 1998 the large gull seemed able to reach more of the nests within the study site, including nests in the high density clusters. Although it is possible that the large gulls were taking eggs that had already failed, it seems unlikely as most eggs disappeared early in the incubation period from nests where incubation appeared to be proceeding normally.

4.3.2.2.4 Fledging success

As with brood size, there was no difference in the number of chicks fledging per nest from the Skomer sub-colonies between 1997 and 1998 (Table 12; $G = 0.28$, 2 d.f., $P > 0.05$). Within years, however, there were different patterns of fledging success among study sites. In 1997 there were no differences among the sites in the number of chicks fledged per nest ($G = 2.68$, 6 d.f., $P > 0.05$). In 1998 there were differences in the number of chicks fledged per nest among Skomer sites ($G = 30.54$, 6 d.f., $P < 0.05$). The lowest fledging success was observed at High Cliff and the highest at the Lower Wick sub-colony (Table 12).

In 1997 the percentage fledging success at the South Stream sub-colony was significantly lower than the other sites (Table 13; $X^2 = 6.98$, 3 d.f., $P < 0.05$). In 1998 percentage fledging success at the High Cliff sub-colony was lower than the other sites (Table 13; $X^2 = 40.84$, 3 d.f., $P < 0.05$), when compared to overall percentage success. Fledging success at High Cliff and Upper Wick in 1997 ($X^2 = 4.21$, 1 d.f., $P > 0.05$) and at South Stream, Upper Wick and Lower Wick in 1998 ($X^2 = 2.5$, 2 d.f., $P > 0.05$) did not differ from the optimum fledging success of 87% recorded by Coulson and Wooller (1984).

On Skomer Island potential predators of chicks were present at all sub-colonies in both years. In 1997 there were two incidences of herring gulls taking chicks from study site nests during observation periods at South Stream. In 1998 peregrine falcons were observed apparently hunting in all areas where kittiwakes were nesting. At High Cliff in 1998, it is probable that predation by peregrine falcons nesting on the same cliff was the major cause of chick mortality, although incidences of predation from the study nests did not occur during observation periods. Early in the breeding season an adult kittiwake at one of the High Cliff study site nests was killed by a falcon.

All sub-colony sites on Skomer experienced some nest losses in 1997 due to physical factors in the environment. Weather conditions affected South Stream (one nest being washed away during incubation) and Lower Wick (southerly gales washing away 6 nests during incubation). Rock falls affected both Upper Wick (losing two nests during incubation) and High Cliff (losing one nest during chick rearing).

4.3.2.2.5 Nest cluster density and breeding success

In 1997 in the Skomer sub-colonies there were significant differences between nests in high and low density clusters in the number of chicks fledged per well built nest ($G = 8.0$, 2 d.f., $P < 0.05$), laying date (Mann Whitney, $U = 1209$, $n = 110$, $P = 0.009$) and hatching date (Mann Whitney, $U = 664$, $n = 80$, $P= 0.037$). Pairs in high density clusters fledged more young and laid and hatched earlier than pairs in low density clusters (Table 14). There were no differences between high and low density clusters in clutch size ($G = 5.9$, 3 d.f., $P > 0.05$) or brood size (Table 14; $G = 5.6$, 2 d.f., $P > 0.05$).

Table 14. Breeding success of nests in high and low density clusters in terms of clutch size, the number of chicks hatched and fledged per well built nest, and laying and hatching dates at Skomer in 1997.

	Low Density			High Density		
	n	Mean	S.E.	n	Mean	S.E.
Clutch size	39	1.5	0.14	60	1.8	0.07
Brood size	57	1.0	0.12	59	1.3	0.11
No. fledging	60	0.6*	0.10	61	0.9*	0.10
Laying Date	52	28/5*	0.96	58	25/5*	0.47
Hatching Date	34	24/6*	1.26	46	21/6*	0.47

To determine whether nest cluster density or the overall density of the sub-colony site was affecting the timing of breeding and fledging success, I performed two-way analyses of the number of chicks fledging per nest and laying date by nest cluster density and sub-colony density (low density – High Cliff and South Stream; medium density – Lower Wick; high density – Upper Wick). There were significant differences in the number of chicks fledging per nest from nests in high and low density clusters, when sub-colony density was controlled, but no differences in the number of chicks fledged among sub-colonies of different density when local cluster density was controlled (Two-way ANOVA: cluster density $F_{1,120} = 6.65$, $P = 0.011$; sub-colony density $F_{1,120} = 0.51$, $P = 0.60$, no significant interactions). Pairs nesting in high density clusters fledged more chicks than pairs nesting in low density clusters (Table 15).

Table 15. No. of chicks fledging per nest among pairs nesting in high and low density clusters in sub-colonies of different density (low – High Cliff and South Stream; medium – Lower Wick; high – Upper Wick) at Skomer in 1997.

Sub-colony Density	Nest Cluster Density	No. Fledging		
		n	mean	S.E.
Low	Low	46	0.63	0.12
	High	5	0.80	0.37
Medium	Low	10	0.40	0.22
	High	23	0.96	0.16
High	Low	4	0	0
	High	33	0.91	0.15

When sub-colony density was controlled there was no difference in the laying date between birds nesting in high and low density clusters (Two-way ANOVA: cluster density $F_{1,109} = 0.42$, $P = 0.52$; sub-colony density $F_{1,109} = 0.62$, $P = 0.62$, no significant interactions).

In contrast to the results for the 1997 breeding season, in the Skomer sub-colonies in 1998 there were no differences in clutch size ($G = 0.16$, 2 d.f., $P > 0.05$) brood size ($G = 0.82$, 2 d.f., $P > 0.05$), the number of chicks fledged per well built nest ($G = 0.90$, 2 d.f., $P > 0.05$), laying date (Mann Whitney, $U = 905.0$, $n = 93$, $P = 0.23$) or hatching date (Mann Whitney, $U = 500.0$, $n = 66$, $P = 0.60$) between pairs nesting in high or low density clusters (Table 16).

Table 16. Breeding success and timing of breeding for nests in high and low density clusters at Skomer in 1998.

	Low Density			High density		
	n	Mean	S.E.	n	Mean	S.E.
Clutch size	36	1.7	0.10	54	1.7	0.08
Brood size	42	1.2	0.13	57	1.0	0.12
No. fledging	43	0.6	0.12	58	0.8	0.10
Laying date	40	2/6	0.85	53	1/6	0.47
Hatching date	30	28/6	0.87	36	28/6	0.53

In both 1997 and 1998, high density clusters were associated with more synchronised breeding, reflected in lower standard deviations of laying date in the Skomer sub-colonies (Table 17).

Table 17. Laying date for nests in high and low density clusters at Skomer in 1997 and 1998 .

Year	Low density clusters			High density clusters		
	n	mean	S.D.	n	mean	S.D.
1997	52	28/5	7.0	58	25/5	3.5
1998	40	2/6	5.4	53	1/6	3.5

4.4 Discussion

4.4.1 Typical or atypical seasons for the colonies in the study

Breeding was late in the Tyneside colonies in 1996, in comparison with observations made at Marsden in the early 1990's (Strowger 1993) and observations at the North Shields colony, where the mean laying dates from 1954-1990 were 19/5 +/- 9 days (Fairweather 1994). The earliest and latest means for individual years were 14/5 and 25/5. Estimating laying date for 1996 by subtracting 27 (the mean incubation period for kittiwakes (Coulson & White 1958; Maunder & Threlfell 1972)) from recorded hatching date in 1996 yields an overall mean laying date of 4/6. Even if this date is further corrected to 31/5, allowing for the maximum error in recording actual hatching dates at every nest in 1996 of four days, the resultant mean laying date still indicates that 1996 was a late season. Delayed breeding is usually associated with lowered breeding success. The mass mortality of kittiwakes in the Tyneside area may also be expected to have lowered fledging success. The number of chicks fledged per nest on Tyneside in 1996 was, however, consistent with the breeding successes recorded for the North Shields colony between 1954-1983 (0.94 to 1.61) (Coulson & Thomas 1985), for the North Shields colony 1986 – 1990 (Walsh et al 1992) and for the Marsden Rock colony 1986 – 1990 (Walsh et al 1992). The 1996 breeding season can, therefore, still be regarded as a typical season for Tyneside in terms of the overall breeding success.

The numbers of chicks fledging per nest from the Skomer colonies in 1997 and 1998 were similar to the figures for Skomer Island in 1996, with 0.72 fledged per nest (Hamer & Turner 1997), and within the range of breeding success recorded since 1986 (Walsh et al 1992). Although laying was significantly later in 1998 than in 1997 there was no difference in the fledging success between the two years. It would appear that a one week delay did not adversely affect breeding success.

Breeding success at the North Shields colony has been consistently high compared to other kittiwake colonies, while the breeding success recorded for the Skomer Island colonies has consistently fallen within the range of breeding success recorded elsewhere. The breeding success of between 30 and 61 colonies monitored throughout the UK from 1986 - 1994 was 0.73 +/- 0.03 (Thompson et al 1995) and studies on individual kittiwake colonies in Norway (Barrett and Runde 1980) and on the Isle of May (Harris and Wanless 1992) yielded breeding successes of similar magnitude. The years of my study do not, therefore, appear to be atypical for their sites, but the North Shields colony, and by implication all the Tyneside colonies included in this study, are atypical.

4.4.2 Factors affecting breeding success in the Tyneside colonies.

Of the factors outlined in the introduction which may have contributed to the consistently high breeding success of the North Shields colony, relative to other kittiwake colonies in the U.K. including the Skomer Island colony, some can be eliminated as reasons for the difference in breeding success I observed between Tyneside colonies in 1996 and the Skomer Island colony in 1997 and 1998. Location on a building rather than a cliff and the freedom from parasites this location conferred can be discounted as it was not applicable to the Tynemouth and Marsden colonies. Colony size and colony age should also be discounted as, although the North Shields and Tynemouth colonies were small, the Marsden colony and the Skomer colony were both large colonies dispersed over several miles of coastline and all colonies studied had been in existence for a considerable time.

Although clutch size was not recorded for Tyneside, a mean clutch size of 2.3 can be calculated from the mean Tyneside brood size in 1996 (1.54) and the long-term hatching success of 67% recorded at the North Shields colony (Coulson & Wooller 1984). The clutch size calculated for the Tyneside colonies was, therefore, higher than the mean clutch sizes recorded on Skomer Island in 1997 (1.72) and 1998 (1.69). Differences in breeding success between the two areas, therefore, occurred at all stages in the breeding cycle, suggesting that the factors which made for consistently good breeding success on Tyneside operated throughout the breeding season.

Coulson & Wooller (1984) argued that the long-term hatching success of 67% and the long-term fledging success of 87% recorded for the North Shields kittiwake colony represented the breeding potential of kittiwakes in the absence of predation and in the presence of at least reasonable food availability. They recorded around 5% of eggs being addled (as a result of infertility or embryo death) and suggested that the failure of approximately one third of eggs to hatch could be attributed to inadequate incubation (Coulson & Wooller 1984).

Coulson and Thomas (1985) further suggested that the most important factor influencing the breeding success of a particular pair of kittiwakes was the quality of the individuals, with quality being a measured by an individual's relative consistency in breeding success over their lifetime. At the North Shields colony good quality kittiwakes lived longer and were more productive each year. Poor quality kittiwakes may lay smaller clutches, be less able to co-ordinate incubation and brooding shifts, be less able to protect eggs or chicks or be unable to provide adequate food during chick rearing.

4.4.3 Factors contributing to the differences in breeding success between Tyneside and Skomer

Factors that may have contributed to the differences observed between the two areas were the respective food availabilities in the North Sea and the Irish Sea, predation intensity within the two areas and a possible overall difference in the quality of birds nesting in the North-East of England, relative to the quality of kittiwakes nesting on Skomer Island which is nearer the edge of the species range. Smaller scale differences in predation pressure and the quality of birds may also have accounted for differences observed between sub-colonies within each area. At the scale of the sub-colony, or the nearby Tyneside colonies, food availability will not differ, but there may be seasonal fluctuations in food availability which will affect the breeding success of the area.

If the overall difference in breeding success between birds in the Skomer colony and Tyneside colonies could largely be attributed to differences in the quality of the bird populations, available food or other factors acting on a large scale among kittiwakes in the two areas, I would expect that percentage hatching and fledging success would be consistent within areas and different between areas. Although nesting density at the three main Tyneside study sites was low and of similar magnitude to the low density sites studied on Skomer Island, visual observations of the secondary monitoring sites indicated they were at least as densely settled as the higher density study sites on Skomer Island. The overall differences in breeding success between the two areas are, therefore, unlikely to be attributable to differences in sub-colony or nest cluster density.

If the percentage hatching or fledging success recorded for any colony or sub-colony at either Skomer or Tyneside accorded with the kittiwake breeding potential, as described by Coulson and Wooller (1984), I suggest that neither food availability nor the overall quality of the kittiwake population was limiting breeding success in that area. This proved to be the case in both colony areas. On Tyneside in 1996 the percentage fledging success at Tynemouth, North Shields, Jack Rock and Marsden Main Cliff did not differ from the kittiwake optimal fledging potential of 87%. On Skomer the percentage hatching success at all sub-colonies in 1997 and at all sub-colonies except Upper Wick in 1998 did not differ from the kittiwake optimal hatching potential of 67%. The percentage fledging success at High Cliff and Upper Wick in 1997, and at South Stream, Upper Wick and Lower Wick in 1998 also did not differ from the optimal. Although the percentage fledging success differed between areas, it was not consistent within areas, suggesting that large scale differences could not account for all the variation in breeding success observed.

4.4.4 Factors contributing to the differences in breeding success within areas.

Within an area, if fluctuations in the food supply during the breeding season were the main factors affecting breeding success, it would be expected that the percentage success at the stage when food was limiting would be lower than the success expected if food was not limiting. This effect would be consistent at all sub-colonies within the area and year. Conversely, if variation in breeding success between sites was to be attributed to differences in the quality of birds or the nesting density at each sub-colony, it would be expected that percentage hatching and fledging success would be consistent for each sub-colony, relative to the average for the breeding season, but would vary among sub-colonies. I would expect some consistency in breeding success between years for each site as, in consecutive breeding seasons, the kittiwake's longevity and nest site fidelity would lead to little turnover in the individuals within a breeding sub-colony. Different predation pressure could, however, act at any stage and at any spatial scale, and could result in inconsistency in breeding success between areas, between colonies and within colonies, between stages and years.

As fledging success was recorded for only one season at Tyneside no firm conclusions can be drawn for this area. The low breeding success at the Marsden Grotto may be attributable to higher predation pressure, lower quality breeding birds or the significantly lower density of nesting at this site. The difference in predation pressure observed between sites does, however, suggest that predation at Marsden Grotto acted to reduce breeding success. During 1996 I observed no instances of predation at either North Shields or Tynemouth. In contrast, the Marsden Grotto site experienced high levels of predation by herring gulls. As no chicks were seen dead on nests in the study area, I suggest that predation of chicks was the more likely agent of mortality than starvation, neglect or poisoning by the toxin that affected adults in the area.

As both percentage hatching and fledging success were recorded over two years from the Skomer colony, more positive conclusions can be drawn. Variations in relative hatching and fledging success were not consistent within sub-colonies, between stages or years. In 1997 hatching success was consistent across all four sub-colonies, while the subsequent fledging success was reduced at South Stream, relative to the other sub-colonies. In 1998 the percentage hatching success at Upper Wick was lower than the other three colonies, but the subsequent fledging success at Upper Wick was higher than the average, while fledging success at High Cliff was reduced. This inconsistency within sub-colonies suggested that differences in the quality of pairs and nesting density could not explain all of the observed variation in breeding success among sub-colonies. Variations in relative hatching and fledging success were also not consistent within stages, between sub-colonies in each year, indicating that seasonal fluctuations in food supply did not account for the observed variation.

The variations in hatching and fledging success did, however, appear to correspond with the different predation pressures observed or predicted from observations of different types of predators at the different sites. For example, in 1997, hatching success at the High Cliff site was relatively low, and the disappearance of eggs, along with the presence of herring gulls, lesser-black backed gulls and jackdaws at the site suggested egg predation, while the fledging success was relatively high, the surviving eggs being, presumably, on nests inaccessible to the larger gulls. In 1998, however, the presence of peregrine falcons nesting at High Cliff may have inhibited the activities of potential egg predators, resulting in high hatching success, while presumed predation of chicks by the peregrines could explain the low percentage fledging success.

The predation pressure observed at the Skomer sub-colonies and at Marsden Grotto, was more typical of kittiwake colonies than the predator free status of the other Tyneside colonies. Herring gulls (Jacobsen & Erikstad 1995; Barrett & Runde 1980; Galbraith 1983), great black-backed gulls (Jacobsen & Erikstad 1995; Barrett & Runde 1980), ravens (Jacobsen & Erikstad 1995; Danchin pers. comm.) and great skuas (*Stercorarius skua*) (Andersson 1976) have all been recorded preying upon kittiwakes. Galbraith (1983) suggested that high levels of gull predation may be associated with poor nest sites on "broken and easy-angled nesting cliffs" and may not be representative of steeper or more typical cliff sites, where nests are denser and less accessible. The situation at Marsden appeared to follow this pattern with predation being concentrated on the easily accessible, low density nesting group above the Grotto, and less intense at the other two Marsden monitoring sites, where nesting density was higher and the nests less accessible. Andersson (1976) suggested that larger kittiwake broods were more vulnerable to predation as the parents could not completely cover, and therefore protect, the whole brood from attacks.

In the Skomer study sites in 1997 and 1998 great black-backed gulls, lesser black–backs and herring gulls were observed taking eggs or chicks. In addition jackdaws were observed acting as opportunistic egg predators, stealing eggs when adults left their nests on the approach of the larger gulls, in nests immediately adjacent to the study site. In 1998 peregrine falcons were also observed taking chicks and adults. Although direct observations of predation were few, differences in percentage and hatching success between sub-colony sites appeared to reflect the different levels of predation observed in each sub-colony in each year. In contrast, the only predation observed during the 1996 breeding season in the Tyneside colonies was restricted to the chick-rearing stage at the Marsden Grotto site.

4.4.5 The influence of nest cluster density on breeding success

My results provide some evidence suggesting location within a colony may impact on breeding success, and the influence of location may operate on a number of spatial levels.

As expected the association was between higher density nesting and enhanced breeding success, in terms of the number of chicks surviving to fledge in a breeding season.

I suggest that the number of pairs nesting within a loosely interacting cluster, within a 1.5m radius, was the scale at which nesting density had a consistent impact on breeding success. Pairs nesting in high density clusters fledged more young than pairs nesting with fewer neighbours in the cluster, independent of the density of the larger, sub-colony grouping at Tyneside in 1996 and at Skomer in 1997. I suggest that the results from the 1997 Skomer Island breeding season, where there was no association between breeding success and sub-colony density, independent of immediate cluster density, would more readily be replicated than the results from the Tyneside season in 1996. The results from Tyneside will have been affected by the relatively low nesting density of the main study sites on Tyneside, the small number of pairs included in the dense cluster category and the consistent differences in breeding success recorded for Tyneside colonies, relative to the breeding success recorded for other kittiwake colonies.

From my study it was not possible to determine the relative contribution to enhanced breeding success of nesting density and individual or pair quality. Coulson and Thomas (1984) have suggested that only birds of high quality could establish nest sites in close proximity to other breeding pairs, so the effects of nesting density and quality would be additive. Where predation levels were particularly high, as at the Upper Wick site during incubation in 1998, the effects of quality and nesting density may be negated by the randomised effects of predation.

At a larger spatial scale, the density of the small colony or sub-colony density did not appear to have a consistent effect on breeding success. I suggest the differences in breeding success recorded between sites of different density on Tyneside in 1996, which persisted when immediate cluster density was controlled, should be attributed to differences in predation between the low density site, Marsden Grotto, and the two higher density sites. Analyses of hatching and fledging success suggested that predation caused the observed differences in breeding success. As already noted, no predation was observed during incubation at any site, while predation of chicks at the Marsden Grotto site was observed. I cannot, however, discount the possibility that the sparse nesting layout at Marsden Grotto contributed to the level of predation observed there, or that differences in sub-colony nesting density and a possible corresponding difference in quality of nesting pairs contributed to the lower breeding success.

Unfortunately, the promising results from the Skomer Island colony in 1997 were not replicated in 1998, where no consistent associations were recorded between nesting density, at either scale, and the timing of breeding or breeding success. The sites on Skomer were selected to reflect differential nesting density and consistent long-term differences in breeding success. In particular, the Upper Wick site was chosen as it formed part of a group for which the highest breeding success on the island had been consistently recorded for over a decade. In 1997 comparatively low breeding success was recorded for part of this group and in 1998 low breeding success was recorded for this entire group (J. Poole pers comm.). My observations suggested that in 1997 a great black-backed gull began to specialise in kittiwake egg predation from this group, facilitated by the broad, close-packed ledges which enabled the kittiwakes to nest densely, and expanded its predation activities in 1998. In 1998 approximately two thirds of the breeding attempts at the Upper Wick study site failed before or during incubation. I consider these results reflect the operation of less predictable factors than nest spacing or bird quality on the breeding success of birds, factors which in small groups for short periods may over-ride and obscure longer term trends.

4.4.6 Advantages of high density nesting

Although kittiwakes lack the full mobbing response of many gulls and terns they do have some anti-predator behaviours. Andersson (1976) observed kittiwakes lunging at great skuas with open beaks when the skuas approached within 2-3m of the cliff, and in some cases birds flew and swooped at the predator, harassing it for up to 20m. I observed similar behaviour, with kittiwakes lunging from their nest sites and chasing lesser black-backed gulls, herring gulls and ravens from the nesting cliffs. On the approach of either peregrine falcon or great black-backed gull, however, the response of adult kittiwakes was quite different, with all adults leaving the nesting cliffs in the vicinity of the predator.

Andersson (1976) suggested that kittiwake defence is probably more efficient in denser parts of the colony, where there are more birds who may join in harassing a predator, and he noted that the number of kittiwakes "mobbing " a skua was significantly higher before unsuccessful attacks than before successful attacks on nests. My results in 1996 and 1997 support the suggestion that nesting in a denser cluster may confer a protective advantage, at least against predators that do not present a threat to an adult kittiwake. In 1998 more losses could be attributed to predators that presented a threat to adults so location of a nest in a high density cluster did not enhance breeding success.

The arguments that better "quality" kittiwakes preferentially nest in the dense centres of colonies, with poorer "quality" birds being forced to breed on the periphery may need to be re-evaluated, taking into consideration the improvement in breeding success expected from the presence of neighbours (Coulson and Thomas 1985, Fairweather 1994). It may, however, be that because of the advantages of being in a denser cluster of birds, only good quality birds can gain and retain such sites. The relationship between aggressive behaviour, kittiwake quality and nesting density will be examined in chapter 5.

Another factor contributing to the association between clustering and breeding success may be that breeding success is enhanced and the timing of breeding brought forward in denser clusters as a result of more intense social stimulation. Burger and Gochfield (1991) suggested using the standard deviation of laying date as the most appropriate measure of breeding synchrony. In the absence of laying dates for Tyneside, I used the hatching date standard deviation as an indicator of synchrony. On Skomer in both years, breeding was more synchronised among nests in high density clusters than among nests in low density clusters. Pairs nesting in high density clusters on Skomer in 1997 also laid significantly earlier than pairs in low density clusters suggesting that social stimulation does influence the timing of breeding.

Chapter 5.

Interactions between behaviour, nesting density and breeding success: behaviour as a guide to quality.

5.1 Introduction

Of the factors influencing the breeding success of a pair of kittiwakes in any breeding season, Coulson & Thomas (1985) stressed the prime importance of phenotypic quality. Differences in breeding success between individuals were more consistent than variation between years, and longer-lived kittiwakes also exhibited higher initial and later breeding success, leading to greater overall lifetime reproductive success. Although in any given year the highest quality phenotype may alter slightly in accordance with prevailing conditions, birds that are of good quality will generally perform well in the range of conditions experienced during their lifetimes. Differences in quality would be expected to be reflected in differential breeding success and survival. More successful breeding individuals of a number of species have been found to be more likely to survive to the next breeding season (e.g. Smith 1981, Newton (ed) 1989).

Breeding success can be directly equated with Darwinian fitness only in the ideal situation where the number of young which survive to join the breeding population can be quantified. In most species of birds, the number of young which survive to fledging is used as a rough index of breeding success, as the young of many species, including kittiwakes, disperse to other areas to breed. Fledgling quality has also been used as an indicator of eventual breeding success. Heavy fledglings have been shown to be more likely to survive to breeding age (Barber & Evans 1995) and food shortages during the breeding season have been demonstrated to reduce post-fledging survival in herring gulls (Parsons et al 1976 in Fairweather 1994) and manx shearwaters *Puffinus puffinus* (Perrins, Harris & Britton 1973 in Fairweather 1994). When considering the impact of quality on breeding success it is difficult to avoid a circular argument as quality is itself measured by breeding success so, by definition, good quality birds will be those that consistently fledge more young.

The proportion of time spent by a pair of kittiwakes in behaviours directly related to breeding (aggressive and pairing behaviours) may reflect both the quality and current condition of individuals. Francis (1988) noted that levels of aggressive behaviour are an acceptable measure of social dominance, which in the case of the kittiwake would be equated with the ability to obtain and hold a breeding territory. If quality was of prime importance in determining the breeding success of kittiwakes, there may be a quantifiable relationship between breeding success and the proportion of time allocated to aggressive and/or pairing behaviours. It may, therefore, be possible to use the proportion of time allocated to these behaviours as an indicator of quality.

As both members of the pair share incubation, brooding and foraging duties, co-operation within the pair is crucial to the survival of young kittiwakes. Chardine (1983) found that newly formed pairs allocated more time to pairing displays than established pairs. New pairs were less securely bonded and potentially less well coordinated than pairs that had been formed in previous breeding seasons. New pairs spent more time together at the nest site and performed the greeting ceremony more frequently than established pairs, presumably to reduce the time period needed for familiarisation, the reduction of within pair aggression and the establishment of a viable pair bond. Frequent performance of the greeting ceremony may also be needed to learn the vocalisation pattern of the new mate. Wooller (1978) demonstrated that individual kittiwakes remember their partners vocalisation from year to year, so established pairs would not need to vocalise as frequently. Among established pairs better quality birds may be able to allocate a greater proportion of time to displays reinforcing the pair bond or, conversely, may not need to allocate so much time to pairing displays to achieve the necessary within-pair co-operation for a successful breeding attempt.

A large body of research has focused on the intense competition between kittiwakes for good nest sites in the central or more densely occupied areas of colonies, and the consequent benefits conferred by a good nest site in terms of higher breeding success (e.g. Coulson and White 1960, Coulson 1968, Coulson and Thomas 1983, Coulson and Thomas 1984, Falk and Møller 1993). Birds able to allocate more time to aggressive behaviour may, therefore, be expected to be more successful breeders.

Behaviour also reflects the current environment, including the presence and behaviours of conspecifics in the proximity of the nest. Danchin (1988) observed that the behaviour of kittiwakes in the vicinity of mating pairs differed from behaviour at other times, being characterised by stronger general activity with an emphasis on pairing and aggressive activity. Chardine (1983) suggested that spontaneous greeting was triggered by external factors such as the behaviour of other birds in the colony, whereas the return of the male to its mate and subsequent greeting was more likely to be controlled by intrinsic, within-pair factors and was more frequently followed by courtship behaviours. Wooller (1979 cited in Chardine 1983) observed higher greeting rates among pairs nesting in the centre of the colony than pairs at the edge of the colony. Head tossing was also more likely to follow the greeting ceremony among pairs at the centre and Chardine suggested this reflected social facilitation in the more densely settled centre of the colony.

Nest cluster density may, therefore, be an important factor impacting on the behaviour of an individual. Among many colonial species, however, increasing nesting density, of itself, would be associated with higher aggression levels. More interactions between conspecifics would be expected in high density nesting clusters relative to low density nesting clusters, regardless of the quality of the nesting birds. The potential for interactions would increase with an increase in the number of birds in the group. This trend would be reinforced among kittiwakes by the contagious nature of some displays.

Among many colonial birds, including kittiwakes, the effects of density and quality would be additive, as good quality, aggressive birds would be expected to dominate the denser parts of each colony . If more aggressive birds experienced higher breeding success, when nesting density was controlled, the level of aggression could be used as an indicator of quality. Intense competition for nest sites in high density nest clusters should be most apparent in differences in levels of aggressive behaviour during the pre-laying period.

Coulson and White (1960) recorded that kittiwakes responded to neighbouring pairs performing the greeting ceremony only at relatively short distances. Around 80% of the responses (greeting or aggressive displays) occurred at distances less than 2 feet, and no responses were observed more than 5 feet from the displaying pair. The reaction to alighting birds was significantly greater in denser, rather than less dense sub-colonies at Marsden, suggesting that excitation is more intense at higher nest densities. In this chapter, I extend this work by examining the scale at which density impacts on behaviour, whether at the small scale of a cluster of interacting nests within approximately 1.5m radius or at the larger scale of the sub-colony.

5.2 Methods

Refer to chapter 2.

5.3 Results

5.3.1 Aggressive behaviour during the pre-laying stage in relation to sub-colony density, nest cluster density and fledging success

5.3.1.1 Tyneside in 1996

There were significant differences among the three Tyneside sub-colonies in the proportion of time kittiwakes allocated to aggressive displays during the pre-laying stage in 1996 (Oneway AOV: F = 5.65, 2 d.f., P = 0.006). A Tukey-HSD test indicated that the proportion of time spent in aggressive behaviour at Marsden, the least dense sub-colony, was significantly lower than that at Tynemouth (Figure 1). There were, however, no differences in the proportion of time allocated to aggressive displays, between pairs nesting in low density (fewer than 4 neighbours within 1.5m) and high density (4 or more neighbours within 1.5m) clusters (t = -0.16, 55 d.f., P = 0.87). The expected relationship between location in a high density cluster and higher levels of neighbour interaction may not have been evident because behaviour was recorded for only a small number of nests in the high density category in the Tyneside colonies (14 nests).

Successfully breeding pairs were more aggressive than pairs which were less successful in their breeding attempts, success being measured as the number of chicks fledged (F = 3.83, 2 d.f., P = 0.03) or whether or not at least one chick survived to fledge (Figure 2; t = -2.11, 56 d.f., P = 0.039). A Tukey-HSD test indicated that pairs which fledged 2 chicks were more aggressive than pairs which failed to fledge any chicks.

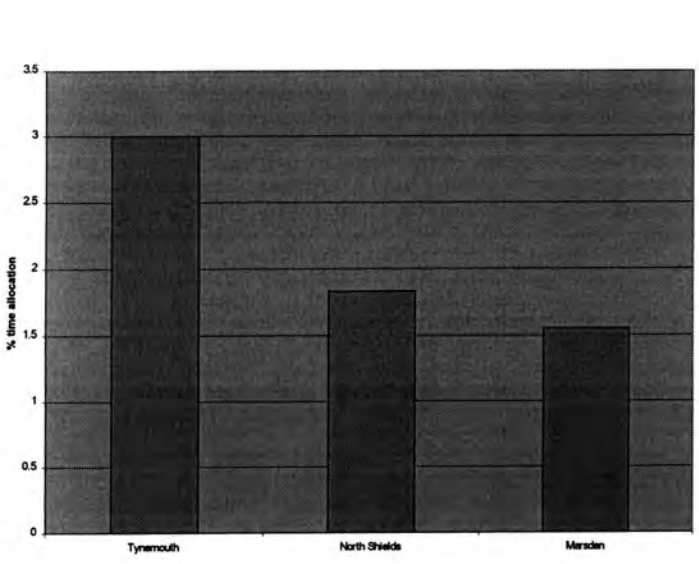

Figure 1. Aggressive behaviour in colonies of different density at Tyneside during the pre-laying period in 1996.

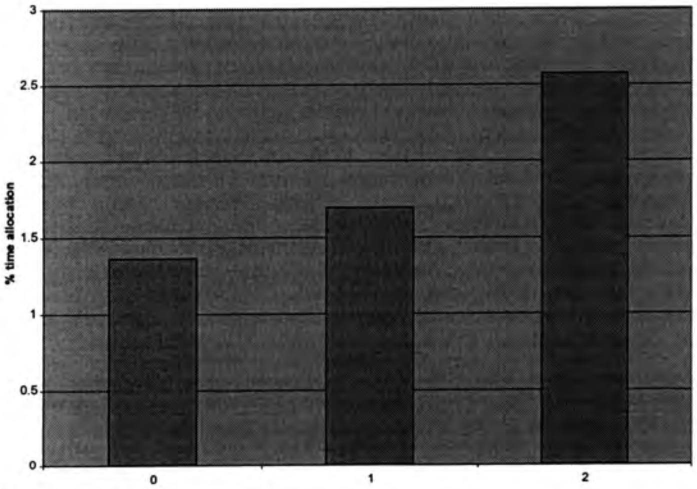

Figure 2. Aggressive behaviour during the pre-laying period among pairs with different breeding success.

When the effects of colony site, nest cluster density and breeding success were separated, the difference in aggression levels among sub-colony sites remained significant. When nesting density was controlled, however, there were no differences in allocation of time to aggressive displays among pairs with different fledging success (Three-way ANOVA: sub-colony density $F_{1,56} = 4.66$, $P = 0.015$; cluster density $F_{1,56} = 0.12$, $P = 0.73$; breeding success $F_{1,56} = 0.83$, $P = 0.44$; no significant interactions).

5.3.1.2 Skomer in 1998

In 1998 there were significant differences among sub-colonies in the proportion of time spent in aggressive behaviour during the pre-laying stage ($F = 5.9$, 3 d.f., $P = 0.001$). A Tukey HSD test indicated that pairs at the Upper Wick, the most densely clustered sub-colony, allocated more time to aggressive displays than pairs at the other three sites (Figure 3). At the smaller spatial scale, there were also differences in allocation of time to aggressive behaviour between pairs nesting in high and low density clusters within a radius of 1.5m ($t = -2.49$, 98 d.f., $P = 0.014$). Pairs in high density clusters allocated more time to aggressive displays than pairs in low density clusters (Figure 4). The increased potential for neighbour interactions associated with higher density nesting was, therefore, reflected in higher aggression levels at both scales of density measured, both immediate cluster and sub-colony.

There were no differences in the percentage of time spent in aggressive behaviour between successful and unsuccessful birds, when either number fledged ($F = 0.64$, 2 d.f., $P = 0.53$) or success or failure ($t = 1.13$, 98 d.f., $P = 0.26$) were considered.

When the effects of nest cluster density and sub-colony site were separated, there were, however, no differences in aggression levels between pairs nesting at different cluster densities or sub-colony sites (Two-way ANOVA: sub-colony density $F_{1,99} = 1.46$, $P = 0.23$; cluster density $F_{1,99} = 0.009$, $P = 0.93$; no significant interactions)

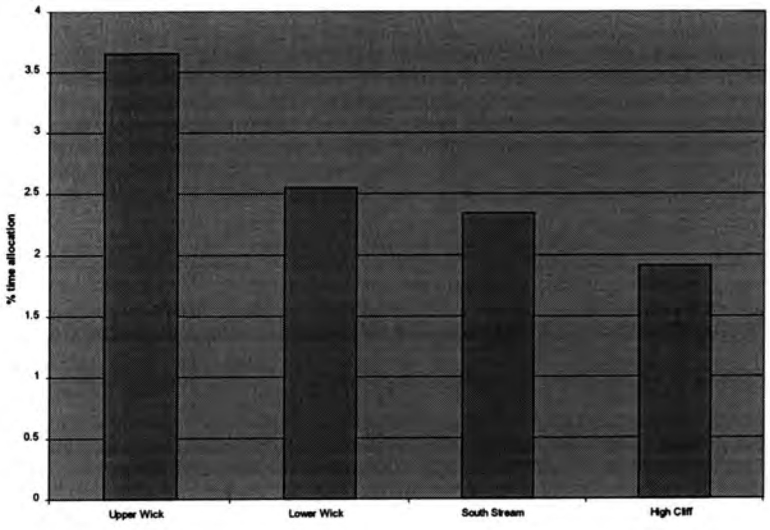

Figure 3. Aggressive behaviour in sub-colonies of different density at Skomer during the pre-laying period in 1998.

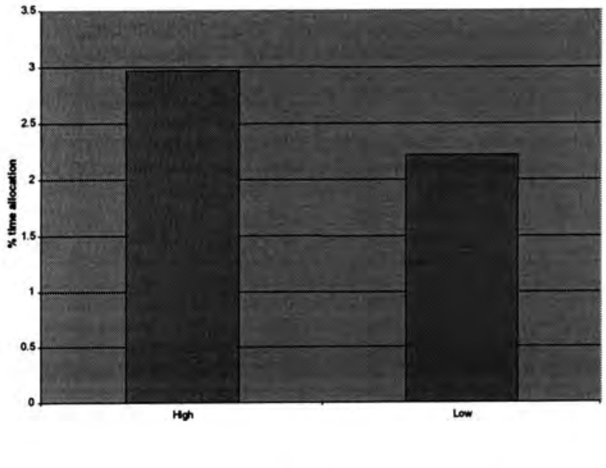

Figure 4. Aggressive behaviour of pairs nesting at different density at Skomer during the pre-laying period in 1998.

5.3.2 Aggressive behaviour during incubation at Skomer Island in 1997 and 1998 in relation to sub-colony density, nest cluster density and fledging success

During incubation in the Skomer Island colony in 1997 there were differences among sub-colony sites in the proportion of time spent in aggressive displays (F = 5.04, 3 d.f., P = 0.0026). A Tukey HSD test indicated that levels of aggression at South Stream were lower than aggression levels at High Cliff and Lower Wick, and that levels of aggression at the Upper Wick, the cub-colony with highest nesting density, were higher than at the other sites (Figure 5). In 1998, however, there were no differences during incubation among sub-colonies in time allocated to aggressive behaviour (F = 1.54, 3 d.f., P = 0.21).

At the smaller spatial scale, during incubation in the 1997 breeding season pairs nesting in high density clusters allocated a higher proportion of time to aggressive behaviour than pairs nesting in low density clusters (Figure 6; t = -2.17, 108 d.f., P = 0.032). In 1998, however, there was no difference in aggressive behaviour between nests in high and low density clusters (t = -0.19, 91 d.f., P = 0.85).

In both the 1997 and 1998 breeding seasons there were no differences in levels of aggressive behaviour among pairs with different breeding success, either in terms of the number of chicks fledged (1997: F = 0.10, 2 d.f., P = 0.90; 1998: F = 0.50, 2 d.f., P = 0.61) or whether or not a pair fledged at least one chick (1997:t < 0.0001, 108 d.f., P >0.99; t = -0.65, 91 d.f., P = 0.51).

When the effects of nest cluster density and sub-colony were separated for the 1997 breeding season, there were no differences in aggression levels between pairs nesting at different cluster densities or sub-colony sites (Two-way ANOVA: sub-colony density $F_{1,109}$ = 2.10, P = 0.11; cluster density $F_{1,109}$ = 0.053, P = 0.82, no significant interactions).

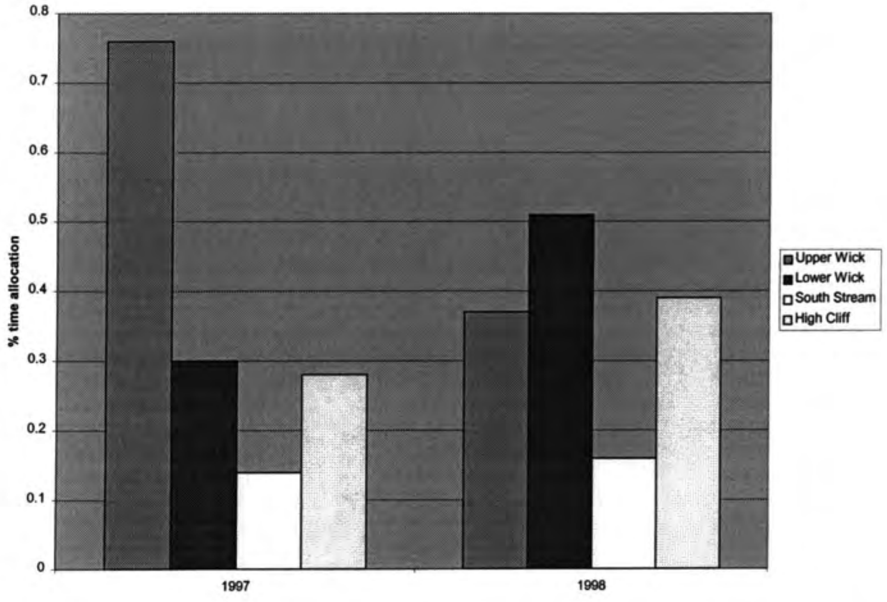

Figure 5. Aggressive behaviour among pairs nesting in sub-colonies of different density during incubation at Skomer in 1997 and 1998.

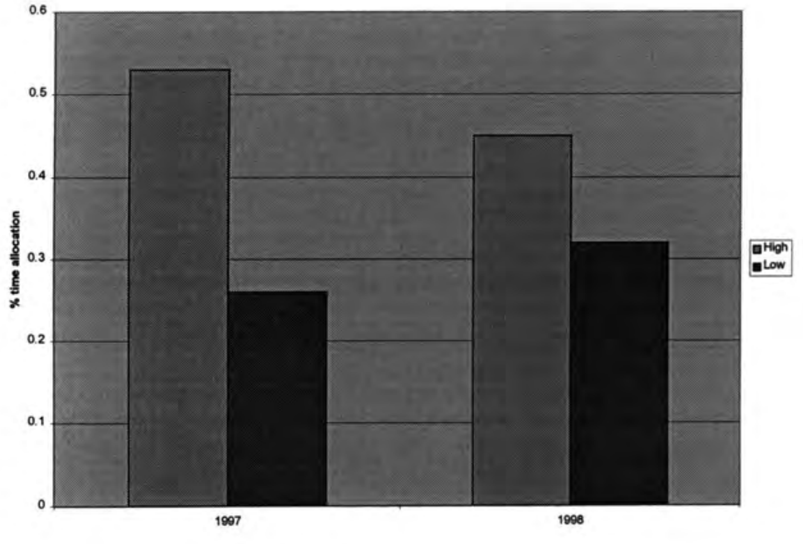

Figure 6. Aggressive behaviour of pairs nesting at different density at Skomer during incubation in 1997 and 1998.

5.3.3 Aggressive behaviour during chick rearing at Skomer in 1997 and 1998 in relation to sub-colony density, nest cluster density and fledging success

There were differences among Skomer Island sub-colonies in the proportion of time allocated to aggressive behaviour during chick rearing in both 1997 ($F = 3.92$, 3 d.f., $P = 0.012$) and 1998 ($F = 3.09$, 3 d.f., $P = 0.034$). Tukey HSD tests indicated aggression levels at South Stream were significantly lower than those at Lower Wick in 1997, while in 1998 no two sub-colony sites were significantly different in the time allocated to aggressive behaviour (Figure 7).

In 1997 during chick rearing, pairs nesting in high density clusters were more aggressive than pairs nesting in low density clusters (Figure 8; $t = -2.52$, 77 d.f., $P = 0.014$). In 1998 there were, however, no differences in levels of aggression between pairs nesting in high or low density clusters ($t = -1.03$, 64 d.f., $P = 0.31$).

In both the 1997 and 1998 breeding seasons, during chick rearing there were differences in the proportion of time allocated to aggressive displays among pairs with different breeding success, measured as the number of chicks fledging per nest (1997:$F = 3.7$, 2 d.f., $P = 0.029$; 1998: $F = 9.01$, 2 d.f., $P = 0.0004$) or whether or not at least one chick survived to fledge. (1997: $t = -2.13$, 77 d.f., $P = 0.036$; 1998: $t = -3.74$, 64 d.f., $P < 0.0001$). Tukey-HSD tests for both years indicated pairs which fledged two chicks were most aggressive, followed by pairs which failed to fledge any chicks, while pairs which fledged 1 chick spent the least time in aggressive displays (Figure 9).

When the effects of sub-colony site, nest cluster density and breeding success were separated for 1997, there were no differences in time allocated to aggressive behaviour relating to sub-colony site or cluster density, while a trend for differences in aggression associated with fledging success approached significance (Three-way ANOVA: sub-colony density $F_{1,78} = 1.97$, $P = 0.13$; cluster density $F_{1,78} = 0.42$, $P = 0.52$; breeding success $F_{1,78} = 2.41$, $P = 0.098$; significant interactions between sub-colony density and breeding success $F_{1,78} = 2.30$, $P = 0.046$).

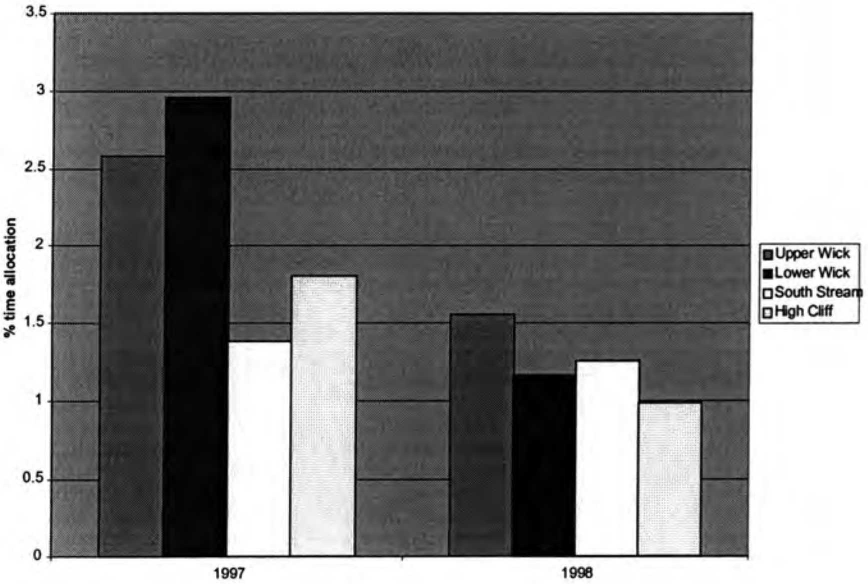

Figure 7. Aggressive behaviour during chick rearing of pairs nesting in sub-colonies of different density at Skomer during 1997 and 1998.

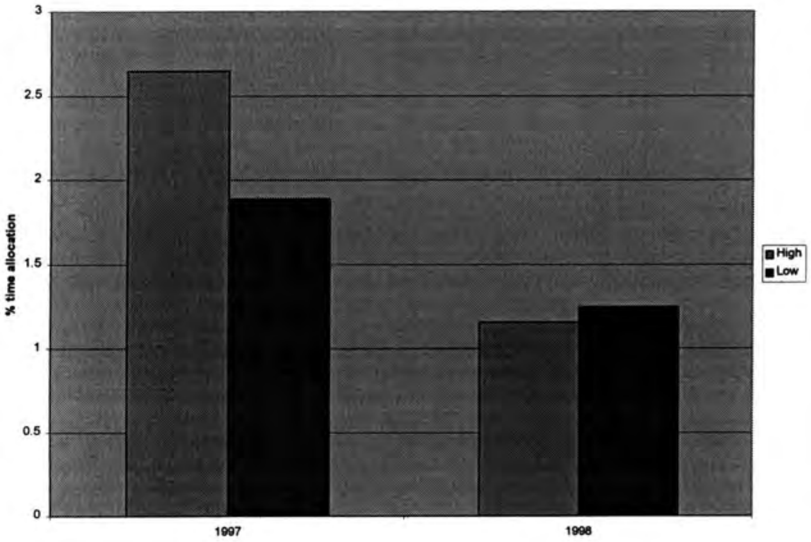

Figure 8. Aggressive behaviour during chick rearing of pairs nesting at different density at Skomer during 1997 and 1998.

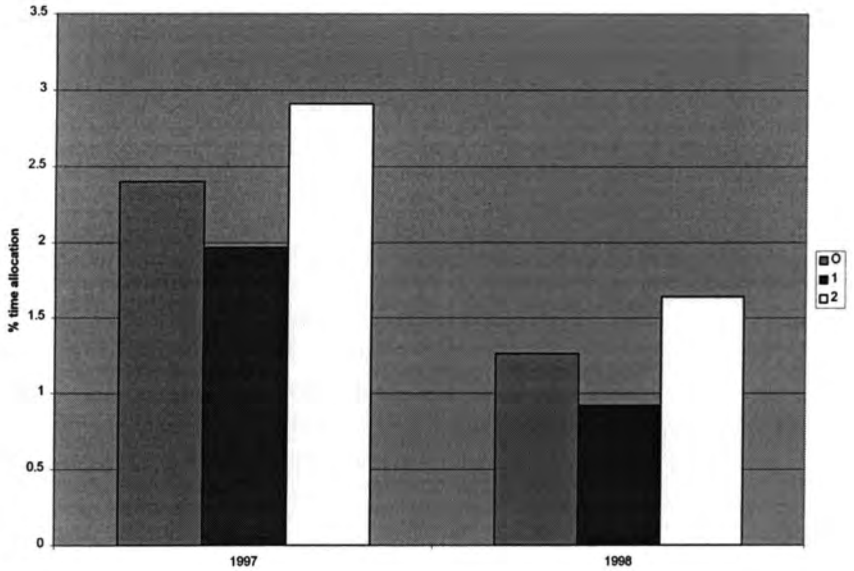

Figure 9. Aggressive behaviour during chick rearing of pairs with different nesting success at Skomer in 1997 and 1998.

In 1998, however, there were differences in time allocated to aggressive behaviour among pairs with different fledging success, when sub-colony density was controlled (Two-way ANOVA: sub-colony density $F_{1,65} = 0.23$, $P = 0.87$; breeding success $F_{1,65} = 3.96$, $P = 0.024$, no significant interactions).

5.3.3.1 Comparison of nest cluster density between 1997 and 1998

As many pairs nesting in high density clusters at the Upper Wick site failed to hatch chicks in 1998, I examined the relative density of pairs rearing chicks in 1997 and 1998. A lower density of active nests during chick rearing in 1998, compared with 1997, may have explained the lower levels of aggression observed during chick rearing during 1998 (see chapter 2), as at lower cluster densities there are likely to be fewer interactions between neighbours. There were, however, no differences in the density of pairs whose breeding attempts continued until the point where they hatched or fledged chicks between 1997 and 1998 in terms of the percentage of nests in high or low density clusters (Table 1). There were also no differences between years in the number of neighbours within 1.5 m of nests where breeding attempts continued through to hatching or fledging (Table 2; Mann Whitney U test hatch: $Z = -1.18$, $n = 145$, $P = 0.28$; fledge: $Z = -1.18$, $n = 113$, $P = 0.24$).

Table 1. Comparison of the percentage of nests in high or low density clusters where breeding attempts continued to the point of hatching or fledging in the 1997 and 1998 breeding seasons at Skomer.

	Nests where chicks hatched			Nests where chicks fledged		
	Low(%)	High (%)	n	Low (%)	High (%)	n
1997	43	57	79	37	63	62
1998	45	55	66	37	63	51

Table 2. Comparison of the mean number of neighbouring nests (within a cluster of radius 1.5m) where breeding attempts continued to the point of hatching or fledging in the 1997 and 1998 breeding seasons at Skomer.

	Nests where chicks hatched			Nests where chicks fledged		
	n	mean	SD	n	mean	SD
1997	79	4.03	2.4	62	4.42	2.35
1998	66	3.53	1.84	51	3.86	1.8

5.3.3.2 Proximity of failed nests

During chick rearing in 1997 and 1998 there were no differences in aggression levels among pairs with no failed neighbours, one failed neighbour or more than one failed neighbour within 1.5m (1997: F = 1.22, 2 d.f., P = 0.30; 1998: F = 0.75, 2 d.f., P = 0.48). In 1998, however, there were differences in fledging success among pairs with no, one or more than one failed neighbour within 1.5m (K-W One-way AOV, Chi-square = 11.23, 2 d.f., P = 0.0036), while in 1997 the difference approached significance (KW AOV, Chi-square = 5.41, 2 d.f., P = 0.067). In 1998 the highest fledging success was recorded for pairs with no failed neighbours, while in 1997 the highest fledging success was recorded for pairs with one failed neighbour.

When the effects of failed neighbours, nest cluster density and fledging success were separated there were no differences in levels of aggression among pairs with different numbers of failed neighbours within 1.5m in either year. When failed neighbours were controlled, however, there were differences in aggression between nests with different fledging success in both years, and between nests in different cluster densities in 1997 (1997 Three-way ANOVA: failed neighbours $F_{1,77} = 1.63$, P = 0.20; breeding success $F_{1,77} = 3.54$, P = 0.035; cluster density $F_{1,77} = 6.96$, P = 0.011; no significant interactions; 1998 Three-way ANOVA: failed neighbours $F_{1,64} = 0.59$, P = 0.56, breeding success $F_{1,64} = 7.35$, P = 0.002; cluster density $F_{1,64} = <0.0001$, P = 0.996, significant interactions between failed neighbours and breeding success $F_{1,64} = 2.69$, P = 0.042).

5.3.4 Pairing behaviour in relation to breeding success, nest cluster density and sub-colony site.

During the pre-laying stage at Tyneside in 1996, the pre-laying stage at Skomer in 1998, incubation and chick rearing stages at Skomer in 1997 and 1998 there were no differences in the time allocated to pairing behaviour between pairs nesting in low and high density clusters, among pairs with different breeding success or among pairs at the different sub-colonies (Tables 3 -5). Although there was a trend toward a difference in time spent in pairing displays between pairs in high and low density nest clusters during chick rearing in the Skomer colony in 1998, the difference was not significant.

Table 3 T-test results testing for differences in the proportion of time allocated to pairing behaviour during pre-laying, incubation and chick rearing between pairs nesting in high and low density clusters.

Stage	Year	t	d.f.	P
Pre-laying	1996	-0.79	55	0.44
	1998	-0.21	98	0.83
Incubation	1997	-1.38	108	0.17
	1998	-0.45	91	0.65
Chick rear to min fledge	1997	-0.44	77	0.66
	1998	-1.75	64	0.085

Table 4. One-way Anova testing for differences in the proportion of time allocated to pairing behaviour during pre-laying, incubation and chick rearing between pairs which fledged different numbers of young

Stage	Year	F	n	d.f.	P
Pre-laying	1996	0.26	56	2	0.77
	1998	0.81	99	2	0.45
Incubation	1997	1.19	110	2	0.31
	1998	0.98	92	2	0.38
Chick rear to min fledge	1997	1.67	78	2	0.19
	1998	1.08	65	2	0.35

Table 5 One way Anova test results for differences in the proportion of time allocated to pairing behaviour during pre-laying, incubation and chick rearing among different sub-colony sites

Stage	Year	F	n	d.f.	P
Pre-laying	1996	0.82	58	2	0.44
	1998	2.10	99	3	0.11
Incubation	1997	2.09	110	3	0.11
	1998	1.75	92	3	0.16
Chick rear to min fledge	1997	1.14	78	3	0.34
	1998	0.59	65	3	0.62

5.4 Discussion

I began this study expecting there would be differences in the time allocated to aggressive and pairing behaviours between pairs nesting in clusters of different density and between pairs with different breeding success. As previous studies suggested that better quality kittiwakes tended to nest in the denser, central areas of colonies (Coulson and White 1960, Coulson 1968, Coulson and Thomas 1983, Coulson and Thomas 1984, Falk and Møller 1993), I expected the effects of quality and nesting density would combine to make high density clusters very different in behaviour to low density clusters. I did not, however, find clear and consistent differences in time allocated to aggressive or pairing behaviours. There were some indications that the time allocated to aggressive behaviour was influenced by the quality of breeding birds, as measured by fledging success, and nesting density, at both large and small spatial scales. There were no indications that nesting density or differences in quality influenced the time allocated to pairing behaviours.

The proportion of time spent in aggressive displays during the pre-laying and chick-rearing stages appeared to reflect the quality of the pair, indicated by the breeding success in that season. Initial analysis suggested more successful pairs in the Tyneside colonies allocated more time to aggressive behaviour before eggs were laid than less successful pairs. This relationship did not, however, persist when nest cluster density and sub-colony site were controlled. The positive association between nest density and breeding success (see chapter 4) on Tyneside suggests there were differences in quality among pairs nesting at the different cluster and sub-colony densities and that higher aggression may be a result of proximity to more birds and not separately associated with individual quality. Differences in the time allocated to aggression among pairs with different breeding success during chick-rearing in the Skomer Island sub-colonies were recorded for both the 1997 and 1998 breeding seasons. The highest levels of aggression were associated with pairs which fledged 2 chicks which were presumably the highest quality pairs. This relationship was at least partly independent of the effects of density. The difference in aggression levels among birds with different fledging success was significant in 1998, and approached significance in 1997, when nesting density was controlled.

Nesting density also appeared to have some impact on the proportion of time birds allocated to aggressive displays at all stages in the breeding season. Initial results indicated a difference in aggressive behaviour between birds in high and low density clusters during pre-laying at Skomer in 1998, and during incubation and chick rearing at Skomer in 1997. In all cases, these differences did not persist when separated from the effect of location in sub-colonies of different density. From my results I could not, therefore, clearly distinguish at which of the two spatial scales nesting density had most impact on the allocation of time to aggressive behaviour. Although responses to aggressive displays have been noted only among birds within approximately 1.5m of a displaying bird, responses have been observed to radiate from the initiating bird or cluster, each group acting like the interlocking links in "chain-mail" (Coulson and Dixon 1979).

In the Tyneside colonies in 1996 there were no differences in level of aggressive behaviour associated with nesting in clusters of different density. In the areas where colour-ringed birds were concentrated and behavioural observations conducted, there were only 14 pairs nesting in high density clusters. I suggest that there were too few nests in the high density category, and insufficient hours of observations undertaken, to identify possible differences in aggressive behaviour between nests in high and low density clusters, although the results indicating differences related to quality do suggest some difference associated with density. Differences in aggressive behaviour among pairs nesting in the different sub-colonies on Tyneside during the pre-laying period, which persisted when immediate cluster density and breeding success were controlled, suggested that levels of aggressive behaviour in the Tyneside colonies may have been controlled at the larger spatial scale of the sub-colony, or that factors other than density may have caused the differences in aggression between sub-colonies.

Unfortunately, the only year in which I was able to undertake observations at all stages of the breeding season, 1998, did not yield the expected results. Although breeding success overall was within the usual range for the Skomer Island colony, the breeding season was unusual in the intensity of localised predation at the Upper Wick site. Although there were relationships between breeding density and aggression levels, the expected differences in aggression related to breeding success were not evident. The breeding attempts of a high proportion of the good quality, aggressive pairs at the Upper Wick sub-colony failed due to predation shortly after eggs were laid (see chapter 4). During the pre-laying stage the pairs at this site were more aggressive than at the other three sites, as expected, but the number of chicks fledged per nest was low compared to the other

Skomer sub-colonies. The Upper Wick site had been selected for this study because its breeding success at this site had consistently been the highest recorded among the sub-colonies monitored on Skomer Island over a period of ten years (J. Poole, pers. comm.). The expected relationships between quality, measured as breeding success, and levels of aggression were evident during chick rearing in 1998, in spite of the small numbers of Upper Wick nests where breeding attempts were still in progress, as predation was not intense at this site during chick rearing.

Although there were no differences in the proportion of nests in high and low density clusters at the start and finish of chick rearing between 1997 and 1998, nor any difference in the mean number of neighbours at nests still active, there was a marked difference in the distribution of failed nests. Approximately half of the Upper Wick sub-colony nests were deserted shortly after incubation commenced. This desertion probably contributed to the lower aggression levels observed during incubation and chick rearing relative to aggression in 1997 (see chapter 3).

There were differences in breeding success among pairs with different numbers of failed neighbours, lower breeding success being associated with increasing numbers of failed neighbours. Increased levels of aggression at nests with failed neighbours in response to disturbance from birds on the failed nests, either the failed residents or prospectors, may have provided a mechanism to explain lower breeding success. There were, however, no differences in aggressive behaviour associated with increasing numbers of failed neighbours within a radius of 1.5m. The proximity of failed nests may, however, have impacted on aggressive behaviour at a larger spatial scale than that of the cluster of nests within 1.5m, the basic unit for this study. Clustering of failed birds was more likely to be attributable to collective vulnerability. If one nest in a cluster was vulnerable, e.g. to predation or destruction by wave action, other nests in the cluster were also likely to be vulnerable. At the Upper Wick site the nature of the nesting ledges meant that in many cases predators could readily move between nests in a cluster.

A kittiwake whose breeding attempt had failed would be unlikely to restrict its prospecting activities to nests in the immediate vicinity of its own nest site. Kittiwakes were more likely to relocate to a different colony after a breeding failure if other nests in the vicinity had also failed (Danchin and Monnatt 1992). Cadiou (1999) also observed that failed birds prospected in more successful areas within their own colony or nearby colonies rather than in the immediate vicinity of the failed nest. Furthermore Danchin et al (1998) found that failed breeders on productive cliffs remained on their nest sites for the rest of the season, while failed breeders on less productive cliffs tended to desert the nest after failure and prospect on successful nests elsewhere in the colony. More aggressive interactions would therefore be expected in more successfully breeding areas, especially during the latter stages of chick rearing, when the incidence of prospecting peaks (Cadiou et al 1994) and nest attendance is reduced (e.g. Galbraith 1983, Wanless and Harris 1992). Without individual identification of most birds in the study area it was not possible to differentiate between failed residents and prospectors at failed nest sites. Similarly, although intruders could normally be identified when chicks were present on a nest, it was not possible to determine whether or not the intruder was a failed neighbour, a new recruit, or a failed breeder from elsewhere in the colony.

I suggest that during the pre-laying and chick-rearing stages, levels of aggressive behaviour may be used as an index of the quality of a pair of birds, when the effects of nesting density are controlled, and their eventual breeding success in that season will reflect this measure of quality. This trend can, however, be over-ridden on the small scale by less predictable circumstances, in this case more intense predation in a small area.

The importance of the strength of the pair bond and the quality of individual birds influencing their ability to co-ordinate activities with a partner have been emphasised as factors determining kittiwake breeding success (e.g. Coulson and Thomas 1984, Coulson and Wooller 1984). I found no differences in the proportion of time allocated to pairing displays among pairs nesting at different densities or with different breeding success; time allocated to pairing displays cannot be used as an indirect index of quality. My results cannot, however, be used to question the importance of the pair bond and pair co-ordination to breeding success, as time allocated to pairing behaviour does not necessarily reflect the quality of the pair-bond. As had been found in the determination of a kittiwake breeding activity budget (see chapter 3),time allocated to pairing behaviour appeared to be relatively fixed in comparison to time allocated to aggressive behaviour. Levels of aggressive behaviour appeared to be more flexible, changing with nesting density and the quality of the pair.

Chapter 6.

General Discussion

Although there is a considerable body of research relating to the breeding behaviour of the kittiwake, there are still some areas where little work has been done. I consider that it is worthwhile to endeavour to bridge some of these gaps as greater understanding of the breeding dynamics of one colonial breeding species may shed insight on more general relations within breeding colonies and assist in the ongoing debate on the evolution of colonial breeding.

Considerable efforts have been made to describe and interpret the significance of the behaviour of kittiwakes in their breeding colonies (e.g. Cullen 1957, Tinbergen 1958, 1959, Cadiou et al 1994, Danchin 1987) facilitating the study of the allocation of time at the nest site to various categories of behaviour described in chapter 3. This work is intended to complement the considerable body of work on kittiwake activity budgets, in terms of nest attendance and the duration of time allocated to foraging (e.g. Braun and Hunt 1983, Galbraith 1983, Coulson and Wooller 1984, Wanless and Harris 1992, Hamer et al 1993, Cadiou and Monnat 1996, Falk and Møller 197, Regehr and Montevecchi 1997).

I found patterns of change in the proportion of time allocated to the seven behavioural categories studied which were consistent across years and colonies for the stages of the breeding season where repeat observations were made. Most of a kittiwake's time on the nest site was allocated to the categories of "inactive behaviours", sitting or standing on the nest either obviously alert or appearing to sleep, followed in terms of time allocation by maintenance behaviour while only small proportions of time were allocated to behavioural interactions with conspecifics or nest building.

Relatively large amounts of time were allocated to both pairing and aggressive displays during the pre-laying period, while nest sites and pairs for the season were being established. Aggression at this stage was most frequently expressed through choking and bow and moan displays, denoting aggression at medium to long distance within the colony. Although kittiwakes exhibit both nest site and partner fidelity, there will always be some changes in breeding partners caused by the death of one member of the pair, and changes in both nest site and partner are not uncommon even when both members of the pair return to the colony to breed. When such divorces occur the male is more likely to retain the nest site, breeding with a new partner, while the female is more likely to breed elsewhere in the colony (Coulson 1978, Coulson and Thomas 1983). Danchin and Monnat (1992) have also shown that under the stimulus of breeding failure kittiwake pairs may move to a different nest site. In many species the territory owner has an advantage in any territorial dispute (e.g. Davies 1978, Beletsky and Orians 1987) and there is no reason to suppose that the situation differs among kittiwakes. The presence of young birds seeking to breed for the first time, as well as experienced birds seeking new sites or partners will ensure that there will always be competition for sites and partners when the breeding colony is reoccupied at the beginning of the breeding season. Pairing displays, including frequent copulations, may also be essential to bring the female into breeding condition as well as reinforcing the strength of the pair-bond, ensuring adequate within pair coordination throughout the breeding season, and may pay a role in paternity assurance.

Once a pair commenced incubation there were significant reductions in the percentage of time allocated to both pairing and aggressive displays and aggressive interactions were largely confined to immediate neighbours. At this stage the resident pair will have invested too much in the breeding attempt for a prospector to find it worth the effort needed to displace them. The very energetic and active displays prominent in the pre-laying behavioural repertoire may be inhibited by the presence of eggs, to minimise the risk of eggs being dislodged from the nest. Unlike ground-nesting gulls which will retrieve eggs displaced from the nest site (Tinbergen 1959) a dislodged egg means failure for the cliff nesting kittiwakes. Once chicks hatched there was a gradual increase in the time allocated to aggressive displays and the relative frequency of medium and long distance aggression increased. There was, however, no corresponding rise in the allocation of time to pairing displays. At nest sites where breeding attempts had failed, relatively large amounts of time were allocated to both pairing and aggressive displays, and the highest levels of aggression were recorded for intruders on nests during chick rearing. These results accord with those of Cadiou and Monnat (1996) as aggression presumably increased in response to an increasing incidence of prospecting in the latter stages of chick rearing, as residents acted to maintain their breeding sites for the subsequent breeding season.

The time allocated to maintenance behaviours was second to inactive behaviours, except during incubation, when a significant decrease was noted, presumably to minimise the risk of dislodging eggs. Kittiwakes allocated the same overall proportion of time to maintaining the integrity of the nest during incubation, as was allocated to building behaviours at the nest site, while after the eggs hatched nest maintenance ceased. Even within the time categorised as inactive there were patterns as time on the nest alert, as opposed to non-alert, increased once eggs were laid and remained high during chick rearing, when time on the nest non-alert decreased, suggesting that kittiwakes altered vigilance levels in response to perceived predation risks (Bednekoff and Lima 1998).

Although the pattern of change in time allocation was consistent, there were differences in the actual proportions of time allocated to some behaviours during some breeding stages. Most notable were differences in the time allocated to aggressive interactions during the pre-laying stage at Skomer in 1998 compared to Tyneside in 1996 and during chick rearing at Skomer in 1997 relative to 1998, while the time allocated to pairing behaviour remained fixed within apparently narrow limits. I interpreted these differences to reflect greater flexibility in the allocation of time to aggressive behaviours, relative to pairing behaviours, enabling pairs to respond to specific environmental circumstances such as density of nesting, considered in chapters 4 and 5.

The second part of my study was an investigation of the impact on breeding success of nesting density at the scale of the sub-colony and at the smaller scale of a cluster of interacting nests. As expected from previous work on kittiwakes (e.g. Coulson and White 1960, Falk and Møller 1997) there was association between denser nesting and enhanced breeding success, particularly at the scale of a loosely interacting cluster of nests. Positive association between nesting density and breeding success was not, however, consistently evident. At the Tyneside study sites high breeding success at sites where nest density was low, in comparison to the study sites at Skomer, may be attributed to factors, such as low predation intensity, associated with nesting in an urban environment. At the "natural" colony on Skomer less predictable factors, in this case variable predation intensity at the level of the sub-colony, appeared to over-ride the predicted trend, at least in small groups for short periods.

I then looked at interactions between aggressive and pairing behaviours, nesting density and breeding success. As I had found in chapter 3, time allocation to pairing behaviour appeared to be fixed while aggressive behaviour was more flexible. I found no indications that nesting density or differences in quality of the pair, measured as breeding success, influenced the time allocated to pairing behaviours. My results did, however, suggest that the time allocated to aggressive behaviour was influenced by both the quality of breeding birds and nesting density, at the scale of the immediate cluster and at sub-colony level. Aggression during the pre-laying and chick-rearing stages may therefore be a useful index of the quality of a pair of birds, when the effects of nesting density are controlled. Better quality birds and birds nesting at higher density allocated more time to aggressive behaviour during pre-laying and chick rearing. These trends were not, however, consistently apparent during the three breeding seasons included in the study, being obscured by variable predation pressure operating at the level of the sub-colony described in chapter 4. Differences in breeding success associated with proximity to failed neighbours could not be related to disturbance arising from the high levels of aggression observed at failed nests.

References

Altmann, J. 1974, Observational study of behaviour: sampling methods, Behaviour, 49, 227-267.

Andersson, M. 1976, Predation and kleptoparasitism by skuas in a Shetland seabird colony, Ibis, 118, 208-217.

Åström, M. 1993, Time allocation in canada geese during the breeding season, Ornis Fennica, 70, 89-95.

Barber, C. A. and Evans, R. M. 1995, Clutch-size manipulations in the yellow-headed blackbird: A test of the individual optimization hypothesis, Condor, 97, 352-360.

Barrett, R. T. and Runde, O. J. 1980, Growth and survival of nestling kittiwakes *Rissa tridactyla* in Norway, Ornis Scandinavica, 11, 228-235.

Bednekoff, P. A. and Lima, S. L. 1998, Randomness, chaos and confusion in the study of antipredator vigilance, Trends in Ecology and Evolution, 13, 284-287.

Beletsky, L. D. and Orians, G. H. 1987, Territoriality among male red-winged blackbirds: II Removal experiments and site dominance, Behavioural Ecology and Sociobiology, 20, 339-349.

Berg, S., Nilsson, G. and Bostrom, U. 1992, Predation on artificial wader nests on large and small bogs along a south-north gradient. Ornis Scandinavica, 23, 13-16.

Birkhead, T. R. 1977, The effect of habitat and density on breeding success in the common guillemot *(Uria aalge),* Journal of Animal Ecology, 46, 751-764.

Birkhead, T. R, Atkin, L. and Møller, A. P. 1987, Copulation behaviour of birds, Behaviour, 101, 101-138.

Boulinier, T. and Danchin, E. 1996, Population trends in kittiwake *Rissa tridactyla* colonies in relation to tick infestation, Ibis, 326-334.

Braun, B.M, and Hunt, G. I. 1983, Brood reduction in black-legged kittiwakes, The Auk, 100, 469-476.

Brown, R. G. B. 1967, Courtship Behaviour of the lesser black-backed gull *Larus fuscus*, Behaviour, 29, 122-153.

Brown, C. R. and Bomberger Brown, M. 1987, Group-living in cliff swallows as an advantage in avoiding predators, Behavioural Ecology and Sociobiology, 21: 97-107.

Brown, C. R. and Bomberger Brown, M. 2000, Nest spacing in relation to settlement time in colonial cliff swallows, Animal Behaviour, 59, 47-55.

Brunton, D. H. 1997, Impacts of predators: centre nests are less successful than edge nests in a large nesting colony of least terns, Condor, 99, 372-380.

Bunin, J. S. and Boates, J. S. 1994, Effects of nesting location on breeding success of arctic terns on Machias Seal Island, Canadian Journal of Zoology, 72, 1841-1847.

Burger, J. and Gochfeld, M. 1991, The Common Tern: It's breeding biology and social behaviour, Columbia University Press, New York.

Burger, J. and Gochfeld, M. 1996, Use of space by nesting black-billed gulls *Larus bulleri*: Behavioural changes during the Reproductive Cycle, Emu, 96: 73-80.

Cadiou, B. 1999, Attendance of breeders and prospectors reflects the quality of colonies in the Kittiwake *Rissa tridactyla*, Ibis, 141, 321-326.

Cadiou, B. and Monnat, J.-Y. 1996, Parental attendance and squatting in the kittiwake *Rissa tridactyla* during the rearing period, Bird Study, 43, 164-171.

Cadiou, B., Monnat, J. Y. and Danchin, E. 1994, Prospecting in the kittiwake, *Rissa tridactyla*: different behavioural patterns and the role of squatting in recruitment, Animal Behaviour, 47, 847-856.

Chardine, J. W. 1983, Aspects of the Breeding Behaviour of the Kittiwake *(Rissa tridactyla)* before egg-laying, unpublished Ph. D. thesis, University of Durham.

Chardine, J. W. 1986, Interference of copulation in a colony of marked black-legged kittiwakes, Canadian Journal of Zoology, 64, 1416-1421.

Clode, D. 1993, Colonially breeding seabirds: predators or prey? Trends in Ecology and Evolution, 8, 336-338.

Clutton-Brock, T. H. 1988, Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems, University of Chicago Press, Chicago.

Coulson, J. C. 1962, Kittiwake, in Bannerman, D. A, The Birds of the British Isles, Vol 11, Oliver and Boyd, Edinburgh.

Coulson, J. C. 1963, The status of the kittiwake in the British Isles, Bird Study, 10, 147-179.

Coulson, J. C. 1966, The influence of the pair-bond and age on the breeding biology of the kittiwake gull *Rissa tridactyla*, Journal of Animal Ecology, 35, 269-279.

Coulson, J. C. 1968, Differences in the quality of birds nesting in the centre and on the edges of a colony, Nature, 217, 478-9.

Coulson, J. C. 1978, A study of the factors influencing the duration of the pair-bond in the kittiwake gull *Rissa tridactyla*, Symposium on Biological Significance of the Pair-Bond.

Coulson, J.C. and Dixon, F. 1979, Colonial Breeding in Sea-birds, Biology and Systematics of Colonial Organisms, Larwood, G. and Rosen B. R. (Ed), Academic Press, London.

Coulson, J. C. and Johnson, M. P. 1993, The attendance and absence of adult kittiwakes *Rissa tridactyla* from the nest site during the chick stage, Ibis, 135, 372-378.

Coulson, J. C. and Thomas, C. 1983, Mate choice in the kittiwake gull, Mate Choice, Bateson (ed) Cambridge University Press.

Coulson, J. C. and Thomas, C. 1984, Differences in the breeding performance of individual kittiwake gulls, *Rissa tridactyla (L.),* Behavioural Ecology: Ecological Consequences of Adaptive Behaviour, Sibley, R. M. and Smith, R. H. (ed), Blackwell Scientific Publications, Oxford.

Coulson, J. C. and White, E. 1960, The effect of age and density of breeding birds on the time of breeding of the kittiwake *Rissa tridactyla,* Ibis, 102, 71-86.

Coulson, J. C. and White, E. 1961, An analysis of the factors influencing the clutch size of the kittiwake, Proceedings of the Zoological Society London, 136, 207-217

Coulson , J. C. and Wooller, R. D. 1976, Differential survival rates among breeding kittiwake gulls *Rissa tridactyla (L.),* Journal of Animal Ecology, 45, 205-213.

Coulson, J. C. and Wooller, R. D. 1984, Incubation under natural conditions in the kittiwake gull, *Rissa tridactyla,* Animal Behaviour, 32, 1204-1215.

Cramp, S. and Simmons, K. E. L. 1983, The Birds of the Western Palearctic Vol III, Oxford University Press, Oxford.

Cullen, E. 1957, Adaptation in the kittiwake to cliff nesting, Ibis, 99, 275-302.

Danchin, E. 1987, The Behaviour associated with the occupation of breeding site in the kittiwake gull *Rissa tridactyla*: the social status of landing birds, Animal Behaviour, 35, 81-93.

Danchin, E. 1988, Social interactions in kittiwake colonies: social facilitation and/or favourable social environment, Animal Behaviour, 36, 443-451.

Danchin, E., Boulinier, T. and Massot, M. 1998, Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality, Ecology, 79, 2415-2428.

Danchin, E. and Monnat, J. Y. 1992, Population dynamics modeling of two neighbouring kittiwake *Rissa tridactyla* colonies, Ardea, 80, 171-180.

Danchin, E. and Nelson, J. B. 1991, Behavioural adaptations to cliff nesting in the kittiwake *(Rissa tridactyla)*: Convergences with the gannet *(Sula bassana)* and the black noddy *(Anous tenuirostris),* Colonial Waterbirds, 14, 103-107.

Daniels, D. Heath, J. and Rawson, W. 1984, A declaration of intent in the kittiwake gull (*Rissa tridactyla*), Animal Behaviour, 32, 1151-1156.

Davies, N. B. 1978, Territorial defence in the speckled wood butterfly *(Pararge aegeria):* the resident always wins, Animal Behaviour, 26, 138-147.

Eberhardt, L. E. Books, G. G. Anthony, R. G. and Rickard, W. H. 1989, Activity budgets of canada geese during brood rearing, The Auk, 106, 218-224.

Fairweather, J.. A. 1994, A study of colonial organisation of the kittiwake *Rissa tridactyla*, Unpublished Ph. D. thesis, University of Durham.

Falk, K. and Møller, S. 1997, Breeding ecology of the fulmar *Fulmarus glacialis* and the kittiwake *Rissa tridactyla* in high-arctic northeastern Greenland, 1993, Ibis, 139, 270-281.

Fowler, J. Cohen, L. and Jarvis, P. 1990, Practical Statistics for Field Biology, Open University Press.

Francis, R. C. 1988, On the relationship between aggression and social dominance, Ethology, 78, 223-227.

Galbraith, H. 1983, The diet and feeding ecology of breeding kittiwakes *Rissa tridactyla,* Bird Study, 30, 109-120.

Hamer, K. C. Monaghan, P. Uttley, J. D. Walton, P. and Burns, M. D. 1993, The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland, Ibis, 135, 255-263.

Hamer, K. C. and Tuner, V. 1997, Productivity and nest attendance patterns of kittiwakes on Skomer following the Sea Empress oil spill, Unpublished Report to the Sea Empress Environmental Evaluation Committee, Dyfed Wildlife Trust and C. C. W.

Harris, M. P. 1980, Breeding performance of puffins *Fratercula arctica* in relation to nest density, laying date and year, Ibis, 122, 193-209.

Harris, M. P. and Wanless, S. 1990, Breeding success of British kittiwakes *Rissa tridactyla* in 1986-88: Evidence for changing conditions in the Northern North Sea, Journal of Applied Ecology, 27, 172-187.

Hunter, F. M. Burke, T. and Watts, S. E. 1992, Frequent copulation as a method of paternity assurance in the northern fulmar, Animal Behaviour, 44, 149-156.

Jacobsen, K. and Erikstad, K. E. 1995, An experimental study of the costs of reproduction in the kittiwake *Rissa tridactyla,* Ecology, 76, 1636-1642.

Krebs, J. R. and Davies, N. B. 1981, An Introduction to Behavioural Ecology, Blackwell Scientific Publications, Oxford.

Lack, D. 1966, Population Studies of Birds. Clarendon Press, Oxford.

Lack, D. 1968, Ecological Adaptations for Breeding in Birds, London, Methuen.

Nelson, J. B. 1967, Colonial and cliff nesting in the gannet compared with other *sulidae* and the kittiwake, Ardea, 55, 60-90.

Newton, I, (Ed), 1989, Lifetime Reproduction in Birds, Academic Press, London.

Palestis, B. G. and Burger, J. 1998, Evidence for social facilitation of preening in the common tern, Animal Behaviour, 56, 1107-1111.

Pearson, T. H. 1968, The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland, Journal of Animal Ecology, 37, 521-552.

Petrie, M. 1992, Copulation frequency in birds: why do females copulate more than once with the same male? Animal Behaviour, 44, 790-792.

Petrie, M. and Kempenaers, B. 1998, Extra-pair paternity in birds: explaining variation between species and populations, Trends in Ecology and Evolution, 13, 52-57.

Pierotti, R. 1981, Male and female parental roles in the western gull under different environmental conditions, The Auk, 98, 532-549.

Porter, J. M, 1985, Recruitment to the colony and other aspects of the biology of the kittiwake *(Rissa tridactyla (L.))* unpublished Ph. D. thesis, University of Durham.

Porter, J.M, 1990, Patterns of recruitment to the breeding group in the kittiwake *Rissa tridactyla,* Animal Behaviour, 40, 350-360.

Pöysä, H. 1994, Group foraging, distance to cover and vigilance in the teal, *Anas crecca*, Animal Behaviour, 48, 921-928.

Raven, S. J. 1997, Aspects of the ecology of gulls in the urban environment, unpublished Ph. D. thesis, University of Durham.

Regehr, H. M. and Montevecchi, W. A. 1997, Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species, Marine Ecology Progress Series, Vol 155, 249-260.

Roberts, G. 1996, Why individual vigilance declines as group size increases, Animal Behaviour, 51, 1077-1086.

Smith, J. N. M, 1981, Does high fecundity reduce survival in song sparrows? Evolution, 35, 1142-1148.

Spear, L. B. 1993, Dynamics and effect of western gulls feeding in a colony of guillemots and brandt's cormorants, Journal of Animal Ecology, 62, 399-414.

Stamp Dawkins, M. 1986, Unravelling animal behaviour, Longman.

Strowger, J. 1993, Aspects of the breeding biology of the kittiwake gull *Rissa tridactyla* at Marsden Bay, Tyne and Wear, unpublished M. Sc. thesis, Durham University.

Tasker, C. R. and Mills, J. A. 1981, A functional analysis of courtship feeding in the red-billed gull, *Larus novaehollandiae scopulinus,* Behaviour, 77, 221-241.

Thomas, C. 1980, Certain aspects of the breeding biology of the kittiwake *Rissa tridactyla*, unpublished Ph. D. thesis, University of Durham.

Thompson, K. R., Brindley, E. & Heubeck M., (1995) Seabird numbers and breeding success in Britain and Ireland 1995, UK Nature Conservation no. 20, JNCC.

Tinbergen, N. 1953, The Herring Gull's World, Collins, London.

Tinbergen, N. 1958, Curious Naturalists, Country Life Ltd. London.

Tinbergen, N. 1959, Comparative studies of the behaviour of gulls *(Laridae)*: a progress report. Behaviour, 15, 1-70.

Tinberben, N. 1972, The Animal in its World Vol. 1, Allen & Unwin, London.

van Vessem, J. and Draulans, D. 1986, The adaptive significance of colonial breeding in the gray heron *Ardea cinerea*: inter- and intra-colony variability in breeding success. Ornis Scandinavica, 17, 356-362.

Villarroel, M. Bird, D. M. and Kuhnlein, U. 1998, Copulatory behaviour and paternity in the American kestrel: the adaptive significance of frequent copulations, Animal Behaviour, 56, 289-299.

Walsh, P. M., Sim, I. & Heubeck, M., (1992) Seabird numbers and breeding success in Britain and Ireland 1992, UK Nature Conservation No.10, JNCC

Wanless, S. and Harris, M. P. 1992, Activity budgets, diet and breeding success of kittiwakes *Rissa tridactyla* on the Isle of May, Bird Study, 39, 145-154.