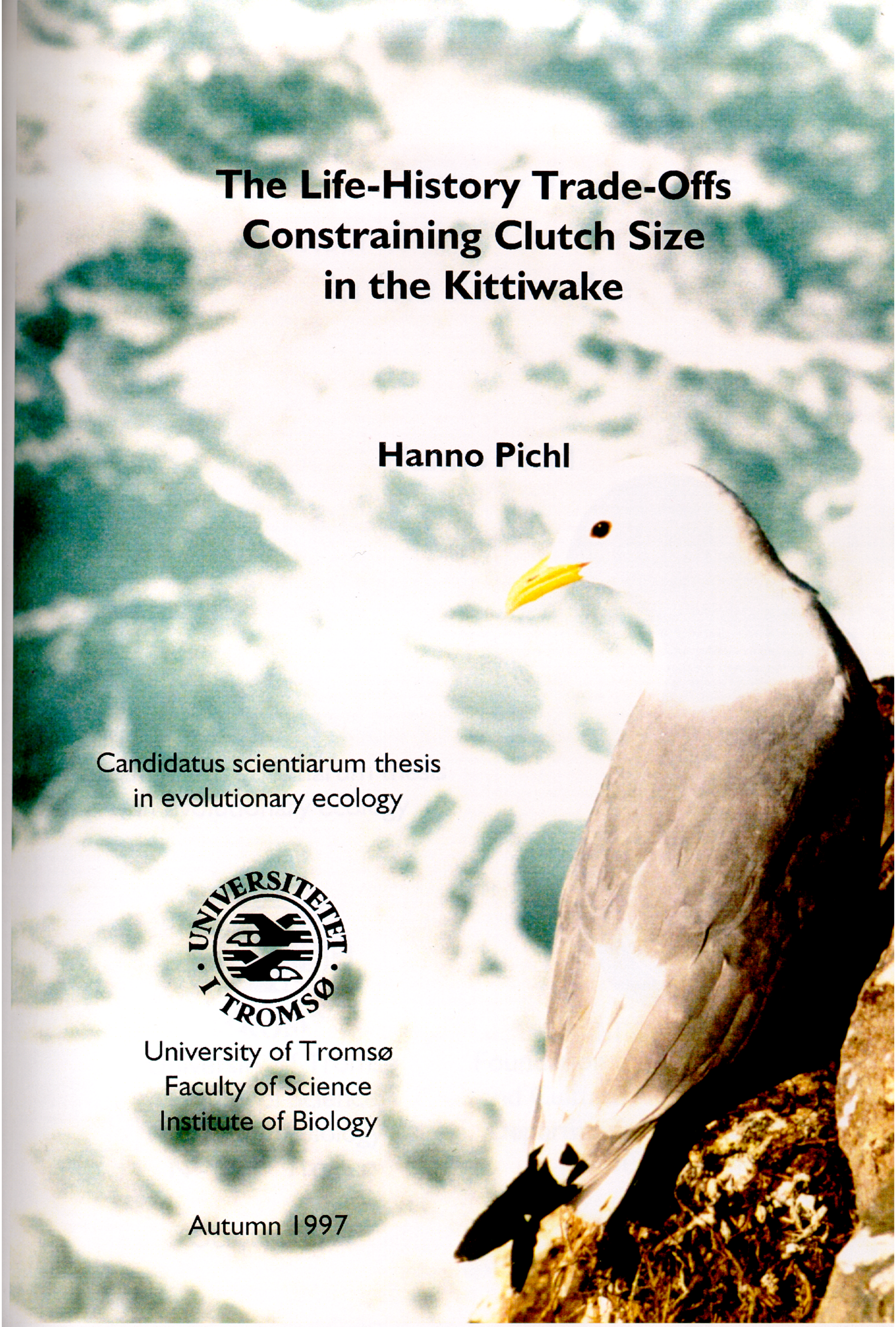

The Life-History Trade-Offs Constraining Clutch Size in the Kittiwake

Hanno Pichl

Candidatus scientiarum thesis
in evolutionary ecology

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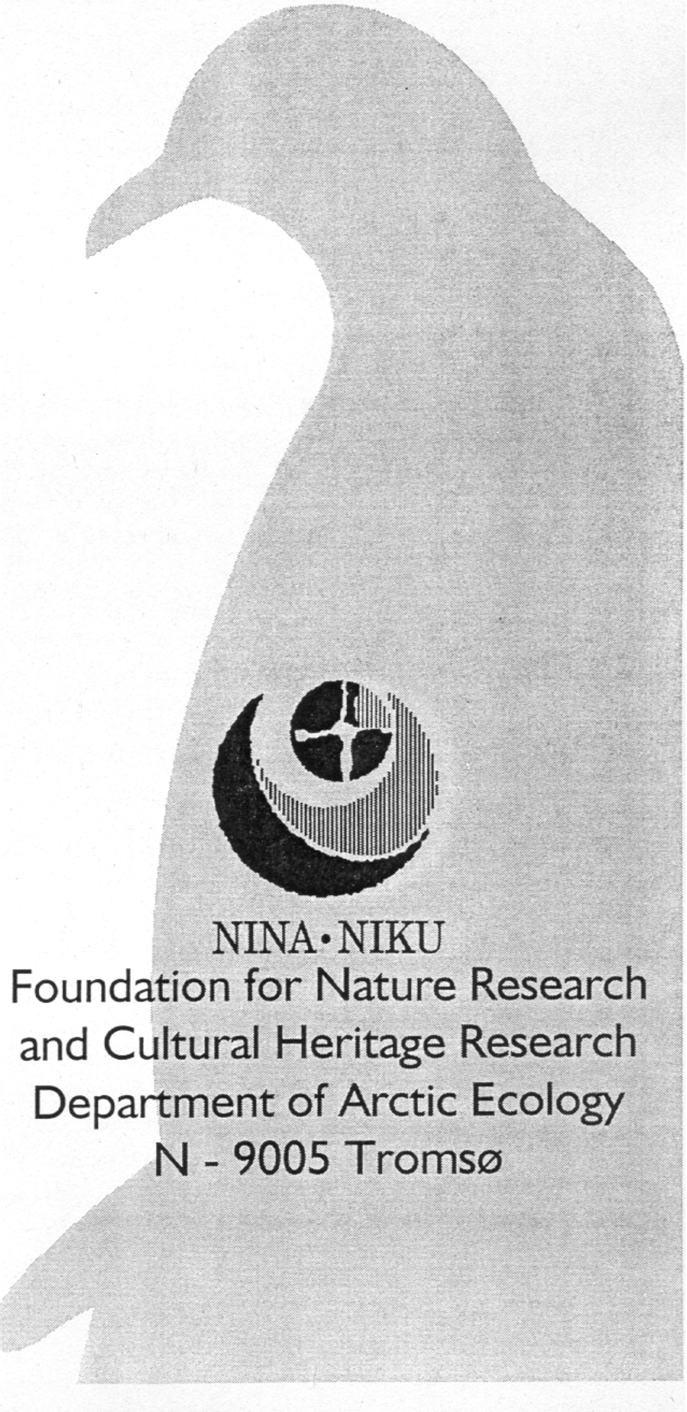

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Contents

A

Abstract

Pichl H (1997): The life-history trade-offs constraining clutch size in the Kittiwake. - University of Tromsø: Master thesis, Institute of Biology. 76 pages. Though the costs of reproduction in birds have recently received much attention, and many brood size manipulation experiments have been conducted, most of them have been restricted to short-lived species. I carried out a brood size manipulation of the Kittiwake, a seabird with an intermediate annual survival rate. Manipulation assigned experimentally enlarged (three chicks), reduced (one) and control broods (two) by random to a sample of 267 breeding pairs. The manipulated brood sizes were within the natural range of Kittiwake clutch sizes. Among the parameters recorded were proportion of nests losing young, age at chick loss, fledging success, and number of offspring produced; parental body mass, mass loss, and body condition early and late in the chick rearing period; re-sighting rate of adults in the following breeding season, frequency of mate and nest-site change; clutch sizes, egg volumes, hatching success and proportion of chick loss during the following breeding season. I found clear evidence of both inter- and intragenerational trade-offs within and between seasons: among others, fledgling weight of chicks and late body condition of female parents decreased with increasing brood size. Also fledging success decreased with increased brood size, but the Kittiwakes were nevertheless able to raise additional chicks. This did, however, not result in a significant relation between treatment and adult re-sighting rate in the following year. But hatching success, and frequency of chick losses and total breeding failure indicated the existence of costs of reproduction in the Kittiwake. I discuss these findings in relation to trade-offs and the optimal clutch size in the Kittiwake. Considering some model assumptions on chick recruitment and adult reproductive value, I come the conclusion that my findings cannot explain why the most common clutch size in Kittiwakes is two, rather than three eggs. I discuss further hypotheses which could explain the difference between the most common and the seeming optimal clutch size. As the stochastic environment Kittiwakes are adapted to can be responsible for that difference, I compare my findings with the results of a previous, very similar study which was carried out in the same colony. I can give some support to the hypothesis that responses to treatment should vary between years

KEYWORDS: Life history evolution, cost of reproduction, brood size manipulation, adult survival, offspring recruitment, *Rissa tridactyla*.

Sammendrag

Pichl H (1997): Livshistorie-karakterene som begrenser kullstørrelsen hos krykkje. - Universitetet i Tromsø: Cand scient-oppgave, Institutt for Biologi. 76 sider. Manipulering av kullstørrelse hos fugler har blitt en vanlig måte å estimere reproduktive kostnader på. De fleste manipuleringseksperimenter har imidlertid blitt gjennomført på kortlevende arter. Jeg gjennomførte et eksperimentelt studie på krykkje, en sjøfugl med en middels livstidslengde. Manipuleringen besto i å randomisere 267 krykkje-reir som inneholdt to egg. Etter klekking ble ungene byttet mellom forskjellige reir slik at noen reir fikk tre, noen to, og noen én unge(r). Disse manipulerte kullstørrelsene er innenfor de naturlige rammene for kullstørrelse hos krykkje. Jeg undersøkte en rekke livshistorie-karakterer både hos ungene og hos de voksne: hyppighet av og alder ved ungetap, antall og andel flygedyktige unger per reir, massen til ungene; masse, massetap og kondisjon til foreldrene både tidlig og sent i hekketiden; gjensynsrate av voksne året etter, samt deres reproduktive suksess i året etter. Jeg fant tydelige tegn på "avveininger" ("trade-offs"): Vekt sent i sesongen av både unger og voksne var lavere jo større kullet hadde vært. Færre unger overlevde til flygedyktighet hvis kullstørrelsen hadde blitt økt. Likevel klarte krykkjene å fostre opp flere unger enn den "planlagte" kullstørrelsen. Dette førte imidlertid ikke til redusert returneringsrate til neste hekkesesong. Men jeg fant andre tegn på reproduktive kostnader, bla hadde hunner i begynnelsen av den neste sesongen fortsatt en lavere kroppskondisjon hvis de hadde økt kullstørrelse året før, klekkesuksessen minket med økende kullstørrelse, og sannsynligheten for ungetap økte. Jeg diskuterer disse resultatene i henhold til trade-offs og den optimale kullstørrelsen til krykkje. Med hjelp av forskjellige modeller om ungenes rekrutteringssjanser og de voksnes reproduktive verdi (reproductive value), konkluderer jeg med at de karakterene jeg undersøkte ikke kan forklare kullstørrelsen. Blant de grunnene som kan føre til dette avviket, diskuterer jeg det stokastiske miljøet som krykkjene hekker i som en mulig årsak. Dette utsagnet støtter jeg på en sammenlignelse med et tidligere studium gjennomført i samme koloni. Jeg kan dermed støtte hypotesen at krykkjenes respons til kullstørrelsesmanipulering varierer mellom år.

Z

Zusammenfassung

Pichl H (1997): Die Begrenzung der Gelegegröße durch Faktoren der Lebensgeschichte bei der Dreizehenmöwe. - Universität Tromsø: Diplomarbeit, Institut für Biologie. 76 Seiten. Vögel sind ein beliebtes Objekt der Evolutionsökologie, da sich ihre Lebensgeschichte (life history) über Manipulation der Gelegegröße leicht experimentell erforschen läßt. Der Schwerpunkt der Forschung hat aber bisher auf kurzlebigen Arten gelegen. Ich führte eine Studie an der Dreizehenmöwe durch, einem Seevogel mit mittlerer Lebenserwartung. Das Experiment bestand aus dem randomisierten Austausch von Jungen nach dem Schlüpfen, so daß Brutpaare, die zwei Eier gelegt hatten, mit Brutgrößen von ein bis drei Jungen konfrontiert wurden. Diese Brutgrößen kommen auch natürlich bei der Dreizehenmöwe vor. Ich studierte im Verlauf der weiteren Brutsaison und des darauffolgenden Frühjahres eine Reihe von Lebensgeschichts-Merkmalen: Anzahl der flüggen Jungen pro Nest sowie deren Masse, Ausmaß und Zeitpunkt von Brutverlusten; Masseverlust und Kondition der Eltern; die Quote der wiedergesehenen Vögel im darauffolgenden Jahr und ihr Bruterfolg dieses Jahres, d. h. die Gelegegröße, das Eivolumen, die Schlüpfquote und die Häufigkeit von Brutverlusten. Es zeigte sich, daß sowohl innerhalb als auch zwischen Generationen und Saisonen "Abwägungen" (trade-offs) stattfanden: Mit zunehmender Gelegegröße nahm die Masse der Jungen ab, ebenso Masse und Kondition der Eltern. Letzteres wirkte sich nicht auf die Wiedersehenswahrscheinlichkeit aus. Es gab jedoch andere, klare Anzeichen von Vermehrungskosten: Der Schlupferfolg des darauffolgenden Jahres und die Überlebenswahrscheinlichkeit der Jungen waren reduziert, wenn die Eltern im Vorjahr vergrößerte Gelege bebrütet hatten. Ähnliche Effekte sind bisher weitgehend nur von kurzlebigen Arten beschrieben. Ich diskutiere diese Erkenntnisse daher im Lichte der "Lebensgeschichts-Evolution" und des Begriffs der optimales Gelegegröße. Dabei nehme ich insbesondere Rücksicht auf die Rekrutierung von Jungen in Abhängigkeit von ihrer Masse und auf den "Fortpflanzungswert" (reproductive value) von Adulten. Ich komme zu dem Schluß, daß die von mir erhobenen Parameter nicht erklären können, warum Gelege mit drei Eiern nicht häufiger vorkommen. Von den verschiedenen Hypothesen, die ich zur Erklärung dieses Widerspruchs anführe, gehe ich besonders auf die Stochastizität der Umweltbedingungen ein, an die Dreizehenmöwen angepaßt sind. Anhand des Vergleichs mit einer älteren, sehr ähnlichen Studie kann ich die Hypothese unterstützen, daß langlebige Arten in variablen Umwelten sehr unterschiedlich auf Manipulationen der Brutgröße reagieren.

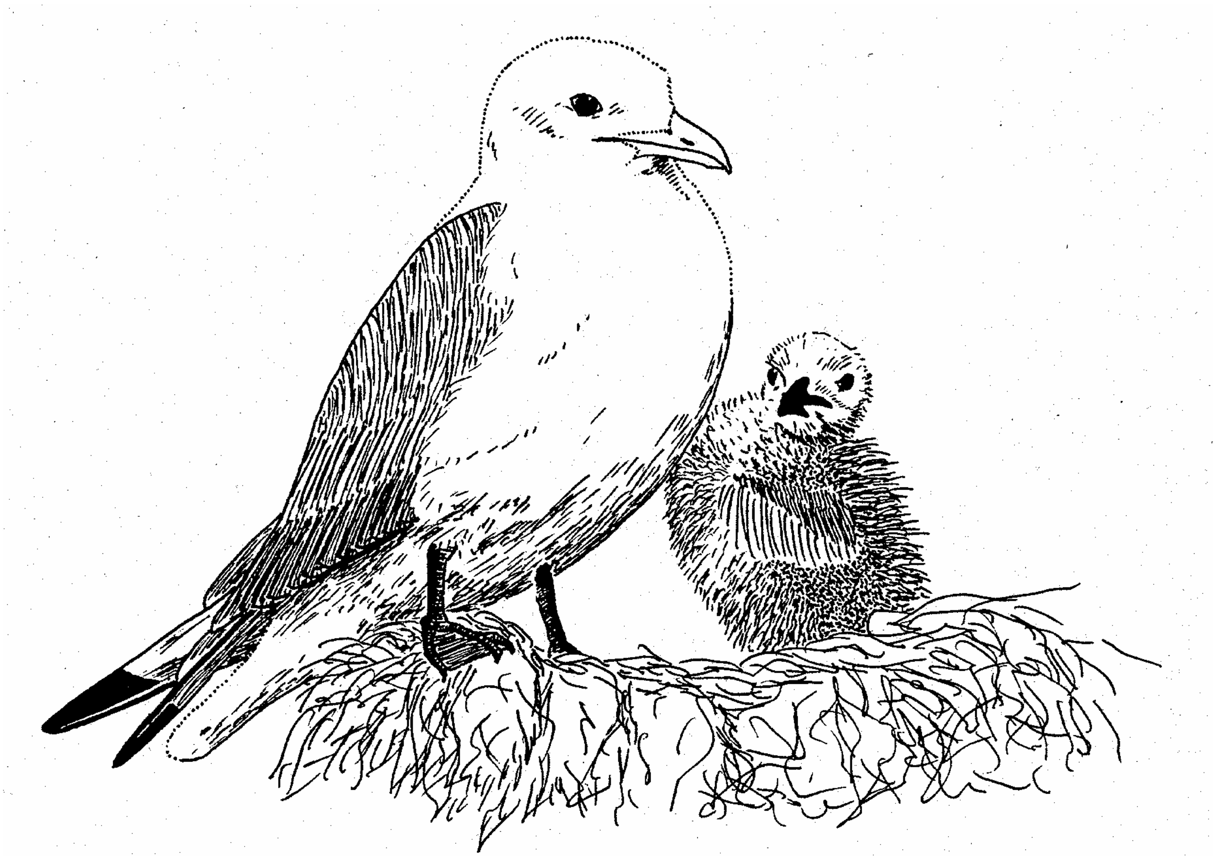


Figure 1: Adult Kittiwake and chick at the nest.

Figure 2: Kittiwake cliff on Hornøya. This picture illustrates how Kitiwake nests are situated, and shows the metal number pins that I used for marking nests, the colour rings that I used for identifying birds, and some birds that were dyed at their heads to avoid double catching. Chicks are younger than one week.

1

Introduction

Why does the Kittiwake lay two eggs per year? Why doesn't it lay a dozen like the Great Tit or some millions per day like tapeworms? Questions like this are addressed by life-history theory. As in evolutionary ecology generally (Maynard Smith, 1978; Grafen, 1991; but see Stearns, 1980), in life-history theory the adaptedness of organisms is not the hypothesis to be tested; instead, it is considered the premise on the basis of which one is able to assess the contribution of a given trait or behaviour to fitness.

In the case of clutch size in birds, this approach was first taken by Lack (1947) who suggested that parental fitness should be maximized not by the largest possible clutch size, but, as a consequence of past selection, by the most common one. A clutch size below the optimum would fledge fewer chicks simply because of fewer hatchlings; and a clutch size above the optimum would fledge fewer chicks "through the inability of the parents to get enough food for their young, so that some or all of them die before or soon after fledging, with the result that few or no descendants are left with their parent's propensity to lay a larger clutch" (p. 319).

The number of fledglings, the only parameter considered by Lack, is, however, merely one of several traits that are important for an organism's life-history. Others are size and sex ratio of offspring, age and size at maturity, frequency of reproductive events, and duration of the reproductive life span (Stearns, 1992). Life-history theory predicts that not all of these traits can be maximized simultaneously, or, as Reznick (1985) put it: "To be best in all possible worlds is not biologically possible; to be well adapted to even one world requires compromise. Theoretical studies of life history evolution embody such compromises as 'tradeoffs' between life history variables." (p. 258). Trade-offs, i.e. negative relations between two traits, occur when "a change in one trait that increases fitness is linked to a change in another trait that decreases fitness" (microevolutionary trade-offs sensu Stearns, 1992: 75).

The mechanism constraining clutch size according to Lack (1947), is simply a trade-off between clutch size and survival of offspring to fledging. The optimal clutch size predicted on the basis of this trade-off is called the Lack clutch. However, many studies have shown that the most productive clutch size is larger than the most common one. For instance, in 46 of 66 studies reviewed by Ydenberg & Bertram (1989), Dijkstra et al. (1990) and VanderWerf (1992), addition of eggs or chicks to the median clutch or brood size increased the number of fledglings raised. This evidence falsified Lack's hypothesis as it indicated that decreasing chick survival does not necessarily outweigh chick addition.

One reason is that Lack's "most productive clutch size" does not consider offspring fitness, but only the offspring's chances of survival until fledging. This view ignores long-lasting costs to fitness of, e.g., low weight at fledging (Charnov & Skinner, 1984). In general life history evolution, "Lack's solution clutch size" is, therefore, used in a different meaning (Godfray, 1987), depicting the "clutch which maximizes the number of offspring surviving to adulthood" (Charnov & Skinner, 1984: 8).

The falsification of Lack's hypothesis was further in accordance with predictions made by Williams (1966) on theoretical grounds. He argued that parental traits also could influence the optimal clutch size because current parental effort should at any given time be balanced against the residual reproductive value. An organism's fitness depends, in other (here, Bell, 1980's: 45) words, "not only on the total quantity of reproduction, but also on the distribution of this reproduction through the life history, a set of data which is usually summarized in the form of a life table" (cf. tab. A1).

Both of these trade-offs, the intergenerational one of clutch size versus offspring fitness, and the intraindividual one of clutch size versus future reproduction or survival, result in a smaller than expected optimal clutch size. The latter of these trade-offs is also called the "cost of reproduction" (Bell, 1980; Reznick, 1985).

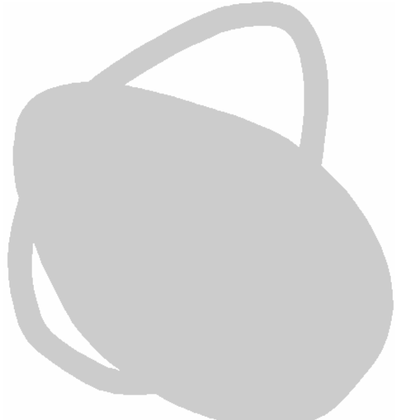
Manipulation experiments are good tools to use when investigating the mechanisms constraining clutch size (Bell & Koufopanou, 1986; Partridge & Harvey, 1985, 1988; Gustafsson & Sutherland, 1988; but Reznick, 1985). A large number of clutch/brood size manipulation experiments has been conducted (reviewed by Lindén & Møller, 1989, Ydenberg & Bertram, 1989, Dijkstra et al., 1990, and VanderWerf, 1992), but most of them involved short-lived Passeriformes. In these species, the probability that an individual will survive between two breeding seasons is often so low that a large investment in the current breeding attempt will be expected. It was already predicted by Williams (1966) that especially species with low annual mortality rates will show a low reproductive effort in a given season, compared to the effort which would maximize reproduction for that season. Later, also Goodman (1974), Charlesworth (1980) and Wooller, Bradley & Croxall (1992) pointed out that a negative impact of current reproduction on future survival will have the greatest consequences for the optimal clutch size in long-lived species. On the other hand, long-lived species with a phylogenetically fixed clutch size of one, such as Procellariiformes, will not be expected to respond readily to changes in offspring demands because even a small reduction in adult survival rate will have great consequences for the lifetime reproductive success (Ricklefs & Minot, 1991). That is why species with intermediate adult survival are especially suited to document survival costs of clutch size enlargements (Jacobsen, Erikstad & Sæther, 1995).

In this study, I performed an experiment very similar to the one carried out earlier by Jacobsen (1993). The brood size of Kittiwakes (*Rissa tridactyla*) in a stable population was manipulated within the natural range of brood sizes. The primary goal was to estimate parameters of future reproduction that have not been examined before. It has recently been claimed that long-lived seabirds should respond differently to brood-size manipulations in different years (Erikstad et al., in press). The second goal of this study was, therefore, to find whether results in Kittiwakes can support this hypothesis.

In particular, the questions investigated and hypotheses tested by this study are:

- Is there a trade-off between clutch size and offspring survival?
  Prediction: the relation between manipulated brood size and number of offspring surviving to fledging is negative.
- Is there a trade-off between number and quality of offspring?
  Prediction: the relation between manipulated brood size and fledgling mass is negative.
- Is there a trade-off between reproduction and parental state?
  Prediction: the relation between manipulated brood size and adult mass loss during the breeding period is positive, but negative between manipulated brood size and late adult body condition.
- Is there a trade-off between reproduction and adult return rate?
  Prediction: the relation between manipulated brood size and adult return rates in the following breeding season is negative.
- Is there a trade-off between current and future reproduction?
  Prediction: birds have poorer breeding performance the larger broods they had reared in the previous year. Poor breeding performance will be indicated by one or more of the following parameters: low pair-bond stability, nest-site fidelity, clutch size, egg volume, and/or hatching success; late laying date; large hatching asynchrony.
- Are there differences between this study and the ones of Jacobsen (1993), and if so, can these differences be explained by a variation of breeding conditions between years?
  Prediction: In a year where breeding conditions lay just above the breeding threshold, both breeding performance and survival will be relatively poor; both will be better in a better year; in a year where breeding conditions lie beneath the breeding threshold, reproductive output will be zero, while survival is high.

I will use the data obtained to calculate whether they can explain why two-egg clutches are the most common ones in the Kittiwake.



Material & methods

2

2.1 Subject & study site

The Kittiwake

The Black-legged Kittiwake *Rissa tridactyla* (L), Aves: Laridae, is a holarctic, cliff-nesting seabird (fig. 1 & 2). It is found on both sides of the Atlantic Ocean, as far east as Novaya Zemlya, and in the northern Pacific Ocean. Kittiwakes feed on pelagic animals and spread across the whole North Atlantic or Pacific, respectively, after breeding (Coulson, 1966b).

The most extensive studies on the Kittiwake stem from Great Britain (references in tab. 1). Their results cannot simply be transferred to Kittiwakes breeding farther north, because both birds and eggs are larger and heavier towards the north of their range (Bergman's rule; Coulson, 1963a; Barrett et al., 1985). Furthermore, day-night rhythms that are well-known in the Kittiwake from other colonies (Coulson & Wooller, 1984; Coulson & Johnson, 1993), are not as obvious under the constant light conditions within the Arctic Circle (Furness & Barrett, 1985; M. Jansson, pers. comm.). Also onset of breeding, clutch size, breeding success, and other life-history traits are not directly comparable as both mean values and variation between years differ between British and Norwegian colonies (Coulson & White, 1961; Barrett & Runde, 1980). This can be illustrated with the survey in table 1 (see also tab. A1, p. 59).

Data from North Norway are included, where available. The British data can be supplied with further results: Clutches increase in size with breeding

Table 1: Life history traits in the Kittiwake. The column "North Shields" refers to the data obtained at the Kittiwake colony at North Shields, Great Britain, by Coulson and co-workers. Data from North Norway come from the Kittiwake colonies at Hekkingen, Hornøya, and Runneskholmen by Barrett and co-workers.

Trait	North Shields	North Norway	Sources
Clutch size (c/1 : c/2 : c/3)	9 : 73 : 18	24 : 70 : 6	Coulson & White (1961); Barrett (1978)
Hatching success	67 %	54 %	Coulson & Thomas (1984); Barrett (1978)
Fledging success	88 %	59 %	Coulson & Thomas (1984); Barrett & Runde (1980)
Age at first breeding, ♀	5.1 a	–	Wooller & Coulson (1977)
Age at first breeding, ♂	4.7 a	–	Wooller & Coulson (1977)
Intermittent breeding[a], ♀	5 %	–	Wooller & Coulson (1977)
Intermittent breeding[a], ♂	2 %	–	Wooller & Coulson (1977)
Annual survival, ♀	82 %	90 %	Aebischer & Coulson (1990); Erikstad et al. (1995)
Annual survival, ♂	78 %	94 %	Aebischer & Coulson (1990); Erikstad et al. (1995)

[a] among birds with at least 1 year breeding experience

experience from 1.8 to 2.2 eggs (Thomas, 1983). Hatching success increases also for the first c. 5 years of breeding life from 56 % to 74 %, and then decreases for the rest of the life span down to 67 % (Coulson & Thomas, 1985a). Fledging success is, in contrast, relatively constant. Intermittent breeding occurrs mainly among new breeders, 29 % in females and 19 % in males, whilst the lower values in table 1 apply to more experienced birds (Wooller & Coulson, 1977). Annual survival shows a decrease of 11% after 12 years of breeding experience (Aebischer & Coulson, 1990).

As this thesis studies experimentally the life-history traits constraining the clutch size in the Kittiwake, it is important to have a closer look at which factors have been found by observational studies to influence clutch size in natural populations (Coulson & White, 1961): (1) an *individual component*, as variation in clutch size between years is smaller in individuals than in the whole population; (2) *breeding experience*, as older birds tend to lay larger clutches; and (3) *laying date*, as there is a seasonal decline in clutch size, also after controlling for breeding experience. All these factors are, however, controlled for by randomizing the manipulation (see pp. 12 and 65 for further details).

Study site

The experiment was carried out on the island of Hornøya on the south coast of the Barents Sea. Hornøya is situated off Vardø in eastern Finnmark, Norway (70° 22' N, 31° 10' E). The climate is arctic, that means only three months have a mean temperature of more than 5°C; no monthly mean is above 10°C (Schulz, 1995). The island has an area of c. 900 m · 650 m. It consists of sandstone and shale which form cliffs at its north and west face. In the area of the breeding colony that was used for this study, the cliff is divided into single terraces that are between 5 m and 10 m high; thus many Kittiwake nests are easily accessible (fig. 2). The study area covered about 100 m · 50 m on the north-west part of Hornøya.

Hornøya and the neighbouring island of Reinøya are protected as a nature reserve, and the seabird populations have been monitored annually since 1980 (Lorentsen, 1990; Anker-Nilssen, Erikstad & Lorentsen, 1996). The Kittiwake population was estimated to 23,000 breeding pairs in 1983 (Furness & Barrett, 1985). Since then, the population has been relatively stable (Anker-Nilssen et al., 1996; R. Barrett, pers. comm.).

Other species breeding on Hornøya and potential predators on Kittiwake eggs, chicks and partly adults are Herring Gulls *Larus argentatus*, Great Black-backed Gulls *L. marinus*, and some Common Ravens *Corvus corax* (Barrett & Runde, 1980; Burger & Gochfeld, 1984; Maccarone, 1992; pers obs). Additionally, Gyr Falcons *Falco rusticolus* are regularly visiting Hornøya and are known to prey upon Kittiwakes (R. Barrett, pers. comm.).

The Barents Sea is one of the most productive seas in the world (Sakshaug et al., 1994), and along its coast are some of the largest seabird colonies in the North Atlantic (Norderhaug, Brun & Møllen, 1977). Kittiwake diet at Hornøya is mainly capelin *Mallotus villosus* (Furness & Barrett, 1985), but in recent years, the proportion of herring *Clupea harengus* in diet has been larger (Barrett & Krasnov, 1996) and constituted about 68 % of Kittiwake diet in 1995 (R. Barrett, pers. comm.).

Timing of the study

The study took place between 21 June and 25 July 1995. This encompassed the main hatching period, and it terminated shortly before fledging of the first chicks.

In 1996, Hornøya was visited in the beginning of May in order to record the return rate of adults (see below). At that time, the adults had not begun incubating, so their colour rings were readily visible (Harris & Calladine, 1993). An additional trip was made in mid June 1996, to record clutch sizes, egg volumes and hatching dates.

2.2 Treatment

Marking nests

At the beginning of the first field season, 267 nests were marked with numbered metal pins (fig. 2). Only nests with two eggs were chosen, and all such nests in this part of the island that were easily accessible were included into the sample. At the end of the breeding season, photographs were taken of all breeding sites to enable me to identify nests the following year.

Manipulation of brood size

Within the first 3 days after hatching of a nest's second chick, clutch sizes were manipulated by exchanging chicks between nests (tab. 2). To do this, nests were randomized, assigning them with the same probability to one of three categories: "reduced", "control", and "enlarged". The treatment, as summarized in table 2, resulted thus in manipulated brood sizes of 1 chick, 2 and 3 chicks, respectively.

Randomization included primarily all nests that hatched 2 days before the respective day of manipulation. When randomization resulted in an odd number of nests – i.e. number of "reduced" nests ≠ number of "enlarged" nests, or number of "control" nests was not even –, additional nests were used; these were chosen at random from the sample of nests that hatched 1 day before the respective day of manipulation. The latter nests were excluded from randomization and manipulation on the next day. Nests that were preyed upon before manipulation were excluded from the sample.

Table 2: Experimental treatment of the nests. The three categories used in the experiment with the respective brood sizes after manipulation (number of chicks). Brood size prior to manipulation was 2 chicks for all categories.

Category	Manipulated brood size	Treatment
"Reduced"	1	One chick removed to a an "enlarged" nest
"Control"	2	One chick exchanged with another "control" nest
"Enlarged"	3	One chick added from a "reduced" nest

As chick movements between nests are quite common (Pierotti & Murphy, 1987; Roberts & Hatch, 1994; pers obs), especially when nests are grouped on larger ledges, neighbouring nests had to be isolated. This was done using small planks, erected in such a way that they functioned as fence between nests.

2.3 Field measurements & observations

Offspring production and quality

When all nests were marked, they were checked for hatching and chick loss once a day. This way, every chick loss and hatching date were recorded during the entire observation period. The hatching date of the second (= last) chick of a nest was defined as the nest's hatching date.

Kittiwake chicks can fly at an age of less than 5 weeks (Maunder & Threlfall, 1972). The experiment was terminated some days before the first chicks were able to fly. This procedure avoided investigator-caused loss of chicks caused by premature flight from the nest. On the other hand, the youngest chicks were then only about 3 weeks old. To ensure a uniform measure of production, the number of chicks per nest 18 days after the nest's hatching date was defined as the respective nest's production of offspring.

Chicks were weighed twice, 9 days and 18 days after hatching of the nest's second chick. Weighing was carried out during the nest checking round with a 300g- or 500g-capacity Pesola® spring balance to the nearest gram.

Parental state

Within 2 days of manipulation, i.e. 1 to 5 days after hatching of the nest's second chick, both parents were caught. The birds were then
– ringed with both a numbered stainless steel ring and an individual combination of five additional coloured PVC rings (fig. 2; Coulson, 1963b) unless they had been ringed before,
– measured: the skull length (head + bill) was measured with a specially adapted calliper (fig. 3) as described by Coulson et al. (1983) to the nearest 0.5 millimetres,
– weighed with a 500g- or 1,000g-capacity Pesola® spring balance to the nearest gram, and
– dyed with Penol® permanent ink on the top of the head (fig. 2) to avoid double catching of the adults.

During ringing and weighing, the birds were kept in textile bags to keep them calm and to avoid injuries of both parts involved.

The adults were caught a second time 18 days later, i.e. 19 – 23 days after hatching of the nest's second chick. Then, they were only weighed and dyed.

Adults were usually caught using a 6 m noose pole (fig. 4). This method was least dangerous to the birds, but was not always successful, especially during the second weighing session, when birds became increasingly difficult to catch. Another method was then used and consisted of a perlon® snare, joined to a c. 20 m long thin cord. The snare was attached to the nest, and when the bird returned to the nest, it was caught by entangling its feet. Finally, a third method was used for the most stubborn birds, a trap con-

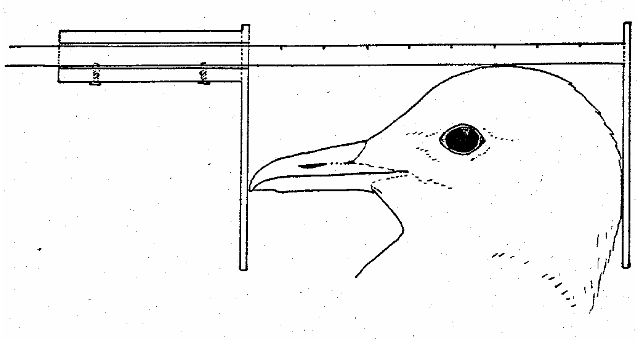


Figure 3: Tool designed for measuring head + bill length as described by Coulson et al. (1983). Scale 1:2.

sisting of a wire construction with four to six perlon® nooses that could be fixed above the nests (fig. 4). The bird was caught as its head entered one of the nooses.

Adult nest attendance was observed in the period from 29 June until 16 July. One observation consisted of a "snap shot" of the colony where I recorded whether nests were attended by no, one or two adult(s). Two such observations were made each day, one in the morning between 9 and 11 a.m., before research activity in the colony had started, and one in the evening at about 7 to 9 p.m. Observations included only nests which contained the complete manipulated brood size, i.e. nests that lost chicks are not considered. One observation round lasted c. 30 to 60 minutes.

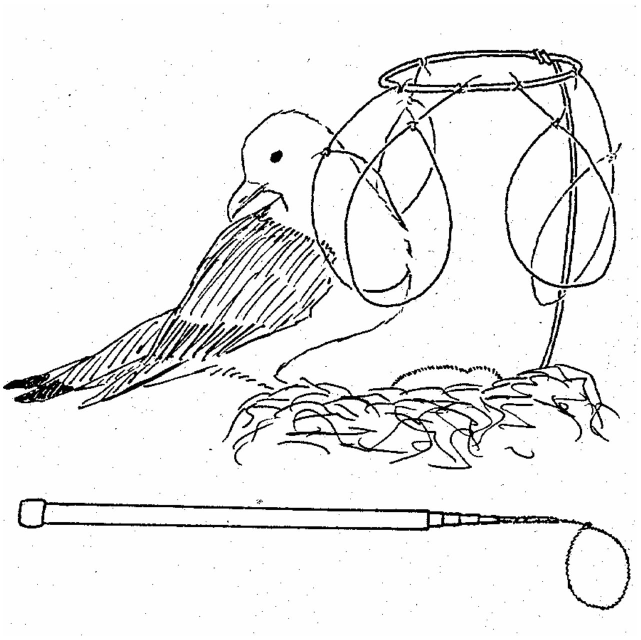


Figure 4: Tools for catching Kittiwakes. The trap (top; with a suspicuous bird) was fixed above the nests (scale 1:5). The noose-pole was used more often (bottom), total length was 6 m (scale 1:10)

Future reproduction

In 1996, the re-sighting rate of the adults from the 1995 season was recorded. Many birds were caught; in addition, the Hornøya colony was regularly searched using 10 × 40 binoculars, recording all colour-ringed Kittiwakes observed. It was thus possible to document changing of nest sites and/or mate change ("divorce rate") of the Kittiwakes.

Also clutch sizes of the sample nests used the previous year were recorded. As predation and re-laying caused some variation in clutch size, the day with the first hatched chick in the colony (18 June) was used as a fixed day for recording clutch sizes. Additionally, egg volume was estimated by measuring egg length and egg width (diameter). Measuring was carried out with a Maub® calliper to the nearest 0.1 mm. Furthermore, hatching dates of all eggs were recorded, and, for the majority of the nests (broods of 2 chicks), also date of chick loss.

2.4 Data processing

Correction and preparation of field data

Some raw data were processed before performing calculations:

- All adults were sexed, and all adult measurements were calculated for females and males separately. Sexing was based on head + bill (skull) length (Coulson et al., 1983), assuming that, within a breeding pair, the bird with larger head + bill length was the male. This method would, due to data from Hornøya (Barrett et al., 1985), sex c. 98 % of the birds correctly (app. B). Some personal observations of copulating birds – though too few (*n* = 3) to test the method statistically – agreed with this method of sexing. In cases of doubt (difference in skull length < 2 mm; 10 of 142 pairs), mass was also considered. In all cases, the larger birds were heavier, and thus treated as males. One pair with identical skull lengths was excluded from the sample. When only one bird of a breeding pair was caught, it could in some cases (3 of 10) be identified, assuming that birds with a skull length of more then 94 mm (2 mm more than the largest female skull in the sample) must be males; otherwise it was excluded from the sample.

- Mass loss was corrected for the differences in the time between the first and second weighing (see tab. 3).
- Body condition was calculated from body masses and skull lengths. Because of the allometric nature of the variables (Cates & Gittleman, 1997) and because logarithms are generally suited for linearizing ratios (Johnson et al., 1985), both measures were log-transformed. Then, the regression was calculated using least squares, and any bird's condition was defined as the residual from that regression. Calculations were made separately for females and males, and for early (1995 and 1996) and late (1995 only) body masses (see app. B). In every calculation, all birds with known body mass and skull length were used in order to get the largest possible sample size; i.e. even birds that were excluded from other calculations – e.g. birds that did not breed for at least twelve days –, were included in the calculation of the regression. Figure 5 shows one of the six regressions calculated.
- As just mentioned, some calculations were not carried out with all birds. This applied to calculations of late body mass, mass loss, re-sighting rate etc. For these parameters, only birds that maintained their manipulated

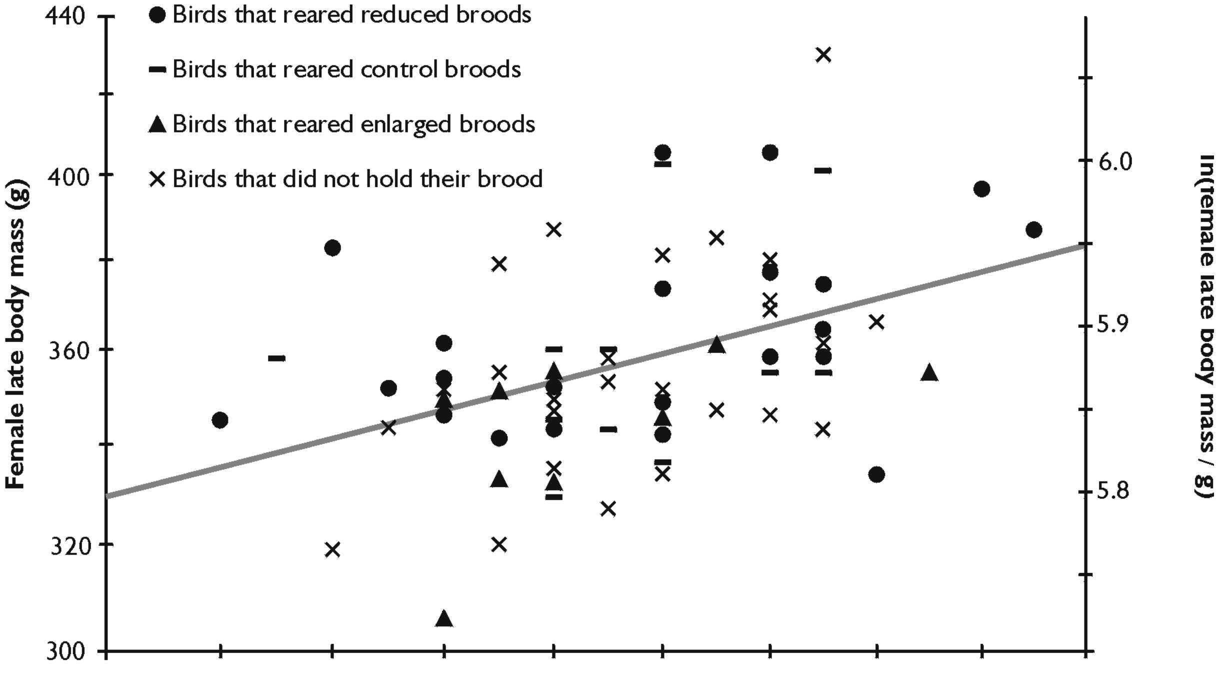


Figure 5: Regression between head + bill length and body mass in Kittiwakes. Exemplified for late female body mass. Note that the x-axis and the left y-axis are logarithmically scaled. The right y-axis gives the natural logarithms of the left y-axis. The grey line shows the regression line ($r^2=0.14$; slope, $p<0.001$; for complete statistics, see app. B). A bird's body condition was calculated as residual from the regression line, i.e. as the distance of the bird's point in this figure from the regression line, as measured in units from the right y-axis and expressed in per thousands (‰).

clutch sizes for at least 12 days were used in comparisons. The parameters affected by such exclusions are all specially marked in table 3.

- A bird was considered re-sighted when its colour rings were recorded during at least two different checking rounds (see app. C for details, p. 69). This procedure resulted in two birds that were not considered re-sighted in spite of observing them once. In the result chapter, both possibilities are considered for these two birds.
- Egg volumes were calculated using Coulson's (1963a) formula

  $$V = k \cdot b^2 \cdot l \qquad \text{(eqn. 1)}$$

  with k, constant factor (0.4861; Runde & Barrett, 1981); b, egg breadth; l, egg length.

Table 3 summarizes the different parameters used in this study; they were either directly recorded or calculated from recorded data. The expression "parental state" will be used to refer to the two state-dependent measures recorded, i.e. adult body mass and adult body condition as defined in table 3.

Statistics

All statistical tests were carried out with SAS® software (SAS Institute, 1989a). Analyses of variance (ANOVA) and covariance (ANCOVA) were calculated with PROC GLM, based on type `III` sum of squares, because all samples were unbalanced, and PROC GLM is to be preferred to PROC ANOVA under these conditions (SAS Institute, 1989b). In one case, I used PROC GLM with linear contrast to test differences by an ordered null hypothesis, i.e. by the underlying assumption that: body condition for "reduced" birds > condition for "control" > condition for "enlarged" ones.

According to Bortz & Lienert (1990), parametric tests (such as ANOVA) are robust enough to tolerate violation of one precondition. But when more conditions were violated, e.g. when the data were neither normally distributed nor cardinally scaled (checked graphically), I used a nonparametric test (χ^2-approximation to Kruskal-Wallis, PROC NPAR1WAY WILCOXON). Differences in frequency distributions were tested using Kolmogorov-Smirnov tests (PROC NPAR1WAY EDF).

Binary responses were analysed with maximum likelihood estimates of logistic regressions, i.e. with PROC CATMOD when treatment was the only independent variable. PROC GENMOD was used when one of the categories only showed one response (options LINK=LOGIT, DIST=BINOMIAL, and TYPE3; Stokes, Davis & Koch, 1995), or for dates and continuos variables.

Pairwise comparisons of cardinally scaled parameters were carried out with *t*-tests (PDIFF option in LSMEANS statement in PROC GLM) and controlled for the type `I` experimentwise error rate by Bonferroni tests (BON option in MEANS statement in PROC GLM). Pairwise comparisons of discrete variables were carried out with a Wilcoxon two-sample test (PROC NPAR1WAY WILCOXON).

Pearson product-moment correlations were conducted with PROC CORR; for nonparametric measures I used Spearman's rank-order correlation (PROC CORR SPEARMAN).

When not otherwise stated, tests are one-tailed. Probabilities of less than 0.05 were considered significant. In figures, significance levels are indicated by

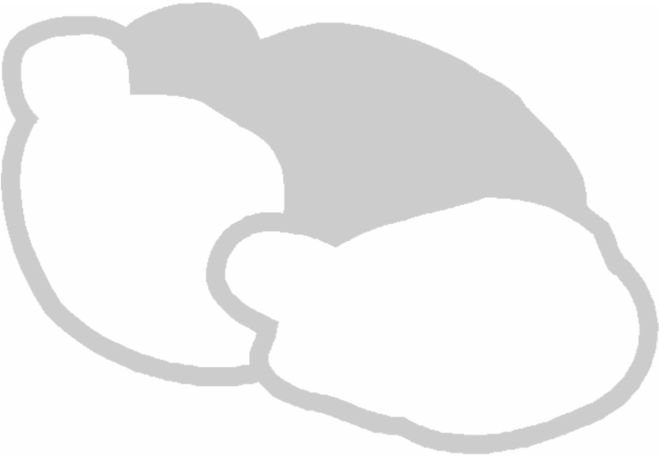
Table 3: List of parameters used and definitions adopted in the study.

Parameter	Unit	Definition	Year [a]
NB			
Hatching		Hatching date of a nest's **second** (=last) chick	95
OFFSPRING PRODUCTION & QUALITY			
Offspring production		Number of chicks alive 18 days after hatching	95
Fledging success	%	Quotient of offspring production divided by manipulated brood size	95
Failed nests	%	Proportion of nests that lost all chicks	95, 96
Chick loss	%	Proportion of nests that lost at least one chick	95, 96
Time of first chick loss	d	Time between manipulation and a nest's first chick loss	95, 96
Chick loss within 3d	%	Proportion of nests that lost its first chick within 3 days after manipulation	95
Chick survival until day 9	%	Proportion of chicks that survive to day 9 after hatching	95, 96
Chick survival from day 9 to day 18	%	Proportion of chicks alive at day 9 after hatching that survive to day 18 after hatching	95
Early chick body mass	g	Mean body mass of a nest's chicks, 9 days post-hatch	95
Late chick body mass [b]	g	Mean body mass of a nest's chicks, 18 days post-hatch	95
Chick growth [b]	g	Difference between late and early chick body mass	95
PARENTAL STATE			
Female/male early body mass	g	Adult body mass, 1 - 3 days after manipulation	95, 96
Female/male late body mass [b]	g	Adult body mass, 18 - 21 days after manipulation	95
Absolute female/male mass loss [b]	g	Difference between early and late adult body mass, corrected for number of days between measurements, correction factor used: 18d · (weighing date 2 - weighing date 1)	95
Relative female/male mass loss [b]	%	Quotient of absolute adult mass loss divided by early body mass	95
Early/late[b] female/male body condition in 1995/1996[b]	‰	Residuals from the regression between $\log_e$(adult body mass / g) and $\log_e$(adult skull length / mm)	95, 96
Nest attendance [c]	%	Number of adults present at the nest during a snap shot	96
FUTURE REPRODUCTION			
Female/male re-sighting rate [b]	%	Proportion of adults re-sighted	96
Pair-bond stability [b]	%	Proportion of pairs observed that had the same partners as in the preceeding year	96
Nest-site fidelity [b]	%	Proportion of pairs observed that had the same nesting site as in the preceeding year	96
Clutch size [bd]		Number of eggs in a nest before hatching of the colony's first chick (= 18 June)	96
Egg volume [bd]	ml	Mean volume (0.4861 · egg length · egg breadth · egg breadth) of a nest's eggs	96
Hatching success [bd]	%	Quotient of number of chicks hatching divided by clutch size	96
Hatching date [bd]	d	Hatching date of a nest's **first** chick (1 = 1 June)	96
Hatching asynchrony [bd]	d	Time between hatching of the first and second chick in a nest with a clutch size of two	96

[a] year of recording the respective parameter
[b] calculated for nests only that kept their manipulated clutch size for at least twelve days
[c] recorded twice daily during 18 days for nests only that had not lost any chick prior to observation
[d] calculated for pairs only that retained the same mate

asterisks (*, $0.01 \leq p < 0.05$; **, $0.001 \leq p < 0.01$; ***, $p < 0.001$) or "ns" ($p \geq 0.05$). In tables, asterisks are used in addition to the exact significance level.

Throughout the following text, all measures are expressed as mean ± one standard error. That applies also to figures, were the standard error is indicated by error bars, and to tables. In text, "$n =$ " refers to sample sizes, in figures and tables they are given in brackets. Degrees of freedom (df; in text, indicated as indices to test observators) are not mentioned when the effect investigated is solely the effect of treatment (3 categories ⇒ 2 df; in pairwise comparisons, 2 categories ⇒ 1 df) and when sample sizes are given.



3

Results

3.1 Offspring production and quality

Chick losses

Table 4 shows the fate of the 267 nests, 125 of which lost eggs or chicks before manipulation and were excluded from all further calculations. Also after manipulation, chick losses were considerable. In all three groups, a large proportion of nests did not fledge any young at all (45 %, 52 %, and 39 % in reduced, control and enlarged broods, respectively). This proportion of failed pairs was not related to experimental treatment (logistic regression: $\chi^2 = 1.27$, $p = 0.265$).

The total proportion of nests that lost one or more chicks, increased significantly with increasing manipulated brood size from 45 % to 82 % (fig. 6; tab. 5, row 1). This difference was due to a lower proportion of nests preyed upon among "reduced" nests compared to the other two groups, which did not differ from one another (Wilcoxon: reduced vs. control, $Z = 3.07$, $p < 0.002$; control vs. enlarged, $Z = -0.65$, $p = 0.257$; reduced vs. enlarged, $Z = -3.74$, $p < 0.001$). In contrast, the percentage of nests that lost exactly one chick decreased significantly with increasing manipulated brood size from 45 % (reduced) to 16 % (enlarged; tab. 4; logistic regression: $\chi^2 = 8.81$, $p < 0.013$).

Table 4: Overview over all marked nests. Number of nests used in the experiment and assigned to the different treatment categories, and their production at the end of the experiment. Every line summarizes the subordinated lines (symbolized by indentation) below it. The "Proportion" columns give the percentages of nests in relation to the superordinated category: left hand, considering all nests; right hand, considering only nests that fledged young (see footnotes).

	Number	Proportion	
Original sample size	267		
Preyed upon before manipulation	125	47 % [a]	
Manipulated nests	142	53 % [a]	
"Reduced" nests	**47**	33 % [b]	
1 chick fledged	26	55 % [c]	100 % [d]
0 chicks fledged	21	45 % [c]	–
"Control" nests	**46**	32 % [b]	
2 chicks fledged	10	22 % [c]	45 % [d]
<2 chicks fledged	36	78 % [c]	55 % [d]
1 chick fledged	12	26 % [c]	55 % [d]
0 chicks fledged	24	52 % [c]	–
"Enlarged" nests	**49**	35 % [b]	
3 chicks fledged	9	18 % [c]	30 % [d]
<3 chicks fledged	40	82 % [c]	70 % [d]
2 chicks fledged	8	16 % [c]	27 % [d]
1 chick fledged	13	27 % [c]	43 % [d]
0 chicks fledged	19	39 % [c]	–

[a] of original sample size
[b] of manipulated nests
[c] of all nests in the respective category "reduced", "control", or "enlarged"
[d] of the nests in the respective category "reduced", "control", or "enlarged" that fledged at least one chick

Time of chick loss

There was no seasonal effect on chick loss, i.e. the chances of a complete nest to lose a chick, did not change with calendar date (two-tailed logistic regression: $\chi^2_{1,94} = 0.32$, $p = 0.572$). Chick loss was, however, significantly influenced by the age of the chicks (two-tailed logistic regression: $\chi^2_{1,94} = 4.59$, $p < 0.033$). This is evident from figure 7 which shows that the chick loss peaked, in all three experimental categories, during the first three days after manipulation. The trend in height of the peak of the chick loss curve suggests that enlarged nests suffered more during the first three-days interval (fig. 7). This trend was, however, not significant (tab. 5, row 2).

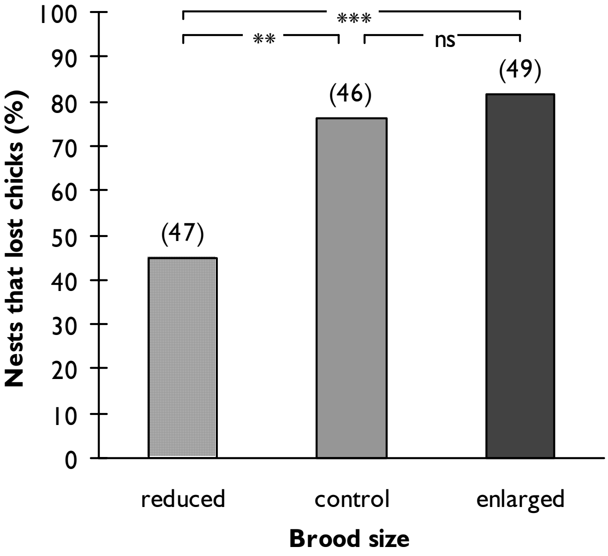


Figure 6: Proportion of nests that lost at least one chick. Chick loss in Kittiwakes that reared manipulated brood sizes. Differences were tested with Wilcoxon.

The mean time of chick loss was not affected by manipulated brood size, though there was a tendency towards an earlier chick loss from enlarged broods than from control broods, which themselves tended to lose chicks earlier than reduced broods (tab. 5, row 3). This became apparent when comparing the distribution of time of chick loss between groups: "reduced" nests differed significantly from the other two categories (two-tailed Kolmogorov-Smirnov: reduced vs. control, $D = 0.36$, $p < 0.006$; control vs. enlarged, $D = 0.17$, $p = 0.524$; reduced vs. enlarged, $D = 0.46$, $p < 0.001$).

The hatching date did not differ between groups (ANOVA: $F = 0.15$; $p = 0.859$). Therefore, I do not need to control for this factor in the calculations.

Chicks fledged

The percentage of chicks fledged did not differ between groups, varying between 38 % (control) and 55 % (reduced; fig. 8; tab. 5, row 4). However, after excluding nests that did not fledge any chicks at all (failed), the relation be-

Table 5: Chick loss and production. Survey of different measures related to chick loss and offspring production in manipulated Kittiwake broods.

	Parameter	Brood size			Statistics	
		reduced	control	enlarged	χ^2	p
1	Chick loss (%)[a]	45±8	76±7	82±6	16.02[e]	0.001***
2	Chick loss within 3d (%)[b]	29±19	37±9	53±8	3.63[e]	0.082
3	Time of first chick loss (d)[b]	8.0±1.2	6.4±0.9	5.2±0.7	4.08[f]	0.065
4	Chicks fledged (%)[ad]	55±8	38±7	39±6	3.39[f]	0.184
5	Chicks fledged (%)[cd]	100±0	73±6	61±6	29.11[f]	0.001***
6	Offspring produced[ad]	0.55±0.08	0.76±0.13	1.16±0.17	6.50[f]	0.039*
7	Offspring produced[cd]	1.00±0.00	1.46±0.11	1.84±0.16	21.06[f]	0.001***

[a] all nests (sample sizes: reduced, n=47; control, n=46; enlarged, n=49)
[b] only nests that lost at least one chick (sample sizes: reduced, n=21; control, n=35; enlarged, n=40)
[c] only nests that fledged at least one chick (sample sizes: reduced, n=26; control, n=24; enlarged, n=31)
[d] two-tailed test
[e] test performed was logistic regression
[f] test performed was Kruskal-Wallis

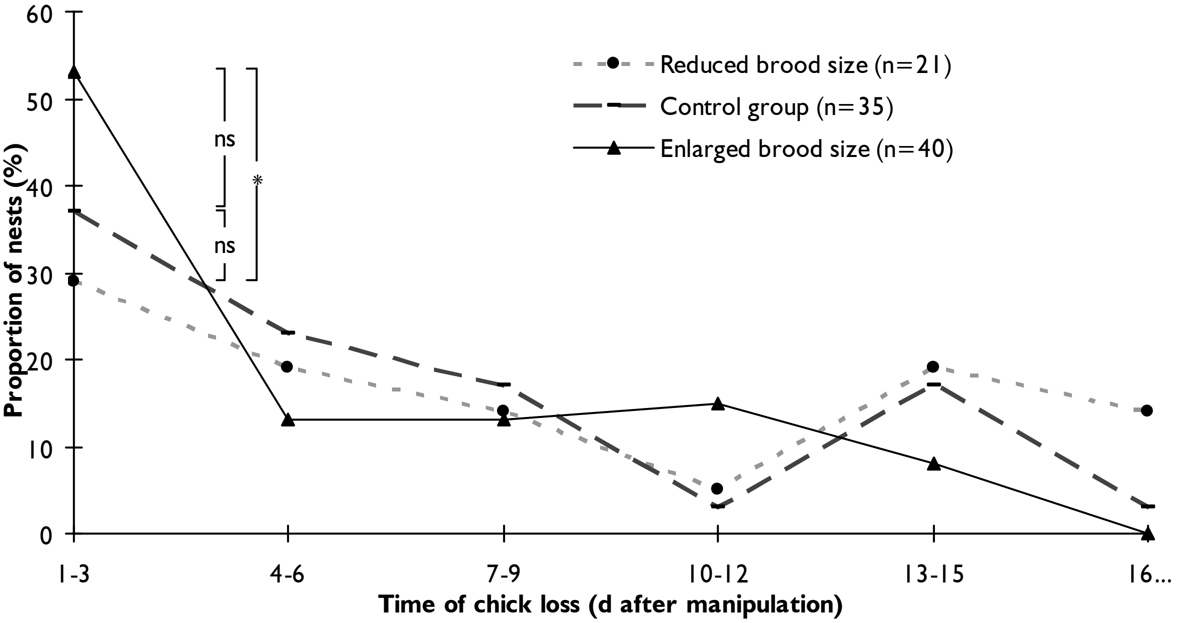


Figure 7: Timing of chick loss. Distribution of chick losses occurring in nests of Kittiwakes rearing manipulated broods; plotted as proportion of chick losses in relation to when these chick losses occurred. Chick losses were computed as fraction of nests losing their first chick within a certain three-day period, divided by the total amount of nests in the same experimental category that lost chicks; time of first chick loss was expressed in days after manipulation. Differences between the proportions of nests that lost their first chick within the first three days after manipulation, were tested with Wilcoxon.

tween fledging success and treatment became significant (tab. 5, row 5): reduced broods had a higher fledging success than control broods, which in turn had a higher fledging success than enlarged broods (Wilcoxon: reduced vs. control, $Z = -4.31$, $p < 0.001$; control vs. enlarged, $Z = 1.79$, $p < 0.037$; reduced vs. enlarged, $Z = 5.28$, $p < 0.001$).

The production of offspring increased with increasing manipulated brood size, both when including all nests and when excluding failed ones (fig. 8; tab. 5, rows 4 & 5). In pairwise comparisons, only reduced and enlarged broods differed when all nests were included (Wilcoxon: reduced vs. control, $Z = 0.92$, $p = 0.179$; control vs. enlarged, $Z = -1.63$, $p = 0.051$; reduced vs. enlarged, $Z = -2.47$, $p < 0.007$). The difference between control and enlarged broods was only marginally significant, also when excluding failed nests (Wilcoxon: reduced vs. control, $Z = 3.86$, $p < 0.001$; control vs. enlarged, $Z = -1.53$, $p = 0.063$; reduced vs. enlarged, $Z = -4.39$, $p < 0.001$).

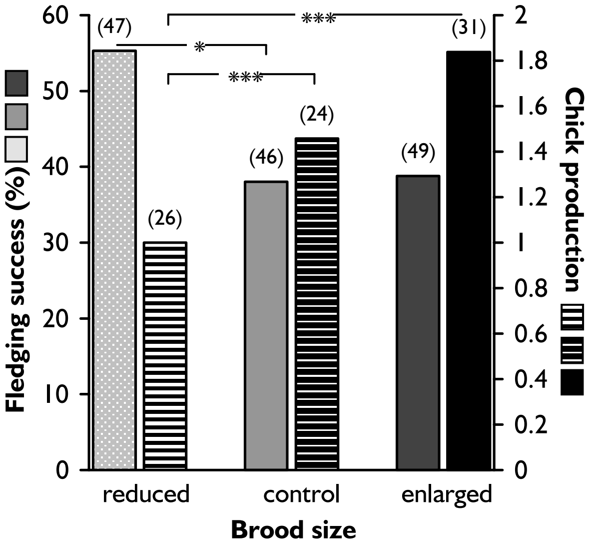


Figure 8: Percentage and number of chicks alive 18 days after hatching. Fledging success (left x-axis; all nests) and chick production (right x-axis; without failed nests) of Kittiwakes rearing manipulated broods. Differences were tested with Wilcoxon; insignificant differences are not shown.

Chick survival

Table 6 shows the probability of each offspring surviving to day nine after hatching, and the probability of all offspring which were alive on day nine surviving to day eighteen. The treatment effect on the chances of offspring survival was statistically significant in the first nine-day period only: survival decreased with increasing manipulated brood size. No such effect was apparent in the second period. The probability of surviving from hatching to day eighteen has the same numerical value as the percentage of chicks fledging (tab. 5, row 4).

Table 6: Chick survival (%). Chances of surviving to day 9 post-hatch for Kittiwake chicks with a given manipulated brood size, and chances of surviving to day 18 post-hatch for the chicks alive on day 9 post-hatch. Test performed was Kruskal-Wallis.

Brood size	Until day 9	From day 9 to day 18
reduced	79±7 (47)	70±3 (37)
control	66±7 (46)	59±8 (37)
enlarged	64±6 (49)	61±7 (40)
χ^2	6.65	1.93
p	0.019*	0.191

Chick body mass

Chick growth in the three experimental groups is listed in table 7. Early chick mass, i.e. 9 days after hatching, was not related to treatment. Late chick mass, i.e. 18 days after hatching, exhibited a negative relation with manipulated brood size (fig. 9): "reduced" chicks were heaviest (322 g ± 7 g), "enlarged" chicks lightest (282 g ± 9 g). Chicks from reduced and from control broods did not differ in mass in a pairwise comparison.

Table 7: Chick body masses (g). Body masses of Kittiwake chicks from manipulated broods 9 days (early) and 18 days (late) after hatching, and mass gain during this period. Test performed was ANOVA.

Brood size	Early chick body mass	Late chick body mass [a]	Chick mass gain [ab]
reduced	175.8±5.7 (37)	322.2±6.5 (26)	144.7±7.0
control	180.6±5.1 (37)	309.7±12.3 (14)	134.3±12.9
enlarged	175.6±3.6 (40)	282.4±8.5 (11)	110.1±6.9
F	0.35	4.72	3.33
p	0.352	0.007**	0.023*

[a] only nests that maintained their manipulated brood sizes for at east 12 days

[b] same sample sizes as for late chick body mass

Chick mass gain showed a similar pattern as late chick mass: mass gain decreased significantly from 145 g ± 7 g in "reduced" chicks to 110 g ± 7 g in "enlarged" chicks, this relation being significant (tab. 7).

3.2 Parental state

Time and sex effects

In all groups and both sexes, the time effect in body mass was highly significant: adults were heavier early (1 – 5 d post-hatch) than late (19 – 23 d post-hatch) in the chick-rearing period (tab. 8).

A calculation of the sex × treatment interaction of the mass loss data showed that both sexes responded differently to treatment (tab. 9). Therefore, all further results concerning the treatment effect will be presented for both sexes separately.

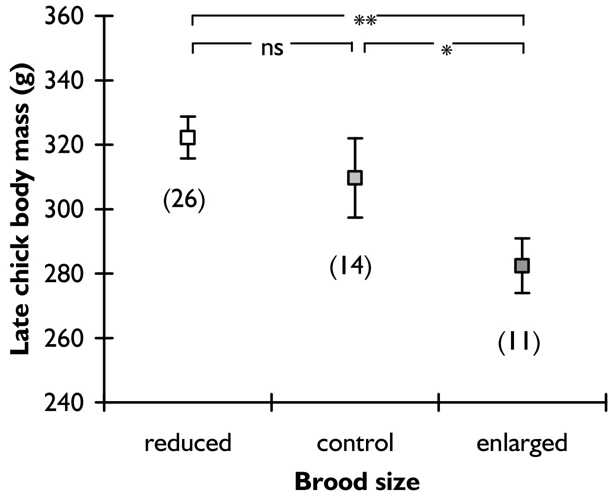


Figure 9: Body mass of Kittiwake chicks reared in manipulated broods, 18 days after hatching. Differences were tested with *t*-test.

Table 8: Adult body mass (g). Early (1-5 d post-hatch) and late (19-23 d post-hatch) body masses of adult Kittiwakes that reared manipulated broods. The statistics columns to the right show the treatment effect of the data; test performed was ANOVA. The statstics rows at the bottom show the time effect of the data; test performed was paired t-test.

	Reduced brood size		Control group		Enlarged brood size		F	p
EARLY[a]								
	403.7±3.5 (42)		409.4±4.3 (42)		394.4±4.0 (47)		3.80	0.025*
		457.8±4.0 (44)		453.3±4.3 (43)		457.7±3.9 (47)	0.39	0.750
LATE[b]								
	364.1±4.5 (22)		359.1±7.2 (11)		343.4±5.6 (9)		3.10	0.029*
		402.3±5.0 (25)		402.1±6.8 (13)		414.9±7.6 (9)	0.99	0.811
t	9.27	11.48	9.66	9.51	7.52	8.96		
p	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***		

[a] two-tailed test

[b] only nests that maintained their manipulated brood sizes for at least 12 days

Female state

Female body mass early in the breeding period, i.e. within three days of manipulation, differed between the treatment categories: females with enlarged broods were lightest (394 g ± 4 g; tab. 8). This difference in female body mass between the treatment categories was less pronounced late in the breeding season (tab. 8), though the tendency stayed the same.

When considering absolute female mass loss, there was a significant increase with increasing manipulated brood size (ANOVA: $F = 4.01, p < 0.014$). In a pairwise comparison, "reduced" females (39.5 g ± 4.6 g, $n = 22$) differed from both "control" (59.4 g ± 6.1 g, $n = 11$) and "enlarged" ones (55.1 g ± 6.7 g, $n = 9$), while the latter two did not differ from one another (t-test [Bonferroni]: reduced vs. control, $t = -2.59, p < 0.007$ [*]; control vs. enlarged, $t = 0.46, p = 0.677$ [ns]; reduced vs. enlarged, $t = -1.89, p < 0.033$ [ns]).

The positive relation between mass loss and manipulated brood size became even more accentuated when calculating relative mass losses (fig. 10; ANOVA: $F = 4.29, p < 0.011$): females caring for reduced broods lost 9.7 % ± 1.1 % of their original mass, while the control females lost 14.1 % ± 1.4 % in body mass. Relative mass loss of birds with control and with enlarged broods (13.6 % ± 1.5 %) did not differ.

The observations in female body condition differed somewhat from body mass (fig. 11; tab. 10): the early effect of treatment on condition was not statistically significant, whereas the late effect was. Accordingly, "reduced" and "enlarged" females differed significantly in their late body condition.

Male state

In males, body mass did not show any relation to treatment, neither early nor late in the breeding season (tab. 8). The tendency was, however, that males with enlarged broods weighed slightly more late in the breeding season than those in the other two groups.

Neither absolute nor relative mass loss were unequivocally related to manipulation (fig. 10; ANOVA: $F = 1.61$, $p = 0.894$). "Reduced" males lost 54.6 g ± 4.8 g (11.9 % ± 1.1 %), "control" males 66.7 g ± 5.7 g (14.1 % ± 1.2 %), and "enlarged" ones lost 48.4 g ± 11.3 g (10.2 % ± 2.4 %). These values did not differ from one another at the 5 % level when compared with pairwise *t*-tests, except for the relative mass losses of "control" and "enlarged" males.

The picture of male body condition is not clearer, though late condition at least tends towards a positive relation with manipulated brood size (fig. 11; tab. 10).

Adult nest attendance

Figure 12 shows the nest attendance during the experiment for the three experimental groups. The overall mean nest attendance was 100.7 % ± 0.6 % ($n = 749$) for nests with reduced broods, and 96.2 % ± 0.2 % for both control nests ($n = 443$) and ones with enlarged broods ($n = 315$). The relation with treatment was significant, as was the relation between chick age and adult nest attendance (logistic regression: treatment, $\chi^2_{2,1504} = 21.53, p < 0.001$; chick age, $\chi^2_{1,1505} = 50.56, p < 0.001$). As is evident from figure 12, also the chick age × treatment interaction is significant (logistic regression: $\chi^2_{2,1501} = 83.11, p < 0.001$). This means that the decrease in nest attendance with the progressing age of the chicks was the sharper, the larger manipulated broods the parents reared.

Table 9: Sex × treatment interaction in relative mass loss of Kittiwakes rearing manipulated broods. Only nests that maintained their manipulated brood sizes for at least 12 days were included; test performed was ANOVA.

Variables	*df*	*F*	*p*
Treatment	2	3.78	0.014*
Sex	1	0.20	0.671
Sex × treatment	2	2.57	0.042*
Error	83		

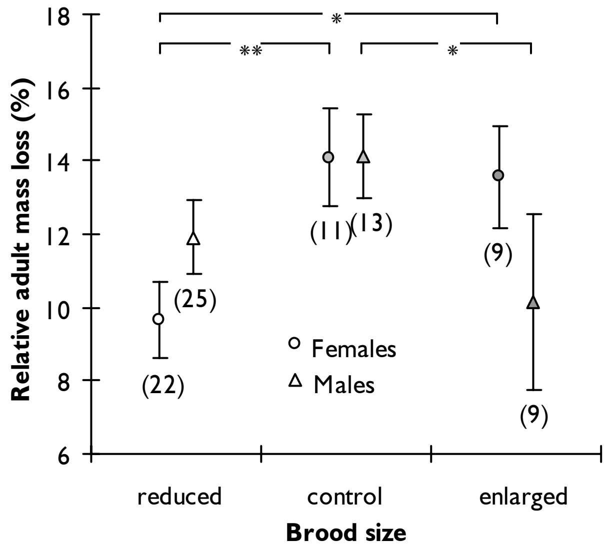


Figure 10: Relative mass loss of adult Kittiwakes. Female and male mass loss during 8 days of rearing manipulated broods, compared to early (1 – 5 days post-hatch) body mass. Differences were tested with t-test; insignificant differences are not shown.

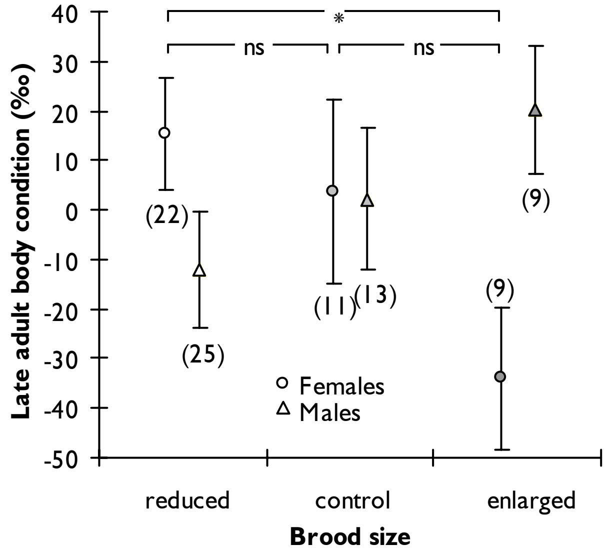


Figure 11: Late adult body condition. Body condition (as defined in tab 3) of adult Kittiwakes that reared manipulated broods, 19 – 23 days after hatching. Differences were tested with *t*-test; in males, no difference was significant.

Table 10: Adult body condition (‰). Early (2–5 d post-hatch) and late (19–23 d post-hatch) body conditions (as defined in tab 3) of adult Kittiwakes that reared manipulated broods. Test performed was ANOVA.

Status		Brood size			Statistics	
Time	Sex	reduced	control	enlarged	F	p
EARLY[a]	♀	3.4±6.4 (42)	13.2±10.2 (42)	−14.8±9.4 (47)	2.65	0.074
EARLY[a]	♂	2.0±7.8 (44)	−1.2±9.1 (43)	−0.8±8.3 (47)	0.04	0.959
LATE[b]	♀	15.3±11.4 (22)	3.8±18.6 (11)	−34.0±14.2 (9)	2.72	0.040*
LATE[b]	♂	−12.1±11.8 (25)	2.1±14.3 (13)	20.3±12.9 (9)	1.26	0.854

[a] two-tailed test

[b] only nests that maintained their manipulated brood sizes for at least 12 days

3.3 Future reproduction

Adult re-sighting rate

There was a tendency for females, but not for males, to have a decreasing probability of being observed the following year with increasing manipulated brood size (fig. 13). In females, 79 % of birds rearing reduced broods, and 82 % of birds rearing control groups were re-sighted, while only 73 % of "enlarged" females were seen. This tendency was, however, not significant (logistic regression: $\chi^2 = 0.37$, $p = 0.416$). The tendency became even weaker when also including the two birds that were only seen once (cf. p. 69; reduced, 79 %; control, 83 %; enlarged, 75 %; logistic regression: $\chi^2 = 0.32$, $p = 0.429$). In males, the control category had the lowest probability of being re-sighted (83 %), compared with 88 % in "reduced" and 100 % in "enlarged" males, although this relation was also insignificant (logistic regression: $\chi^2 = 2.13$, $p = 0.828$). Among "enlarged" birds, males had a higher probability of being re-sighted the next year than females (two-tailed logistic regression: $\chi^2 = 4.92$, $p < 0.027$).

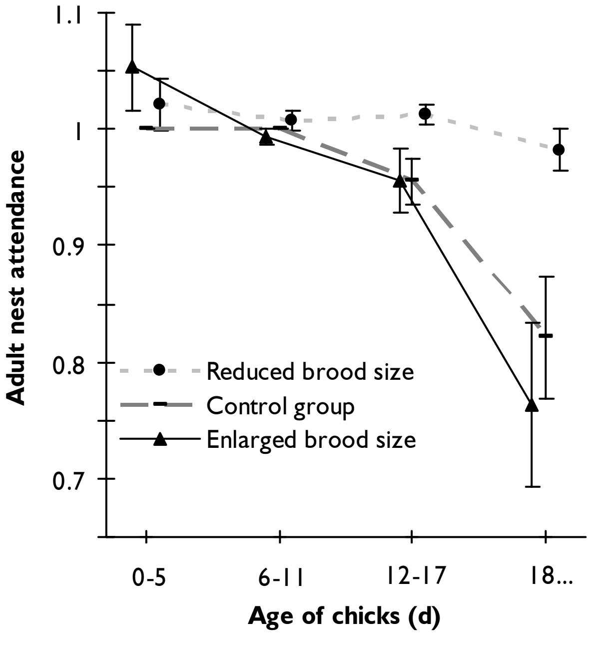


Figure 12: Nest attendance of adult Kittiwakes rearing manipulated broods. Number of adult Kittiwakes present at the nest during a snap-shot observation which was made twice daily, in relation to the age of the nest's chicks. Sample sizes, i.e. number of nest-observations (reduced/control/enlarged): 0-5, 46/54/38; 6-11, 267/178/148; 12-17, 322/155/91; 18-23, 114/56/38.

Change of mate or nest site

A similar picture was true for nest-site fidelity (tab. 11): the lowest value occurred in the control group, but here, the effect of experimental treatment the year before was significant when considering all birds, including divorced ones and "widow(er)s". When the test is restricted to pairs where both mates were re-sighted, the significant effect of treatment disappeared (logistic regression: $\chi^2_{2,42} = 1.56$, $p = 0.229$). When one further restricts analysis to pairs that did not divorce, it appears that no single pair moved together to a new nesting site ($n = 34$).

The tendency in divorce was a decrease with increasing brood size. None of the birds that reared enlarged broods the year before, divorced. This tendency was insignificant.

Parental early body condition

Table 11 gives a survey of early body mass and condition in 1996 of the birds whose broods were manipulated in 1995.

In females, there was a marginally significant trend of body mass decreasing with increasing manipulated brood size. The same trend was apparent in female body condition (fig. 14; tab. 11), and here it turned out to be statistically significant using ANOVA with linear contrast (body mass, $F_{1,19} = 3.97$, $p = 0.061$; body condition, $F_{1,19} = 4.60$, $p < 0.046$).

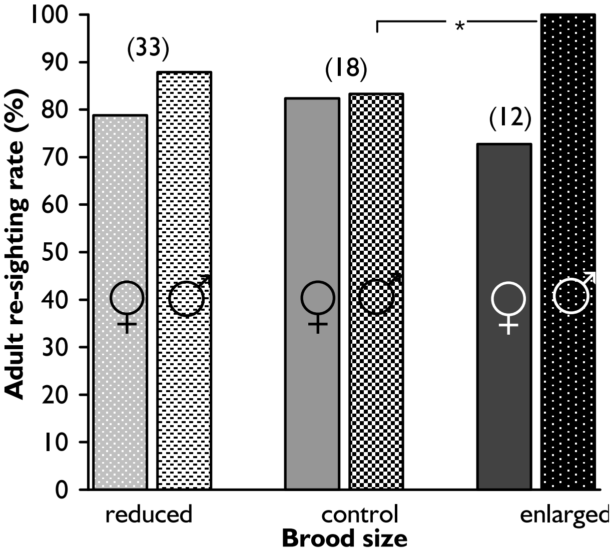


Figure 13: Re-sighting rates of adult Kittiwakes. Percentage of birds rearing manipulated broods in 1995, that were re-sighted in 1996. Differences were tested with Wilcoxon; non-significant differences are not shown.

Males did not show similar trends. On the contrary, birds of the "enlarged" group tended to be heavier and in better condition than other males. But this tendency, and all other ones concerning male body mass and condition, were not significant (fig. 14; tab. 11).

Next year's clutches

Table 12 shows some traits related to offspring of the following year.

Neither clutch size nor egg volume were related to treatment in the previous year. Most females laid two eggs; clutches of one egg were only laid by 3 of 17 "reduced" birds, 1 of 9 "control" birds and 1 of 7 "enlarged" birds. The only clutch of three eggs was laid by a "control" female. The effect of treatment on egg volume was also calculated for clutches of two only (tab. 12, row 3). But neither this nor controlling egg volume for female body mass could render the trend significant (ANOVA with residuals from regression of egg volume on

Table 11: Adult traits in the beginning of the following breeding season. Survey of different measures related to status of adult Kittiwakes one year after they reared manipulated broods. Only nests that maintained their manipulated brood sizes for at least 12 days the previous year are included.

Parameter		Brood size			Test observator	*p*
		reduced	control	enlarged		
Pair-bond stability (%)		78±9 (23)	75±14 (12)	100±0 (7)	2.08[a]	0.823
Nesting-site fidelity (%)		97±4 (30)	71±12 (17)	100±0 (12)	5.61[a]	0.031*
Early body mass (g)	♀	399.3±4.6 (13)	390.8±11.0 (4)	380.8±8.1 (5)	2.04[b]	0.078
Early body mass (g)	♂	444.0±6.7 (14)	442.0±14.0 (2)	449.0±7.8 (7)	0.13[b]	0.560
Early body condition (‰)	♀	7.7±13.0 (13)	–24.3±32.9 (4)	–47.4±17.6 (5)	2.49[b]	0.055
Early body condition (‰)	♂	–1.1±14.9 (14)	–6.0±26.4 (2)	9.3±15.8 (7)	0.12[b]	0.444

[a] test observator is χ^2 from logistic regression

[b] test observator is *F* value from ANOVA

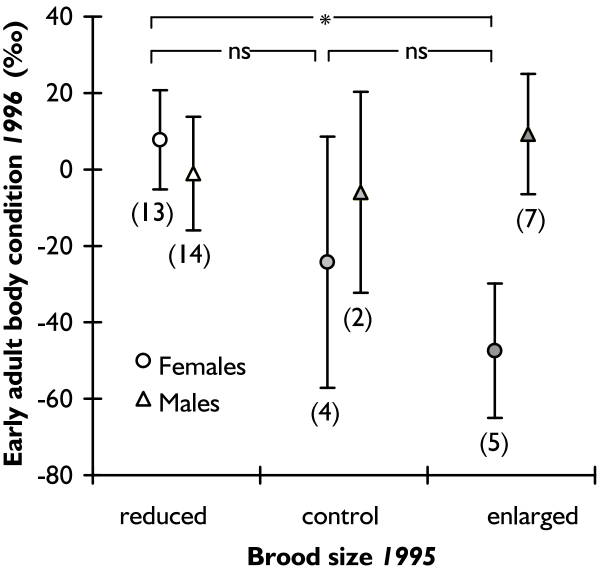


Figure 14: Body condition of adult Kittiwakes early in the following breeding season. Body condition 1 – 5 days post-hatch in 1996 of birds that reared manipulated broods in 1995. Differences were tested with *t*-test; in males, no difference was significant.

female early 1996 body mass: $F = 0.17$, $p = 0.576$).

Next year's offspring

Hatching success the year after the experiment did not exhibit any relation to treatment when tested for all nests (tab. 12, row 4). When calculated for clutches of two only, it showed, however, an effect of treatment (row 5). The lowest value (57 %) occurred in the control group and was significantly lower than among "reduced" nests (93 %); the other groups did not differ from one another in pairwise tests (Wilcoxon: reduced vs. control, $Z = -2.73$, $p < 0.004$; control vs. enlarged, $Z = 1.42$, $p = 0.924$; reduced vs. enlarged, $Z = -0.55$, $p = 0.290$).

The hatching date decreased slightly with increasing manipulated brood size (tab. 12, row 6), but not significantly so. Neither restricting the analysis to clutches of two (row 7), nor controlling for hatching date in the previous year rendered the treatment effect significant (Kruskal-Wallis with residuals from regression of 1995 on 1996 hatching date: all clutches, $\chi^2 = 0.39$, $p = 0.589$; clutches of 2, $\chi^2 = 0.26$, $p = 0.561$). In hatching asynchrony, there was no significant relation, nor was there any unambiguous

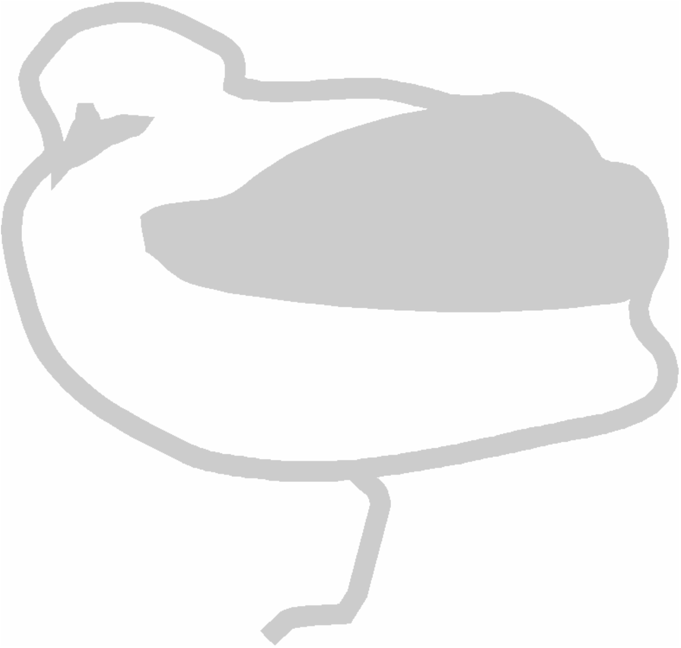
Table 12: Traits in offspring of the following breeding season. Survey of different measures related to future reproduction of adult Kittiwakes one year after they reared manipulated broods. Only pairs that held their manipulated brood sizes for at least 12 days the previous year and retained the same mate in 1996 are included.

	Parameter	Brood size			Test observator	*p*
		reduced	control	enlarged		
1	Clutch size	1.82±0.10 (17)	2.00±0.17 (9)	1.86±0.15 (7)	0.97[b]	0.691
2	Egg volume (ml)	48.64±0.83 (17)	47.86±0.88 (9)	48.06±1.25 (7)	0.21[c]	0.407
3	Egg volume (ml)[a]	49.19±0.91 (14)	47.56±1.07 (7)	49.06±0.89 (6)	0.72[c]	0.248
4	Hatching success (%)	82±10 (17)	63±13 (8)	71±19 (7)	2.88[b]	0.118
5	Hatching success (%)[a]	93±8 (14)	57±14 (7)	83±17 (6)	5.38[d]	0.034*
6	Hatching date (d)	28.93±1.11 (14)	28.38±0.97 (8)	28.20±2.04 (5)	0.49[b]	0.609
7	Hatching date (d)[a]	28.77±1.19 (13)	27.83±1.20 (6)	28.20±2.04 (5)	0.48[b]	0.607
8	Hatching asynchrony (d)[a]	1.46±0.19 (13)	2.00±0.00 (2)	1.80±0.20 (5)	2.23[b]	0.164
9	Predation (%)	23±13 (13)	50±50 (2)	100±0 (5)	8.22[b]	0.009**
10	Predation date (d)	2.7±0.7 (3)	1.0 (1)	5.6±2.3 (5)	3.07[b]	0.892
11	Total breeding failure (%)	8±8 (13)	50±50 (2)	60±25 (5)	4.65[d]	0.049*
12	Chick loss within 3d (%)	67±34 (3)	100 (1)	60±25 (5)	0.04[d]	0.509

[a] calculated for clutches of 2 only
[b] test observator is χ^2 from Kruskal-Wallis test
[c] test observator is F value from ANOVA
[d] test observator is χ^2 from logistic regression

trend (row 8).

The frequency of chick losses increased with increasing manipulated brood size in the previous year (tab. 12, row 9). Nests of "reduced" birds suffered a level of chick loss roughly half as large as "control" birds, and chick loss was again half as frequent among "control" than among "enlarged" birds, afflicting literally all nests of the latter group. This trend was statistically significant. Chick loss date was, on the other hand, not related to treatment (row 10), nor did an analysis of the distribution show any differences between single experimental groups (Kolmogorov-Smirnov: reduced vs. control, $D = 1.00$, $p = 0.441$; control vs. enlarged, $D = 1.00$, $p = 0.375$; reduced vs. enlarged, $D = 0.40$, $p = 0.925$). Total breeding failure, i.e. loss of the whole brood, was related to previous-year treatment, exhibiting the same trend as chick loss, and was statistically significant (row 11). The proportion of nests that lost chicks within the first three days after manipulation, did not differ between treatments (row 12).



4

Discussion

In an experimental study, I examined the effect of manipulating brood sizes (cf. tab. 2) of Kittiwakes on different life history traits. In this chapter, I discuss the results in the light of life history evolution. I first look at the trade-offs acting within the broods (4.1). Then I discuss the evidence for an intergenerational trade-off between brood size and parental state (4.2), and for costs of reproduction (4.3). In section 4.4, I put the evidence of the previous sections together in an attempt to calculate overall adult fitness in relation to manipulated brood size. In section 4.5, I have a closer look at the differences between my results and the ones of Jacobsen (1993; Jacobsen et al., 1995) who conducted a very similar study in another year, and discuss them as adaptations to a stochastic environment. Section 4.6 comprises the conclusions of this thesis. The discussion of the methods used can be found in appendix C.

4.1 The trade-off between number and quality of offspring

The Lack clutch

Lack (1947) was the first to point out that the number of fledglings is neither simply a linear function of clutch size nor adjusted to mortality rates in a manner requiring group selection (e.g., Rensch, 1938). Instead, he claimed that fledging success decreased with increasing brood size because the parents could not supply enough food to large broods, thus resulting in an optimal clutch. Above this optimal clutch size, called the *Lack clutch*, parents would not benefit from laying further eggs. The prediction was thus that the most commonly-laid clutch size in a given population had, as a result of selection past, to be the optimal one.

Many experimental studies that have manipulated brood sizes, reported a negative correlation between brood size and nestling survival to hatching (31 of 47 studies reviewed by Lindén & Møller, 1989, and Dijkstra et al., 1990). However, for Laridae, there are many studies that showed conflicting evidence (6 of 6 species reviewed by Ydenberg & Bertram, 1989, and VanderWerf, 1992). Only evidence from Harris & Plumb (1965) in Lesser Black-backed Gulls *Larus fuscus* could be interpreted as supporting the existence of a decline in chick survival with increasing brood size.

My findings are in accordance with the Lack clutch only for fledging success and chances of chick loss. Occurrence of chick losses in this study, measured as the proportion of nests that lost at least one chick, was positively related to manipulated brood size (fig. 6 & tab. 5, p. 20). Accordingly, the fledging success decreased with increasing brood size (fig. 6, p. 20; tab. 5, p. 21). These relations could be explained by Lack's postulate that the food supply per chick decreased with increased brood size and vice versa.

The evidence presented in appendix C (p. 66) suggests that total breeding failure was due to factors other than brood size. It is thus sensible to examine fledging success also after an exclusion of those failed nests, as I did here.

As regards offspring produced, however, Lack (1947) predicted a lower production in both reduced and enlarged, compared with control broods. This proved true for reduced broods in this study. But the number of fledglings is larger among enlarged broods than among controls (fig. 6; tab. 5) – even though this trend is only marginally significant.

This last finding is in accordance with many other studies (46 of 66 studies reviewed by Ydenberg & Bertram, 1989, Dijkstra et al., 1990, and VanderWerf, 1992; Heaney & Monaghan, 1995) that were able to show that Lack's assumptions (1947) were simplified, as the only trade-off they take into consideration is number versus survival of offspring. The hypothesis was therefore extended to include offspring quality in the prediction of optimal clutch size (Charnov & Skinner, 1984), which is now commonly called *Lack's solution clutch size* (Godfray, 1987).

To see whether Lack's solution clutch size gives a better fit to my data, I will now take a look at offspring quality.

Lack's solution clutch size

Late chick body mass, i.e. 18 days after hatching, was significantly negatively related to manipulated brood size (tab. 7 & fig. 9, p. 22). This clearly indicates a trade-off between number and body mass of offspring, and was the result expected according to Lack's solution clutch size.

Many studies were able to demonstrate this trade-off (29 of 42 studies reviewed by Lindén & Møller, 1989, Dijkstra et al., 1990, and VanderWerf, 1992; Martins & Wright, 1993; Møller, 1993). But other studies present conflicting results:

Of the studies of Laridae that did not show such effects (Harris & Plumb, 1965; Harris, 1970; Haymes & Morris, 1977), one (Haymes & Morris, 1977) reported "locally abundant artificial food sources (e.g., commercial fish refuse)", and one (Harris & Plumb, 1965) was carried out in an increasing population, thus probably biasing the results (but see Ydenberg & Bertram, 1989).

A previous comparable study (Jacobsen, 1993) reported a significant treatment effect in Kittiwake chick mass at about the same time as late weighing took place in my experiment (19 – 24 days after hatching). But, as he recorded chick masses until 36 days post-hatch, he was able to show that the difference in body mass disappeared again later, closer to fledging. I am not able to demonstrate such an effect because of the described changes in the experimental design (cf. p. 13). But I doubt that I would have observed the same tendency. The reason is that Jacobsen (1993) reported a peak of chick loss in the same period (19 – 24 days). He supposed that loss of chicks resulted in an adjustment of the broods' food requirement to food supply, thus equalizing chick masses after that time. In my study, most chick losses occurred early after hatching (fig. 5). Therefore, I believe that such brood size adjustments did not take place after I terminated the experiment, such that the chick body masses I have recorded, might give a good estimate of fledging mass.

So far, my findings are in accordance with Charnov & Skinner's (1984) assumption that offspring size or mass should decrease with brood size. To test the predictions of Lack's solution clutch size, one has to know the fitness of the offspring. But there is no simple equation to calculate the fitness value of a single offspring from its body mass. Charnov & Skinner based their paper on parasitoid insects which have an indeterminate growth and several-fold size variation among reproductive adults. These patterns do not occur in birds. Therefore, the influence of offspring body mass on their chances of survival and, more important, their chances of recruitment to the breeding population, has not been given as much attention. There is, however, some evidence that offspring fitness is heavily influenced by fledging mass: Coulson & Porter (1985) found an effect of growth rate during the nestling period on recruitment in the Kittiwake. Also for other species, it has been demonstrated that weight at fledging was a good indicator of post-fledge survival (Perrins, Harris & Britton, 1973; Ward, 1973, cit. in Haymes & Morris, 1977; Newton, Marquiss & Village, 1983; Lundberg & Alatalo, 1992).

Recruitment of chicks to the breeding population

In table 13, I calculated three different models of relations between fledgling mass and recruitment, the extremes of which might embrace the true value of recruitment to the breeding population (see app. A for algorithms).

- The first version ("Lack") assumes *no correlation* between offspring mass and their chances of recruitment to the breeding population. This extreme is identical with Lack's (1947) original assumption that only the number of chicks is significant.
- The second model ("Proportionality") assumes that a chick's chance of recruitment increases *proportionally* with its body mass.
- The third version ("Coulson") uses the chick return rates calculated by Coulson & Porter (1985). This is the other extreme considered in table 13, because return rates increase *more than proportionally* with increasing growth rates: a 10 % higher growth rate during the nestling period leads, according to Coulson & Porter (1985), to an about 22 % higher chance of being recruited to the breeding colony.

Table 13: Recruitment of chicks. Number (recruits per nest) of Kittiwake chicks reared in manipulated broods that survive to reproduce. The different models are explained in the text.

Model	Brood size		
	reduced	control	enlarged
ALL NESTS	n=47	n=46	n=49
"Lack"	0.19±0.03	0.26±0.05	0.39±0.06
"Proportionality"	0.20±0.03	0.25±0.05	0.36±0.05
"Coulson"	0.21±0.04	0.26±0.05	0.35±0.05
MIN 12 d [a]	n=33	n=18	n=12
"Lack"	0.27±0.03	0.47±0.07	0.82±0.11
"Proportionality"	0.29±0.03	0.45±0.08	0.68±0.11
"Coulson"	0.30±0.04	0.46±0.08	0.64±0.11

[a] only nests that maintained their manipulated brood sizes for at least 12 days

It is impossible to infer from my data, which one of the three models is most realistic. I prefer, however, model "Coulson" as it is the only one which is based upon empirical data from Kittiwakes. But even this most "radical" model cannot explain why clutches of three are not more common in the Kittiwake: even when assuming that chances of recruitment decrease over-proportionally with decreasing fledging mass, the number of recruits is positively related to brood size (ANOVA: all nests, $F = 2.91$, $p < 0.029$; nests that maintained their brood size for 12 days, $F = 7.27$, $p < 0.001$), and enlarged broods are the most productive ones. However, not even recruitment rates explain all variation in fitness: also individuals that survive to maturity can vary greatly in reproductive performance (e.g., Coulson & Thomas, 1985a; Clutton-Brock, 1988; Newton, 1989), and there is evidence that also such variation is influenced by weaning/fledgling quality (Gustafsson & Sutherland, 1988; de Kogel, 1997). It might thus be the case that my model "Coulson" represents recruitment rates correctly, but that I still overestimate fitness of light chicks because they, for instance, acquire low-quality nest sites (Porter, 1990) or die after having reproduced only once.

Timing and causes of chick losses

It is important to note that my definition of chick loss used in this study (tab. 3, p. 17), also includes chick loss that occurred as a result of factors other than just predation. Other causes of chick losses are adverse weather conditions (see app. D) and, particularly, siblicide. The reason for treating all chick losses as the same event was that it was not possible to distinguish between the different causes. This point is discussed in more detail in the critique of methods (appendix C, p. 65).

Chick loss peaked during the first three days after manipulation (i.e. 2 – 5 days post-hatch), as is apparent from figure 7 (p. 21). Further, there was a tendency that chick loss occurred earlier with increasing brood size (tab. 5, p. 20), and, consequently, a tendency that the proportion of nests preyed upon within three days after manipulation, also increased with brood size (fig. 5). The distribution of the time of chick loss was different between reduced broods and the other experimental categories.

That chick losses occurred early in the chick rearing period is not surprising, as Barrett & Runde (1980) found that about half of all chick losses occurred within the first 10 days after hatching. Braun & Hunt (1983) and Coulson & Porter (1985) also reported an age-dependent decline in mortality rate for chicks, with the highest risk of dying during the first five to eight days post-hatch. There is, however, some evidence that human disturbance might be an additional reason for chick losses in my study (Pichl & Barrett, in prep.), thus enhancing the peak of chick loss during the first hatchling days.

It is interesting to note, that the rate of chick loss with its peak during the first three days, differed from the curve reported by Jacobsen et al. (1995). In the latter, the peak appeared between day 19 and 24 post-hatch for "control" and "enlarged" nests, and even later for "reduced" nests. I terminated my study before that time (at day 18), in order to avoid observer-caused chick losses (see section 2.3). But also the trend that was apparent in Jacobsen (1993; Jacobsen et al., 1995) before day 18, namely that chick loss increased with time, contradicts my observations. But taking into account the evidence presented by Barrett & Runde (1980) and Coulson & Porter (1985), it seems that Jacobsen's study, rather than mine, might represent an exception.

The differences between the experimental groups can be interpreted such that increased brood size reduced the ability of the parents to maintain the respective brood size over a given period of time. Possible explanations for that phenomenon are that brood size affects (1) the parents' *nest attendance*, (2) the parents' ability to protect offspring from *predation*, and/or (3) the strength of *competition* between siblings.

1) Wanless & Harris (1989) have shown that "the likelihood of an adult being present on a nest decreased with brood size and broods of two were more than twice as likely to be left alone as single chicks, while broods of three were twice as likely to be left alone as broods of two" (p. 157+8). They summarized the potential risks for unattended chicks as (a) increased probability of predation, as predators will generally chose the easiest way to prey and, therefore, prefer unattended nests; (b) other Kittiwakes ("squatters", see p. 69) that were frequently observed being aggressive against chicks in the squatted nest – there is, however, no documented case of chick mortality that could be assigned to squatting birds; (c) increased susceptibility to adverse weather conditions (cf. app. D); (d) droppings from Kittiwakes nesting above the unattended nest which, in turn, lower the insolation effect of the chicks' downs and enhance factor (c). Also Cadiou & Monnat (1996) observed that single-chick broods were left unattended later than larger broods. On the other hand, Coulson & Johnson (1993) were unable to show any effect of brood size on attendance patterns.
2) Galbraith (1983) reported that parents were not able to cover all chicks of three-chick broods. It is, therefore, possible that increased brood size leads to an increased risk of predation even when parents attend the nest.
3) Brood reduction is common among birds (reviewed by Nilsson, 1995, Amundsen & Slagsvold, 1996, and Stenning, 1996). In most species, brood reduction is mediated by chick aggression and dominance of the first-hatched over later-hatched siblings, resulting in food monopolization by the dominant chicks. The role of the parents in this interaction is uncertain. In some cases, chick reduction might be a result of a parent-offspring conflict over clutch size (Trivers, 1974; O'Connor, 1978; Lazarus & Inglis, 1986; Nilsson, 1995). In other cases, it seems evident that parents enhance dominance of chicks over others by laying eggs that hatch asynchronously, thus creating an age and size hierarchy between chicks. Facultative brood reduction is in these cases interpreted as an adaptation to changes in food availability that could not be forecasted at the time of egg-laying (Lack, 1966; Wiebe, 1995). As the Kittiwake belongs to facultatively brood-reducing species (Runde & Barrett, 1981), brood reduction might here be a method to adjust brood size to food availability (Braun & Hunt, 1983; Wiebe, 1996).

These three explanations are not mutually exclusive, and I will discuss their possible contribution in the following paragraphs.

Adult nest attendance

In my data, nest attendance of the parents decreased significantly with increasing manipulated brood size. The common explanation has been food shortage: Wanless & Harris (1989) stated that "adults with the biggest demands [i.e., the ones having the largest broods] were most likely to leave their young" (p. 160), and Roberts & Hatch (1993) observed that parents that were unable to feed hungry, begging chicks often deserted their nests. However, Cadiou & Monnat (1996) presented alternative explanations for the absence of parents from the nest: space in or near the nest might be scarcer with larger broods, especially where nests are close to one another; and adults might avoid increasing begging pressure by resting on nearby ledges.

My findings, both the relation between attendance and brood size and the seasonal decline in attendance (fig. 12, p. 25), are in accordance with both explanations: food stress and space scarcity. These explanations are also compatible. But in combination with my data on parental body conditions (see below), it appears that attendance mirrors the level of food stress the parents are subjected to by their chicks. However, attendance levels can only explain a minor part of all chick losses, namely the ones occurring late in the breeding season. This is because attendance was still high when most chicks were lost.

As I showed in appendix D, weather conditions are clearly related to chances of chick loss. I also found a significant treatment × wind speed interaction which indicated that chick loss related to strong wind occurred more frequently in broods of three chicks than in smaller broods (p. 73). The effect of adverse weather might thus have contributed to the differences in chick loss between the treatment categories.

As regards the role of undernourishment, it does not seem that this can explain the relation between treatment and chick survival prospects to day 9 post-hatch in my study (tab. 6, p. 22). There were no differences in chick body mass between groups when chances of survival differed, and vice versa (tabs. 5 & 6). Also starvation cannot, therefore, explain the early peak in chick losses because there were no differences in early chick body masses at that time. The two first factors invoked to explain chick losses are thus unlikely to occur as early in the chick rearing period as the peak in chick loss was observed. I think therefore that brood reduction, brought about by siblicide, accounts for a large part of chick losses.

This allows for two explanations. Either parents do not supply the chicks with enough food to prevent brood reduction – this would be the case when the parents have a threshold for parental expenditure. The chicks "translate" then this food shortage into aggression against siblings. An alternative explanation is that chicks and parents have different optimal brood sizes, and that the chicks have "won" this intergenerational conflict (Trivers, 1974; O'Connor, 1978; Lazarus & Inglis, 1986). The latter hypothesis is, however, somewhat speculative. Therefore, I prefer the first one which views the siblicide occurring as evidence for that the parents are not willing to meet the offspring demands completely.

Synthesis

I showed that the Lack clutch could not explain the most common clutch size in the Kittiwake. Chick loss was related to treatment, but not all of, let alone more than, the additional chicks in enlarged broods were lost. I than looked at offspring quality as inferred from body mass 18 days post-hatch, and found a negative relation to brood size as assumed by Lack's solution clutch size. But, calculating three models with different relations between offspring mass and their subsequent chances of recruitment, I was unable to show that even a overproportional effect of fledging mass could explain the most common clutch size.

Chick loss occurred probably mainly due to brood reduction, i.e. siblicide. Undernourishment, adverse weather and attendance patterns could not explain why chick loss occurred so early in the breeding period.

However, as the growth rate of chicks is a very sensitive measure of the amount of food received by a chick – with an "amplification factor" of about 4 (Coulson & Porter, 1985) –, late chick body mass will mirror parental readiness to follow offspring demands. Therefore, not only traits in chicks may be significant; adult traits have also to be considered because reproduction happens at a cost to the parents. Therefore, maximizing reproductive output in one season is, in iteroparous species, not the same as maximizing lifetime reproductive success – which means it would have been surprising when the Lack solution clutch size *did* correctly predict the number of fledglings in my study.

4.2 The trade-off between reproduction and parental state

Also Lack's solution clutch size does not take into consideration all trade-offs relevant to life history. Williams (1966) was the first to argue that parental traits also have to be taken account of. His definition of residual reproductive value as

$$RRV = \mathbf{\Phi} - \phi \qquad \text{(eqn. 2)}$$

with $\mathbf{\Phi}$, reproductive value prior to a season's reproduction; and ϕ, the "part of $\mathbf{\Phi}$ that is immediately [i.e., in the respective reproductive season] at stake",

expresses that there must be a trade-off between current and future reproduction: increased reproductive effort during the current reproductive event will necessarily reduce the residual reproductive value. This trade-off has to be mediated by the parents, since it is an intraindividual trade-off. Therefore, and because *RRV* is not directly measurable, measurements of the body condition of adults after one breeding season are often used as an estimate of the parental expenditure incurred by them. Many studies have subsequently been able to demonstrate such trade-offs between current reproduction and body mass (7 of 17 studies reviewed by Lindén & Møller, 1989 and Dijkstra et al., 1990; Martins & Wright, 1993; Weimerskirch, Chastel & Ackermann, 1995; Tombre & Erikstad, 1996).

Mass loss

It is well-documented that Kittiwakes (Barrett et al., 1985), as many other birds (reviewed by Moreno, 1989), lose body mass during the breeding season. Though it has been pointed out that mass loss reduces flight costs and could be adaptive (Freed, 1981; Norberg, 1981), "mass losses are normally considered as evidence of physiological exertion due to reproductive work-loads (Drent & Daan, 1980; Yom-Tov & Hilborn, 1981)" (Moreno, 1989: 298).

My data confirm that adult Kittiwakes lose mass during the chick rearing period (tab. 8, p. 23; fig. 10, p. 24), as masses early and late in the breeding season differed very significantly, irrespective of sex or treatment.

Female state

I used different parameters to assess adult state after, or parental expenditure incurred by, rearing manipulated broods: late body mass, late body condition, absolute and relative mass loss. The relations revealed by these measures are unequivocal: in females, late body mass and condition decreased with increasing brood size (tabs. 8 & 10), while mass losses increased (fig. 8). This can safely be interpreted as evidence for a trade-off between number of offspring and female state.

The bias in the early body mass data (see tab. 8) cannot be related to treatment, because early body mass was measured within the first three days of manipulation, when the chicks were between one and five days old. That brood size can influence a parent's body mass in such a short period of time is unlikely, among others because chick food requirements are relatively low in this period (Galbraith, 1983; Coulson & Pearson, 1985; Voß, Hartwig & Vauk, 1987). Instead, this bias must have arisen from a sampling bias, creating a type I error. The results for *late* female state are, however, not devaluated by this bias in early masses, because individual variation in early body mass is controlled for by calculating both mass *loss* and body *condition* (cf. app. C, p. 68).

There are no statistically significant differences between "enlarged" and "control" birds. This result suggests that adults reduce the use of own body reserves when brood sizes are reduced – as is also indicated by "reduced" chicks not being heavier than "control" chicks –, but are not willing to increase the use of own body reserves when brood sizes are enlarged. The same findings are reported by Jacobsen (1993; Jacobsen et al., 1995) and three of four studies of seabirds reviewed by Dijkstra et al. (1990). An explanation for this finding is a threshold in parental expenditure which the parents are not willing to cross (Masman et al., 1989; Ricklefs & Minot, 1991; Sæther, Andersen & Pedersen, 1993; Erikstad et al., in press).

Male state and differences between the sexes

In males, there is no relation whatsoever between their state and treatment. Neither early nor late body mass (tab. 8, p. 23), nor mass loss (fig. 10, p. 24), nor condition (fig. 11, p. 24; tab. 10, p. 25), were related to manipulated brood size. This result is in accordance with the findings of Jacobsen (1993; Jacobsen et al., 1995). The only trend that could be discovered was that "enlarged" males lost significantly less body mass than "control" males (fig. 8).

The differential response between the sexes was illustrated by the sex × treatment interaction in relative mass loss (tab. 9, p. 24) and becomes evident from the tendencies in the figures 8 and 9: in both figures, the curves for the sexes have slopes of different signs and intersect in the control group. This means that the sexes differed in their response to a manipulation of brood sizes: females were more readily responding to brood size enlargement than the males and lost more body mass during breeding. Males even seemed to reduce their contribution when broods were enlarged. It is interesting to note that Coulson & Porter (1985) found that the breeding experience of females, but not of males, was correlated with chick growth rate. This finding could suggest that males did not contribute as much to chick rearing as do females.

My data support the view that Kittiwake females have a higher parental expenditure than males. This is an indicator for a conflict on clutch size between the sexes (cf. Jacobsen et al., 1995). It is known also from other species with biparental care that the sexes contribute differentially to chick rearing (e.g., Moreno et al., 1995). It must be regarded as a sign of different strategies in the two sexes (Houston & Davies, 1985) that females are more willing to invest in offspring at their own costs than are males. One reason for males investing less is that their paternity is not as equally certain as is the females' maternity. This is known from other species (Davies, 1991), but I know of no evidence for extra-pair copulations in the Kittiwake (but see Coulson & Wooller, 1984).

Synthesis

The evidence for a trade-off between reproduction and state was convincing in female Kittiwakes. The largest difference occured, however, between "reduced" and "control" females, indicating that there may be a threshold in parental expenditure that females did not cross. State of males was not related to treatment; the tendency was a decrease in paternal expenditure with increasing brood size, indicating an even lower threshold for males.

Body condition is, however, only relevant to life-history when it reduces subsequent survival or future reproduction. It is known that individuals can recover during non-reproductive phases, because, by definition, parental care is not identical with parental care (cf. Clutton-Brock & Godfray, 1991). Body mass has, for example, been shown to have no influence on survival in the Willow Ptarmigan *Lagopus lagopus* (Robb, Martin & Hannon, 1992). I will therefore now look at survival of Kittiwakes to, and their breeding performance in, the next breeding season.

4.3 The trade-off between current and future reproduction

Adult re-sighting rate

Survival is subjected to considerable selection pressure in long-lived species (e.g., Wooller et al., 1992). Reproductive life span is, for instance, the single most explanatory factor in the variation of lifetime reproductive success in Kittiwakes (Coulson, 1988; Thomas & Coulson, 1988). Few studies have been able to demonstrate a trade-off between production and adult survival in long-lived birds (Reid, 1987; Jacobsen et al., 1995), mainly because few such studies have been performed with long-lived birds so far (reviewed by Dijkstra et al., 1990). A failure to document costs of reproduction in these species should however, according to theory (Williams, 1966; Gadgil & Bossert, 1970; Charlesworth, 1980), not be interpreted as a weakness of the studies conducted, but as evidence that "parents shunt all experimentally increased reproductive costs to their offspring" (Mauck & Grubb, 1995).

Support for this theoretical reasoning comes among others from the observations that annual survival decreases at the end of the life span (Botkin & Miller, 1974) and that parental investment increases with age (Curio, 1983). Both claims have been substantiated for several seabird species (Aebischer & Coulson, 1990, and references therein; reviewed by Wooller et al., 1992).

With this background, it is not surprising that I did not find any significant relation between experimental treatment and re-sighting rate to the next year, in either females or males (fig. 10). The tendencies differed between sexes: females tended to have decreasing re-sighting rates with increasing manipulated brood sizes, the highest value occurred, however, in the control group. In males, on the other hand, "control" birds had the lowest, and "enlarged" birds the highest chances of being re-sighted.

This lack of decline in survival with increasing brood size can be seen in connection with my finding that "control" and "enlarged" females did not differ in their late body condition, though the latter ones produces more offspring. This pattern can be brought about by some birds – of low quality – neglecting their broods while others were able to raise more offspring without incurring survival costs because they apparently were of higher quality. Also this hints at a threshold in parental expenditure (cf. pp. 36 & 47), which, of course, will differ between individuals.

The tendencies observed in this study are similar to those reported by Jacobsen (1993; Jacobsen et al., 1995). He was, however, able to demonstrate a significant difference between the return rate for "enlarged" and that of the (pooled) other females.

It is important to draw attention to the sex differences in re-sighting rate in my data. Return rates reported in literature are consistently higher for female than for male Kittiwakes. In Coulson & Thomas's (1985b) figure 9, for instance, the mean annual survival rates of females and males never cross in spite of considerable oscillations in the course of 28 years of observations (cf. Aebischer & Coulson, 1990). From this perspective, my finding that the re-sighting rate of "enlarged" birds was significantly lower among females than among males, might mirror an effect of the experiment, even when the overall comparison between experimental groups was not significant. An alternative explanation is, however, that mortality patterns differ between Britain and northern Norway (Erikstad et al., 1995).

A problem with the parameter "re-sighting rate" as used in this study (tab. 3) is that it is not necessarily identical with survival rate. I discuss this problem in more detail in the critique of methods (app. C, p. 69) were I conclude that even when a bird not re-sighted is alive, but changed either the breeding colony – and thereby most probably also its mate (see below) – or simply did not breed in the following year (intermittent breeding; Wooller & Coulson, 1977), it will incur fitness costs. Therefore, re-sighting rate *does* indicate a cost of reproduction, although, when interpreted as survival, it may overestimate the true costs.

I will now try to calculate whether the re-sighting rate can explain why the most common clutch size in Kittiwakes is two eggs. Table 14 shows the residual reproductive value (*RRV*) after the 1996 breeding season. I did not regard the possibility that birds moved to another breeding site, as Coulson & Wooller (1976; but see Danchin & Monnat, 1992) did not record any such movement in 20 years of observation. The *RRV* for birds alive in 1996 was 2.40 ± 0.09 (app. A, p. 61),assuming that the age distribution of the birds used in the experiment was the same as in the rest of the population. I also used the same life table for male Kittiwakes, results for males can, therefore, probably only give a rough estimate. Table 14 considers two models with different assumptions.

- The first model ("Wooller") assumes that 9.6 % of females and 4.5 % of males are intermittent breeders. These numbers are calculated from data of Wooller & Coulson (1977; cf. p. 61) and the age distribution of the population that follows from table A1 (p. 59). Missing birds beyond the ones taken to be intermittent breeders, are assumed to be dead.
- The second model ("Mortality") assumes that all birds that were not re-sighted have died.

Both models amplify the observations for adult re-sighting rate from figure 10: the *RRV* is highest for females that reared control broods and for males that reared enlarged broods. This could explain why single-egg clutches are not more common in the Kittiwake. As regards three-egg clutches, it seems that males and females have different optima (cf. Jacobsen et al., 1995): females should indeed prefer two-egg clutches, but males should favour three-egg clutches.

There are, however, parameters involved in the term "future reproduction" other than just the chances of surviving to the next reproductive event. Costs of reproduction can also lower future reproduction without leading to an increase in mortality (Nur, 1984; Gustafsson & Sutherland, 1988). These other aspects will be discussed in the rest of the section.

Table 14: Residual reproductive value in 1996. Residual reproductive value (*RRV*) of adult Kittiwakes that reared manipulated broods in 1995. The different models are explained in the text. Calculation of the mean *RRV* of birds alive is based on table A1 for both females and males.

Model		Brood size		
		reduced	control	enlarged
ALL NESTS				
"Wooller"	♀	1.97	2.17	1.87
"Wooller"	♂	2.19	1.85	2.10
"Mortality"	♀	1.74	1.94	1.64
"Mortality"	♂	2.09	1.75	1.99
MIN 12 d[a]				
"Wooller"	♀	2.12	2.21	1.98
"Wooller"	♂	2.22	2.11	2.40
"Mortality"	♀	1.89	1.97	1.75
"Mortality"	♂	2.11	2.00	2.40

[a] only nests that maintained their manipulated brood sizes for at least 12 days

Change of mate or nest site

Many colonial seabirds exhibit an intense breeding site tenacity which is associated with a high incidence of between-year mate fidelity (e.g., (Coulson, 1972; Richdale & Warham, 1973; Ollason & Dunnet, 1978). I discuss this aspect in more detail in appendix E. The levels of mate retention in my study (tab. 11, p. 26) are close to the one reported in literature (73 %, Fairweather & Coulson, 1995). As regards nest site fidelity, Coulson & Wooller (1976) stated that Kittiwakes very seldom move. Accordingly, I did not observe any pair that moved together to a new nest site ($n = 34$). When also divorced pairs were considered, change in nest site was still low in "reduced" and "enlarged" pairs. Only among "control" birds was the rate of nest change surprisingly high, with both partners moving in 42 % of the pairs. But these differences between treatments were not significant. However, when also pairs with one non-resighted bird were included, the relation between treatment and nest site change was significant. But this relationship was probably brought about by chick loss in the previous year (app. E).

I am not able to demonstrate any effect of treatment on mate retention, the tendency was, however, opposite to the one expected (tab. 11). The manipulated brood size of the previous year did thus not affect the birds' decision in favour or against divorce. It is rather the fact whether or not a breeding failure occurred, that is significant (see app. E).

Parental early body condition

As could be seen from table 11, female early body condition is related to treatment. This indicates that the birds were unable to compensate for costs incurred in the previous season. This is one of the crucial assumptions underlying the concept of reproductive costs and can be verified with my data.

However, female state at the beginning of a breeding season is not the only factor determining the females' reproductive success in the respective year. In some species, it has even been shown that body condition did not have any obvious influence on reproductive performance (Naylor & Bendell, 1989; Marjakangas & Aspegren, 1991; Meathrel et al., 1993). Therefore, I will now consider other factors affecting the reproductive output.

Next year's clutches

A positive relation between clutch size and body condition – which itself can, as just shown, be a function of the previous year's brood size – is reported from several species (Nisbet, 1977; Ankney & MacInnes, 1978; Drent & Daan, 1980; Houston, Jones & Sibly, 1983; Coulson & Porter, 1985). In the Kittiwake, however, one would expect that the effect of treatment would have to be enormous before it significantly affects the clutch size laid the year after treatment. This is because, with a median clutch size of two eggs, one egg more or less equals 50 % of the egg production. It is unlikely that the thresholds for the decision as to whether one additional / one less egg should be laid, are affected strongly enough to cause an observable deviation. Accordingly, I was not able to detect any treatment effect in clutch size (tab. 12, row 1, p. 27).

Egg volume, on the other hand, can vary at much smaller scales. It is considered the biologically most relevant egg measurement as it indicates "how much energy was put into the egg and the amount of reserves available for the hatching chick" (Coulson, 1963a; cf. Ricklefs, Hahn & Montevecchi, 1978). Accordingly, a positive relation between egg volume and both hatching and fledging success in Kittiwakes was reported by Thomas (1983; app. B, p.63), and is also known from other species (Bolton, 1991, and references therein). I discuss this question in more detail in appendix B. In my data, there is, however, no obvious tendency in egg volume (tab. 12, row 2).

As Coulson (1963a) reports a correlation between egg volume and clutch size – which was, however, not present in my own data (see app. B)–, I additionally tested the effect of treatment restricting the analysis to the egg volumes of two-egg clutches in 1996 (tab. 12, row 3). But not even this test showed any treatment effect, probably due to a further diminished sample size.

The expected relation between treatment and next year's hatching success should be negative when a cost of reproduction is involved. The effect is, however, difficult to interpret in my data because the lowest value occurs in the control group (tab. 12, row 4), but the differences are not significant anyway. Restricting analysis to clutches of two eggs renders the logistic regression significant (tab. 12, row 5). Indeed, the also the correlation is negative – which would meet the expectations –, but not significantly so (Spearman: $r = -0.28$, $p = 0.165$). The evidence is thus equivocal, but, especially taken together with my finding that female body condition was related to treatment, allows for an interpretation as reproductive costs. Birds with low body condition may for instance fail to incubate continuously because they have to spend more time feeding, and can consequently only take shorter incubation "shifts".

The significance of laying date is ambiguous (see app. F for details). But Lessells (1986) was, for example, able to document that Canada Geese *Branta canadensis* that had reared enlarged broods bred later in the following season.

I was not able to record laying dates, but hatching dates should give a good estimate of laying date (cf. app. C, p. 71). In my data on hatching date (tab. 12, row 6), the direction of the tendency is opposite to that expected: eggs hatch later, the smaller the brood sizes their parents had the year before. But this tendency was not significant. Neither restriction of the analysis to clutches of two eggs (tab. 12, row 7), nor correction for hatching dates of the previous year, changed the picture. The most parsimonious explanation is thus that hatching date was not affected by treatment.

As regards hatching asynchrony, this phenomenon was discussed earlier in connection with facultative brood reduction (p. 33). Evidence was presented showing that parents may enhance brood reduction by creating a hierarchy among offspring. They can do so by means of hatching asynchrony, i.e. by starting to incubate before all eggs are laid (Runde & Barrett, 1981). If this is so in the Kittiwake, one could expect weakened parents to take smaller risks concerning brood size by enhancing dominance differences between offspring. Brood reduction can then, later in the chick rearing period, be a possibility to adjust brood size to food availability and parental state. Parents with high body condition might rely more on their ability to feed any brood size regardless of later environmental conditions (Wiebe, 1995). Therefore, the expectation is an increase in hatching asynchrony with increasing manipulated brood size in the year before. Again, the tendency in my data is ambiguous, as "control" birds, though only with a sample of 2, have the highest hatching asynchrony. In spite of that, the overall tendency meets the expectations, but is not statistically significant (tab. 12, row 8).

Next year's offspring

The significance of the proportion of nests that lost chicks and of time of chick loss was discussed in section 4.1 in connection with intra-seasonal effects of treatment. When there are costs of reproduction, one could expect a decreasing ability of parents to maintain their brood sizes with increasing manipulated brood size the year before. This was the case, both when the proportion of nests that lost at least one chick (tab. 12, row 9) and the ones that lost all chicks (tab. 12, row 11) were considered.

I know of no other study that has been able to show similar effects of treatment on the future reproductive success of long-lived birds. The present study is thus the first one to document such effects. From short-lived species, such trade-offs are well-known (e.g., Slagsvold, 1984).

Synthesis

The re-sighting probability of Kittiwakes was not related to the brood size in the year before. This finding is, even though in contradiction to the one of Jacobsen et al. (1995), not surprising, because there are only very few studies that could show such effects in long-lived species (Reid, 1987). But there was other evidence for costs of reproduction: there was an ambigous trend in hatching success and a very clear tendency in chick loss that must be interpreted as a consequence of a trade-off between current (1995) and future (1996) reproduction. In combination with the relation I found between early female body condition to treatment, this interpretation seems to be appropriate.

4.4 Parental overall fitness

I shall now attempt to calculate adult fitness in relation to experimental treatment. When I use the equation used by Jacobsen et al. (1995),

$$W = N \cdot p_j \cdot S + p_a \qquad \text{(eqn. 3)}$$

with N, number of fledglings; p_j, juvenile survival rate one year after fledging; S, sex ratio; p_a, adult survival,

and let $p_j = 0.79$ (Coulson & White, 1959), $S = 0.5$, I obtain the fitnesses given in table 15.

As is apparent from table 15, all birds, regardless of sex and of whether failed nests were excluded, maximized their fitness by rearing enlarged broods. This is in contradiction to both the study of Jacobsen et al. (1995), were females with reduced, and males with control broods had maximum fitness, and expectations from life-history theory: organisms that are adapted to their environment should behave optimally (Grafen, 1991). But, according to the fitness values calulated with equation 3, Kittiwakes with experimentally enlarged broods do better than the majority of Kittiwakes in the Hornøya colony – which only lay two eggs (tab. 1, p. 10).

Table 15: Adult fitness. The contribution of individuals to the next year by adult Kittiwakes rearing manipulated broods. Calculated according to equation 3.

		Brood size		
		reduced	control	enlarged
All nests	♀	0.94	1.11	1.14
	♂	1.09	1.03	1.28
Excluding failed nests	♀	1.18	1.40	1.45
	♂	1.27	1.41	1.73

Equation 3 does not, however, take into consideration offspring fitness or the future reproduction of adults surviving; an adult bird surviving is weighted just as much as two single juveniles. This does not correctly represent the reproductive value of an adult bird (cf. tab. A1, p. 59). I use, therefore, another method of calculating adult fitness. As it is – under some conditions discussed by Schaffer (1979) and met in the Kittiwake – possible to view the maximization of fitness as equivalent to maximizing reproductive value of each age class, I shall consider reproductive value instead of fitness. Following the definition of reproductive value in a stationary population ($r = 0$),

$$v_x = l_x^{-1} \cdot \sum_{i=x}^{\omega} m_i \cdot l_i \qquad \text{(eqn. 4)}$$

with x, age in years; l_x, survival from fledging to age x; ω, age at last reproduction; m_x, fecundity at age x,

the reproductive value of the birds in the experiment can be written as

$$v_x = m_x + p_x \cdot m_{x+1} + RRV_{x+1} \qquad \text{(eqn. 5)}$$

with p_x, survival from age x to age $x+1$; RRV_x, residual reproductive value at age x.

I will now use means, rather than individual values, and indicate that by using years (95 and 96), not ages, as indices:

$$v_{95} = \sum_{i=\alpha}^{\omega} v_i \cdot c'^{-1}_i \qquad \text{(eqn. 6)}$$

with α, age at first reproduction; c'_x, proportion of birds aged x in the breeding population.

Then, the mean reproductive value is

$$v_{95} = m_{95} + p_{95} \cdot m_{96} + RRV_{96}. \qquad \text{(eqn. 7)}$$

m_{95} can be taken from table 5. m_{96} can be calculated from table 12, letting

$$m_{96} = cs_{96} \cdot hs_{96} \cdot fs \cdot S \qquad \text{(eqn. 8)}$$

with cs_{96}, clutch size; hs_{96}, hatching success; fs, fledging success,

and $fs = 0.59$ (Barrett & Runde, 1980), $S = 0.5$. p_{95} is unknown (see p. 69), but as fecundity is zero in the year following a year with zero survival, it does not have to be known, either, when m_{96} is calculated. But then it has to be known when calculating RRV_{96}. I solve this problem by adopting the values from table 14 for the RRV of adults in 1996.

Further, offspring fitness is not taken into account. Here, I can use correction factors obtained by dividing the recruitment rates from table 13 by average recruitment (0.339, tab. A1). This is better than using first-year survival, as in equation 3, for two reasons:

- Values from literature on first-year survival (Coulson & White, 1959; Aebischer & Coulson, 1990) do not take into account individual differences in offspring quality.
- The first spring after fledging is anyway an unusual moment for determining the parents' reproductive success of the previous year. Normally, one uses either hatching, fledging (independence), or recruitment. This is because the "currency" used for determining offspring production should be the same as for reproductive value. Under field conditions, the currency "offspring alive after their first winter" is difficult to obtain.

By using different models from tables 12 and 13, one obtains different estimates of reproductive value. I show three examples in table 16. What becomes clear is that, besides the case that also failed nests are considered, only the combination of the two most radical models leads to the conclusion that females rearing control broods maximized their reproductive value: this result relies upon on overproportional effect of fledging mass on chances of recruitment (model "Wooller", tab. 13) and on that all birds not re-sighted had died (model "Mortality", tab. 14). While the first assumption appears to be justified (Coulson & Porter, 1985), I criticize the latter one in the critique of methods (p. 69) and in appendix E (p. 75). It is thus more likely that females rearing enlarged broods maximized their reproductive value, as is the case in all other combinations of models. This also applies to all model combinations in males. The finding of Jacobsen et al. (1995) that there is a conflict about clutch size between sexes can thus also only be supported by combining the two most radical models.

The result can be shown graphically using a constraint function (fig. 15). In this diagram, current reproduction is plotted against future reproduction. The grey line represents conditions of equal fitness. The expectation when conducting a manipulation experiment is that the control group maximizes fitness, i.e. that the fitness curve does not intersect the grey line, but merely meets it in one point (broken line with open symbols in fig. 15). My findings are, however, that the fitness curve intersects the grey line, and that enlarged broods maximized fitness. This is shown by the black line with solid symbols in figure 15, which uses data from table 5 for the axis "current reproduction" (offspring production in 1995 times sex ratio), and data from table 13 for the axis "future reproduction" (reproductive value from tab. 16, based on model "Wooller").

Table 16: Adult reproductive value. Some illustrating calculations of adult reproductive value of Kittiwakes that reared manipulated broods. Model names refer to tabs. 13 & 14.

Models		Brood size		
		reduced	control	enlarged
ALL NESTS				
"Lack +	♀	2.61	2.86	2.77
Wooller"	♂	2.89	2.51	3.07
"Proportionality	♀	3.05	3.07	3.25
+ Survival"	♂	3.13	3.04	3.32
"Coulson +	♀	2.41	2.63	2.38
Mortality"	♂	2.84	2.41	2.90
MIN 12d[a]				
"Lack +	♀	2.87	2.95	3.47
Wooller"	♂	3.01	2.85	4.00
"Proportionality	♀	3.18	3.37	3.36
+ Survival"	♂	3.22	3.37	3.47
"Coulson +	♀	2.68	3.28	2.97
Mortality"	♂	2.94	3.31	3.73

[a] only nests that maintained their manipulated brood sizes for at least 12 days

To summarize my findings so far, I was not able to demonstrate why Kittiwakes do not lay clutches of three eggs more often, as this seems to be the clutch size that maximizes their reproductive value. One possible reason for this difference was mentioned earlier (p. 32), namely that even offspring recruitment does not take into consideration all relevant variation in offspring quality. Further, costs of reproduction might act over time scales larger than just the following breeding season because they, for example enhance parasitic infections (Daan & Tinbergen, 1997). There are, however, some additional factors that could explain the difference between the most common and the optimal clutch (Stearns, 1992) which were not taken account of by this study:

1) Frequent brood parasitism should favour adults that decrease the clutch laid by them.
2) Gene flow from other populations that face other environmental conditions prevents adaptation to the local conditions.
3) Asymmetric offspring survival curves punish parents more for producing one additional young than for producing one less young than the optimum.
4) The costs incurred by parents prior to reproduction or during egg production and incubation are too high to lay additional eggs.
5) Temporal variation in environmental conditions and/or the inability of parents to forecast such changes will lead to suboptimal clutch sizes in single years.

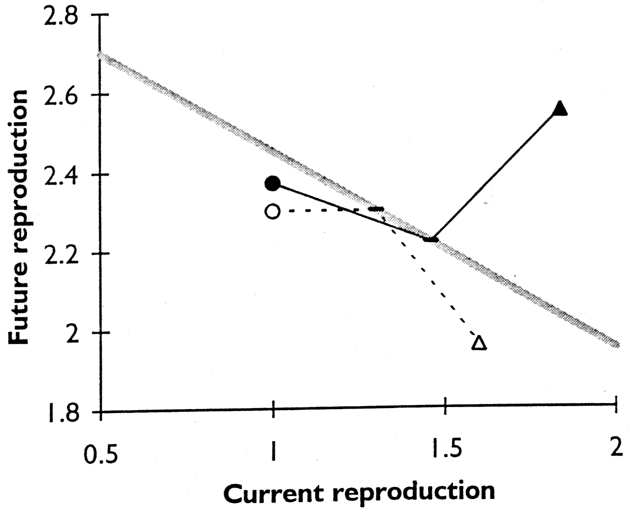


Figure 15: Constraint function depicting the cost of reproduction. Diagram relating current to future reproduction. The bold grey line represents conditions of equal fitness. Symbols represent treatment (circle, reduced brood size; triangle, enlarged brood size). The broken line with open symbols shows the expectation in a manipulation experiment. The black line with solid symbols depicts my findings (based on model "Wooller"; cf. tab. 13).

The first three hypotheses cannot, in my opinion, explain the patterns observed by me. First, there is no known evidence that brood parasitism normally occurs in the Kittiwake. As regards the second hypothesis, there does not seem to be much exchange with breeding colonies further south in Europe as is indicated by the general differences, for instance in size, between British and Norwegian Kittiwakes. That environmental conditions along the Norwegian and Russian coast are so different that adaptation can be hindered by gene-flow between these colonies, seems quite unlikely to me. There are, however, no data that are able to monitor these hypothetical differences. The third hypothesis would only make sense in the Kittiwake when clutches with four eggs occur, but there is no such record.

The fourth point, however, very recently received some attention: Price & Liou (1989) addressed costs prior to reproduction that might be neglected. Further, Monaghan & Nager (1997) reviewed the evidence that laying and incubating eggs is more costly than widely appreciated. Lack (1947) assumed that the costs of egg production is not a factor limiting clutch size. Though it is true that feeding young is most often more costly than producing or incubating eggs (Drent & Daan, 1980), this does not justify a neglection of this factor. As regards the costs of incubation in the Kittiwake, this issue is currently being addressed by Eriksen (1997). His findings show that incubating is indeed costly, as paternal body mass is negatively related to the manipulated clutch size incubated. Furthermore, there is a tendency that chick loss occurs earlier in nests that contained enlarged clutches during incubation. Eriksen's (1997) data can, however, not explain my finding that enlarged broods maximized reproductive value, because fledgling production was not related to manipulated clutch size. It is therefore important to combine Eriksen's (1997) and my approach in one experiment to assess the combined costs of both incubating and rearing enlarged clutches/broods (Monaghan & Nager, 1997), and to further address the costs of egg laying, for instance by inducing re-laying by removing newly laid eggs. It is possible that the costs of incubating and of rearing are not demonstrated when examined separately, but that they become apparent when the same birds are exposed to both of them.

The point made by the fifth hypothesis is that conditions may be different in different years. I will discuss this idea in the following section by comparing my results with the one of a similar study in another year.

4.5 Differences between years

As already mentioned, a study with an experimental design very similar to this study was carried out five years before mine (Jacobsen, 1993; Jacobsen et al., 1995). It is thus possible to compare some of the results from 1990 and from 1995. I cannot, however, establish any trends or final results from only two years of observation, but I can point out some striking differences.

Some of the differences will be attributable to improvements in the experimental design. This applies most probably to the fact that Jacobsen (1993) did not find differences between early and late body masses in "control" and "reduced" males. The differences were highly significant in my study (tab. 8, p. 23; fig. 10, p. 24). This could be due to the narrower time intervals I used for catching and weighing the adults (cf. p. 13).

In other cases, the reasons for differences between the both studies might not have anything do to with the experiment or with Kittiwakes at all. For example the differences in the

Table 17: Comparison between results from brood size manipulations in 1990 and 1995. Data from 1990 come from Jacobsen et al. (1995; chick loss & fledging success, fig. 1; chicks fledged, tab. 1; chick late body mass, fig. 3; female late body mass, fig. 4; female re-sighting rate, fig. 5). Data from 1995 come from this study. Tests are two-tailed.

Variable	df	test observator	*p*
CHICK LOSS [a]			
Treatment	2	30.81	0.001***
Year	1	1.68	0.195
Treatment × year	2	1.18	0.553
Error	115		
CHICKS FLEDGED [a]			
Treatment	2	28.97	0.001***
Year	1	1.23	0.268
Treatment × year	2	2.17	0.338
Error	115		
FLEDGING SUCCESS [a]			
Treatment	2	21.24	0.001***
Year	1	0.01	0.920
Treatment × year	2	5.18	0.075
Error	115		
CHICK LATE BODY MASS [b]			
Treatment	2	8.64	0.001***
Year	1	0.18	0.755
Treatment × year	2	0.17	0.842
Error	161		
FEMALE LATE BODY MASS [b]			
Treatment	2	1.40	0.252
Year	1	110.30	0.001***
Treatment × year	2	0.50	0.606
Error	115		
FEMALE RE-SIGHTING RATE [a]			
Treatment	2	4.28	0.118
Year	1	0.10	0.755
Treatment × year	2	2.50	0.286
Error	103		

[a] test performed was logistic regression, test observator is χ^2

[b] test performed was ANCOVA, test observator is *F* value

timing of chick loss between the studies (p. 32) may reflect different abundances or activity patterns of the predators, especially the *Larus* species, rather than differential behaviour of Kittiwakes in 1990 and 1995.

There are, however, some other aspects of more interest which are summarized in table 17 (parts of this section have been presented before as a poster, Pichl et al., 1997). The two traits I want to focus on are number of fledglings and female re-sighting rate:

- Kittiwakes were not able to rear an additional chick in 1990, while *production of offspring* was higher among enlarged broods than among controls in 1995. This trend was only marginally significant. In fledging *success*, the treatment × year interaction was also marginally significant.
- Females rearing enlarged broods had the lowest probability of being re-sighted in the 1991 breeding season. The tendency was the same in 1995/1996, i.e. *re-sighting rate* decreased with increasing brood size, but, in contrast to 1990/1991, not significantly so.

The effects of treatment were discussed in the previous sections. The effect of year is not surprising as marine ecosystems exhibit high levels of stochasticity (Aebischer, 1986; Ainley et al., 1990; Ashmole, 1991; Murphy, Springer & Roseneau, 1991; Sakshaug et al., 1994). It is obvious that changes in for instance food supply will affect chick growth such that chick growth is faster in a better year (1995). It is thus mainly the treatment × year interactions that are of interest. In spite of the differences summarized above, only in the case of fledging success was the interaction marginally significant (tab. 17).

This interaction and the other tendencies observed, challenge the prevalent view that long-lived birds do not increase parental effort. This belief was built upon the hypothesis that natural selection favours a more reluctant response to offspring demands in long-lived birds (e.g., Charlesworth, 1980; Wooller et al., 1992). So far, only a few brood-size manipulation experiments have been carried out on long-lived bird species. Their evidence does not, however, fully support the expectations, as many seabirds are able to successfully rear increased broods (Ydenberg & Bertram, 1989). The willingness to feed additional chicks in seabirds demands an explanation. Erikstad et al. (in press) proposed that part of that explanation is that the mentioned assumptions are only met in some years, namely in average and below-average years as expressed in breeding condition. One might think of an upper threshold in breeding conditions that has to be crossed before seabirds are willing to increase their investment into current offspring (fig. 16). In both of

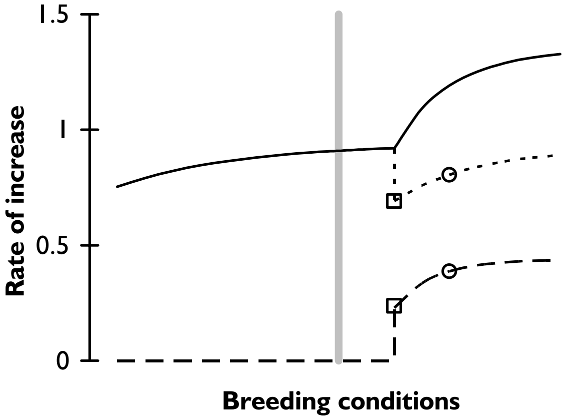


Figure 16: Breeding performance in a stochastic environment. The figure shows the rate of increase (λ) of a seabird genotype in relation to breeding conditions which are normally distributed around the mean (grey line). Reproductive output (broken line) increases first when conditions reach a threshold above the mean, accompanied by a steep decrease in survival (dashed line). Under still more favourable conditions, both reproductive output and survival increase. The solid line depicts the total rate of increase. Source: Erikstad et al. (in press). Squares indicate breeding conditions for the Kittiwake in 1990, circles indicate breeding conditions for the Kittiwake in 1995.

the two years considered here, breeding conditions obviously lay above the threshold, as indicated by the open squares and circles in figure 16. But breeding conditions in 1990 (squares) obviously lay just above the threshold, i.e. adults did not abandon their broods (dashed line), but this was accompanied by a steep decrease in survival (dotted line). In 1995 (circles), under still better conditions, the Kittiwakes were able to rear still more young, but without incurring a survival cost.

In conclusion, it can be said that the Kittiwake is adapted to stochastic marine environments in which responses to brood size manipulation will differ between years. Questions of whether a certain trade-off exists, e.g. reproduction versus adult survival, need, therefore, several breeding seasons of observations to be answered thoroughly. This agrees with the theoretical predictions made by, among others, Schaffer (1974; cf. Stearns, 1976, and references therein) that fluctuating environments favour reductions in per capita reproductive output. In fact, the observed clutch size in species adapted to variable environments are close to that which maximizes geometric mean fitness (Boyce & Perrins, 1987; Partridge & Harvey, 1988).

As mentioned above, two years of observation are not enough to answer the question of which environmental factors are responsible for whether breeding conditions for Kittiwakes lie above or below the threshold. Besides climatic conditions (Aebischer, Coulson & Colebrook, 1990), one important factor will, however, be food availability (Harris & Wanless, 1990; Murphy et al., 1991). Barrett & Krasnov (1996) found, for instance, a clear relation between the proportion of capelin in Kittiwake diet and the breeding success of the respective year. But, as already mentioned, two data points are not enough to see whether these factors account for the variation on the "breeding condition" axis in figure 16.

4.6 Conclusions

I studied the life-history trade-offs of the Kittiwake by subjecting randomized breeding pairs to a brood size manipulation. I then studied various traits in relation to whether the respective broods were reduced (one chick), controls (two) or enlarged (three chicks). My aim was to identify the factors that constrain the Kittiwake clutch to a median size of two eggs.

I found some evidence that supported Lack's (1947) assumption that fledging success would decline with an increase in brood size beyond the optimum as a consequence of the parents' inability to meet the chicks' food demands: Fledging success was lower in enlarged broods, and survival probability to day 9 post-hatch was inversely related to brood size. However, in contradiction to Lack's predictions and in accordance with a large body of experimental evidence (reviewed by Ydenberg & Bertram, 1989, Dijkstra et al., 1990, and VanderWerf, 1992), I found that the number of fledglings produced was slightly larger in enlarged broods.

I then checked whether Lack's solution clutch size (Charnov & Skinner, 1984) could explain this difference by taking into consideration the quality of offspring. Indeed, chick body mass 18 days post-hatch was inversely related to brood size, indicating a trade-off between number and quality of offspring. I then calculated different models of how fledging mass would influence the chicks' chances of being recruited to the breeding population. I found that not even the most radical model considered could explain the clutch size in Kittiwakes, thus also falsifying Lack's solution clutch size.

I then concentrated on adult traits and found clear evidence for a trade-off between reproduction and adult state in females, both when calculated as late body mass, as mass loss, or as late body condition. Male Kittiwakes did not show similar trends. These differences in late female state did, however, not affect female survival as inferred from re-sighting rates. A trade-off between reproduction and survival was thus not documented. But the relation between brood size and body condition was still present at the beginning of the next year. Accordingly, there were some other relations between brood size and next year's offspring that can be interpreted as evidence for a cost of reproduction: hatching success decreased and the chances of chick loss increased with increasing brood size the previous year. The latter findings are rather unexpected for a long-lived bird species as the Kittiwake (Wooller et al., 1992).

Nevertheless, I was not able to show that any convincing combination of these trade-offs explained the median clutch size of two eggs. Only when one assumes that all birds that were not re-sighted died – an assumption that I could not support (pp. 69 & 75) – females with control broods had a slightly larger reproductive value than had females rearing enlarged broods. Among the factors I discussed that could explain this deviation from the optimal clutch size, are the costs of producing and incubating the eggs (Monaghan & Nager, 1997), and the fact that marine environments exhibit high degrees of stochasticity (Schaffer, 1974; Ashmole, 1991). The latter hypothesis leads to the conclusion that birds should react differently to experimental treatment in different years. The year observed by me could simply have been a better-than-average one, such that the trade-offs constraining clutch size did not become evident. The evidence collected so far does not allow us to identify the factors that are important for making a year better than others.

This finding supports the need for a repetition of this study over several years. In the future, some improvements should be taken into account in the experimental design. Among these suggestions are that chicks could be individually marked, that recruitment should be estimated by ringing fledglings (p. 67), and that studies on the costs of egg production and of incubation should be combined with this experiment (p. 46).

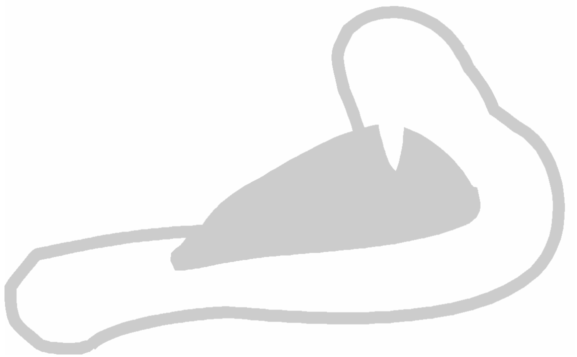


Figure 17: The fyrmesterbakken.

5

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* * *

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Appendix A

Demography

As could be seen from the survey in table 1 (p. 10), life-history data vary considerably between Kittiwake colonies in North Norway and the one studied by Coulson and co-workers in North Shields, England. This is propbably due not only to latitude, but also to the fact that there was virtually no nest predation at North Shields. Therefore, it would be optimal to use North Norwegian data for the following calculations. But there are not yet enough data available to construct a life table. Estimates of age at first breeding are lacking as well as frequency of intermittent breeding, nor have changes of survival or fecundity with breeding experience been documented. To take the lacking values from the North Shields data can produce artefacts which in the worst case differ more from reality than when all data would have been taken from Coulson et al.'s data. Therefore, I calculated both chick recruitment and parental overall fitness with the North Shields data. My calculations will thus not meet the real conditions, but merely illustrate trends. Clearly, there is need for more accurate life-history data on Kittiwakes breeding in the Arctic.

Life table

It is possible to construct a life table from the life-history parameters given in table 1 (p. 10) for the Kittiwakes studied at North Shields. This life table is presented in table A1. The calculations it is based upon are given in the following equations.

Fecundity denotes the number of female fledglings produced by a female Kittiwake of the given age. As literature only gives clutch size and hatching success in relation to breeding age *y*, not to real age *x*, I let

$$x = \alpha + y \qquad \text{(eqn. A1)}$$

with α, age at first reproduction (5.1 a; Wooller & Coulson, 1977); y, breeding age.

Fecundity can thus be calculated as

$$m_{\alpha+y} = cs_{\alpha+y} \cdot hs_{\alpha+y} \cdot fs \cdot S \qquad \text{(eqn. A2)}$$

with $cs_{\alpha+y}$, clutch size at breeding age y (Thomas, 1983); $hs_{\alpha+y}$, hatching success at breeding age y (Coulson & Thomas, 1985a); fs, fledging success (0.88; Coulson & Thomas, 1985a); S, sex ratio of offspring (0.50).

A mean age at first reproduction of 5.1 years means that, on average, 90 % of females reproduce for the first time at an age of 5 years, while 10 % do so one year later. Furthermore, intermittent breeders do not reproduce at all in the given age, so that their proportion has to be excluded from the calculation of mean fecundity at age *x*:

$$m_x = (0.9 \cdot (1 - ib_{5+y}) \cdot cs_{5+y} \cdot hs_{5+y} + 0.1 \cdot (1 - ib_{6+y}) \cdot cs_{6+y} \cdot hs_{6+y}) \cdot fs \cdot S \qquad \text{(eqn. A3)}$$

with $ib_{\alpha+y}$, frequency of intermittent breeding at breeding age *y* (Wooller & Coulson, 1977).

The same correction for age at first reproduction is necessary to calculate the annual survival rate:

$$p_x = 0.9 \cdot p_{5+y} + 0.1 \cdot p_{6+y} \qquad \text{(eqn. A4)}$$

with $p_{\alpha+y}$, annual survival at breeding age *y* (Aebischer & Coulson, 1990).

Assuming no decline in survival rate, one female in the Hornøya colony should be 94 years old (ln[1/20.000]/ ln[90%]), as Botkin & Miller (1974) demonstrated. They criticize this assumption to be unrealistic. Unfortunately, there are no data available on the potential natural longevity in Kittiwakes. I therefore arbitrarily chose the year when l_x dropped beneath 0.0005, to finish the life table by letting $p_x = 0$.

There are no reliable estimates of Kittiwake juvenile survival. It is commonly assumed that second-year survival equals adult survival (Lack, 1954). On this assumption, Coulson calculated Kittiwake yearling survival to amount to 0.79 (Coulson & White, 1959), later correcting this estimate with a larger sample size to 0.70 (Coulson, 1988). I calculated a p_0 that would lead to a stable population (see below), and found it to amount to 0.775. This estimate lies between the ones of Coulson, thus I took it to be acceptable. When trying to calculate a life table for male Kittiwakes with the same

Table A1: Life table of female Kittiwakes. List of annual fecundity (m_x, number of female fledglings), survival (p_x, chance of surviving from age *x* to age *x*+1; l_x, chance of surviving from fledging to age *x*), residual reproductive value (RRV_x, mean expectancy of female fledglings during the rest of life for a female aged *x*), and fraction (c'_x, proportion of *breeding* population aged *x*) as an function of age (*x*, years) in female Kittiwakes. Table is based on combined vertical and horizontal data from Wooller & Coulson (1977), Coulson & Thomas (1984), Aebischer & Coulson (1990), and assumes a stable population (r=0).

Age x	Fecundity m_x	Survival p_x	 l_x	RRV_x	Fraction c'_x
0	0.00	0.775	1.000	1.00	–
1	0.00	0.813	0.775	1.29	–
2	0.00	0.813	0.630	1.59	–
3	0.00	0.813	0.512	1.95	–
4	0.00	0.813	0.417	2.40	–
5	0.41	0.813	0.339	2.54	0.187
6	0.42	0.823	0.279	2.67	0.154
7	0.59	0.824	0.227	2.69	0.125
8	0.61	0.824	0.187	2.65	0.103
9	0.63	0.821	0.154	2.59	0.085
10	0.64	0.821	0.126	2.51	0.070
11	0.65	0.821	0.104	2.41	0.057
12	0.65	0.821	0.085	2.29	0.047
13	0.65	0.810	0.070	2.13	0.039
14	0.65	0.809	0.057	1.98	0.031
15	0.60	0.809	0.046	1.84	0.025
16	0.60	0.809	0.037	1.68	0.020
17	0.60	0.723	0.030	1.47	0.017
18	0.60	0.713	0.022	1.44	0.012
19	0.60	0.713	0.015	1.42	0.008
20	0.60	0.713	0.011	1.39	0.006
21	0.60	0.713	0.008	1.35	0.004
22	0.60	0.713	0.006	1.29	0.003
23	0.60	0.713	0.004	1.22	0.002
24	0.60	0.713	0.003	1.11	0.002
25	0.60	0.713	0.002	0.95	0.001
26	0.60	0.713	0.001	0.73	0.001
27	0.60	0.713	0.001	0.43	0.001
28	0.60	0.000	0.001	0.00	0.000

assumptions, I arrived, however, at a first-year survival that amounted to 0.856. This assumption is quite unrealistic (Lack, 1954; Sæther, 1989) because male first-year survival would then be higher than the annual survival rate of any other age group. That is the reason why I did not construct a life table for male Kittiwakes, as well.

Survival to age *x* can be calculated from annual survival:

$$l_x = \prod_{i=0}^{x-1} p_i. \qquad \text{(eqn. A5)}$$

From these parameters it is possible to calculate reproductive value which is defined as

$$v_x = l_x^{-1} \cdot \sum_{i=x}^{\omega} m_i \cdot l_i \qquad \text{(eqn. A6)}$$

when the population is neither growing nor declining ($\lambda = 1$, $r = 0$). As should be expected under these conditions, reproductive value of fledglings is 1.0 (tab. A1).

Further, it is possible to calculate the age distribution from l_x, also given that the population is stable. The fraction c_x of individuals of age x in the total population is

$$c_x = l_x \cdot (\sum_{i=0}^{\omega} l_i)^{-1}. \qquad \text{(eqn. A7)}$$

I am, however, not interested in the total, but only in the breeding population. The last column in table A1 gives this fraction c'_x of individuals of age *x* in the breeding population, which was obtained by replacing the zero in equation A7 with α.

Recruitment of chicks

Coulson & Porter (1985) presented data on the relation between the growth rate of chicks and their chances of recruitment to the breeding population. I calculated the regression between their data on growth rate and recruitment chances (logistic regression: df = 1,3, $r^2 = 0.98$; intercept, $t = -4.52$, $p < 0.021$; slope, $t = 11.74$, $p < 0.002$) as

$$rc = 0.234\ \% \cdot \partial m^{1.369} \qquad \text{(eqn. A8)}$$

with ∂m, change in chick body mass per day.

By dividing the chick mass gain by $\partial m_{\text{control}}$ which was taken from table 7 (p. 22), the recruitment equals the one in table A1 (l_α) for control broods. The algorithms for the three models in table 13 (p. 31) are thus as follows:

$$rc = l_\alpha \qquad \text{(eqn. A9)}$$

for the model "Lack",

$$rc = l_\alpha \cdot \partial m / \partial m_{\text{control}} \qquad \text{(eqn. A10)}$$

for the model "Proportionality", and

$$\mathrm{rc} = l_{\alpha} \cdot (\partial m/\partial m_{\mathrm{control}})^{1.369} \qquad \text{(eqn. A11)}$$

for the model "Coulson". The values in table 13 are attained by multiplying *rc* with the number of fledglings *N*.

Residual reproductive value

To calculate the *RRV* of the birds used in the experiment, I first had to find a figure of the ages of the birds. Assuming that the age distribution was the same in the experimental sample as in the rest of the population, I could use the row *c*' in table A1. Then using the residual reproductive values of the respective age classes from the same tables, I was able to calculate an average *RRV*:

$$RRV_{96} = \sum_{i=\alpha}^{\omega} RRV_{i+1} \cdot c'_{i}. \qquad \text{(eqn. A12)}$$

I found the average *RRV* of birds used in the experiment in 1995 to amount to 2.40 in 1996. This value was used in table 14 (page 39).

Furthermore, I needed to know the proportion of intermittent breeders. I also calculated it by using the age distribution from table A1, replacing *RRV* in equation A12 with *ib* and taking these numbers from Wooller & Coulson (1977).

Appendix B

Biometry

Use of skull length in sexing

Coulson et al. (1983) proposed to use head + bill length in sexing of gulls. Barrett et al. (1985) found that 87 % of adult Kittiwakes on Hornøya were sexed correctly by using a head+bill length of 92.1 mm as discriminant value. I sexed birds by comparing head+bill lengths within a pair (cf. p. 14), thus reducing the risk of a wrong sexing to 1.6 % when one assumes random mating and normally distributed skull lengths in both sexes.
The latter assumption can be checked in figure B1 which shows the distribution of head+bill lengths. When female and male head+bill lengths are plotted separately, both appear to be normally distributed. In contrast to the study of McGowan & Zonfrillo (1995), I find a clearly bimodal distribution when I plot the sums of both sexes (broken grey line in fig. B1).

Use of skull length for calculating body condition

Skull length can be assumed to be independent of short-term changes in nutritional state. Therefore, it can be used as a state-independent correction factor for calculating body condition from body mass, as recommended by Johnson et al. (1985). In a first step, I log- transformed both measurements and then calculated the regression from $\log_e$(body mass / g) on $\log_e$(head+bill length / cm). Table B1 gives the results of the six regression performed. One of them (late female body condition in 1995) is also shown graphically in figure 5 (p. 15). Deviations from this regression line are assumed to be state-dependent. Therefore, I used the residuals from that regression as measurement of body condition.
Using rounded means of the different estimates, the relation between body mass *m* and the numerical value of head+bill length in cm, *hn*, can be expressed with the formula

$$m = 14.6\ \mathrm{g} \cdot hn^{1.5} \qquad \text{(eqn. B1)}$$

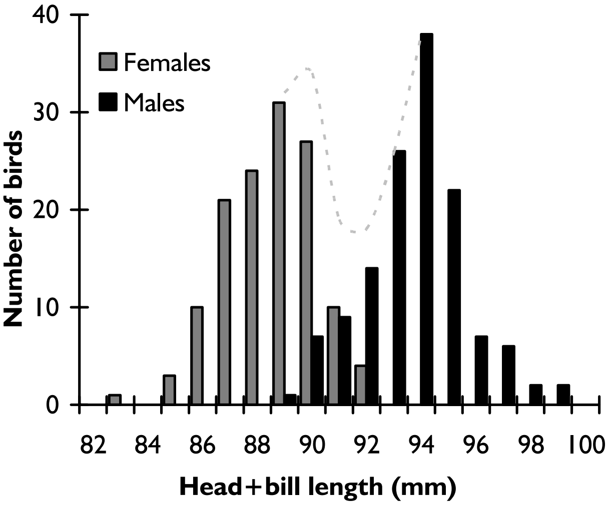

Figure B1: Distribution of head + bill lengths of adult Kittiwakes on Hornøya. Grey bars represent female skull lengths, black bars male skull lengths, the broken line represents the sums of all adult skull lengths.

for females, and

$$m = 59.9\ \mathrm{g} \cdot hn^{0.9} \qquad \text{(eqn. B2)}$$

for males.

Table B1: Regressions between head + bill length and body mass in Kittiwakes. Statistics for the six regressions that were used in calculating adult body condition. Intercepts were all highly significant.

Time[a]	r^2	df	Intercpt	Slope		
			est.	est.	t	p
FEMALES						
early 95	0.19	1,129	15.0	1.50	5.47	0.001***
late 95	0.18	1,66	13.7	1.49	3.79	0.001***
early 96	0.14	1,104	15.1	1.49	4.11	0.001***
MALES						
early 95	0.10	1,132	54.9	0.95	3.91	0.001***
late 95	0.14	1,70	40.3	1.03	3.43	0.002**
early 96	0.06	1,99	97.7	0.68	2.46	0.016*

[a] early, 1 – 5 d post-hatch; late, 19 – 23 d post-hatch

Significance of body condition

To test whether body condition influences reproductive performance, I checked the relation between female body condition and egg volume and found a significant positive one (ANOVA: $F_{1,95} = 5.07, p < 0.014$). However, body condition explained only 5 % of the variation in egg volume.

The influence of body mass on hatching date in examined in app. F.

Significance of egg volume

Variation in individual quality of females is often responsible for a positive correlation between egg volume and clutch size (Coulson, 1963a). In my data, I did not find such a relation (tab. B2). Egg volume was independent of clutch size. This might be a consequence of low variation in clutch size in 1996, i.e. very few clutches contained either more or less than two eggs.

As mentioned earlier (p. 40), it is assumed that the egg volume is related to the survival chances of a hatchling. Such a relationship between egg volume and hatchling mass and/or fledging success was found in several species (e.g., Parsons, 1970; Ricklefs et al., 1978; Birkhead & Nettleship, 1982; Thomas, 1983). While it has been argued that this result also can be created by maternal effects (Davis, 1975), some studies demonstrated the mentioned correlations also after cross-fostering (Nisbet, 1973; Nisbet, 1978). Only one study (Bolton, 1991) calculated, however, the relative contribution of both egg volume and parental quality on chick survival. Bolton (1991) concludes that chick survival is related to both factors, but that egg size contributes less than parental quality.

I checked the significance of egg volume in my data by calculating a logistic regression using egg volume as independent variable for hatching success of two-egg clutches (tab. B2). The relation was highly significant. It can also be seen from table B2 that birds which only hatched one of two eggs, had laid smaller eggs than birds which hatched both eggs. I can, however, not distinguish between the significance of egg volume itself and a maternal effect.

Table B2: Clutch size and hatching success, and their relation to egg volume. Egg volume in relation to clutch size (*cs*, left half; test performed was *t*-test) and to hatching success (*hs*, right half; clutches of two, only; test performed was logistic regression). *df*= 1.

cs	egg volume	*hs*	egg volume
1	47.12±1.68 (10)	0	50.69±3.16 (4)
2	48.71±0.29 (126)	½	45.86±0.89 (8)
3	50.27 (1)[a]	1	48.84±0.29 (114)
t	−1.42	χ^2	8.34
p	0.079	p	0.002**

[a] this nest was not used in the test

Appendix C

Critique of methods used

Appropriateness of the species examined

As hypothesized by Cullen (1957) and demonstrated by Storey et al. (1992; but equivocal evidence in Roberts & Hatch, 1994), Kittiwakes use the nest location as a recognition cue, and parent-young recognition is absent early after hatching. This decision rule might be interpreted as an adaptation to nesting in the steepest areas of cliffs because behavioural excitement might lead to the chicks falling from the nest, and any return to the nest cannot normally occur even if recognition was present.

This is an optimal situation for manipulation experiments that exchange chicks between broods. Furthermore, Maunder & Threlfall (1972) stated that "marking [Kittiwake] nests and making daily visits did not lead to their desertion" (p. 796). Also this is a necessary condition for carrying out experiments like the one described in this thesis.

As Lindén & Møller (1989) pointed out, it is important in brood size manipulations that the manipulated brood sizes lie within the natural range of brood sizes. This is also taken account of, as can be seen from tables 1 and 2 (pp. 10 & 12).

Also the Kittiwake population examined met the conditions for studies of life-history trade-offs. As the population was neither decreasing nor increasing, it was assumed to be in an evolutionary equilibrium. This is important because studies in evolutionary ecology build upon the assumption that animals are adapted to their environments (cf. Maynard Smith, 1978; Grafen, 1991).

A further problem with many manipulative studies pointed out by Lindén & Møller (1989; Møller, 1993) is that nest boxes were cleaned every year and/or set up in too high densities. Both factors can bias the results by creating an environment other than the one the birds are adapted to. This is in contradiction to Bell's (1980) claim that manipulations have to be carried out in the field and that there must be no change in any other factor than the one examined. By using natural nests in natural surroundings, my study is not biased by these factors. Neither prevalence of parasites (e.g., Barton, Harris & Wanless, 1995; cf. Danchin & Monnat, 1992; Richner & Heeb, 1995) nor density of nests was influenced by the study itself.

Brood size manipulation

Manipulation experiments have been both criticized (Bell, 1980; Reznick, 1985) and recommended (Partridge & Harvey, 1985, 1988; Bell & Koufopanou, 1986; Gustafsson & Sutherland, 1988). There is, however, little dissence that manipulative studies have clear advantages over observational studies that merely state phenotypic correlations. Manipulations will thus, at least in species with too long a generation length to perform selection experiments (Bell, 1980), be the preferred method of investigating trade-offs. By restricting manipulation experiments to studies that meet the conditions discussed in the above paragraphs, even Bell's (1980) and Reznick's (1985) criticisms are taken into account (but see Lessells, 1991).

Stearns (1992) summarizes some reasons why one might not detect a trade-off in spite of its existence. The most wide-spread of these is probably the "variation in acquisition and allocation of energy". The advantage of manipulative studies is that allocation rules are partly broken up by assigning randomized costs to individuals, regardless of their genetic quality or conditional state. The most controversial field in this respect might be the trade-off between clutch size and survival: "should there be a positive or a negative correlation between clutch size and survival", asked for example Högstedt (1981). He presented an example of a positive correlation between clutch size and survival (because of territory quality) which he thought could falsify "Charnov & Krebs's (1974) [i.e. Williams's (1966)] theory". What he did not realize, was that both approaches are not mutually exclusive because they deal with totally different phenomena and levels of explanation. Also Bell & Koufopanou (1986) had predicted that phenotypic correlations tend to be negative only when resources were scarce. It is, therefore, not true that experimental manipulations of brood sizes make the assumption "that all parents are of equal quality" (Coulson & Porter, 1985: 461). Rather, randomization and manipulation allow for statements about reproductive effort that are independent of differences in nest-site or individual quality. Individual differences in quality between birds might represent the single most important factor determining reproductive success in individual Kittiwakes (Thomas & Coulson, 1988), but do not explain the underlying evolutionary mechanisms: which traits are responsible for natural selection making certain birds and not others appear to be good-quality ones. Using quality in answering that question leads to a circularity.

Under some conditions, however, even observational studies can contribute to the identification of trade-offs: "If it is assumed that, for inexperienced breeders especially, there is a cost associated with breeding, the reduced clutch size and chick production of Kittiwakes breeding for the first time (Thomas, 1983) look like an adaptation for young birds to gain valuable experience without incurring the higher cost of a large brood which may jeopardize future chances of reproduction (sensu Curio, 1983)" (Aebischer & Coulson, 1990).

Chick loss and production of offspring

In order to interpret chick losses in a life-history context, it is crucial to distinguish between losses that are related to brood size, and chicks that are lost independently of brood size. Unfortunately, I was not able to distinguish between the different possible causes of chick loss.

In the cases where I found dead chicks in or next to the nest, siblicide was the most probable explanation (Braun & Hunt, 1983; Galbraith, 1983). But when one chick was simply missing, it was impossible to say whether the loss was due to predation of an attended or of an unattended nest, or whether a predator had just removed a chick that was pushed out of the nest by a sibling. Chick loss might thus in many cases have been caused by siblicide, and might as such reflect competition for food between siblings which again must be regarded as being a function of brood size (Galbraith, 1983).

Total loss of the brood, on the other hand, hints at that the cause was predation, or perhaps related to weather, e.g. a collapse of the whole nest as a consequence of storm. While losses of the whole brood can also be a function of the parents' nest attendance and thus of brood size (see p. 33), weather influence is independent of experimental treatment.

In tables 4 and 5 (pp. 19 & 20), I considered both the possible interpretations, either including or excluding all failed nests. Including these nests also includes in the calculations nests that lost chicks independently of manipulation, such that the statistical noise in the data increases. Excluding these nests also excludes single chick losses in one of the experimental groups (reduced!) and total losses that were due to treatment, which might produce a bias in the data.

There is no solution to that dilemma, as the truth will be some place between the two mentioned extremes. But there is some evidence that excluding nests that lost all chicks is more sensible than including them:

- Prior to manipulation, nearly half of all nests of the original sample size of 267 were preyed upon (tab. 4), indicating that predation levels are generally quite high.
- Multiple chick loss was strongly related to weather conditions (app. D).
- The proportion of nests not producing any young, was similar in all three experimental groups (tab. 4), and significantly independent of treatment.
- Previous studies (Jacobsen, 1993; Jacobsen et al., 1995) were able to show a treatment effect in offspring production only when nests that did not fledge young were excluded.

I therefore assumed it to be justified to exclude failed nests from many of the calculations performed.

Fledging success

My use of the term "fledging success" is somewhat blurred, as I define it as the proportion of chicks alive 18 days after hatching – i.e. c. two weeks before the chicks are able to fly (Maunder & Threlfall, 1972). The reasons were, as mentioned (p. 13), to avoid premature flight of chicks in neighbouring nests. This is, however, only problematic when comparing my numerical values of fledging success with other studies using other definitions, or when chick loss after that time would bias my results. The former should thus be avoided. The latter possibility is unrealistic, because in my study levels of chick loss were higher in larger broods. This trend would have to be reversed between day 18 and fledging in order to render my results incorrect. There is no reason to believe that this should have happened.

Offspring growth & survival

It was problematic to calculate chick mass gain in broods where one or two chicks had died between weighings. I simply used the mean weights from both weighings to calculate mass gain (tab. 7, p. 22), but it would, of course, have been better to band the single chicks and then calculate the mean of mass gains instead of the gain in mean mass. It could thus be an advantage to mark chicks in future studies. However, late chick mass seemed to be more revealing a measurement than mass gain (tab. 6). In order to minimize disturbance of the colony, it is, therefore, better to keep to the method I used unless one wants to study maternal effects. As every nest contains both own and foster chicks, the effect of parental quality and manipulation could be sorted out. Also the effect of transferring a chick on the chick itself could be controlled for (Haymes & Morris, 1977).

In order to correctly calculate the costs of reproduction, it is important to have better estimates of offspring recruitment than just fledging/weaning success (Partridge & Harvey, 1988). Few studies have done this so far. I approximated recruitment using data by Coulson & Porter (1985). They might, however, have underestimated chick survival as they only recorded return to the natal colony, and many birds, especially females (Wooller & Coulson, 1977, Porter & Coulson, 1987), might breed in other colonies than the one in which they were born. However, when the chicks' chances of changing the colony are not influenced by their growth rates, return to the natal colony can at least give an estimate of the relation between fledgling growth rate and chances of recruitment, even when the total values for recruitment might be biased.

Nevertheless, instead of relying on such data, it is to be preferred to investigate recruitment rates. Therefore, all fledglings should be ringed in future studies. This has not been done so far, I therefore suggest to ring chicks during the last weighing session (18 days post-hatch).

It might also be interesting to see whether there are sex-specific differences in chicks' fledging success, their growth rate and/or chances of recruitment, or whether parents skew their sex-ratio of offspring produced in the year following a brood size manipulation. Sexing immature Kittiwakes morphologically is not possible, but molecular sexing could be an alternative (Ellegren & Sheldon, 1997).

Parental state

The state of adults is a rather abstract term that is difficult to attribute to any measurable parameter. Johnson et al. (1985) proposed to use a lipid index (ratio of fat to fat-free dry mass) as measurement for body condition. As this measurement is only obtainable after killing the birds in question, they compare different other measurements and their reliability. Body mass alone "is a fair index" (Johnson et al., 1985: 574), but not very reliable as individual differences between birds might bias the weights or at least increase the statistical noise (i.e. the standard deviation) of the data. Therefore, a better measurement is obtained by controlling body mass for another – state-independent – measurement of individual body size. I used skull length as such a measurement, assuming that differences in skull length are largely state-independent. Furthermore, Johnson et al. (1985) recommended logarithms instead of ratios.

Calculation of the body condition measurement used in this study, was explained in table 3.

I will here shortly summarize the pros and cons of using body condition and body mass:

- While early female body mass indicates a treatment effect (tab. 8) – a type I error caused by individual variation in mass (see p. 36) –, there is no type I error in body condition. This illustrates the advantages of controlling for individual differences.
- When only late body condition is used as a measurement of late adult state, one does not need to catch adults early in the chick rearing period and can thus reduce disturbance of the colony.
- A relation to treatment in the following season was found in early body condition only. But this necessitates weighing also early in the chick rearing period.
- It is not possible to calculate a change in body condition. Nor can conditions be compared between sexes. This is because values of early and late, or male and female, condition cannot be compared directly. They are relative measurements that depend on body conditions of all birds measured at a certain moment of the experiment.
- Also by calculating relative mass losses, individual differences can be partly removed. Relative mass loss has the further advantage that it can be used in comparisons between sexes. But relative mass loss is an indicator of state change rather than of parental state.

The results I obtained from my different measures of adult state (late body mass, late body condition, absolute mass loss, relative mass loss), were largely of equal value, as they indicated exactly the same trends. In some cases, body condition was to be preferred, while mass loss was better in other cases. As early measurements are needed anyway to demonstrate effects of previous-year treatment, and as head+bill length has to me measured anyway to sex the birds, it will be best to use *both* measurements in future.

Head + bill length

The accuracy of measurements of head+bill length could be examined for birds that were caught and measured in both 1995 and 1996. In 9 out of 84 cases, differences between the measurements were larger than 2 mm. Though the maximum difference (6.5 mm) most probably was a writing mistake rather than a measuring error, there is some variation in measuring accuracy which can lead to erroneous calculates of body condition. The measurement of head + bill length is quite susceptible to changes in the angel between the bill's lower edge and the calliper (cf. fig. 3, p. 13). A field worker not aware of this problem can easily produce wrong measures. A head+bill length underestimated by 3 mm would lead to an overestimation of body condition by 48 ‰. But as long as the number of birds with inaccurate measurements is low, as seems to be the case (11 %), the results will not be biased.

The sexing of the birds in question was, however, not influenced by the measuring error in any of these cases.

Parental attendance

According to Coulson & Johnson (1993), a frequency of counts of two per day overestimates the first occasion of a nest being left alone by both adults by about 9.3 days. But, as they state further, "spot-observations [...] are [...] unsuitable unless [...] the study is restricted to making comparisons between categories of birds" (p. 377). As this was exactly the aim of recording attendance, and not an estimation of the first nest absence, a frequency of two counts per day seems acceptable.

There are two opposing error sources of recording nest attendance (Coulson, 1959; Wanless & Harris, 1989; Cadiou & Monnat, 1996; pers obs): Kittiwakes often stand on ledges near the nest from where they will defend their young. The nest thus appears unattended, although only one parent is at sea feeding. On the other hand, squatting is a frequent phenomenon that can lead to an overestimation of attendance. "Squatters" are prebreeders or failed breeders prospecting nests that are left alone by its owners (Cadiou & Monnat, 1996). However, the large sample size obtained by observing a large number of nests twice daily during two weeks, seem to outweigh these error sources.

Parental re-sighting rate

Some colours used in ringing Kittiwakes are difficult to distinguish (brown – red, or white – light blue). To reduce the risk of wrong observations, I therefore only considered a bird as being re-sighted when its colour ring was observed at least twice during independent checking rounds. However, a single observation was assumed sufficient in the cases when the bird was caught, or where the colour combination was observed at the same nest as in the year before. The latter procedure is justifiable because congruence in nesting place was first recognized after the field season – i.e. the observer did not know what colour rings were to be expected at a certain nest –, and the number of nests made it improbable that an incorrect colour combination was observed in the respective right place by chance. There were two birds that maintained their 1995 manipulated brood sizes for more than twelve days, that were observed only once, and were, therefore, excluded from calculating re-sighting rate.

An important issue is the question of whether re-sighting can be equated with survival. The answer is that it cannot, because re-sighting rate consists of three factors: the probability of surviving, of being present when alive, and of being re-sighted when present (Clobert, 1995). Two years of re-sighting are the minimum necessary to obtain separate estimates of these probabilities, but three years are advisable because "the last estimable survival probability (the one of interest in the event of only two recapture occasions) may be biased" (Clobert, 1995: 994). I used only one year of re-sighting and am thus not able to distinguish between the three factors contributing to a re-sighting. Re-sightings of the following years are beyond the scope of this study, but are available (H. Pichl et al., unpublished data) though they may be biased by the fact that the same experiment as described in this study was carried out in the subsequent years and birds thus can have had their broods manipulated in several years. On the other hand, this had an advantage, because birds that were part of both years' samples have been re-sighted with an probability of 1. Therefore, only the probability of not being present can bias the estimate of survival rates. Not being present includes two possibilities: intermittent breeding (see app. E!) and change of nest site. Both these possibilities represent costs to the birds as they will reduce reproductive output in the respective year (see p. 74). It is therefore correct to use re-sighting rate as a measure for costs of reproduction, even though it is incorrect to equate failure of re-sighting with death - which, of course, has a higher cost than intermittent breeding or changing nest site.

The same can be said about the possibility that weakened birds may fail early in the breeding season and then desert the colony. Though I also searched the colony for ringed birds before the onset of incubation (see p. 12), this method was not as effective as capturing the birds later in the breeding season during next year's manipulation experiment. But according to the previous paragraph, those cases can be viewed as intermittent breeders which also incur fitness costs.

The study of Jacobsen et al. (1995) has been criticized for committing exactly the mistakes discussed above (Boulinier et al., 1997). This critique is generally correct. But the results of Jacobsen et al. (1995) are nevertheless valid: in calculating parental fitness, the future reproduction was – as criticized by me on other grounds on page 42 – not taken into account (tab. 2 in Jacobsen et al., 1995). This can be interpreted such that reproductive performance two years after manipulation was not regarded. This fact wipes out the differences between intermittent breeders and birds that died. Besides this theoretical reasoning, re-sighting rates in Jacobsen et al. (1995) were estimated not only in the year after manipulation, but in two additional years, and only one bird not re-sighted in the year following the manipulation was re-sighted later (K. E. Erikstad, pers. comm.).

As regards change of nest site, Coulson & Wooller (1976; Coulson & Thomas, 1985b) found, by checking neighbouring colonies to a colony where all breeding and many prospecting Kittiwakes had been marked, strong evidence that the disappearance of a breeding bird can be equated with its death, in contrast to prospecting birds that often were found in neighbouring colonies. Danchin & Monnat (1992) corrected this observation, however, by pointing out that this was only valid "if the conditions remain good" (p. 176) – i.e. in prospering colonies.

Next year's clutches

The factor *k* in equation 1 (p. 16) was calculated to amount to 0.4866 by Coulson (1963a) and to 0.4861 by Runde & Barrett (1981). I adopted Runde & Barrett's value because it was obtained from Kittiwakes in a North Norwegian breeding colony and because the difference of the values is less than the measuring accuracy.

A possible error source was that replacement clutches contain smaller eggs (Runde & Barrett, 1981), but I was not able to distinguish them from first-laid eggs. This could have contributed to the fact that I failed to find a relation between treatment and next year's egg volumes.

Hatching date

As mentioned above (p. 41), I did not record laying dates, but used hatching dates as a substitute. In calculating the effect of previous year's treatment, this should, however, not produce any bias. Otherwise one would have to expect that the duration of the incubation period should be inversely related to manipulated clutch size in the year before. This is an unreasonable assumption.

A bias can, however, occur when calculating the relation between hatching date and egg volume or hatching success. These two cases are discussed in connection with the respective calculations in appendix F (p. 76).

Appendix D

The effect of weather on chick loss

Using data from the Norwegian Meteorological Institute (Det norske meteorologiske institutt, Vervarslinga for Nord-Norge, pers. comm.) on weather conditions in Vardø, I tested different meteorological parameters for their relation to chick loss. These parameters were daily minimum temperature, mean temperature, precipitation, maximum wind speed, and mean wind speed. Chick loss was calculated as proportion of chicks lost, based upon the total number of chicks alive that were younger than 19 days. Except for precipitation, all parameters were significantly related to probability of chick loss (tab. D1).

Table D1: Relation between different meteorological parameters and chick loss in Kittiwakes on Hornøya. Relation between a day's chick loss and the respective same day's or previous day's weather conditions. Tests performed were logistic regressions, $n = 72$.

Variable	Same day		Previous d	
	χ^2	p	χ^2	p
Minimum temperature	8.69	0.002**	13.01	0.001***
Mean temperature	6.86	0.005**	8.83	0.002**
Precipitation	1.27	0.129	0.03	0.569
Maximum wind speed	3.76	0.027*	13.56	0.001***
Mean wind speed	6.90	0.005**	15.78	0.001***

The daily minimum temperature is also plotted in figure D1. It can be seen that the chick loss curve is somewhat delayed in phase compared to

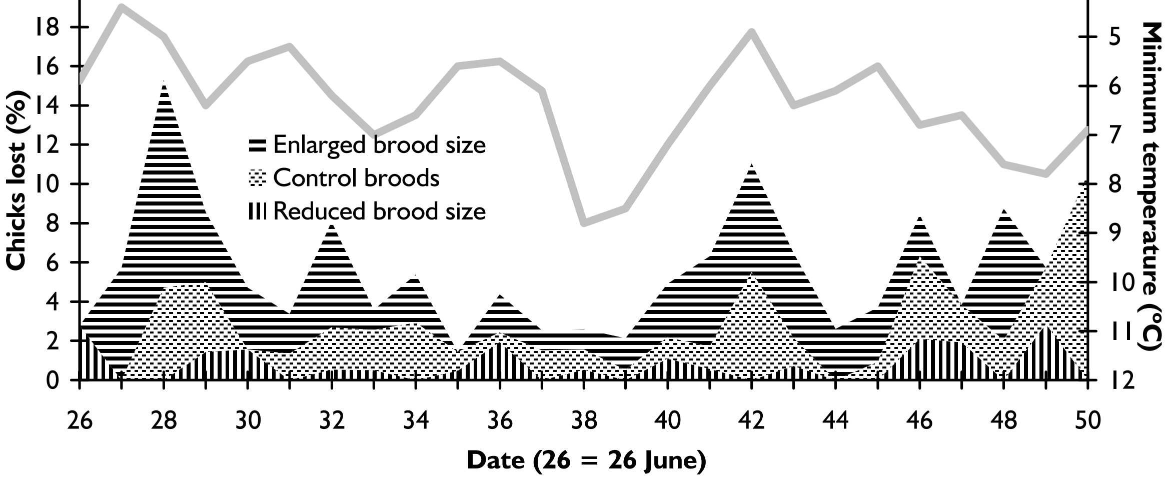

Figure D1: Chick loss and minimum temperature. Chick loss (hatched and grey areas) was calculated as the proportion of chicks aged 2 - 18 days, that were lost at a given day; proportions for the three treatment categories are plotted cumulatively. Minimum temperature (broken line; data from Det norske meteorologiske institutt, Vervarslinga for Nord-Norge) is plotted with reversed axis.

the temperature curve. This is because chick loss occurring late at any given day will first be recorded one day later. I therefore also tested the relation between chick loss and the previous day's weather conditions (tab. D1). The results were even more pronounced, suggesting that most chicks died after the checking round. When including all variables into one model, and subsequently eliminating insignificant variables, the best model consisted of the previous day's minimum temperature, maximum wind speed, and experimental treatment (logistic regression, $n = 72$: temperature, $\chi^2_1 = 14.30$, $p < 0.001$; wind, $\chi^2_1 = 14.89$, $p < 0.001$; treatment, $\chi^2_2 = 8.05$, $p < 0.018$).

Table D2: Correlation between chick loss and the previous day's temperature / wind speed. Test performed was Spearman correlation, $n = 24$.

Variable	Statistics	Brood size		
		reduced	control	enlarged
Minimum temperature	r	+0.08	+0.02	-0.45
	p	0.696	0.922	0.024*
Maximum wind speed	r	+0.00	+0.06	+0.45
	p	0.985	0.789	0.027*

Figure D1 shows also the responses of the three experimental groups. The correlation between chick loss and both temperature and wind speed was significant only in enlarged broods (tab. D2). It was, however, only wind speed that exhibited a significant weather × treatment interaction (two-tailed logistic regression, $n = 72$: treatment × temperature, $\chi^2_2 = 1.20$, $p = 0.548$; treatment × wind, $\chi^2_2 = 6.63$, $p < 0.037$).

Table D3: Relation between different meteorological parameters and multiple chick loss in Kittiwakes on Hornøya. Relation between a day's multiple chick loss (as defined in the text) and the respective same day's or previous day's weather conditions. Tests performed were logistic regressions, $n = 23$.

Variable	Same day		Previous	
	χ^2	p	χ^2	p
Minimum temperature	14.32	0.001**	4.92	0.014*
Mean temperature	5.14	0.012*	7.87	0.003**
Precipitation	4.08	0.022*	0.96	0.836
Maximum wind speed	0.50	0.240	4.77	0.015*
Mean wind speed	1.83	0.088	7.88	0.003**

Finally, I tested whether chances of multiple chick loss were related to weather conditions. I defined multiple chick loss as the loss of a nest's two last chicks at the same day, i.e. the total loss of a control brood or an enlarged brood, or the loss of the remaining chicks in an enlarged brood that previously had lost one chick. The proportion was computed as the number of thus defined multiple chick losses divided by the number of control and enlarged broods that contained at least two chicks which were younger than 19 days. Also here, I considered both the same day's and the previous day's weather conditions. The results are given in table D3 and demonstrate that also multiple chick loss is clearly related to weather conditions.

Appendix E

Mate retention, nest-site fidelity, and intermittent breeding

Many colonial seabirds exhibit an intense breeding site tenacity which is associated with a high incidence of between-year mate fidelity(Coulson, 1972; Richdale & Warham, 1973; Ollason & Dunnet, 1978; Morse & Buchheister, 1979; Boersma et al., 1980; Morse & Kress, 1984; Ainley, Ribic & Wood, 1990; Bradley et al., 1990). It is further known in both Kittiwakes (Coulson, 1966a, 1972; Coulson & Thomas, 1980) and other monogamous seabirds (Mills, 1973; Fleet, 1974, cit in Cuthbert, 1985; Davis, 1976; Ollason & Dunnet, 1978, 1988; Bradley et al., 1990) that changes of mates lead to a decrease in breeding success in the following season: Coulson & Thomas (1983) reported a 10 % reduction in clutch size and a 12 % reduction in the number of fledglings in divorced Kittiwakes. This is explained as being the result of a highly complex pair relationship which "can be more productive than the simpler position seen in many other bird species" and "becomes more efficient through individual experience of a mate. The long term pair-bond seems to induce a greater reproductive drive resulting in a better all-round breeding performance" (Coulson, 1972: 433, 432; cf. Coulson & Wooller, 1984). It has, therefore, been hypothesized that the retention of the same nest sites might serve to increasing the probability of the pair-bond reforming (Morse & Kress, 1984). For the Kittiwake, however, it has been demonstrated that nest-site fidelity is not the only factor guaranteeing the re-forming of the pair-bond, but that individual, presumably vocal (Wooller, 1978), recognition is involved (Fairweather & Coulson, 1995). Furthermore, competition for nest sites (Birkhead & Furness, 1985) suggests that there is an advantage in retaining good-quality sites (Coulson, 1968; Wooller & Coulson, 1977). One should, consequently, expect that change of either mate or nest site is selected against unless it can compensate for another, heavier cost to fitness. Birds that divorce or move must thus "assume" that breeding failure in the previous breeding season was due to a low quality mate, or nest site, respectively. Change of breeding partner and nest site can, therefore, be hypothesized to give an estimate of how the birds themselves "estimate" their breeding success of the previous year (McNamara & Forslund, 1996). This can be further supported by observations that divorce rate was significantly higher after failed breeding (Coulson, 1966a, 1972; Brooke, 1978; Ollason & Dunnet, 1988; Hatch, Roberts & Fadely, 1993).

I tested some parameters related to breeding success in 1995 on their relation to chances of mate or nest-site change and of re-sighting in 1996. I found the following relations (all tests on this page are two-tailed):

- *Chick loss*: Pairs that lost chicks in 1995 had a higher probability of divorcing in 1996 (Pearson: $\chi^2_{1,\,92} = 5.12$, $p < 0.024$), and of changing the nest-site (Fisher's exact: $p < 0.020$). Re-sighting rate in males, but not in females was also significantly lower after chick loss (logistic regression: ♀♀, $\chi^2_{1,140} = 0.95$, $p = 0.330$; ♂♂, $\chi^2_{1,140} = 3.40$; $p < 0.039$).
- *Total breeding failure*: Only the probability of changing nest-site was higher following a total breeding failure (logistic regression: $\chi^2_{1,122} = 10.60$, $p < 0.002$).
- Re-sighting rate was not related to *relative mass loss* in 1995 (♀♀, $\chi^2_{1,66} = 0.46$, $p = 0.499$; ♂♂, $\chi^2_{1,70} = 0.21$, $p = 0.646$), nor to late *body condition* of the parents (logistic regression: ♀♀, $\chi^2_{1,66} = 1.01$, $p = 0.316$; ♂♂, $\chi^2_{1,70} = 0.00$, $p = 0.964$).

This evidence does not support the view that a bird not re-sighted should be assumed to have died. In this case one should expect a relation with mass loss or body condition. Instead, intermittent breeding seems to be a more frequent cause.

That also divorce and intermittent breeding show this pattern is in accordance with the findings quoted above.

Appendix

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The significance of hatching date

It is known from some species (e.g., Chastel, Weimerskirch & Jouventin, 1995; Daan & Tinbergen, 1997; but Tombre et al., 1996), among others the Kittiwake (Coulson, 1968; Porter & Coulson, 1987; Porter, 1990) that high-quality individuals return earlier to the breeding colony and start egg laying earlier. Accordingly, Lessells (1986) documented that Canada Geese that had reared enlarged broods bred later in the following season. I examined the relation between female body condition and hatching date (two-tailed ANOVA: $F_{1,96} = 5.67$, $p < 0.020$, estimate +5.2‰) and found a positive one. This resembles more the findings in the Barnacle Goose *B. leucopsis* (Tombre et al., 1996) than the ones in other Kittiwake studies. One has, however, to be quite careful interpreting these results. As I measured body mass shortly after hatching of the chicks, the result might just mirror a seasonal effect in body mass – food supply could have been better at the end of the hatching period than at its beginning. Indeed, controlling for weighing date rendered the trend insignificant (two-tailed ANOVA with residuals from regression of 1996 early body condition on weighing date: $F_{1,93} = 0.76$, $p = 0.385$, estimate +1.6‰).

A further factor influencing laying date according to Coulson (1966a) is mate change, as newly formed pairs tend to lay later than established pairs. I could not test this relation because all females with known hatching date in my sample had retained their previous year's mates.

As regards the significance of laying/hatching date, Coulson reported that egg volume decreases with increasing laying date, even after controlling for the parents breeding experience (Coulson & White, 1961), and attributed both lower clutch size and hatching success to later laying date (Coulson & Thomas, 1985a; Coulson & Thomas, 1985b). Similar effects are known from other species (e.g., Perrins et al., 1973; Ollason & Dunnet, 1978; Brinkhof, Cavé & Perdeck, 1997)

I did not find a relation between egg volume or hatching success and hatching date (egg volume, ANOVA: $F_{1,120} = 0.46$, $p = 0.250$, estimate –0.05; hatching success, logistic regression: $\chi^2_{1,121} = 0.15$, $p = 0.349$). That these trends were not significant, can have different reasons. One is that the sample size of nests with a hatching success of 50 % was quite low ($n = 8$, hatching date 30.0 June ± 1.1 d) compared to clutches where all chicks hatched ($n = 115$, hatching date 29.5 June ± 0.4 d). Another problem is the one mentioned on page 71, that I did not record laying, but only hatching dates. In the above calculations, that can bias the results, because smaller eggs might need a shorter incubation period to hatch, and because the hatching date of clutches with 50 % hatching success might be the second, not the first egg's hatching date.