

Atlantic Seabirds



Vol. 1, no. 1 (1999)

*Quarterly journal of The Seabird Group
and of the Dutch Seabird Group*

ISSN 1388-2511

Atlantic Seabirds

Edited by C.J. Camphuysen & J.B. Reid

ATLANTIC SEABIRDS is the quarterly journal of the SEABIRD GROUP and the DUTCH SEABIRD GROUP (Nederlandse Zeevogelgroep, NZG), and is the continuance of their respective journals, *SEABIRD* (following no. 20, 1998) and *SULA* (following vol. 12 no. 4, 1998). *ATLANTIC SEABIRDS* will publish papers and short communications on any aspect of seabird biology and these will be peer-reviewed. The geographical focus of the journal is the Atlantic Ocean and adjacent seas at all latitudes, but contributions are also welcome from other parts of the world provided they are of general interest. *ATLANTIC SEABIRDS* is indexed in the Aquatic Sciences and Fisheries abstracts, Ecology Abstracts and Animal Behaviour Abstracts of Cambridge Scientific databases and journals.

The SEABIRD GROUP and the DUTCH SEABIRD GROUP retain copyright and written permission must be sought from the editors before any figure, table or plate, or extensive part of the text is reproduced. Such permission will not be denied unreasonably, but will be granted only after consultation with the relevant author(s).

Editors

C.J. Camphuysen (NZG), Ankerstraat 20, 1794 BJ Oosterend, Texel, The Netherlands, tel/fax + 31 222 318744, e-mail kees.camphuysen@wxs.nl

Dr J.B. Reid (Seabird Group), c/o Joint Nature Conservation Committee (JNCC), Dunnet House, 7 Thistle Place, Aberdeen AB10 1UZ, Scotland, U.K., e-mail reid_j@jncc.gov.uk.

Offers of papers should be addressed to either editor.

Editorial board

Dr H. Brazier, Dublin, Ireland; Dr S. Garthe, Kiel, Germany; Dr C.J. Hazevoet, Lisboa, Portugal; M. Heubeck, Shetland, U.K.; B. Koks, Groningen, The Netherlands; P.L. Meininger, Vlissingen, The Netherlands; Dr S. Wanless, Banchory, U.K.

Members of The Seabird Group and of the Dutch Seabird Group receive *Atlantic Seabirds* free. Back issues are available at £ 3,00, Euro 4,25 or f 9,25 per copy (including postage) from: Secretary Dutch Seabird Group, De Houtmanstraat 46, 1792 BC Oudeschild, Texel, The Netherlands.

Published by **THE SEABIRD GROUP**, c/o The Lodge, Sandy, Bedfordshire SG19 2DL, U.K., charity number: 260907

and the **DUTCH SEABIRD GROUP** (Nederlandse Zeevogelgroep), section of the Dutch Ornithological Union (NOU), c/o De Houtmanstraat 46, 1792 BC Oudeschild, Texel, The Netherlands

Editorial

This is the first issue of a new journal, jointly issued by *The Seabird Group* and the *Nederlandse Zeevogelgroep* (Dutch Seabird Group) and which is the continuance of their respective journals, *SEABIRD* (1969-1998, 20 volumes) and *SULA* (1987-1998, 12 volumes). *SEABIRD* was published annually and all papers were peer reviewed. *SULA* was published quarterly and while most full papers, especially in later years, were refereed, most of the short notes were checked and edited only by the editorial board. *SULA* served primarily as an accessible publication platform for the largely amateur membership of the Dutch group.

With *ATLANTIC SEABIRDS* we aim at the continuing and consolidating the strengths of both journals: a peer reviewed, quarterly journal, that aims to meet the requirements and expectations of not only the professional ornithologist, but also the large group of amateur seabirders on either side of the North Sea. *ATLANTIC SEABIRDS* will publish papers and short communications on any aspect of seabird biology. The geographical focus of the journal is the Atlantic Ocean and adjacent seas at all latitudes, but contributions are also welcome from other parts of the world provided they are of general interest. *ATLANTIC SEABIRDS* is indexed in the Aquatic Sciences and Fisheries abstracts, Ecology Abstracts and Animal Behaviour Abstracts of Cambridge Scientific databases and journals.

Contributions to *ATLANTIC SEABIRDS* will be published in English, but all articles will be summarised in Dutch and tables and diagrams will also be subtitled in Dutch. We strongly encourage contributions from authors whose first language is not English; the editorial board will do what ever is possible to get these papers in a publishable format. At the outset of this new venture, we have established an editorial board with representatives from different parts of Europe. We have been successful in appointing representatives from Portugal (Kees Hazevoet), Germany (Stefan Garthe), and Ireland (Hugh Brazier), from as remote an area as Shetland (Martin Heubeck), and from specific sites such as the Dutch Delta area (Peter Meininger) and the Wadden Sea (Ben Koks). The former editor of *SEABIRD*, Sarah Wanless, also kindly agreed to serve a few more years on the editorial board of this new journal.

Dit is het eerste nummer van een nieuw tijdschrift dat gezamenlijk door de Britse Seabird Group (Zeevogelgroep) en de Nederlandse Zeevogelgroep wordt uitgegeven, als voorzetting van hun eerdere tijdschriften, SEABIRD (1969-1998, 20 nummers) en SULA (1987-1998, 12 jaargangen). SEABIRD

verscheen elk jaar één keer en alle hierin gepubliceerde artikelen werden door referenten beoordeeld. SULA was een kwartaaluitgave en ofschoon in latere jaren een steeds groter deel van de afgedrukte artikelen werd gerefereerd, werden vooral de korte bijdragen dikwijls alleen door de redacteurs nagekeken. SULA was vooral een laagdrempelig medium, bij uitstek geschikt om artikelen te publiceren van de amateur zeevogelaars waaruit de Nederlandse groep hoofdzakelijk bestaat.

Met ATLANTIC SEABIRDS wordt getracht de sterke punten van beide tijdschriften voort te zetten: een gerefereerd kwartaalblad, waarbij de redactiecommissie het als haar taak ziet om auteurs met raad en daad bij de publicatie van hun werk ter zijde te staan. Het tijdschrift richt zich in eerste instantie op het Atlantische gebied, maar bijdragen uit alle delen van de wereld zijn welkom, vooropgesteld dat de inhoud voor een breed publiek interessant is. Een overzicht van de in ATLANTIC SEABIRDS afgedrukte artikelen wordt gepubliceerd in Aquatic Sciences and Fisheries abstracts, Ecology abstracts en Animal Behaviour abstracts van Cambridge Scientific databases and journals.

De voertaal in het nieuwe blad is Engels, maar alle artikelen worden voorzien van een Nederlandse samenvatting en Nederlandstalige bijschriften van figuren en tabellen. De redactie is zich bewust van de achtergrond en belangstelling van het merendeel van de leden van beide organisaties en zal dan ook bijzondere aandacht besteden aan publicaties over zeevogels in het Noordzeegebied. Ook auteurs die de Engelse taal onvoldoende machtig zijn willen wij aanmoedigen om hun manuscripten, desnoods geheel in het Nederlands gesteld, aan de redactie van ATLANTIC SEABIRDS voor te leggen. De redactie heeft zich voorgenomen al het mogelijke doen om ook zulke bijdragen voor publicatie geschikt te maken.

We hebben geprobeerd om een brede redactie te formeren en menen daarin geslaagd te zijn met vertegenwoordigers uit Portugal (Kees Hazevoet), Duitsland (Stefan Garthe) en Ierland (Hugh Brazier), uit een afgelegen gebied zoals de Shetland Eilanden (Martin Heubeck), of van karakteristieke gebieden zoals de Zeeuwse/Zuid-Hollandse Delta (Peter Meininger) en het Waddengebied (Ben Koks). Tegelijkertijd bleek Sarah Wanless, voorheen eindredacteur van SEABIRD bereid haar enorme ervaring voor het nieuwe blad te blijven aanwenden.

Kees Camphuysen,
Oosterend

Jim Reid,
Aberdeen

ON THE FUNCTION OF PRE-LAYING BREEDING
SITE ATTENDANCE IN THE NORTHERN FULMAR
FULMARUS GLACIALIS
OVER DE FUNCTIE VAN DE AANWEZIGHEID OP DE
BROEDPLAATS VOORAFGAANDE AAN DE EILEG BIJ DE
NOORDSE STORMVOGEL

FIONA M. HUNTER^{1,2}

¹Department of Animal and Plant Sciences, P.O. Box 601, University of
Sheffield, Sheffield, S10 2UQ, England, U.K.; ²Present address:

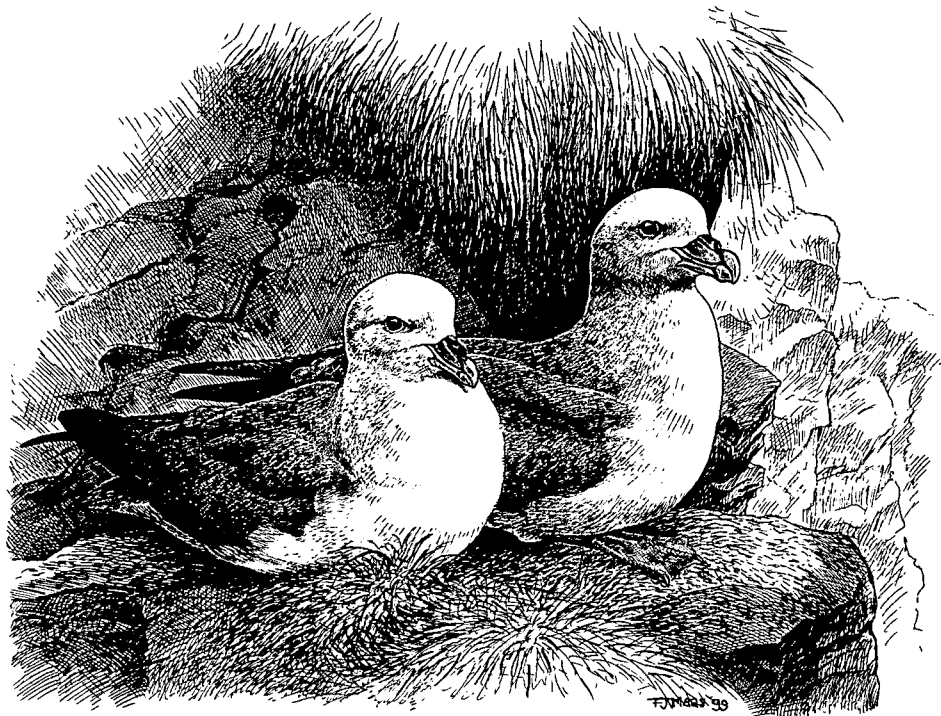
Department of Zoology, University of Cambridge, Downing Street,
Cambridge, CB2 3EJ, England, U.K.

Northern Fulmars spend considerable periods of time at their breeding sites in the months before egg laying. In this study the function of pre-laying breeding site attendance was investigated. Three potential benefits of prolonged pre-laying colony attendance were considered: (1) site defence; (2) opportunities for engaging in either pair or extra-pair copulations (EPCs); and (3) mate defence. There was no evidence that the function of pre-laying colony attendance was site defence: sites were left unguarded for long periods during the pre-laying period and were not subsequently lost to conspecifics. Neither did it appear that individuals maintained a high frequency of attendance to engage in pair copulations. The available evidence is consistent with the idea that females attended the colony to engage in EPCs; females present at the colony on a high proportion of days during the pre-laying period were more likely to be involved in EPC attempts. Although the possibility that females attended the colony for an as yet unidentified reason and engage in EPCs simply because they were there could not be ruled out. It appeared that males attended the colony in an attempt to prevent their partners from engaging in EPCs. Males maintained a higher level of attendance than females throughout the pre-laying period and seldom left their female partners unaccompanied during the presumed fertile period.

Hunter F.M. 1999. On the function of pre-laying breeding site attendance in the Northern Fulmar *Fulmarus glacialis*. *Atlantic Seabirds* 1(1): 3-16.

INTRODUCTION

Seabirds tend to spend the majority of their lives at sea, coming to land only to breed. Individuals must return to their breeding sites to rendezvous and to copulate with their partners after spending the winter apart. In many colonial species individuals are present at the colony for a prolonged period up until the



Northern Fulmars at nest site *Noordse Stormvogels op het nest* (F.J. Maas)

time of laying (e.g. Common Guillemot *Uria aalge*, Birkhead 1978; Least Auklet *Aethia pusilla*, Jones 1992; Northern Fulmar *Fulmarus glacialis*, Dunnet *et al.* 1963). Attendance at the colony is likely to carry costs such as loss of time otherwise available for feeding. However, there are also three potential benefits of prolonged pre-laying colony attendance: (1) site defence; individuals may attend the colony in order to defend their breeding site from others. A number of studies of colonial seabirds have shown that breeding sites vary in quality and that breeding success is affected by site quality (Potts *et al.* 1980; Hudson 1982; Birkhead *et al.* 1985; Hatchwell 1991). As a result there is likely to be competition for good sites, and pairs that have secured good sites may have to defend them. One or both members of the pair could carry out site defence. (2) Opportunities for engaging in either pair copulations or extra-pair copulations (EPCs); individuals may attend the colony in order to seek opportunities to engage in pair copulations with their breeding partner or extra-pair copulations with others (Gladstone 1979; Wittenburger & Hunt 1985; Birkhead & Møller 1992). Both genetic and non-genetic benefits can be gained from engaging in extra-pair copulations. Genetic benefits take the form of additional offspring for males and good or diverse genes for females. Non-genetic benefits include fertilisation assurance, courtship feeding and paternal care (Birkhead & Møller 1992). For long-lived seabirds, the most important non-genetic benefit of engaging in EPCs may be the potential for gaining future reproductive partners (Hatch 1987); (3) mate defence; males may attend the colony in order to defend their mates from the extra-pair copulation attempts of others (Hatch 1987; Hatchwell 1988). Mate defence would carry genetic benefits for males and females similar to those outlined above.

The Northern Fulmar is a long-lived, socially monogamous seabird that breeds colonially and is site- and mate-faithful (Dunnet & Ollason 1978a; MacDonald 1977a; Ollason & Dunnet 1978). Breeding is highly synchronous within any local population (Dunnet & Ollason 1978b; Dunnet *et al.* 1963). The female lays one egg in each breeding season and does not relay if that egg is lost (Hatch 1987). Extra-pair copulation attempts are frequent and 16% of females are involved in behaviourally successful EPCs, although paternity is always secured by the pair male (Hunter *et al.* 1992). In some groups of seabirds and particularly in the Procellariiformes, a pre-laying exodus from the colony occurs immediately prior to egg-laying (Warham 1990). Yolk deposition in the Northern Fulmar takes 23 days, similar to other Procellariiformes, and the function of the pre-laying exodus may be to allow females to feed at sea during this costly egg production period, while males

may feed during the exodus in preparation for their first long incubation shift (Dunnet *et al.* 1963; Astheimer & Grau 1990).

The aim of this study is to report the pattern of pre-laying attendance of Northern Fulmars in a colony on Fair Isle, Shetland (UK) and to assess whether patterns of attendance are related to site or mate defence or extra-pair activity.

METHODS

The study was carried out on a cliff dwelling colony of Northern Fulmars on Fair Isle (59°32'N, 01°37'W), Shetland. The study population consisted of 91 breeding pairs, occupying an area of about 15 m x 15 m of cliff-face. Dates of egg laying were obtained for 77 of these pairs allowing patterns of attendance relative to egg-laying to be determined. Day 0 was defined as the day the egg was laid, day -1 was one day before the egg was laid, day -2 was two days before the egg was laid and so on. All individuals in the study site could be observed simultaneously and were recognisable by unique colour ring combinations and/or distinctive culmen markings (Hatch 1987; Hunter *et al.* 1992). Individuals were sexed by their positions during copulation. The presence or absence of individuals at each site and the identity and hence sex, of single individuals were recorded at 12.00 h GMT each day for the duration of the pre-laying season, from 27 March until the day the last egg was laid on 29 May 1988.

During the pre-laying period a record was made of all copulation attempts and related behaviours. The birds were observed continuously by two recorders alternating 4 hr observation periods, from dawn until dusk each day. The following information was recorded for each copulation attempt: 1) the identity of the male and female involved (i.e. whether it was a pair or extra-pair copulation); and 2) the outcome, that is whether the copulation attempt was behaviourally successful. A copulation was recorded as behaviourally successful if cloacal contact was observed (Hunter 1998).

RESULTS

A partial pre-laying exodus occurred during the period 2-13 May (the first egg was laid on 14 May). On 2 and 3 May there were very high winds which may have resulted in exceptionally low numbers of birds at the colony. On the remaining days of the exodus between 19% and 37% of breeding birds were present at the colony on any one day.

If the function of pre-laying attendance in the Northern Fulmar is site defence, it would be predicted that a high proportion of sites would be occupied by at least one member of the pair throughout the pre-laying period up to the day of egg-laying. This was not the case (Fig. 1). During the period 1-10 April, more than 75% of sites were unoccupied on any one day and during the periods 2-4 and 7-11 May, more than 50% of sites were unoccupied. Furthermore, if individuals attend the colony to defend their sites, it would be predicted that breeding sites left unguarded would be lost to incoming individuals. Although nest sites were sometimes temporarily taken over during the absence of a pair, no such take-over was seen to persist after the return of the original site holder(s). So it seems unlikely that nest site defence is the primary reason for colony attendance.

Alternatively, individuals may attend the colony in an attempt to gain genetic benefits by engaging in either extra-pair or pair copulations. If so, it would be predicted that individuals with high levels of pre-laying attendance would be involved in more copulation attempts than those with low attendance.

Comparing males involved in EPC attempts with those not involved, there was no difference in the proportion of time spent at the colony between individuals engaging in EPCs and those not (Mann-Whitney *U*-test: $z = 1.46$, $n = 32,45$, $P = 0.1$). By contrast, females involved in EPC attempts were present at the colony on a higher proportion of days than those not involved in any EPC attempt (Mann-Whitney *U*-test: $z = 2.20$, $n = 44,33$, $P = 0.03$). This pattern may arise simply as a result of males directing EPCs towards females that spend more time at the colony. This potentially confounding factor would be overcome if only females that solicited copulations were considered. However, it was not possible in this study to identify the sex initiating a copulation attempt, except in the small number of cases in which a female went to the site of a male to engage in an EPC. Instead unforced EPC attempts are considered. Unforced EPCs may be initiated by either sex and are behaviourally indistinguishable from pair copulation attempts, indicating a level of co-operation by both male and female. Females involved in unforced EPC attempts were present at the colony on a higher proportion of days during the pre-laying period than those not involved in any unforced EPC attempt (Mann-Whitney *U*-test: $z = 2.53$, $n = 56,21$, $P = 0.01$). By contrast, neither males nor females gained more pair copulation attempts by being present at the colony on a high proportion of days (male: $z = 1.09$, $n = 77$, n.s.; female $z = 0.62$, $n = 77$, n.s.).

It appears, then, that females are involved in more unforced EPCs by maintaining high attendance at the colony. However, there is no evidence for

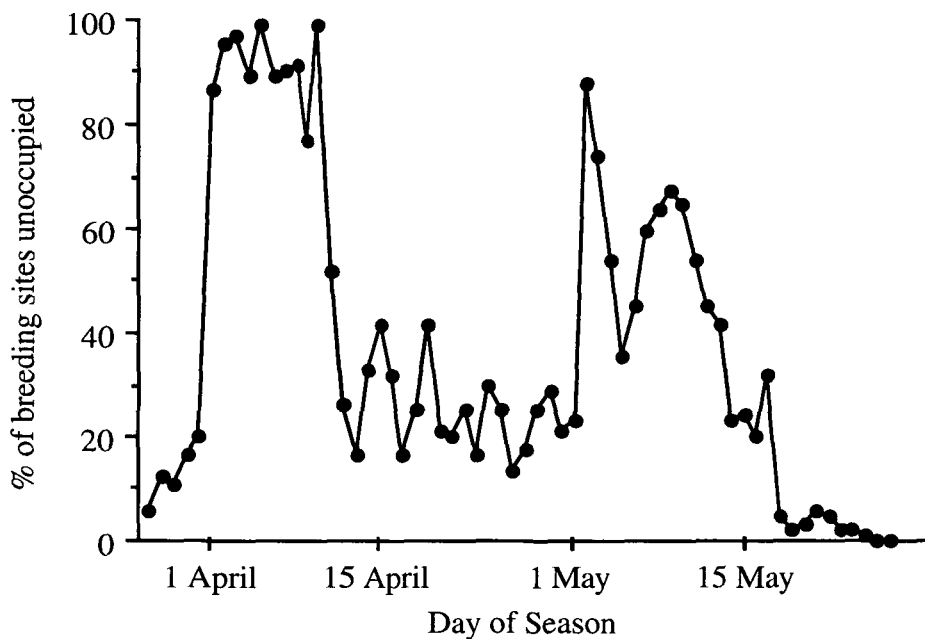


Figure 1. Pattern of site occupancy relative to calendar date. Mean date of egg laying was 18 May (± 3 days SD, $n = 91$ pairs).

Figuur 1. De aanwezigheid van Noordse Stormvogels op de broedplaats gedurende het jaar. De eileg vond gemiddeld rond 18 mei plaats (SD ± 3 dagen, $n = 91$ paren).

females gaining more pair copulations, nor for males gaining either extra-pair or pair copulations by maintaining high attendance at the colony.

Finally, if males attempt to protect the paternity of the offspring they will help to raise by defending their mates from EPCs, then it is predicted that male attendance will be higher than female attendance during the female's fertile period. This will arise because each male will attempt to be at his nest site to defend his female when she returns from feeding. The exact timing of the fertile period is not known for Northern Fulmars. In most species studied, fertilisation occurs 24 hours prior to egg laying and the fertile period ends at

this time, on day -1 (Birkhead & Møller 1992). Hunter (1998) has suggested that in female Northern Fulmars, although fertilisation is likely to take place within a few days of egg laying, the fertile period ends between nine and 20 days prior to egg-laying due to physiological changes in the females reproductive tract. So, inseminations after this time are incapable of fertilising eggs. Hence, if male Northern Fulmars attempt to protect their partners from EPCs it is predicted that male attendance will be higher than female attendance in the period immediately before day -9.

The patterns of male and female attendance varied relative to egg laying during the 52 days prior to laying (Fig. 2a). Attendance was high on days -52 to -50 and reached a peak during the period from day -32 to day -21. After the initial high attendance and during the period day -15 to day -5, attendance was relatively low for both males and females, with less than 60% of individuals of either sex being present. The overall pattern of attendance from day -55 to day +11 was similar for each sex (Spearman rank correlation, $r_s = 0.73$, $n = 67$, $P < 0.001$). Assuming the fertile period to have ended on day -9, then a higher proportion of males than females were in attendance prior to the end of the fertile period (Wilcoxon signed rank test: $z = 5.66$, $n = 46$ days, $P < 0.001$). Even if the fertile period continues to day -1 a higher proportion of males than females were in attendance during the pre-laying period (Wilcoxon signed rank test: $z = 6.20$, $n = 55$ days, $P < 0.001$). By contrast, during the post-laying period there was no difference in the proportion of males and females in attendance (Wilcoxon signed rank test: $z = 1.51$, $n = 12$, $P = 0.1$).

If males attempt to defend their mates, it is predicted that females will rarely be left alone by their partners during the females' fertile periods. The patterns of attendance of unaccompanied males and females varied with respect to egg laying (Fig. 2b). The proportion of females observed to be alone at their sites was very low (4.2%, 2/48) during the period day -34 to day -12. After this time it rose to 14.3% (2/14) on day -9 and remained at this level until day 0 when it increased to 26.7% (20/75) and persisted during the first ten days of incubation. The proportion of males observed to be alone during the period day -20 to day -2 was always greater than 17.7% (6/34) and rose as high as 51.9% (14/27) on day -6. Immediately after laying, the proportion of males observed alone increased to 72.3% (34/47). The post-laying pattern of sex observed alone at the site reflects the tendency for females to take a short (<24 hr) initial incubation shift and males to follow with a long shift (Dunnet *et al.* 1963; Hatch 1990; Mougín 1967). If the fertile period ends on day -9 a smaller proportion of females than males were left alone on any day prior to the end of the fertile period (Wilcoxon signed rank test: $z = 5.62$, $n = 45$, $P < 0.001$).

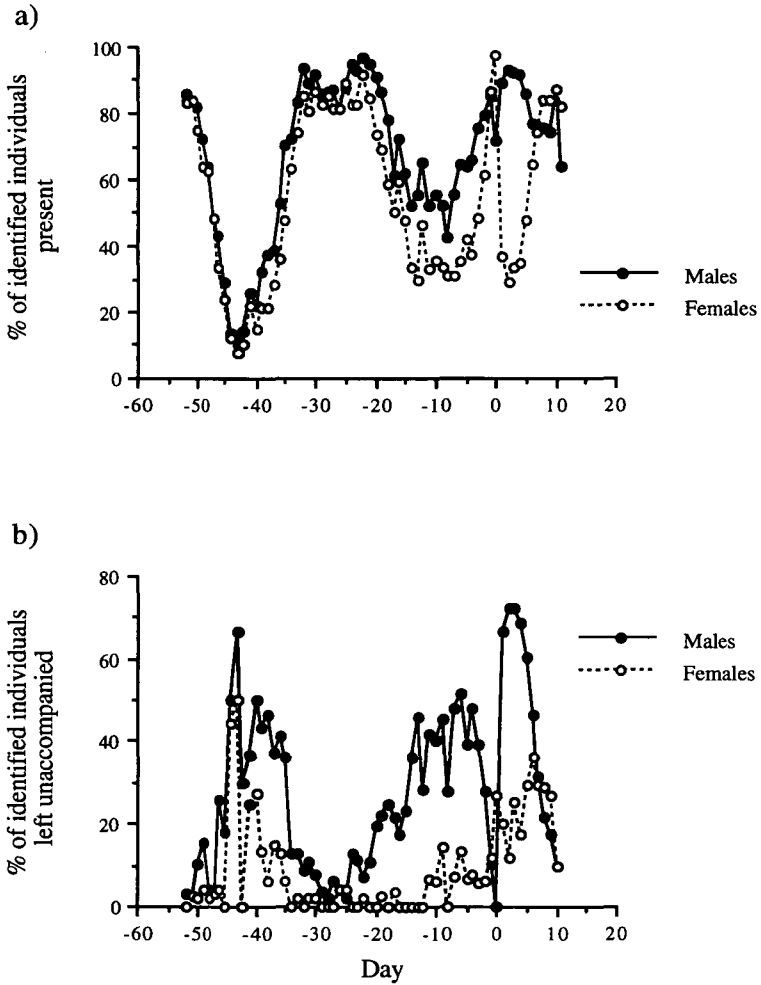


Figure 2. Pattern of attendance of breeding individuals relative to egg-laying for: (a) males and females ($n = 77$ pairs); and (b) unaccompanied males and females ($n = 77$ pairs). Day 0 is the day the egg is laid.

Figuur 2. Aanwezigheid van broedvogels in vergelijking tot de datum van eileg: (a) mannetjes en vrouwtjes ($n = 77$ paren) en (b) niet-begeleide mannetjes en vrouwtjes ($n = 77$ paren). Dag 0 is de datum waarop het ei werd gelegd.

Similarly, if the fertile period continues up until day -1 a smaller proportion of females than males were left alone on any day during the pre-laying period (Wilcoxon signed rank test: $z = 6.18$, $n = 54$, $P < 0.001$). However, during the post-laying period there was no difference between the sexes in the numbers of individuals left alone (Wilcoxon signed rank test: $z = 1.78$, $n = 10$, n.s.). The proportion of females left alone was lower before than after (and including) day -9, the presumed end of the fertile period (Mann-Whitney U -test: $z = 3.18$, $n = 45,20$, $P < 0.001$). Similarly, a lower proportion of females was left alone prior to egg-laying than after egg-laying (Mann-Whitney U -test: $z = 4.48$, $n = 54,11$, $P < 0.001$). There was no difference in the proportion of females left alone during the presumed infertile period prior to laying (day -9 to day -1) and the post-laying period (Mann-Whitney U -test: $z = 0.49$, $n = 9,11$, n.s.).

The higher incidence of male than female attendance, and the finding that females are rarely left alone during the period day -34 to day -12, both support the idea that males are attempting to protect their partners from EPCs. If so, it would be predicted that females involved in EPC attempts will have been left alone by their partner for longer periods than those not involved in EPC attempts. However, females involved in attempted EPCs were not more likely to be left unaccompanied by their mates during the pre-laying period than those that were not involved in any EPC attempt (Mann Whitney U -test $z = 0.48$, $n = 44,33$, n.s.). That is, there was no relationship between the amount of time a female was left unaccompanied by her mate and the likelihood of her being involved in extra-pair copulation activity.

DISCUSSION

Many studies have reported a pre-laying exodus in Northern Fulmars and other Procellariiformes during which individuals are absent from the colony (Fisher 1952; Warham 1990). Dunnet *et al.* (1963) reported a pre-laying exodus during which only 3-10% of their Orkney population was present, MacDonald (1977b) found only 8-23% of his Aberdeenshire population present during the exodus, and Hatch (1987) found less than 10% of individuals present during the exodus in the Semidi Islands, Alaska. In the Fair Isle population studied here, only a partial exodus appears to have occurred over the period 2-13 May. Except for the first two days of this period when high winds occurred and all but a few birds were absent, between 19% and 37% of breeding birds were present. It is possible that food was available relatively close to the colony so foraging individuals could return frequently to the breeding site (Warham

1990). It appears that the pre-laying exodus might have had little or no constraining effect on the behaviour of individuals in this study.

There was no evidence to support the idea that for Northern Fulmars the function of pre-laying colony attendance was site defence. Nest sites were left unguarded for long periods during the pre-laying period and were not subsequently lost to conspecifics. Both MacDonald (1980) and Hatch (1987) in their studies of Northern Fulmar site attendance came to similar conclusions. Females present at the colony on a high proportion of days during the pre-laying period were more likely to be involved in EPC attempts. However, without further study it is not possible to say whether females maintain a presence at the colony specifically to engage in EPCs or whether they attend the colony for some other, as yet unidentified, reason and experience a high rate of EPCs as a consequence. There was no relationship between the amount of time a female was left unaccompanied by her mate and the likelihood of her being involved in extra-pair copulation activity. This might appear paradoxical as a female left alone would be open to the advances of extra-pair males. However, it is possible that only low quality females were left alone for long periods by their partners and such females may have been less attractive to extra-pair males, given the constraints of sperm production (Petrie & Hunter 1994).

Males maintained a higher level of attendance throughout the pre-laying period and seldom left their female partners unaccompanied during the presumed fertile period. Consequently, it appears that males attend the colony in an attempt to prevent their partners from engaging in EPCs. Many studies have assumed that mate guarding, or mate defence, involves a male attempting to prevent any extra-pair male from copulating with his passive mate. The emphasis has been on the pair male responding to the extra-pair male's behaviour. However, this study shows that the threat to a male's paternity may come not from the extra-pair male but from the female instead. Female Northern Fulmars play an active role in securing EPCs; 11% (4/36) of females in the present study went to the breeding sites of extra-pair males to engage in EPC attempts and for an EPC attempt to be successful the female must co-operate with the extra-pair male (pers. obs.). Males might benefit more from attempting to impede their pair female's EPC attempts than from terminating an extra-pair male's advances.

Male and female Northern Fulmars appear to be in conflict over female participation in EPC attempts. Females seek EPCs whereas males attempt to minimise their partner's opportunities for engaging in them. Females seem to be winning the conflict, as males that never left their partners

unaccompanied did not reduce their chances of being cuckolded. The partners of these males still engaged in EPCs, in some cases by going to the sites of other males. However, in their study of paternity in Northern Fulmars, Hunter *et al.* (1992) found no evidence that EPCs resulted in extra-pair paternity. So the question arises, why do females actively seek EPCs if they never result in extra-pair paternity. There are a number of possible reasons: (1) although Hunter *et al.* (1992) found no evidence for EPCs resulting in offspring, their effective sample size meant a level of extra-pair paternity of less than 4.6% could have gone undetected (95% confidence limits, $n = 85$). Extra-pair behaviour could be maintained in the population if even a low level of extra-pair paternity occurred. (2) Females may seek EPCs as insurance against their partner being infertile (Hatch 1987; Westneat *et al.* 1990), (3) females may use EPCs to promote sperm competition and test their males, or (4) there may be some non-genetic benefit to engaging in EPCs. Perhaps the most likely non-genetic benefit for Northern Fulmars is that by engaging in EPCs, long term extra-pair bonds may be maintained, then if a partner dies there will be an alternative mate to take over (Hatch 1987).

Two main forms of paternity assurance have been identified: mate protection, and frequent copulation (Birkhead & Møller 1992). The most commonly described form of mate protection is mate guarding by close following, in which the male actively maintains close contact with the female throughout her fertile period, following her wherever she goes (Birkhead 1979; Lumpkin *et al.* 1982). This strategy is appropriate for territorial birds (Birkhead *et al.* 1987), who remain in a more or less discrete area throughout the female's fertile period, where copulation can occur anywhere within that area and where the habitat gives rise to opportunities for EPCs (Björklund and Westman 1986). For some species however, resources such as food, water or nesting material may be distant from breeding sites, making it difficult for a male to maintain contact with his female (Frederick 1987; Mineau & Cooke 1979; Werschkul 1982). For species that copulate only at the breeding site, including the majority of seabirds, the pair male can still defend his female from the EPC attempts of other males if he ensures that he is at the colony whenever she is present (Birkhead *et al.* 1985; Hatchwell 1988). This form of mate protection is unlike mate guarding in that the male maintains contact passively, by being at the site of copulation, rather than following the female. Male Northern Fulmars appear to use passive mate defence to protect their paternity.

Møller & Birkhead (1991) have shown that mate guarding and frequent copulation are alternative strategies and that colonial species tend not

to protect their mate but instead rely solely on frequent copulation to ensure their paternity. This stems from the finding that in most colonial species one member of the pair must defend the nest site while the other is foraging so there will be times when the female cannot be guarded and must be left alone (Birkhead *et al.* 1987). Male Northern Fulmars appear to employ both mate defence and frequent copulation to protect their paternity (Hatch 1987; Hunter *et al.* 1992; this study). For Northern Fulmars there is no evidence that nest defence acts as a behavioural constraint, so males can forage at the same time as their partners and be present at the breeding site when their partners are present and available for EPCs. However, it appears that male Northern Fulmars cannot rely solely on passive mate defence to protect paternity as females in the present study engaged in extra-pair copulation attempts despite their male's presence. This may explain why male Northern Fulmars use frequent copulation in addition to mate defence to protect their paternity (Hunter *et al.* 1992). The low incidence of extra-pair paternity in this species would suggest that the use of multiple paternity protection strategies is largely successful.

Females participate in EPCs despite their partner's presence at the colony so the final question remains, why do males bother to attempt to prevent their mates from engaging in EPCs if their attempts are unsuccessful? There are two possible reasons. (1) It may be that mate defence behaviour reduces the overall frequency of EPCs and that only the most persistent or the most opportunistic females can overcome their partner's protective behaviour. (2) Males that are present and aware of their female's EPC attempts may be in a better position to respond to these by increasing their copulation rate.

ACKNOWLEDGEMENTS

I am most grateful to Stuart Thomson Sr, the staff of Fair Isle Bird Observatory and especially Sarah Watts for help with fieldwork; and to T.R. Birkhead, T. Bouludier, and S.A. Hatch for helpful comments on the manuscript. The Natural Environment Research Council funded the study.

SAMENVATTING

Noordse Stormvogels brengen veel tijd door op de broedplaatsen in de maanden voorafgaande aan de eileg. In het hier gepresenteerde onderzoek werd de functie van dit verblijf onderzocht. Verondersteld werd dat de aanwezigheid in de kolonie gunstig zou kunnen zijn voor (1) een effectieve verdediging van de nestplaats (het territorium), (2) de extra mogelijkheden voor copulaties met de partner of met andere individuen op de kolonie (EPCs, *extra pair copulations*), of (3) juist ter verdediging van de partner tegen ongewenste intimiteiten van andere Noordse Stormvogels op de kolonie. Er werden geen aanwijzingen gevonden dat de aanwezigheid een rol speelde bij de verdediging van het nest. De nestplaats bleef vaak langdurig onbezet en kon vervolgens weer gewoon door dezelfde vogels worden ingenomen. Evenmin kon worden geconstateerd dat de aanwezige broedparen zich bijzonder actief bezighielden met copulaties. Er werden wel aanwijzingen verzameld dat de op de kolonie aanwezige

wijfjes zich bezighielden met *extra-pair* copulaties (paringen met niet-partners) en er bestond een positief verband tussen de duur van het verblijf op de kolonie en het aantal paringen met niet-partners. Het blijft mogelijk dat de vogels om andere redenen op de kolonie verbleven en dat de *extra-pair* copulaties niet het doel op zich waren, maar plaatsvonden omdat de vogels daar nu eenmaal zaten. De aanwezigheid van mannetjes op de broedplaatsen leek samen te hangen met hun pogingen om deze 'ontrouw' van de partner te voorkomen. Mannetjes waren gemiddeld veel langduriger aanwezig dan wijfjes en in de (verondersteld) vruchtbare periode van de wijfjes weken zij vrijwel niet van de zijde van de partners.

REFERENCES

- Astheimer L.B. & Grau C.R. 1990. A comparison of yolk growth rates in seabird eggs. *Ibis* 132: 380-394.
- Birkhead T.R. 1978. Attendance patterns of Guillemots *Uria aalge* at breeding colonies on Skomer Island. *Ibis* 120: 219-229.
- Birkhead T.R. 1979. Mate-guarding in the Magpie *Pica pica*. *Anim. Behav.* 27: 866-874.
- Birkhead T.R., Greene E., Biggins J.D. & Nettleship D.N. 1985. Breeding site characteristics and breeding success in Thick-billed Murres. *Can. J. Zool.* 63: 1880-1884.
- Birkhead T.R., Atkin L. & Møller A.P. 1987. Copulation behaviour of birds. *Behaviour* 101: 101-138.
- Birkhead T.R. & Møller A.P. 1992. *Sperm competition in birds: causes and consequences*. Academic Press, London.
- Björklund M. & Westman B. 1986. Mate guarding in the Great Tit: tactics of a territorial forest-living species. *Ornis Scand.* 17: 99-105.
- Dunnet G.M., Anderson A. & Cormack R.M. 1963. A study of survival of adult Fulmars with observations on the pre-laying exodus. *Br. Birds*. 56: 2-18.
- Dunnet G.M. & Ollason J.C. 1978a. The estimation of survival rate in the Fulmar *Fulmarus glacialis*. *J. Anim. Ecol.* 47: 507-520.
- Dunnet G.M. & Ollason J.C. 1978b. Survival and longevity in the Fulmar. *Ibis* 120: 124-125.
- Fisher J. 1952. *The fulmar*. Collins, London.
- Frederick P.C. 1987. Extra-pair copulations in the mating system of White Ibis (*Eudocimus albus*). *Behaviour*. 100: 70-201.
- Gladstone D.E. 1979. Promiscuity in monogamous colonial birds. *Am. Nat.* 114: 545-557.
- Hatch S.A. 1987. Copulation and mate-guarding in the Northern Fulmar. *Auk* 104: 450-461.
- Hatch S.A. 1990. Incubation rhythm in the Fulmar, *Fulmarus glacialis*: annual variation and sex roles. *Ibis* 132: 515-524.
- Hatchwell B.J. 1988. Intraspecific variation in extra-pair copulation and mate defence in Common Guillemots *Uria aalge*. *Behaviour* 107: 157-185.
- Hatchwell B.J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of Common Guillemots (*Uria aalge*). *J. Anim. Ecol.* 60: 721-736.
- Hudson P.T. 1982. Nest site characteristics and breeding success in the Razorbill *Alca torda*. *Ibis* 124: 355-359.
- Hunter F.M. 1998. Timing of pair and extra-pair copulations in the Northern Fulmar. *Condor* 100: 141-145.
- Hunter F.M., Burke T. & Watts S.E. 1992. Frequent copulation as a method of paternity assurance in the Northern Fulmar. *Anim. Behav.* 44: 149-156.
- Jones I.L. 1992. Colony attendance of Least Auklets (*Aethia pusilla*) on St Paul Island, Alaska: implications for population monitoring. *Condor* 94: 93-100.
- Lumpkin, S. Kessel K., Zenone P.G. & Erickson C.J. 1982. Proximity between the sexes in Ring Doves: social bonds or surveillance? *Anim. Behav.* 30: 506-513.
- MacDonald M.A. 1977a. Adult mortality and fidelity to mate and nest site in a group of marked Fulmars. *Bird Study* 24: 165-168.

- MacDonald M.A. 1977b. The pre-laying exodus of the Fulmar *Fulmarus glacialis*, (L.). *Ornis Scand.* 8: 33-37.
- MacDonald M.A. 1980. The winter attendance of Fulmars at land in N.E. Scotland. *Ornis Scand.* 11: 23-29.
- Mineau P. & Cooke F. 1979. Rape in the Lesser Snow Goose. *Behaviour* 70: 280-291.
- Mougin J.-L. 1967. Étude écologique des deux espèces de Fulmar: le Fulmar Atlantique (*Fulmarus glacialis*) et le Fulmar Antarctique (*F. glacialisoides*). *Oiseaux* 37: 57-103.
- Møller A.P. & Birkhead T.R. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behaviour* 118: 171-186.
- Ollason J.C. & Dunnet G.M. 1978. Age, experience and other factors affecting the breeding success of the Fulmar, *Fulmarus glacialis*, in Orkney. *J. Anim. Ecol.* 47: 961-976.
- Petrie M. & Hunter F.M. 1994. Intraspecific variation in courtship and copulation frequency: an effect of mismatch in partner attractiveness? *Behaviour* 127: 265-277.
- Potts G.R., Coulson J.C. & Deans I.R. 1980. Population dynamics and breeding success of the Shag *Phalacrocorax aristotelis* on the Farne Islands Northumberland. *J. Anim. Ecol.* 49: 465-484.
- Warham J. 1990. The petrels, their ecology and breeding systems. Academic Press, London.
- Werschkul D.F. 1982. Nesting ecology of the Little Blue Heron: promiscuous behaviour. *Condor* 84: 381-384.
- Westneat D.F., Sherman P.W. & Morton M.L. 1990. The ecology and evolution of extrapair copulations in birds. *Curr. Ornithol.* 7: 331-369.
- Wittenburger J.F. & Hunt G.L. 1985. The adaptive significance of coloniality in birds. *Avian. Biol.* 8: 1-78.

MICROGEOGRAPHICAL VARIATION IN THE CALL OF THE MALE MANX SHEARWATER *PUFFINUS PUFFINUS*

LOCALE VARIATIES IN DE ROEP VAN MANNETJES NOORDSE PIJLSTORMVOGELS

DAVID WOOD

Scottish Natural Heritage, 1 Kilmory Estate, Lochgilphead, Argyll,
Scotland, U.K.

The calls of male Manx Shearwaters at two separate breeding areas on Bardsey Island, Wales were investigated. There was little difference between calls from the two subcolonies when call characteristics were compared separately, but a discriminant analysis placed 75% of the birds into their correct locality. The recent establishment of one of the subcolonies may be responsible for the call variation, rather than any functional explanation.

Wood D. 1999. Microgeographical variation in the call of the male Manx Shearwater *Puffinus puffinus*. *Atlantic Seabirds* 1(1): 17-26.

INTRODUCTION

Compared with work on passerines, patterns of change in seabird calls across geographical areas have received little attention. Where differences have been reported, these have nearly always involved widely separated colonies (Hand 1981; James 1985a; Bretagnolle 1989; Bretagnolle & Lequette 1990; Bretagnolle *et al.* 1991; Tomkins & Milne 1991). The aim of this study was to examine the extent of geographical variation in the calls of male Manx Shearwaters *Puffinus puffinus* on a much smaller scale: between two localities 1.5 km apart on a small offshore island. Manx Shearwaters are nocturnal, colonial burrow-nesters, with a well-developed vocal communication system used for sexual signalling and burrow defence (James 1985b). All male birds can be stimulated to call from nesting burrows by the playback of another male's call, and each male makes an individually distinct variation on a basic, clearly structured, repetitive call pattern (Brooke 1978).

STUDY AREA AND METHODS

The study was carried out on Bardsey, a small island (2.5 km x 1 km) lying 2.5 km from the tip of the Lleyn Peninsula, North Wales. The island comprises low-

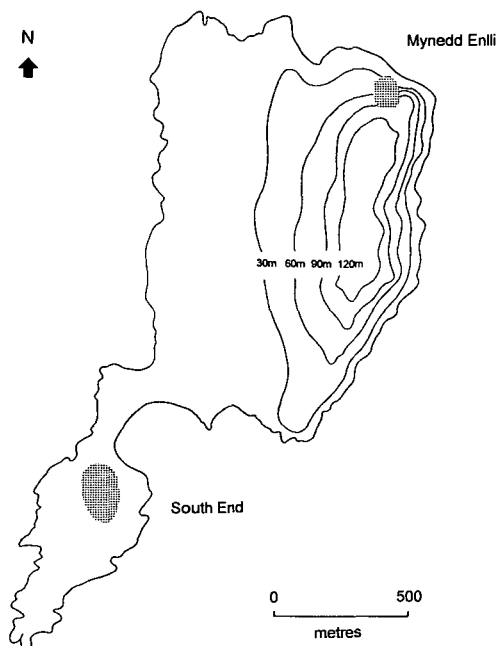
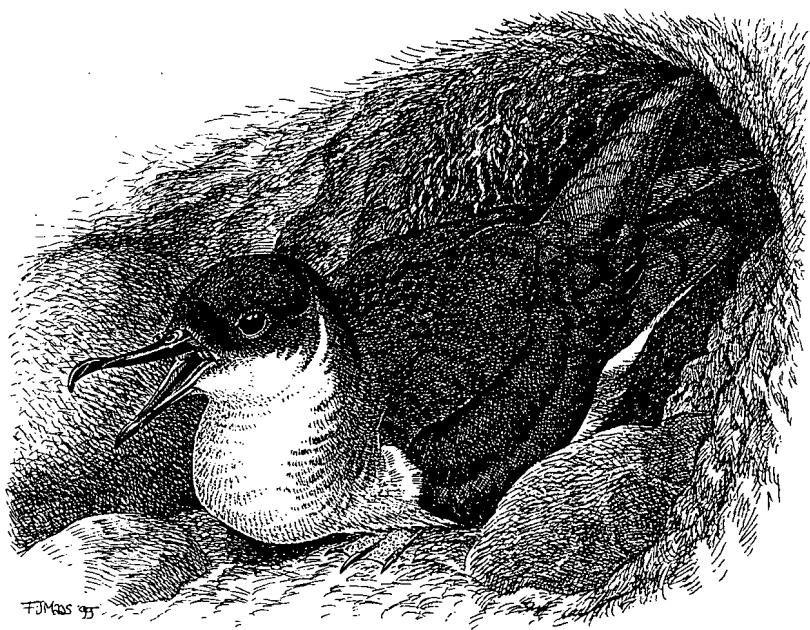


Figure 1. Bardsey Island, showing the locations of shearwater burrows mentioned in the text.

Figuur 1. Bardsey eiland met de plaatsnamen die in de tekst worden genoemd.

lying agricultural land divided by low drystone walls, and a steep hill (Mynedd Enlli) rising to 170 m in the east (Fig 1). Of 2000-4000 pairs of Manx Shearwaters breeding on the island, about half nest at high density in burrows on the north and east slopes of Mynedd Enlli, the remainder being scattered among field walls across the island (Jones 1988). The South End peninsula holds 400-500 pairs (Smart 1986). Reports from the early part of this century suggest that numbers formerly were much lower and changeable, becoming restricted to Mynedd Enlli and possibly reduced to approximately 30-40 pairs by 1913 (Aplin 1902; Ticehurst 1919; Wilson 1930). This occurred when the human population and agricultural impact on the island were at a maximum; 124 people lived on the island in 1901 (Jones 1988). Therefore, shearwater nesting areas away from Mynedd Enlli are likely to have been established or re-established relatively recently. However, the year when this occurred is not known.

During May 1989, a 'playback' method (James & Robertson 1985) was used to record calls of male Manx Shearwaters occupying breeding burrows at



Manx Shearwater *Noordse Pijlstormvogel* (F.J. Maas)

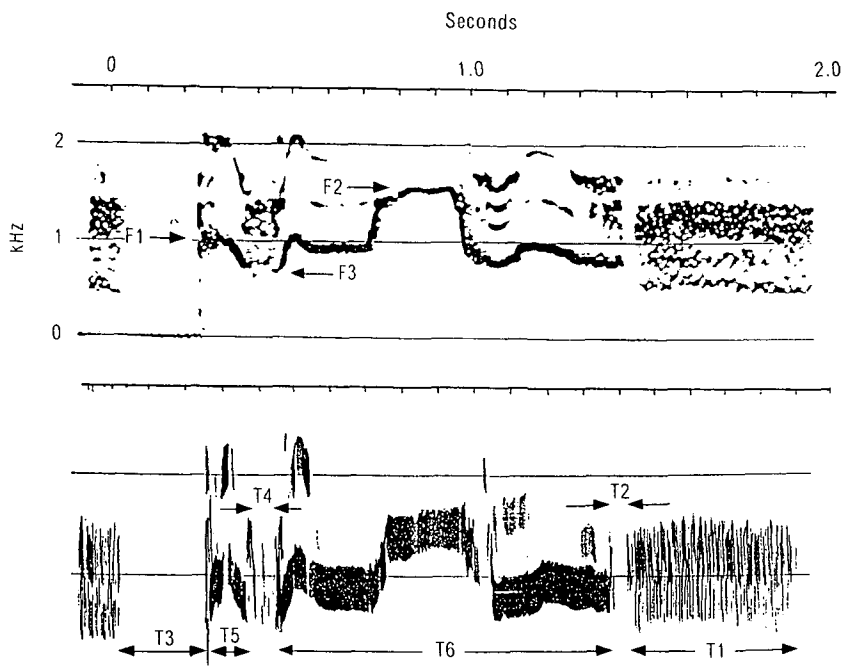


Figure 2. (A) Illustration of three frequency characteristics measured for the call of the male Manx Shearwater: F1 - maximum frequency of first note; F2 - maximum frequency of whole call; F3 - minimum frequency of whole call. (B) Illustration of six temporal characteristics measured for the call of the male Manx Shearwater: T1 - duration of breath intake note; T2 - time gap between breath intake note and rest of call segment; T3 - time gap between successive call segments; T4 - time gap between first note and rest of call segment; T5 - duration of first note; T6 - duration of main part of call segment.

Figuur 2. (A) Illustratie van drie karakteristieke frequenties gemeten bij mannetjes Noordse Pijlstormvogels. F1 = maximale frequentie van de eerste toon, F2 = maximale frequentie van de gehele roep, F3 = minimale frequentie van de gehele roep. (B) zes karakteristieke aspecten van de tijdsduur van onderdelen van de roep. T1 = duur van de toon bij het inademen, T2 = tijdsduur tussen T1 en de rest van het eerste segment van de roep, T3 = tijdsduur tussen opeenvolgende geluidssegmenten, T4 = tijd tussen de eerste toon en de rest van het geluidssegment, T5 = totale duur van het eerste geluidssegment, T6 = duur van het belangrijkste deel van de roep.

[illegible]

Table 2. Discriminant analysis: canonical coefficients (see Fig. 2).
 Tabel 2. Discriminant analyse: canonische coëfficiënten (zie Fig. 2).

F1	-0.37	T3	-0.37
F2	-0.25	T4	0.07
F3	0.53	T5	0.45
T1	0.26	T6	0.21
T2	-0.50		

Table 3. Classification summary for discriminant analysis.
 Tabel 3. Samenvatting classificatie discriminant analyse.

	number of cases <i>aantal gevallen</i>	correctly predicted <i>correct voorspeld</i>	% corr. predicted <i>correct voorsp. (%)</i>
South End <i>zuidzijde</i>	29	23	79%
Mynedd Enlli	28	20	71%
totals <i>totaal</i>	57	43	75%

RESULTS

Mean values and standard deviations of call characteristics from Bardsey (Table 1) generally conformed with Manx Shearwater calls from other British and Irish islands (James 1985a). Unfortunately a detailed comparison between the two studies is not possible for two reasons. Firstly, different recording equipment was used, which may have given rise to systematic errors (Slater 1991). Secondly, drift in the values of the call characteristics, identified by James (1985a), may have occurred between the dates of the two studies.

On Bardsey, call characteristics, when compared individually, were not very different between Mynedd Enlli and South End. Only one characteristic, the maximum frequency of the first note of the call, resulted in a value of t associated with $P < 0.05$, and as the probability of this occurring by chance in a series of nine t -tests is quite high ($P = 0.45$), the result is of little consequence. There was no evidence that temporal or frequency characteristics were systematically higher or lower between one area and the other. The discriminant analysis (see canonical coefficients in Table 2) generates a statistic that tests for overall differences between the means, and again, no significant difference between the two areas was found (Wilks' lambda = 0.76, $F = 1.67$, $df = 9$ and 47, n.s.). However, the same analysis placed 75% of birds into their correct sub-colony (Table 3 and Fig. 3). This is a significantly better classification than would be expected by chance ($Z = 3.87$, $P < 0.01$; Titus *et al.* 1984).

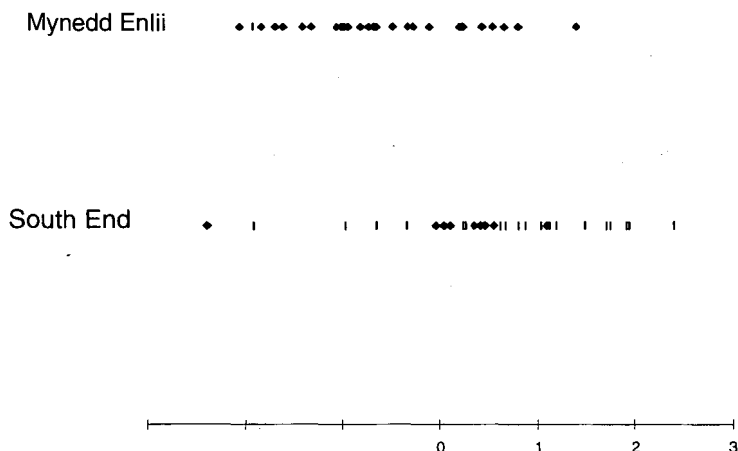


Figure 3. Scatter plot showing the classification of male Manx shearwaters by discriminant analysis of nine call characteristics.

Figuur 3. Puntenwolk op grond waarvan mannetjes Noordse Pijlstormvogels van twee locaties na discriminant analyse van 9 karakteristieken van de roep konden worden geclassificeerd.

DISCUSSION

Microgeographical differences in bird vocalisations can have several explanations. For example, in passerines it is commonly linked to vocal learning. The pattern of geographical variation is then influenced by the site and extent of vocal learning, and the age at which it occurs (Krebs & Kroodsma 1980; Catchpole 1982). However, there appears to be little if any strong evidence for vocal learning in the Procellariiformes (review in Bretagnolle 1996).

The shearwater calls may be adapted to the local environment. A feature of the two subcolonies sampled in my study is that they occupy rather different habitats. The Mynedd Enlli burrows are densely clumped on a steep, exposed hillside, and were probably dug by the birds themselves, whereas South End birds occupy a set of disused rabbit holes, following the lines of old field walls on level ground. The calls may be subtly adapted to provide optimal acoustic propagation according to the different conditions found at each location; there is evidence for this in some passerines (Morton 1975; Hunter & Krebs 1979). However, the subcolonies studied on Skomer by James (1985a) were also in

contrasting locations, especially with respect to topography and degree of noise from the sea, and there was no noticeable variation in calls between them. This difference in findings between the two studies mitigates against adaptation to local environment being the reason for the observed differences between the two areas on Bardsey.

The call differences could arise if higher quality males nested preferentially in one of the areas, and signalled their status through their calls. Male body weight might be a good measure of the quality of individual petrels, and there is evidence that body weight is correlated with call characteristics in some species (Bretagnolle 1996). However, James (1985a) found no significant correlations between body size and call frequency variables in 22 male Manx Shearwaters.

More generally, shearwaters nesting on Skomer and Bardsey presumably have similar functional requirements for their calls. Therefore, the lack of significant call variation between the Skomer subcolonies suggests that functional explanations in general are unlikely to be responsible for the observed differences between the two areas on Bardsey.

An alternative, non-functional explanation for the pattern on Bardsey, which may also account for the contrasting results between the two islands, is suggested by comparing their histories over approximately the last century. On Bardsey, subcolonies away from Mynedd Enlli appear to have been recently established or re-established. This could have happened in two ways. Firstly, a small subset of the breeding birds on Mynedd Enlli could have moved to the South End, possibly in response to reduced human disturbance at the South End. In this case, divergent calls between Mynedd Enlli and the South End could have arisen by a founder effect, with the strongly developed philopatry normally shown by established breeders in this species providing isolation of birds in the new breeding area; Perrins *et al.* (1973) showed that for Manx Shearwaters ringed on Skokholm when fully grown, 97% of those recaptured had moved less than 45 m. Independent vocal lineages could then develop by genetic inheritance. However, with only an estimated 13-15 shearwater generations having passed between the early years of this century and the late 1980s (Harris 1966), it is unlikely that a few emigrants from Mynedd Enlli could have given rise to the substantial numbers nesting at the South End in 1989. A more likely explanation is that shearwaters from other islands colonised the South End and introduced call variation to Bardsey directly; significant vocal differences between well-separated islands have been detected in this species (James 1985a).

Whatever the cause of the call divergence, we would expect that call differences would rapidly become obscured by those young birds that nest away from their natal burrows at first breeding (estimated at 50% of females and an

unknown proportion of males; Brooke 1990). However, on Bardsey, the short period of time that has passed since the present South End colony was established may not have been long enough to fully eliminate the call differences. In comparison, Skomer's large shearwater colony probably has a long history of stability. This can be inferred because only five or six men were needed to work the Skomer farm in the 1860s, when agricultural activity was at its peak, and even at this time only a small proportion of the land was enclosed (Howells 1968). This suggests that shearwaters over much of Skomer were left relatively undisturbed by human activity. In a stable island population, any original vocal patterning would long since have been lost.

Dialect formation by colonisation, followed by isolation, has been suggested in some songbirds (Baker 1975; Lemon 1975; Baker & Cunningham 1985) and may also occur in petrels (Tomkins & Milne 1991). Corroboration of this mechanism in Manx Shearwaters would require investigation of a colony in the process of establishment and expansion (for example, Storey & Lien 1985).

ACKNOWLEDGEMENTS

I thank Michael Brooke, Peter McGregor, Mike Shepherd, John Coulson and two anonymous referees for comments on previous drafts. Emllyn Parry, F.G. Gooding and staff of the Statistics Advisory Unit (University College of North Wales, Bangor), and Michael Shewry (Scottish Natural Heritage), kindly assisted with the multivariate analysis and production of the sonagrams. The fieldwork was conducted while the author was studying for a Master of Science degree at UCNW Bangor, supported by a NERC studentship. Permission to stay and work on Bardsey was given by Bardsey Island Trust.

SAMENVATTING

Roepende mannetjes van de Noordse Pijlstormvogel *Puffinus puffinus* op Bardsey eiland (Wales) werden bestudeerd op twee verschillende plaatsen in de kolonie. Ofschoon er op het eerste gezicht maar weinig verschil bestond in de geluiden die de dieren op beide plaatsen produceerden, bleek na een gedetailleerde studie en een discriminant analyse dat liefst 75% van de vogels op basis van het geluid correct konden worden toegewezen aan één van beide locaties. De recente vestiging van één van beide subkolonies en daarmee het arriveren van 'allochtone' pijlstormvogels in het gebied zou kunnen verklaren hoe het verschil in roep tot stand is gekomen.

REFERENCES

- Aplin O.V. 1902. The birds of Bardsey, with additional notes on the birds of Llyn. *Zoologist* 4(6): 8-17, 107-110.
- Baker M.C. 1975. Song dialects and genetic differences in white-crowned sparrows (*Zonotrichia leucophrys*). *Evolution* 29: 226-241.
- Baker M.C. & Cunningham, M.A. 1985. The biology of song dialects. *Behav. Brain Sci.* 8: 85-133.
- Bretagnolle V. 1989. Calls of Wilson's Storm Petrel: Functions, individual and sexual recognitions, and geographic variation. *Behaviour* 111: 98-112.
- Bretagnolle V. 1996. Acoustic communication in a group of non-passerine birds, the petrels. In: Kroodsma, D.E. & E.H. Miller (eds) *Ecology and evolution of acoustic communication in birds*. Comstock Publishing Associates.

- Bretagnolle V., Carruthers M., Cubitt M., Bioret F. and Cuillandre J.-P. 1991 Six captures of a dark-rumped, fork-tailed storm-petrel in the northeastern Atlantic. *Ibis* 133: 351-356.
- Bretagnolle V. & Lequette B. 1990. Structural variation in the call of the Cory's Shearwater (*Calonectris diomedea*, Aves, Procellariidae). *Ethology* 85: 313-323.
- Brooke M. de L. 1978. Sexual differences in the voice and individual vocal recognition in the Manx Shearwater *Puffinus*. *Anim. Behav.* 26: 622-629.
- Brooke M. de L. 1990. The Manx Shearwater. T. & A.D. Poyser, London.
- Catchpole C.K. 1982. The evolution of bird sounds in relation to mating and spacing behaviour. In: D.E. Kroodsma and E.H. Miller (eds) *Acoustic communication in birds*, 1. Academic Press.
- Hand J.L. 1981. A comparison of vocalizations of Western Gulls *Larus occidentalis occidentalis* and *L. o. livens*. *Condor* 83: 289-301.
- Harris M.P. 1966. Age of return to the colony, age of breeding and adult survival of Manx Shearwaters. *Bird Study* 13: 84-95.
- Howells R. 1968. *The sounds between*. H.G. Walters (Publishers) Ltd., Tenby.
- Hunter M.L. & Krebs J.R. 1979. Geographical variation in the song of the Great Tit (*Parus major*) in relation to ecological factors. *J. Anim. Ecol.* 48: 759-785.
- James P.C. 1985a. Geographical and temporal variation in the calls of the Manx Shearwater *Puffinus puffinus* and British Storm Petrel *Hydrobates pelagicus*. *J. Zool., Lond. (A)* 207: 331-344.
- James P.C. 1985b. The Vocal Behaviour of the Manx Shearwater *Puffinus puffinus*. *Z. Tierpsychol.* 67: 269-283.
- James P.C. & Robertson, H.A. 1985. The use of playback recordings to detect and census nocturnal burrowing seabirds. *Seabird* 8: 18-20.
- Jones P.H. 1988. *The natural history of Bardsey*. National Museum of Wales, Cardiff.
- Krebs J.R. & Kroodsma D.E. 1980. Repertoires and geographical variation in bird song. *Adv. Study Behav.* 11: 143-177.
- Lemon R.E. 1975. How birds develop song dialects. *Condor* 77: 385-406.
- Morton E.S. 1975. Ecological sources of selection on avian sounds. *Am. Naturalist* 109: 17-34.
- Perrins C.M., Harris M.P. & Britton C.K. 1973. Survival of Manx Shearwaters *Puffinus puffinus*. *Ibis* 115: 535-548.
- Slater P.J.B. 1991. Learned song variations in British Storm Petrels? *Wilson Bull.* 103: 55-517.
- Smart E. 1986. The use of playback techniques to investigate population and incubation spells in the Manx shearwater. *Report of Bardsey Bird and Field Observatory* 29: 130-137.
- Storey A.E. & Lien J. 1985. Development of the first North American colony of Manx Shearwaters. *Auk* 102: 395-401.
- Ticehurst M.F. 1919. The birds of Bardsey. *Br. Birds* 13: 42-51.
- Titus K., Mosher J.A. & Williams B.K. 1984. Chance-corrected classification for use in discriminant analysis: Ecological applications. *Am. Midl. Nat.* 111: 1-7.
- Tomkins R.J. & Milne, B.J. 1991. Differences among dark-rumped petrel (*Pterodroma phaeopygia*) populations within the Galapagos archipelago. *Notornis* 38: 1-35.
- Wilson W. 1930. Some further notes on the birds of Bardsey Island. *Br. Birds* 24: 121-123.

THE FOOD OF BREEDING HERRING GULLS *LARUS ARGENTATUS* AT THE LOWER RIVER ELBE: DOES FISH AVAILABILITY LIMIT INLAND COLONISATION?

HET VOEDSEL VAN ZILVERMEEUWEN AAN DE RIVIER DE ELBE: VIS-AANBOD BEPERKEND VOOR KOLONISATIE IN HET BINNENLAND?

OMMO HÜPPOP & KATHRIN HÜPPOP

*Institut für Vogelforschung „Vogelwarte Helgoland“, Inselstation,
P.O.Box 1220, D-27494 Helgoland, Germany,
e-mail: O.Hueppop-IFV@t-online.de*

*In a Herring Gull *Larus argentatus* colony on an island in the lower river Elbe, northern Germany, diet during the breeding season was investigated. Fish was found in 79% of all pellets, followed by crustaceans (39%, presumably Mitten Crabs *Eriocheir sinensis* only) and human refuse (10%). Overall, 77% of all pellets only contained fish and/or crab, suggesting that feeding was predominantly at the river bank near the colony. Of (potential) food remains other than pellets, 46% were fish, 19% gull eggs, 17% crustaceans, 10% small birds and 8% human refuse. The strong tidal rhythm of the adults' attendance at the colony coincides with fishery activities at the river banks and supports their dependence on unwanted bycatches from fisheries. From this and other studies, there is strong evidence to suggest that the inland breeding distribution of Herring Gulls is limited by the availability of fish during the breeding season rather than by the availability of human refuse or by the lack of breeding habitats.*

Hüppop O. & K. Hüppop 1999. The food of breeding Herring Gulls *Larus argentatus* at the lower river Elbe: does fish availability limit inland colonisation? *Atlantic Seabirds* 1(1): 27-42.

INTRODUCTION

The Herring Gull *Larus argentatus* increased considerably in numbers and established many new colonies both in Europe and in North America during the 20th century until the middle of the 1970s. It is generally accepted that extended human activities, typical of improved standards of living, the Herring Gull's broad ability to exploit these activities and a decline in persecution, are the main reasons for the increase and spread (Goethe 1982; Cramp & Simmons 1983; Vauk & Prüter 1987; Lloyd *et al.* 1991, Burger & Gochfeld 1996).

Herring Gulls colonised inland areas mainly from about 1950, mainly moorlands (in Great Britain and Scandinavia), islands in freshwater lakes or rivers, and roofs of buildings (Ludwig 1966; Goethe 1982; Cramp & Simmons 1983; Vauk & Prüter 1987; Lloyd *et al.* 1991; Burger & Gochfeld 1996; Hagemeijer & Blair 1997). Vauk & Prüter (1987), Lloyd *et al.* (1991) and others assumed that the increasing amounts of human refuse enabled the colonisation of inland areas by (marine) gulls. However, although this food source is still available in large amounts and heavily used by gulls throughout the year all over Europe (e.g. Horton *et al.* 1983; Vauk & Prüter 1987), most inland colonies of the Herring Gull remain very small, and settlements generally last for a few years. Possible reasons are: the low nutritional value of human refuse for egg formation and chick growth (Pierotti & Annett 1987, 1991), low availability of alternative food, or the lack of suitable nesting habitats.

We evaluated whether food choice or food availability might explain why the breeding of Herring Gulls is almost exclusively restricted to coastal areas. To do this, we studied the diet and the activity rhythms of a relatively large inland breeding colony in northern Germany. Our results combined with those from other inland colonies in Europe and North America allow testing of the hypothesis that food other than refuse limits the inland breeding of this gull species.

MATERIALS AND METHODS

The study was carried out in a breeding colony of Herring Gulls on a small artificial island in the river Elbe near the island of Lühesand (53°35'N, 9°36'E), 18 km downstream of Hamburg, Germany. This part of the river Elbe, 80 km from its mouth (following the stream, 68 km as the crow flies), is still under strong tidal influence (tidal range *c.* 3 m) but already totally limnic. The artificial island measures 540 m by 75 m and, during our research, was part of a restricted access military area.

The island of Lühesand has been occupied by single Herring Gull pairs from 1952. Later, numbers increased from around 1965 to a maximum of 88 pairs in 1975. In 1976-77, the colony relocated to the small military island. In 1983 and 1985, 57 and 22 breeding pairs, respectively, were found here. From 1990 onwards, numbers increased up to 142 breeding pairs in 1994 (Mitschke 1996).

In spring and summer 1983 and 1985, a total of 192 pellets and 48 other (potential) food remains were collected in the breeding colony. They were taken from the region of the colony exclusively colonised by Herring Gulls in order to exclude the possibility of collecting pellets from Great Black-backed Gulls *Larus marinus* that rest on the island, and from Common Gulls *Larus*

canus, which nest in large numbers in another part of the island. Food remains could be identified immediately, whereas pellets had to be dissected after air-drying. The identification of fish species resulted from pharyngeal teeth (cyprinids) and scales, following Brauer (1909), Grote *et al.* (1909) and Nitsche & Hein (1909), and using self-collected material for comparison (scales, otoliths and bones). Crustaceans could be identified with the help of reference specimens from the collection of the Zoological Institute and Zoological Museum of the University of Hamburg, mainly by the morphology of carapace and claws; molluscs were identified according to Stresemann (1976). Almost all other items (human refuse, earthworms, birds, mammals, plants, etc.) were easily identified.

All results were grouped into three periods according to Hüppop (1987): pre-incubation (till 12 May), incubation (13 May to 10 June), and chick-rearing (11 June onwards). All figures relating to percentages give the number of pellets (or other food remains) in which the respective food category was found. Because more than one food category may be found in one pellet, the total of the percentages may be greater than 100. Frequencies of occurrences in the pellets and in other food remains, respectively, were compared using the G-test (likelihood ratio test) for goodness of fit for all cases with total $n > 5$.

In order to discover if colony attendance showed diurnal or tidal periodicity, all adult Herring Gulls present in the whole colony were counted every hour during daylight, on several days from 5 to 27 May 1985 and from 29 April to 2 May 1986. Reliable counts later in the breeding season were impossible since the vegetation had grown too high. Circular-linear regression techniques (Batschelet 1981) were used for statistical testing of these counts. To enable this, the average tidal cycle (12.38 h, former German Hydrographic Institute) was transformed into angular values.

RESULTS

Fish was the dominant food type throughout the whole breeding period (Table 1). On average it was found in 79% of all pellets, followed by crustaceans (39%, presumably Mitten Crabs *Eriocheir sinensis* only) and human refuse (10%). Although plant material was found in 22% of all pellets and single (gull) feathers in 22%, these two groups are assumed to have been swallowed incidentally, with only four exceptions: cereals were found in three pellets, and the remains of tomato in one (see Appendix). On average, 46% of all (possible) food remains other than pellets were fish, 19% were gull eggs, 17% crustaceans, 10% small birds (including gull chicks) and 8% human refuse (Table 1). On a species level, the fish species mostly taken were cyprinids (identified as *Leuciscus idus*, *Rutilus rutilus*, *Abramis brama*, *Blicca bjoerkna*) and Eel An-

Table 1. Frequency of pellet contents and (potential) food remains of a Herring Gull colony at the lower river Elbe. Periods: 1 = pre-incubation, 2 = incubation, 3 = chick rearing.

Tabel 1. De inhoud van braakballen (n, %) en (potentiële) voedselresten in een zilvermeeuwkolonie aan de rivier de Elbe. 1 = voorafgaande aan het broeden, 2 = tijdens het broeden, 3 = nesten met jongen.

Type of food	pellets				food remains			
	1	2	3	total	1	2	3	total
small mammals	0	0	2 (3%)	2 (1%)	0	0	0	0
birds	0	1 (1%)	3 (5%)	4 (2%)	0	1	4	5
eggs	0	3 (3%)	0	3 (2%)	0	2	7	9
feathers	0	24 (21%)	18 (27%)	42 (22%)	0	0	0	0
fish	10 (83%)	88 (77%)	53 (80%)	151 (79%)	1	19	2	22
crustaceans	5 (42%)	38 (33%)	31 (47%)	74 (39%)	0	3	5	8
other invertebr.	0	9 (8%)	0	9 (5%)	0	0	0	0
plant material	1 (8%)	27 (24%)	14 (21%)	42 (22%)	0	0	0	0
refuse	0	12 (11%)	8 (7%)	20 (10%)	0	1	3	4
other	1 (8%)	3 (3%)	3 (5%)	7 (4%)	0	0	0	0
n =	12	114	66	192	1	26	21	48

guilla anguilla. Nevertheless, many fish remains could not be identified to species level (see Appendix). The spectrum of fish species parallels well with the abundance and accessibility of the fish (see Discussion) at the lower river Elbe (Peters *et al.* 1986; Diercking & Wehrmann 1991; Gaumert & Kämmerleit 1993; Gaumert 1995).

Throughout the breeding season, there were virtually no changes in the proportion of pellets containing fish and crustaceans (Table 1), whereas there was a significant increase in the proportion of pellets containing feathers (G-test, $P < 0.05$). Therefore, all further interpretations of the pellet contents are based on the combined data from the whole breeding season. With respect to (potential) food remains other than pellets, the proportion of fish dropped significantly from the breeding to the chick rearing period ($P < 0.001$), while the proportion of gull eggs increased significantly ($P < 0.05$).

The number of adults present on the island showed a strong tidal rhythm, whereas time of day had a smaller effect. Although time of day is sig-

nificantly correlated with the number present ($r^2 = 0.18$, $P < 0.001$), it explains less than 18% of the variance in the number of adults present in the colony. In contrast, a circular-linear regression revealed that the tidal cycle explained 73% of the variance (Fig. 1). The residuals of this regression further correlate significantly with the time of day and they explain 40% of the variance in numbers (Fig. 2). Hence it is not surprising that tidal cycle and daytime together explain 84% of the variance ($r^2 = 0.84$, $P < 0.001$).

DISCUSSION

The results of food studies in seabirds may heavily be influenced by the method adopted. Pellet analyses can be biased towards hard and larger parts and hence other prey may be under-represented (Duffy & Jackson 1986). Some food, e.g. eggs minus the shell or meat without bones or packing material, will rarely leave detectable remains in pellets. The importance of (potential) food remains found close to a nest is also difficult to evaluate. They may reliably reflect the true spectrum of food items consumed by adults. On the other hand, these food remains may reflect objects too large to be swallowed by the chicks (see discussion e.g. in Duffy & Jackson 1986 and Becker *et al.* 1987) or objects that are rejected by both chicks and adults due to their unpalatability or for other reasons. Nevertheless, our analysis of pellet contents and the analysis of other food remains found show both the same relative importance of the different food classes (with the exception of eggs). Although grass and other plant material may reflect the consumption of earthworms and leather-jackets (Tipulidae), we did not find remains of these animals. Furthermore, in our study Herring Gulls were rarely seen foraging on grassland or arable land. However, grass and other plant material may help pellet formation (Nogales *et al.* 1995).

Table 2. Pellet contents at a Herring Gull colony at the lower river Elbe arranged according to super-categories.

Tabel 2. Braakbalinhoud van Zilvermeeuwen aan de rivier de Elbe, onderverdeeld naar enkele 'super-categoriën'.

super-category	frequency (n, %)	
homogeneous fish	89	46.4%
homogeneous crustaceans	22	11.5%
fish and crustaceans	36	18.8%
homogeneous refuse	8	4.2%
fish, crustaceans and refuse	12	6.3%
other homogeneous	4	2.1%
other heterogeneous	21	10.9%
total number of pellets	192	100%

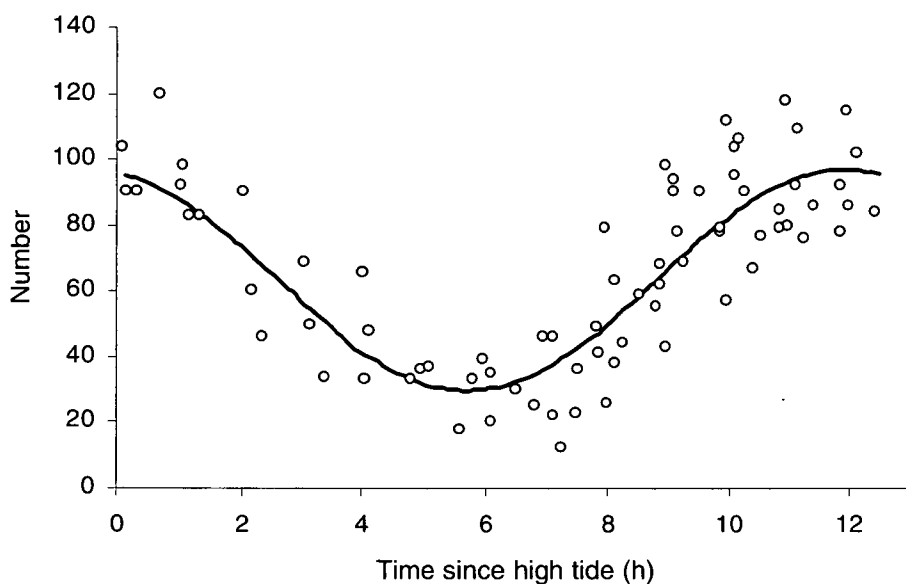


Figure 1. Number of adult Herring Gulls present in the colony at the lower river Elbe during the pre-incubation and early incubation period (29 April to 27 May) in relation to tidal cycle. Low tide = high tide + 5 h 13 min. To calculate a circular regression, the time after high tide was transformed to angular values. $y = 63.4 + 33.7 \cos(t + 0.250)$, $r^2 = 0.73$, $P < 0.001$, t = time (in radians) since high tide = time since high tide (in hours) $\times 12.38 \text{ h}^{-1} \times 2\pi$.

Figuur 1. Aantal volwassen Zilvermeeuwen op de kolonie in het begin van de broedtijd (29 april-27 mei) in relatie tot de getijdencyclus. Laagwater = hoogwater + 5 uur en 13 minuten.

Under these assumptions, our pellet analysis allows quantitative conclusions about *where* the gulls preferably foraged. Pellets containing only fish and/or crustaceans indicate foraging at the river. Those containing only human refuse indicate foraging at refuse tips. Hence, all pellets were regrouped according to these super-categories (Table 2). Of all 192 pellets, 147 (77%) contained exclusively fish and/or crab, whereas not more than 8 pellets (4%) were exclusively refuse pellets, and 12 (6%) contained refuse mixed with fish and/or crustaceans. These findings support our observations that the Herring Gulls breeding near Lühesand feed predominantly at the river banks near the colony and add human refuse or other food items to their diet only to a small extent. At least two refuse tips (Ketzendorf and Neu Wulmstorf, nearly 20 km

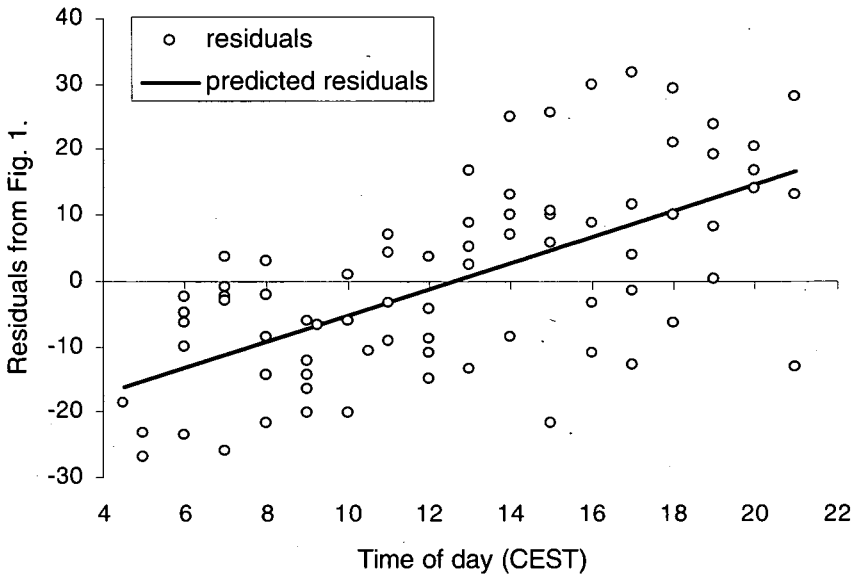


Figure 2. Number of adult Herring Gulls present in the colony at the lower river Elbe during the pre-incubation and early incubation period (29 April to 27 May) as residuals from figure 1 in relation to time of day (Central European Summer Time; GMT + 2), $y = 1.99x - 25.2$, $r^2 = 0.40$, $P < 0.0001$.

Figuur 2. Aantal volwassen Zilvermeeuwen op de kolonie in het begin van de broedtijd (29 april-27 mei) als residu van Fig. 1 in relatie tot de tijd van de dag (Midden-europese Zomertijd; GMT +2).

south-east of the colony; K. Burdorf pers. comm.) were well within the usual feeding range (e.g. Bergman 1951: 35 km; Focke 1959: 35 km; Andersson 1970: 28 km; Spaans 1971: 35 km; Sibly & McCleery 1983: > 30 km).

However, even at the river bank, foraging is based to a large extent on human activities. The strong tidal rhythm of the Herring Gulls at the colony near Lühesand supports the assumption that the gulls feed predominantly at the river bank and explains their access to the aquatic food there. Fishermen empty their fish traps around low tide and then discard unwanted bycatch such as cyprinids, Mitten Crabs and undersized Eel on the tidal flats, where the Herring Gulls can easily feed on these items. Further, low tides render cyprinids that spawn in the bank areas (Diercking & Wehrmann 1991; Gaumert & Kämmerer 1993) and Mitten Crabs migrating up the river (Peters & Panning 1933) accessible to the gulls. The well known tidal influence on coastal Herring Gull foraging activities

(e.g. Drent 1970; Spaans 1971; Verbeek 1977; Galusha & Amlaner 1978) is maintained at the (inland) colony near Lühesand, but it can be assumed that the reasons are different. Natural availability of prey items at the coast versus predominantly anthropogenic availability of food at the river Elbe.

The influence of daytime on the presence of the gulls at the colony can easily be interpreted by hunger. Many birds were seen leaving the colony during the morning twilight before the first count was possible (Hüppop 1987). This corroborates McCleery & Sibly (1986) who found no nocturnal feeding activity of Herring Gulls during the incubation period.

The decrease of fish found in the (potential) food remains in the colony might reflect a higher demand for fish in the chick rearing period (eaten fish cannot be found!). In other breeding colonies of the Herring Gull, increases in

Table 3. Diet composition of inland Herring Gulls. Figures give percentages in pellets, stomachs or prey remains containing the respective categories. A= fish, B= refuse, C= insects, D= other invertebrates, E= mammals, F= birds, G= plants, H= other

Tabel 3. Voedselsamenstelling van Zilvermeeuwen in het binnenland. Weergegeven zijn percentages in braakballen, magen of andere voedselresten. A= vis, B= afval, C= insecten, D= andere ongewervelden, E= zoogdieren, F= vogels, G= plantaardig materiaal, H= overigen.

Locality	period	meth	A	B	C	D	E	F	G	H	ref ⁵
Maine, USA	Jun-Sep	S ¹	77	8					8	7	1
Maine, USA	Jun-Jul	S	76	16	8						2
Michigan, USA	breeding	S,R ²	>85	2	+	1	+	>4		4	3
Järnlunden, S	breeding	P	74	21	37	11	1	2	36	8	4
Manitoba, Can	May-Jun	P	94		+	+	6		2		5
Connecticut, USA	?	S,R	100								6
Gr Lake Plön, D	Apr-May	S	75-87	13-31	34	7	<1			86	7
Hohe Schaar, D	Apr-Jul	P ³	88	3		17		1		1	8
Mühlenb. Loch, D	Jun-Aug	P ³	92	2		26					8
Lake Ontario, Can	Apr-Jun	P	58		32		19	11		11	9
Lake Huron, Can	Apr-Jul	P	22	9	3		27	12	18	2	10
Lake Erie, USA	May-Jul	P	98	1	1	1	1	1	8	<1	11
		R	74	17	1	5	<1	7	2	<1	11
		S ⁴	79	11	3	20	1		13	2	11
Great Lakes, Can/USA	winter-early spring	P	56	19		7	19	11	21		12
Lühesand, D	May-Jul	P	79	10		44		2	22	28	13

¹P= pellet, S= stomach contents, R= prey remains, += present; ²percentages based on number of items detected, excluding insects; ³Herring Gull and Common Gull mixed; ⁴boli from chicks; ⁵1= Mendall (1939), 2 = Vik (1963), 3 = Ludwig (1966), 4 = Andersson (1970), 5 = Vermeer (1973), 6 = Tolonen (1976), 7 = Demuth (1983), 8 = Gruner (1986), 9 = Fox *et al.* (1990), 10 = Allan in Fox *et al.* (1990), 11 = Belant *et al.* (1993), 12 = Ewins *et al.* (1994), 13 = this study.

the proportion of fish consumed were found throughout the breeding season (e.g. Spaans 1971; Vermeer 1973; Fox *et al.* 1990; Noordhuis & Spaans 1992). The increased proportion of eggs in the food remains in the chick-rearing period can be explained by high predation and cannibalism rates by the gulls late in the season (see Discussion in Burger 1984).

The Herring Gull has a very broad food spectrum with large local and seasonal differences. In marine areas, both in Europe and in North America, crustaceans, molluscs, echinoderms, fish and human refuse form the bulk of the food. Where fish is easily available, it may become the most important food category (Goethe 1982 and 1991; Cramp & Simmons 1983; Vauk & Prüter 1987; Pierotti & Good 1994; Burger & Gochfeld 1996). Marine Herring Gulls obtain molluscs and crabs mainly from intertidal areas. Since these are usually not available to inland breeders, it is not surprising that in almost all inland breeding Herring Gulls studied so far, fish is the most important food category (Table 3). However, Herring Gulls are relatively inefficient when foraging on healthy fish in open water (e.g. Goethe 1982; Koop 1990). Hence, fish can only become an important food source where they are concentrated in shallow water, as can be the case in spawning areas (Vermeer 1973; Sjöberg 1989; Fox *et al.* 1990), or where they are available as discards from fisheries (pers. obs.; Nepszy in Ewins *et al.* 1994). The latter is not surprising since Herring Gulls are well-known as scavengers, profiting from human fishing activities at sea or in harbours (Goethe 1982; Hüppop *et al.* 1994; Burger & Gochfeld 1996).

The opportunistic Herring Gull can also successfully exploit other anthropogenic food resources such as refuse. The improved standard of living of men in combination with regular refuse collection and deposition has been interpreted to affect not only the Herring Gull's general increase in numbers and enlargement of its distribution area, but in particular the increased use of inland habitats in the 20th century during the non-breeding season (e.g. Horton *et al.* 1983; SOVON 1987; Vauk & Prüter 1987; Goethe 1991; Arbeitsgruppe Möwen 1996). In some cases, the availability of refuse is assumed to enhance, or even to be essential for, reproductive success (Kadlec & Drury 1968; Hunt 1972; Sibley & McCleery 1983; Pons 1992; 1994). However, the numbers of Herring Gulls breeding inland are still very small (Teixeira 1979; Meltote & Fjeldså 1989; Monaghan 1993; Bauer & Berthold 1996). Is the occurrence of human refuse really important for the inland breeding distribution of Herring Gulls?

In all inland colonies of Herring Gulls studied so far, fish was found in 22 to 100% of the stomachs or pellets, which is on average much more than in marine conspecifics. However, only 0 to 31% of the stomachs or pellets contained refuse (Table 3). Indeed, even the closure of a refuse tip at Great Lake Plön, one of the largest lakes in northern Germany, could not check the growth of the colony (Berndt 1980; Koop in Busche & Berndt 1996). The proportion of

stomachs of Herring Gulls, killed for population management, containing refuse decreased from 31% to 13% after the closure, whereas the proportion of stomachs with fish increased slightly from 75% to 87% (Demuth 1983).

There is some evidence that, at least in marine areas, foraging in natural habitats is preferred to foraging on refuse tips. The latter are mainly visited when access to natural food sources is restricted e.g. during high waters (Spaans 1971; Kihlman & Larsson 1974; Greig *et al.* 1986). Niebuhr (1983) observed that females in the pre-laying period prefer mussels, which provide calcium for egg-shell formation, whereas males feed on refuse. In fact, despite the higher energetic value of refuse, mussel specialists produce more offspring, being larger at all developmental stages compared with refuse specialists (Pierotti & Annett 1987). Black Tern *Chlidonias niger* chicks exclusively fed on insects may die due to calcium deficiency (Beintema *et al.* 1997). In our and other studies (Chudzik *et al.* 1994; Nogales *et al.* 1995) fish bones which are calcium-rich, may substitute for mussel shells. Pairs that switch to a fish diet at the time of hatching have lower chick mortality (Pierotti & Annett 1987; Bukacinska *et al.* 1996). The ability of chicks to digest fish bones in the early phase of growth implies that fish might be an important source of calcium (Spaans 1971). However, Spaans (1971) also found that chicks from broods fed on refuse as well as marine food grew faster than chicks not supplied with refuse. Hence, natural food, such as mussels, crabs and fish, which are rich in protein and calcium, seems to be essential for a high reproductive success, which can be improved even more by high energetic refuse.

Outside the breeding season, however, the availability of human refuse determines to a great extent the inland distribution of Herring Gulls (Monaghan 1980; Goethe 1991; Arbeitsgruppe Möwen 1996). Then, refuse may be an important food and act as an alternative when natural food is unavailable. This could increase life expectancy (Pierotti & Annett 1987) and possibly lifetime reproduction.

The suggestion that the inland breeding distribution of the Herring Gull is limited by the lack of breeding habitats cannot easily be supported. In contrast to the Herring Gull, there exist several very large inland colonies of the Common Gull (Bauer & Berthold 1996; Hagemeyer & Blair 1997), and the inland total of about 6000 pairs in Germany is still increasing (Witt 1976; Koop in Busche & Berndt 1986; Meyer & Sudmann 1996; Mlody 1996; K. Witt pers. comm.). Since Herring Gulls and Common Gulls often nest close together both in coastal and in inland colonies (e.g. Hüppop & Hüppop 1995; Koop in Busche & Berndt 1996; Mitschke 1996; Südbeck & Hälterlein 1997), there are no reasons to assume a lack of inland breeding habitats for Herring Gulls. Correspondingly, Chudzik *et al.* (1994) suggested that food rather than the

availability of breeding habitats limit Herring Gull numbers throughout the Great Lakes of North America.

In conclusion, the food spectrum of Herring Gulls of almost all inland colonies investigated is relatively similar and almost exclusively dominated by fish (Table 3). Further, all larger inland colonies in both Europe and North America (Pierotti & Good 1994; Hagemeyer & Blair 1997) seem to be confined to areas with a sufficient natural or anthropogenic supply of fish (Vermeer 1973; Fox *et al.* 1990; Chudzik *et al.* 1994). For some inland breeding Herring Gulls, e.g. for those in colonies in Brandenburg (eastern Germany, 75-77 pairs in 1995, Haupt & Kaminski 1995) their diet is not known nor whether they have access to fish (H. Haupt pers. comm.), but there is strong evidence that the inland breeding distribution of Herring Gulls is generally limited by the availability of fish during the breeding season rather than by the availability of human refuse or by the lack of breeding habitats.

ACKNOWLEDGEMENTS

The German Army, especially R. Leive, enabled and supported the investigation on the small military island. H. Hudeczek, P. Hunck and J. Wittenberg helped to carry out the field studies. K. Burdorf, V. Dinse, S. Garthe, H. Haupt, D. Landes, R. Schlenker and K. Witt provided literature or additional information. S. Garthe, P. L. Meininger, P. Monaghan and A. Spaans had a critical look at an earlier draft of the manuscript. We are very grateful to all of them!

SAMENVATTING

Zilvermeeuwen zijn deze eeuw zowel in Noord-Amerika als in Europa sterk in aantal toegenomen en tot aan het midden van de jaren zeventig ontstonden talloze nieuwe kolonies. Over het algemeen werd verondersteld dat deze meeuw zich succesvol had aangepast aan de mens en dat de toename vooral een afspiegeling was van onze verhoogde levensstandaard. Behalve dat de Zilvermeeuw profiteerde van nieuwe, door de mens veroorzaakte voedselbronnen (bijvoorbeeld vuilnisbelten, visafval), was ook de verminderde bestrijding van meeuwen een belangrijke voorwaarde voor het succes. Sinds de jaren vijftig werden ook steeds meer vestigingen van Zilvermeeuwen in het binnenland aangetroffen. Vooral deze vestigingen zouden tot stand zijn gekomen door de talrijke (open) vuilnisbelten in West Europa. Toch waren deze meeuwen maar weinig succesvol. Ofschoon dergelijke voedselbronnen nog steeds volop aanwezig zijn, werden dergelijke nieuwe vestigingen dikwijls al snel weer verlaten en het broedsucces bleef vaak gering. Verklaringen voor deze teleurstellende resultaten werden vooral gezocht in de geringe voedingswaarde van menselijk afval in vergelijking met meer natuurlijke prooien, een beperkte toegankelijkheid van alternatieve voedselbronnen en een gebrek aan geschikte nestplaatsen in het binnenland. In dit artikel wordt onderzocht of de voedselbeschikbaarheid verklaart waarom Zilvermeeuwen toch vooral kustgebonden vogels zijn. Hiertoe werd het dieet van Zilvermeeuwen op één van de grootste kolonies in het binnenland (Lühesand, rivier de Elbe, West Duitsland; 53°35'NB, 9°36'OL) onderzocht en vergeleken met gegevens uit de literatuur.

Visresten werden aangetroffen in 79% van alle onderzochte braakballen. Andere veelvoorkomende prooi-soorten waren crustacea (39%; waarschijnlijk uitsluitend de Chinese Wolhandkrab *Eriocheir sinensis*) en menselijk vuilnis (10%). In totaal bevatte 77% van alle braakballen uitsluitend vis- of krabbenresten, waaruit kon worden afgeleid dat deze meeuwen vooral op de rivier voedsel zochten. Andere belangrijke voedselresten in de kolonie, naast de prooiresten

die in braakballen gevonden zijn, waren vis (46%), meeuweneieren (19%), crustacea (17%), kleine vogels (10%) en vuilnis (8%). Op de kolonie werd een duidelijk verband gevonden tussen het foerageergedrag van de meeuwen en het getij, waaruit kon worden afgeleid dat de Zilvermeeuwen hun gedrag voor een belangrijk deel hadden afgestemd op de visserijactiviteiten op de rivier de Elbe, profiterend van de overboord gezette visresten en krabben. Uit de gepresenteerde gegevens, in vergelijking met materiaal uit de literatuur, blijkt dat het succes van Zilvermeeuwen in het binnenland in hoge mate afhangt van de beschikbaarheid van vis in de kuikenfase. De beschikbaarheid van vuilnis en het aanbod van geschikte nestplaatsen lijken aanmerkelijk minder van belang te zijn.

REFERENCES

- Andersson A. 1970. Food habits and predation of an inland-breeding population of the Herring Gull (*Larus argentatus*) in Southern Sweden. *Ornis Scand.* 1: 75-81.
- Arbeitsgruppe Möwen 1996. Die Winterbestände von Möwen (Laridae) in Nordrhein-Westfalen - Ergebnisse dreijähriger Synchronzählungen. *Charadrius* 32: 149-155.
- Batschelet E. 1981. Circular statistics in biology. Academic Press, London.
- Bauer H.-G. & Berthold P. 1996. Die Brutvögel Mitteleuropas. Bestand und Gefährdung. Aula-Verlag, Wiesbaden.
- Becker P.H., Frank D. & Walter U. 1987. Geographische und jährliche Variation der Ernährung der Flußseeschwalbe (*Sterna hirundo*) an der Nordseeküste. *J. Ornithol.* 128: 457-475.
- Beintema A.J., Baarspul, T. & de Krijger, J.P. 1997. Calcium deficiency in Black Terns *Chlidonias niger* nesting on acid bogs. *Ibis* 139: 396-412.
- Belant J.L., Seamans T.W., Gabrey S.W. & Ickes S.K. 1993. Importance of landfills to nesting Herring Gulls. *Condor* 95: 817-830.
- Bergman G. 1951. Unterschiede von Silbermöwe (*Larus a. argentatus*) und Heringsmöwe (*Larus f. fuscus*) in Lebensweise und Stimme. *Vogelwarte* 16: 17-18.
- Berndt R.K. 1980. Bestand und Bestandsentwicklung von Silber-, Sturm- und Lachmöwe (*Larus argentatus*, *canus* und *ridibundus*) in der Seenplatte des Östlichen Hügellandes (Schleswig-Holstein) 1970-1979. *Corax* 8: 131-149.
- Brauer A. 1909. Die Süßwasserfauna Deutschlands. H. 1: Mammalia, Aves, Reptilia, Amphibia, Pisces. Fischer, Jena.
- Bukacinska M., Bukacinski D. & Spaans A.L. 1996. Attendance and diet in relation to breeding success in Herring Gulls (*Larus argentatus*). *Auk* 113: 300-309.
- Burger J. 1984. Pattern, mechanism, and adaptive significance of territoriality in Herring Gulls (*Larus argentatus*). *Ornithol. Monogr.* 34: 1-92.
- Burger J. & Gochfeld M. 1996. Family Laridae (Gulls). In: del Hoyo J., Elliott A. & Sargatal J. (eds): *Handbook of the Birds of the World*, 3: 572-623. Lynx Edicions, Barcelona.
- Busche G. & Berndt R.K. 1996. Ornithologischer Jahresbericht für Schleswig-Holstein 1994. *Corax* 16: 205-236.
- Chudzik J.M., Graham K.T. & Morris R.D. 1994. Comparative breeding success and diet of Ring-billed and Herring Gulls on South Limestone Island, Georgian Bay. *Col. Waterb.* 17: 18-27.
- Cramp S. & Simmons K.E.L. 1983. *The Birds of the Western Palearctic*, 3. Oxford University Press, Oxford.
- Demuth M. 1983. Untersuchungen zur Nahrung der Silbermöwe (*Larus argentatus*) in einer Binnenlandkolonie Schleswig-Holsteins zur Brutzeit. *Seevögel* 4 (2): 19-23.
- Diercking R. & Wehrmann L. 1991. Artenschutzprogramm Fische und Rundmäuler in Hamburg. *Schriftenr. Umweltbehörde Hamburg* 38: 1-126.
- Drent R.H. 1970. Functional aspects of incubation in the Herring Gull. *Behaviour Suppl.* 17: 1-132.
- Duffy D.C. & Jackson S. 1986. Diet studies of seabirds: a review of methods. *Col. Waterb.* 9: 1-17.

- Ewins P.J., Weseloh D.V., Groom J.H., Dobos R.Z. & Mineau P. 1994. The diet of Herring Gulls (*Larus argentatus*) during winter and early spring on the lower Great Lakes. *Hydrobiologia* 279/280: 39-55.
- Focke E. 1959. Zur Ernährung der Silbermöwe (*Larus argentatus*). *Vogelwarte* 20: 86-88.
- Fox G.A., Allan L.J., Weseloh D.V. & Mineau P. 1990. The diet of Herring Gulls during the nesting period in Canadian waters of the Great Lakes. *Can. J. Zool.* 68: 1075-1085.
- Galusha J.G. & Amlaner C.J. 1978. The effects of diurnal and tidal periodicities in the numbers and activities of Herring Gulls *Larus argentatus* in a colony. *Ibis* 120: 322-328.
- Gaumert D. & Kämmerleit M. 1993. Süßwasserfische in Niedersachsen. Niedersächsisches Landesamt für Ökologie, Hildesheim.
- Gaumert T. 1995. Spektrum und Verbreitung der Rundmäuler und Fische in der Elbe von der Quelle bis zur Mündung. Arbeitsgemeinschaft für die Reinhaltung der Elbe, Hamburg.
- Goethe F. 1822. *Larus argentatus* Pontoppidan 1763 und *argentatus argenteus* C.L. Brehm 1822. In: Glutz von Blotzheim U.N. & Bauer K.M. (eds): *Handbuch der Vögel Mitteleuropas*. Band 8/I, Charadriiformes (3. Teil). Akademische Verlagsgesellschaft., Wiesbaden: 515-586.
- Goethe F. 1991. Silbermöwe *Larus argentatus* Pont., 1763. In: Zang H., Großkopf G. & Heckenroth H. (eds): *Die Vögel Niedersachsens. Raubmöwen bis Alken*. Naturschutz Landschaftspfl. Niedersachs. B, H. 2.6: 98-109.
- Greig S.A., Coulson J.C. & Monaghan P. 1986. A comparison of foraging at refuse tips by three species of gull (Laridae). *J. Zool., Lond.* 210: 459-472.
- Grote W., Vogt C. & Hofer B. 1909. *Die Süßwasserfische von Mittel-Europa*. Schlüter u. Mass, Halle a. S.
- Gruner D. 1986. *Die Möwen der Großstadt Hamburg - Beiträge zur Biologie und Ökologie*. Dissertation, Univ. Hamburg.
- Hagemeijer E.J.M. & Blair M.J. (eds) 1997. *The EBBC atlas of European breeding birds: their distribution and abundance*. Poyser, London.
- Haupt H. & Kaminski R. 1995. Sind Silbermöwe und Weißkopfmöwe eigene Arten? *Falke* 42: 68-73.
- Horton N., Brough T. & Rochard J.B.A. 1983. The importance of refuse tips to gulls wintering in an inland area of south-east England. *J. appl. Ecol.* 20: 751-765.
- Hüppop O. 1987. *Der Einfluß von Wachstum, Thermoregulation und Verhalten auf den Energiehaushalt der Silbermöwe (Larus argentatus Pontoppidan, 1763)*. Dissertation, Univ. Hamburg.
- Hüppop O., Hartwig E., Garthe S. & Walter U. 1994. Fischerei und Schiffsverkehr: Vorteil oder Problem für See- und Küstenvögel? In: Lozán J.L., Rachor E., Reise K., von Westernhagen H. & Lenz W. (eds): *Warnsignale aus dem Wattenmeer*. Blackwell, Berlin; p. 278-285.
- Hüppop O. & Hüppop K. 1995. *Der Einfluß von Landwirtschaft und Wegenutzung auf die Verteilung von Küstenvogel-Nestern auf Salzwiesen der Hallig Nordstrandischmoor (Schleswig-Holstein)*. *Vogelwarte* 38: 76-88.
- Hunt G.L. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. *Ecology* 53: 1051-1061.
- Kadlec J.A. & Drury W.H. 1968. Structure of the New England Herring Gull population. *Ecology* 49: 644-676.
- Kihlman J. & Larsson L. 1974. On the importance of refuse dumps as a food source for wintering Herring Gulls *Larus argentatus* Pont. *Ornis Scand.* 5: 63-70.
- Koop B. 1990. Wenig bekannte Nahrung von Silber- und Mantelmöwe (*Larus argentatus* und *L. marinus*). *Corax* 13: 333-334.
- Lloyd C., Tasker M.L. & Partridge K. 1991. *The status of seabirds in Britain and Ireland*. Poyser, London.
- Ludwig J.P. 1966. Herring and Ring-billed Gull populations of the Great Lakes 1960-1965. *Great Lakes Res. Div. Univ. Mich. Publ.* 15 (Proc. 9th Conf. Great Lakes Res.): 80-89.

- McCleery R. H. & Sibly R. M. 1986. Feeding specialization and preference in Herring Gulls. *J. Anim. Ecol.* 55: 245-259.
- Meltofte H. & Fjeldså J. 1989. Fuglene i Danmark. Vol. 2. Dansk Ornitologisk Forening. Copenhagen.
- Mendall H.L. 1939. Food habits of the Herring Gull in relation to fresh-water game fishes in Maine. *Wilson Bull.* 51: 223-226.
- Meyer B.C. & Sudmann S.R. 1996. Bruterfolg einer wachsenden Sturmmöwen-Population in Nordrhein. *Charadrius* 32: 191-196.
- Mitschke A. 1996. Silbermöwe - *Larus argentatus*. In: Garthe S. (ed.): Die Vogelwelt von Hamburg und Umgebung, 3: 230-243. Wachholtz-Verlag, Neumünster.
- Mlody B. 1996. Sturmmöwe - *Larus canus*. In: Garthe S. (ed.): Die Vogelwelt von Hamburg und Umgebung, 3: 208-226. Wachholtz-Verlag, Neumünster.
- Monaghan P. 1980. Dominance and dispersal between feeding sites in the Herring Gull (*Larus argentatus*). *Anim. Behav.* 28: 521-527.
- Monaghan P. 1993. Herring Gull *Larus argentatus*. In: Gibbons D.W., Reid J.B. & Chapman R.A. (eds): The new atlas of breeding birds in Britain and Ireland, 1988-1991: 208-209. Poyser, London.
- Niebuhr V. 1983. Feeding strategies and incubation behavior of wild Herring Gulls: an experiment using operant feeding boxes. *Anim. Behav.* 31: 708-717.
- Nitsche H. & Hein W. 1909. Die Süßwasserfische Deutschlands, ihre Kennzeichen, Fortpflanzung, Verbreitung und wirtschaftliche Bedeutung. Verlag des Deutschen Fischereivereins, Berlin.
- Nogales, M., Zonfrillo B. & Monaghan P. 1995. Diets of adult and chick Herring Gulls *Larus argentatus argenteus* on Ailsa Craig, south-west Scotland. *Seabird* 17: 56-63.
- Noordhuis R. & Spaans A.L. 1992. Interspecific competition for food between Herring *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus* in the Dutch Wadden Sea area. *Ardea* 80: 115-132.
- Peters N. & Panning A. 1933. Die chinesische Wollhandkrabbe (*Eriocheir sinensis* H. Milne-Edwards) in Deutschland. *Zool. Anz.* 104, *Ergänzungsbd.*: 1-180.
- Peters P., Schmidt W., Gercken J., Kranz H. & Watermann B. 1986. Die Fische der Unterelbe im Vergleich der Jahre 1894 und 1982 - eine Richtigstellung. *Arch. FischWiss.* 36: 287-304.
- Pierotti R. & Annett C.A. 1987. Reproductive consequences of dietary specialization and switching in an ecological generalist. In: Kamil A.C., Krebs J.R. & Pulliam H.R. (eds): *Foraging Behavior*: 417-442. Plenum Press, New York.
- Pierotti R. & Annett C.A. 1991. Diet choice in the Herring Gull: constraints imposed by reproductive and ecological factors. *Ecology* 72: 319-328.
- Pierotti R. & Good T.P. 1994. Herring Gull (*Larus argentatus*). In: Poole A.F., Gill F.B. (eds): *The Birds of North America*. No. 124. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union., Washington, D.C.
- Pons J.-M. 1992. Effects of changes in the availability of human refuse on breeding parameters in a Herring Gull *Larus argentatus* population in Brittany, France. *Ardea* 80: 143-150.
- Pons J.-M. 1994. Feeding strategies of male and female Herring Gulls during the breeding season under various feeding conditions. *Ethol. Ecol. Evol.* 6: 1-12.
- Sibly R. M. & McCleery R.H. 1983. The distribution between feeding sites of Herring Gulls breeding at Walney Island, U. K. *J. Anim. Ecol.* 52: 51-68.
- Sjöberg K. 1989. Time-related predator/prey interactions between birds and fish in a northern Swedish river. *Oecologia (Berl.)* 80: 1-10.
- SOVON 1987. Atlas van de Nederlandse Vogels. Arnhem.
- Spaans A.L. 1971. On the feeding ecology of the Herring Gull *Larus argentatus* Pont. in the northern part of the Netherlands. *Ardea* 59: 73-188.
- Stresemann E. 1976. Exkursionsfauna für die Gebiete der DDR und der BRD. Wirbellose I. Volk und Wissen, Berlin.

- Südbeck P. & Hälterlein B. 1997. Brutvogelbestände an der deutschen Nordseeküste im Jahre 1995 - Neunte Erfassung durch die Arbeitsgemeinschaft "Seevogelschutz". *Seevögel* 18: 11-19.
- Teixeira R.M. 1979. Atlas van de Nederlandse broedvogels. Vereniging tot Behoud van Natuurmonumenten in Nederland's-Graveland.
- Tolonen K.E. 1976. Behavioral ecology of *Larus argentatus* and *Larus marinus*: age specific differential in feeding efficiency, a probable factor in the evolution in delayed breeding. Ph. D. thesis, Yale Univ. / New Haven, CT.
- Vauk G. & Prüter J. 1987. Möwen. Arten, Bestände, Verbreitung, Probleme. Niederelbe-Verlag, Otterndorf.
- Verbeek N.A.M. 1977 Comparative feeding ecology of Herring Gulls *Larus argentatus* and Lesser Black-Backed Gulls *Larus fuscus*. *Ardea* 65: 25-42.
- Vermeer K. 1973. Food habits and breeding range of Herring Gulls in the Canada prairie provinces. *Condor* 75: 478-480.
- Vik R. 1963. Notes on the gulls of the Rangeley region, Maine. *Sterna* 6: 195-204.
- Witt H. 1976. Sturm- und Silbermöwe am Franziskus-See (Ville bei Köln). *Charadrius* 12: 1-5.

Appendix. Absolute occurrence of food items found in pellets and (potential) food remains in a Herring Gull colony at the lower river Elbe. Periods: 1 = pre-incubation, 2 = incubation, 3 = chick rearing.

Appendix. De precieze inhoud van braakballen (n) en (potentiële) voedselresten in een zilverbreeuwkolonie aan de rivier de Elbe. 1= voorafgaande aan het broeden, 2= tijdens het broeden, 3= nesten met jongen.

Type of food	pellets				food remains			
	1	2	3	total	1	2	3	total
unident. small mammal	0	0	2	2	0	0	0	0
chick <i>Larus argentatus</i>	0	0	0	0	0	0	1	1
chick <i>L. canus</i>	0	0	0	0	0	0	2	2
<i>Alauda arvensis</i>	0	0	1	1	0	1	1	2
unident. small bird	0	1	2	3	0	0	0	0
<i>Anguilla anguilla</i>	0	2	0	2	1	7	2	10
<i>Osmerus eperlanus</i>	0	0	0	0	0	2	0	2
<i>Abramis brama</i>	1	8	4	13	0	3	0	3
<i>Blicca bjoerkna</i>	0	8	3	11	0	1	0	1
<i>Leuciscus idus</i>	2	13	6	21	0	0	0	0
<i>Rutilus rutilus</i>	3	10	5	18	0	1	0	1
unident. cyprinid	1	12	6	19	0	0	0	0
<i>Gymnocephalus cernua</i>	0	0	0	0	0	1	0	1
unident. perch	0	4	0	4	0	0	0	0
<i>Platichthys flesus</i>	0	1	0	1	0	4	0	4
unident. fish	3	40	31	74	0	0	0	0
unident. beetle	0	3	0	3	0	0	0	0
diptera larvae	0	2	0	2	0	0	0	0
<i>Eriocheir sinensis</i>	5	28	27	60	0	3	5	8
unident. crustacean	0	10	4	14	0	0	0	0
unident. snail	0	1	0	1	0	0	0	0
<i>Succinea putris</i> (terr. snail)	0	2	0	2	0	0	0	0

Type of food	pellets				food remains			
	1	2	3	total	1	2	3	total
unident. earthworm	0	1	0	1	0	0	0	0
tomato	0	1	0	1	0	0	0	0
thorn	0	1	0	1	0	0	0	0
cereal	0	3	0	3	0	0	0	0
grass or other plant material	1	23	14	38	0	0	0	0
bone	0	10	2	12	0	0	2	2
sausage remains	0	5	1	6	0	0	0	0
rind (of bacon)	0	0	0	0	0	0	1	1
thread	0	2	0	2	0	0	0	0
glass	0	5	0	5	0	0	0	0
plastic material	0	8	0	8	0	1	0	1
paper	0	2	2	4	0	0	0	0
tin foil	0	3	3	6	0	0	0	0
metal particle	0	1	0	1	0	0	0	0
pin	0	1	0	1	0	0	0	0
button	0	1	0	1	0	0	0	0
unident. refuse	0	2	2	4	0	0	0	0
human hair	0	0	1	1	0	0	0	0
feather	0	24	18	42	0	0	0	0
egg	0	3	0	3	0	2	7	9
gravel	1	3	2	6	0	0	0	0
total number of pellets/ prey items investigated	12	114	66	192	1	26	21	48

Short notes

THE EFFECT OF A SPRING GALE AND A FREAK WAVE ON A BREEDING GROUP OF COMMON GUILLEMOTS *URIA AALGE*

HET GEVOLG VAN EEN VOORJAARSSTORM EN EEN SUPERGOLF OP EEN BROEDENDE GROEP ZEEKOETEN

MARTIN HEUBECK

Aberdeen University Research and Industrial Services Ltd., East House, Sumburgh Head Lighthouse, Virkie, Shetland ZE3 9JN, UK.

On 19 May 1997, during a north-easterly gale (force 8-9) an exceptionally large swell approached and swept across a rock platform with nesting Guillemots at Sumburgh Head (Shetland). A total of 27 eggs of 110 being incubated on 18 May were lost, but most pairs relaid within 13-20 days. Hatching success of replacement eggs was low and none of the chicks fledged. The storm occurred too late in the incubation period for the replacement eggs to have been successful.

Heubeck M. 1999. The effect of a spring gale and a freak wave on a breeding group of Common Guillemots *Uria aalge*. *Atlantic Seabirds* 1(1): 43-47.

In the British Isles, Common Guillemots *Uria aalge* normally achieve relatively high breeding success, usually fledging c. 0.7-0.8 chicks per breeding pair (Thompson *et al.* 1997). Severe gales can reduce breeding success, although apparently infrequent (Thompson *et al.* 1998). This note describes the effect of a gale on breeding Guillemots in Shetland in May 1997.

Hatching success of the first egg laid by a pair of Guillemots is commonly c. 80%. The main causes of egg loss, where known, are rolling due to an inadequate nest site and/or parents, predation, and infertility (Birkhead 1977, Harris & Wanless 1988). The probability of a replacement egg being laid declines seasonally (Wanless & Harris 1988; Hatchwell 1991), this decline being more closely associated with laying date relative to surrounding pairs rather than to absolute date (Wanless & Harris 1988). However, there is a rapid seasonal decline in the productivity of replacement eggs (Hatchwell 1991).

As part of the Shetland Oil Terminal Environmental Advisory Group's seabird monitoring programme, the breeding success of Guillemots in a single study plot on the east side of Sumburgh Head, at the southern tip of the Shetland Mainland, has been monitored since 1989. The method applied involves the use

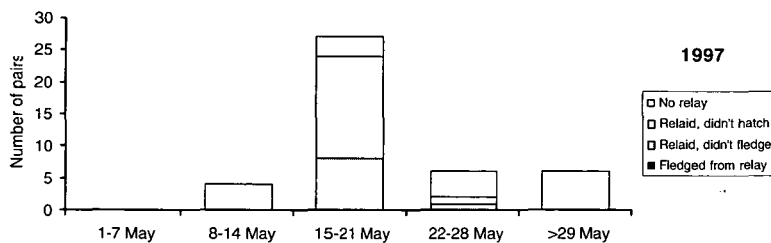
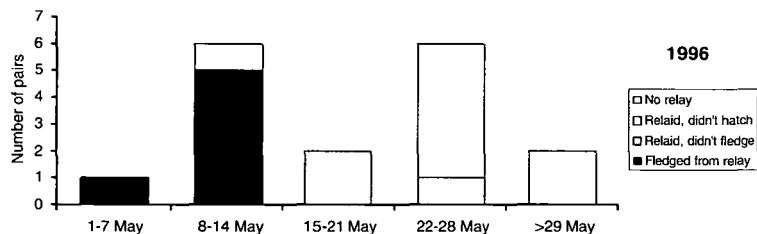
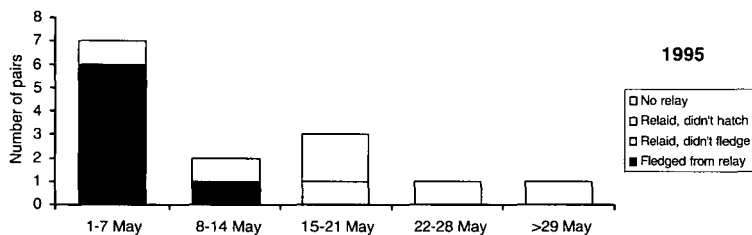
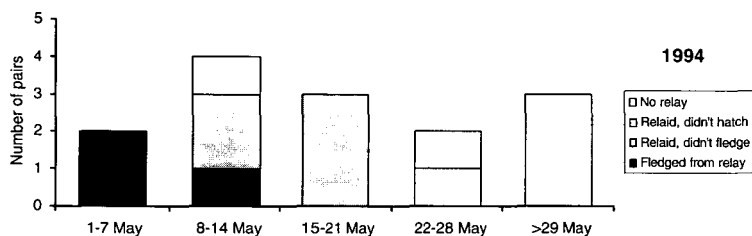
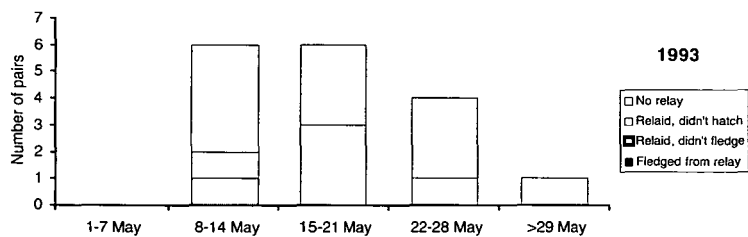


Figure 1. The timing of first egg loss during 1993-97 and the fate of replacement eggs.

Figuur 1. De periode waarin een eerste ei werd verloren en het lot van tweede legfels in de jaren 1993-97. Afgebeeld worden vogels die niet opnieuw legden, vogels die een tweede ei produceerden dat niet uitkwam, tweede legfels waarvan het jong niet uitvloog en succesvolle tweede pogingen.

of marked photographs and daily checks using a telescope. The plot lies on the landward side of a sloping buttress of rock aligned north-west to south-east, the birds nesting 10-15m above sea level. Additional shelter from the open sea is provided from above by a 2-3m high vertical wall of rock, and by a 10m wide rock platform on the seaward side of the base of the buttress. Although heavy spray is sometimes blown over the buttress, there is no evidence that waves washed over the breeding ledges in any of the eight previous summers of monitoring. In 1997, 122 pairs laid eggs in the plot.

During 17-18 May 1997, easterly winds increased in strength and by the morning of 19 May were north-easterly 8-9B, with a heavy north-easterly swell. Of the 110 Guillemots presumed incubating the previous day, 107 remained 'sitting tight', although few eggs were seen in the severe conditions. A very large swell was seen approaching from the north-east, considerably higher than the surrounding waves. It swept across the rock platform and crashed against the seaward side of the buttress, throwing many tonnes of water over the ridge and onto the lower part of the breeding area. Sixteen incubating birds and their eggs, and another 10-15 loafing birds, were washed into the sea in a narrow cleft inside the buttress. None were able to fly out from here but eventually escaped to seaward by flapping and diving through the boiling surf; after 30 min the first of these birds had returned to their breeding sites. By the morning of 20 May a further eight eggs had been lost, the pattern of loss within the plot suggesting that driving spray rather than another freak wave had been responsible.

Thus, a total of 27 (25%) of the 110 eggs being incubated on 18 May was lost during the gale. Most pairs suffering egg loss (23, 85%) relaid within 13-20 days (Figure 1, Table I), with a mean replacement interval of 16.1 days; this is similar to the 16.2 days recorded over a six-year period on the Isle of May (Harris & Wanless 1988). The proportion of pairs relaying in 1997 was higher than during 1993-96, but not significantly so ($\chi^2 = 2.96$, $P = 0.085$). However, excluding early (before 8 May) and late (after 28 May) first egg losses, the replacement rate during the second, third and fourth weeks of May (83%, $n = 36$) was significantly higher in 1997 than in 1993-96 (56%, $n = 45$; $\chi^2 = 7.08$, $P = 0.008$). That 25% of pairs in the plot lost their eggs within 48 hours, and that the losses were mostly in two discrete clusters, may have resulted in such a high rate of relaying relatively late in the season.

Table 1. The response of breeding pairs of Common Guillemots to the loss of their first egg in a study plot at Sumburgh Head, 1993-1996 and (1997).

Tabel 1. De respons van Zeekoeten op het verlies van het (eerste) ei in een studiegebied bij Sumburgh Head op Shetland. Gegeven zijn: datum van eiverlies, aantal gevallen, % tweede legfels, % uitgekomen eieren, % uitgevlogen jongen, aantal uitgevlogen jongen per tweede legfel en uitvliedsucces per broedpaar in 1993-96 en (1997).

First egg lost	Number	% relaid	Hatching success, %	Fledging success, %	Fledged per relay	Fledged per pair
1-7 May	10 (0)	100	90	100	0.90	0.90
8-14 May	18 (4)	67 (100)	83 (0)	70	0.58	0.39
15-21 May	14 (27)	64 (89)	33 (33)	0 (0)		
22-28 May	13 (5)	31 (40)	25 (50)	0 (0)		
>28 May	7 (5)	0 (0)				
Total	62 (41)	57 (73)	66 (30)	70 (0)	0.46 (0.00)	0.26 (0.00)

Hatching success of replacement eggs during the May 1997 gale was the same as for eggs replacing those lost in the third week of May in 1993-96, but as in 1993-96, no chick fledged from an egg replacing one lost after the second week of May. Twenty of the total of 30 replacement eggs laid in the plot in 1997 disappeared, half (possibly including some newly hatched young) after heavy overnight rain on 30 June/1 July. The first chick hatched from a replacement egg on 1 or 2 July, by which time 72% of the 61 chicks that fledged from the plot had done so, 92% having departed the plot by 7 July. By the second week of July, most adults had left the plot and the nine chicks from replacement eggs had disappeared within ten days of known hatching; possibly taken by Herring Gulls *Larus argentatus* or Great Black-backed Gulls *L. marinus*, that had previously been seen predating Guillemot eggs and chicks in the vicinity of the plot.

Both breeding density and synchrony are important factors in Guillemot breeding success, especially at colonies where predation of eggs and chicks occurs (Birkhead 1977; Hatchwell 1991). In this instance, although the synchronous loss of eggs during 18-20 May may have led to a high proportion of females relaying, the storm occurred too late in the incubation period for replacement eggs to have much chance of success.

SAMENVATTING

Zeekoeten leggen slechts één ei, maar over het algemeen hebben de op de Britse Eilanden nestelende Zeekoeten een hoog broedresultaat (0.7-0.8 jongen per paar). Normaal komt ongeveer

80% van de eieren uit en de belangrijkste oorzaken van verlies zijn weggrollen, predatie en onvruchtbaarheid. Indien een ei verloren gaat, worden dikwijls nieuwe pogingen ondernomen, maar de kans op zo'n tweede ei neemt snel af in de loop van een broedseizoen. Het broedsucces van een groep Zeekoeten op de Shetland Eilanden, nestelend bij Sumburgh Head op de zuidpunt van Mainland, wordt sinds 1989 gedetailleerd onderzocht. Bij dit onderzoek worden regelmatig overzichtsfoto's gemaakt en vaste delen van de kolonie worden dagelijks met behulp van een telescoop bekeken. Deze studie-plot bevindt zich aan de landzijde van een rotsblok voor de kust en de broedrichels, waarop in 1997 122 paren nestelden, bevinden zich 10-15m boven zeeniveau.

Op 17 en 18 mei 1997 nam de toch al harde oostelijke wind toe tot stormkracht (NO 8-9B). In de vroege morgen van 19 mei had dit tot gevolg dat er een enorme deining stond en deze zware zeegang zorgde voor de nodige overlast op de kolonies. Van de 110 broedende Zeekoeten die op 18 mei gezien waren zaten deze morgen 107 exemplaren dicht opeen op de eieren. Tijdens de observaties naderde vanuit het noordoosten een ongebruikelijk hoge supergolf en toen deze brak op de rotsen van Sumburgh Head werd de studieplot gedeeltelijk schoongeveegd. Tenminste 16 broedende vogels en hun eieren spoelden van de rotsen. De volgende dag bleken nog eens acht broedvogels hun ei verloren te hebben hetgeen het totale verlies op 27 (25%, $n = 110$) bracht. De meeste paartjes probeerden het opnieuw (23 ex., 85%), door gemiddeld binnen 16 dagen een nieuw ei te produceren. Net als in eerdere jaren vloog er echter geen enkel jong uit van paren die na de tweede week van mei een nieuw ei konden produceren (Fig. 1, Tabel 1). Ofschoon het simultane verlies van eieren dus tot een hoog percentage tweede pogingen heeft geleid, sloeg de supergolf te laat in het seizoen toe om nog met tweede legsels gecompenseerd te kunnen worden.

REFERENCES

- Birkhead T.R. 1977. The effect of habitat and density on breeding success in the Common Guillemot (*Uria aalge*). J. Anim. Ecol. 46: 751-764.
- Harris M.P. & Wanless S. 1988. The breeding biology of Guillemots *Uria aalge* on the Isle of May over a six year period. Ibis 130: 172-192.
- Hatchwell B.J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of Common Guillemots (*Uria aalge*). J. Anim. Ecol. 60: 721-736.
- Thompson K.R., Brindley E. & Heubeck M. 1997. Seabird numbers and breeding success in Britain and Ireland, 1996. UK Nature Conservation No. 21, Joint Nature Conservation Committee, Peterborough.
- Thompson K.R., Brindley E. & Heubeck M. 1998. Seabird numbers and breeding success in Britain and Ireland, 1997. UK Nature Conservation No. 22, Joint Nature Conservation Committee, Peterborough.
- Wanless S. & Harris M.P. 1988. The importance of relative laying date on breeding success of the Guillemot *Uria aalge*. Ornith. Scandinavica 19: 205-211.

Guidelines for contributors to *Atlantic Seabirds*

We welcome papers on any aspect of seabird biology. The geographical focus of the journal is the Atlantic Ocean and adjacent seas, but contributions are also welcome from other parts of the world provided they are of general interest. Manuscripts should be in English, and three copies of the text complete with tables and figures should be provided when submitted. Manuscripts should be printed on white paper, on only one side of the page, with double spacing and broad margins. Figures should have solid black lines on pure white paper. Scientific names of genera and lower taxa should be in italics but may be underlined when typed. Vernacular names of species should start with capitals, e.g. Northern Fulmar. Do not capitalise group names, e.g. grebes, gulls, corvids. Units and abbreviations should conform to the S.I. system where possible. Use 0.01 and not .01. Use 50%, not 50 percent. Details of statistical analysis, which should always be included, are type of test, the value of the relevant test statistic, the sample size and/or degrees of freedom and the probability level. Commonplace statistical abbreviations such as ANOVA, SD, SE, df, *t*-test, χ^2 , *F*, *P*, *n*, *r*, *r*_s should be used. A post-fix to the test statistic symbol can be used to present the degrees of freedom, e.g. χ^2_3 , *F*_{12,34}. and where appropriate, include a reference for the statistic used. Variables, mathematical formulas, and the Latin abbreviation *et al.* should be in italics but may be underlined in the draft version. Do not otherwise use italics or underlining.

The title should be short and concise, a proposal for a 'running head' is welcomed. Avoid too many subdivisions, do not use more than three different types of headings; do not number. Subdivisions should include: Abstract, Introduction, Methods, Results, Discussion, Acknowledgements, and References. The abstract should reflect both content and emphasis of the paper. The Introduction should be restricted to scope, purpose, and the rationale of the study. Limit the information on Material and Methods to what is essential to judge whether the findings are valid. Limit the Discussion to the main contributions of the study in relation to the findings of previous workers. Restrict speculation to what can be supported with reasonable evidence. Acknowledge only those who substantially contributed to the paper. Cited literature should be restricted to significant, published papers. Check your citations carefully against the reference list and vice versa. Examples of literature cited in the text: (O'Connor 1984), (Baudinette & Schmidt-Nielsen 1974) or, in case of more than two authors (Pettifor *et al.* 1988). References in the text should be in order of publication, e.g. (Brown 1974; Anthony *et al.* 1981). In the reference list the literature cited should be in alphabetical order. Titles should be given in the original language. Examples:

Asbjørk S. 1978. Tejsten *Cephus grylle* som ynglefugl i Danmark. Dansk Orn. Foren. Tidsskr. 72: 161-178.

Berger M. & J.S. Hart 1974. Physiology and energetics of flight. In: Farner D.S. & J.R. King (eds) Avian Biology, 4: 415-477. Academic Press, New York.

Greenstreet S.P.R. & M.L. Tasker (eds) 1996. Aquatic predators and their prey. Fishing News Books, Oxford.

Van Eerden M.R. & B. Voslamber 1995. Mass fishing by Cormorants *Phalacrocorax carbo sinensis* at lake IJsselmeer, The Netherlands: a recent and succesful adaptation to a turbid environment. Ardea 83: 199-212.

Provide a 'Samenvatting' in Dutch only if you or one of your friends masters this language; the text should not exceed 250 words. This summary must be easy to read, emphasising biologically relevant findings, while touching only slightly on methods.

Figures need to be definitive, but we prefer to receive raw data underlying figures on file (preferably Excel). Use Arial or Univers for lettering and realise that the diagram may have to be reduced in size. Photographs or slides need high contrast. Illustrations should be numbered in sequence of reference in the text. Legends for the figures should be added after the text, on separate, numbered sheets. Tables should be concise and self-explanatory, carrying a title at the top. Each table should be typed/printed on a separate sheet, numbered in Arabic numerals, with only horizontal lines.

The text of accepted manuscripts should be provided on 3.5 inch diskette, readable for DOS computers, preferably as Microsoft Word file (release 97 or lower), otherwise as ASCII files. Diskettes should be accompanied with a final print produced by the authors. In the proof stage only essential corrections can be made. Corrected proofs should be returned *within two weeks* to the editor.

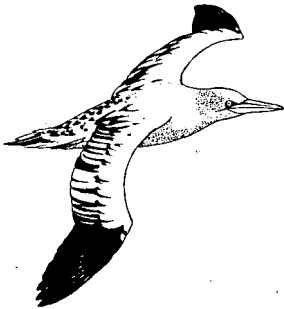
the Seabird Group

was founded in 1966 to circulate news of work in progress on seabirds and to promote research. It is run by an elected Executive Committee and maintains close links with the three major British national ornithological bodies – the British Ornithologists' Union, the British Trust for Ornithology, and the Royal Society for the protection of Birds.



Membership (£10 per annum, £9 if paid by banker's order, £5 for students) is open to all with an interest in seabirds. For details please contact the Membership Secretary (address below) – payment by banker's order helps the Group. Four issues of *Atlantic Seabirds* and three Newsletters are circulated to members each year.

Current Executive Committee Chair S. Wanless, Secretary J. Uttley, Treasurer J.C. Davies, Membership Secretary S. Russell, Editor of *Atlantic Seabirds* J.B. Reid, Newsletter editor M.L. Tasker, also A. Douse, J.D. Okill, E.K. Dunn and S. Sutcliffe.



Nederlandse Zeevogelgroep (NZG)

(*Dutch Seabird Group*), een sectie van de Nederlandse Ornithologische Unie, werd opgericht op 1 januari 1991, als voortzetting van de Club van Zeetrekwaarnemers (1972-1990) en het Nederlands Stookolieslachtoffer-Onderzoek (1977-1990). De Nederlandse Zeevogelgroep stelt zich tot doel: (1) het stimuleren van zeevogelonderzoek in en vanuit Nederland en (2) het uitwisselen van informatie met de uitgave van het tijdschrift, aanvankelijk *Sula*, vanaf 1999 *Atlantic Seabirds*.

Voor zover samenvallend met onderzoek aan zeevogels worden activiteiten aan zeezoogdieren mede in de doelstelling betrokken. Door een viertal werkgroepen wordt onderzoek gestimuleerd naar broedende zeevogels, de verspreiding van vogels en zoogdieren op open zee (offshore), strandingen, zeetrek en de gevolgen van olievervuiling. De contributie van de NZG bedraagt f25 per jaar.

Dagelijks bestuur Voorzitter en Nieuwsbrief redacteur M.F. Leopold, Secretaris J.A. van Franeker, Penningmeester Y. Hermes, Eindredacteur *Atlantic Seabirds* C.J. Camphuysen, en verder A.J. van Dijk, E.W.M. Stienen en C.J.N. Winter.

Atlantic Seabirds

vol 1 no. 1 (1999)

- 1 Editorial by *C.J. Camphuysen & J.B. Reid*
- 3 On the function of pre-laying breeding site attendance in the Northern Fulmar *Fulmarus glacialis* - by *Fiona M. Hunter*
- 17 Microgeographical variation in the call of the male Manx Shearwater *Puffinus puffinus* - by *David Wood*
- 27 The food of breeding Herring Gulls *Larus argentatus* at the lower river Elbe: does fish availability limit inland colonisation? - by *Ommo Hüppop & Kathrin Hüppop*

Short notes

- 43 The effect of a spring gale and a freak wave on a breeding group of Common Guillemots *Uria aalge* - by *Martin Heubeck*
- 48 Guidelines for contributors to *Atlantic seabirds*

Front cover: Northern Fulmar Noordse Stormvogel (C.J. Camphuysen)