PREFACE

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Reproduction is the bottleneck in the life of seabirds, and the constraints obtained during their breeding periods determine their life styles. The energetic demands of breeders are extremely high in consequence of increased resource allocations to supply mates, to produce eggs and to provide for young. This incurs costs and puts high selection pressures on individuals, which is the mainspring behind the evolution of the fascinating life histories of marine birds. Seabird life is characterised by colonial breeding, highly developed social and antipredator behaviour, by extreme foraging strategies, long life and low reproductive output, by sexually divergent parental roles in brood care, and by the specific importance of individual quality and experience.

As "Seabird Reproduction" had not yet been covered as a main topic by earlier Seabird Group Conferences, it was chosen as the main theme of the Seventh International Seabird Group Conference held from 17 to 19 March 2000 in Wilhelmshaven, on the occasion of the EXPO-by-the-Sea, the maritime section of the EXPO 2000 in Hannover. This, the first conference of its kind to be held outside the United Kingdom, was hosted by the Institut für Vogelforschung "Vogelwarte Helgoland", which was founded in 1910 on the island of Heligoland and is one of the oldest and largest ornithological research institutes in the world with a major focus on seabirds. The conference took place in the Wilhelmshaven Stadthalle, where 142 delegates from 16 countries were welcomed by the Local Organising Committee. The Deutsche Forschungsgemeinschaft proved very generous in its support for the participation of seabird biologists from eastern countries. A detailed report on the course of the meeting, its events, atmosphere and success has been presented by Heubeck (2000).

The scientific programme (Tasker 2000, Heubeck 2000) comprised 36 oral and 33 poster presentations of high quality giving insight into reproduction and other aspects of seabird life, and covering a wide spectrum of species and marine areas all over the world. Species-specific or individual-specific reproduction strategies aimed at increasing fitness were the focus of the programme, arranged by the scientific programme committee Peter H. Becker, Kees Camphuysen and Mark Tasker under five main headings: (a) reproductive strategies and parental condition; (b) reproduction and population ecology; (c) breeding ecology of southern hemisphere seabirds; (d) reproductive success, and (e) food provisioning and foraging.

Two notable keynote talks were presented by Ian L. Jones, St. John's, Canada on "Life history implications of mate choice, mating success and sexual selection in seabirds ", and by Pat Monaghan, Glasgow, United Kingdom on "Resource allocation and life history trade-offs in seabirds". The programme reflected the wide diversity of the research that is currently being carried out on marine birds, and the rapid progress that has been made in recent years through the use of new laboratory and field techniques. With most, if not all, marine environments currently threatened by a wide range of anthropogenic activities, the need for research on seabirds has never been greater.

Seabird Group Conferences are well respected for their scientific reputation and for the high quality of contributions. It comes as no surprise, therefore, that just one year after the conference many of the papers given have already been published and can be found spread over the various ecological and ornithological journals. For this reason we have not been able to prepare complete conference proceedings, such as in the last conference co-organised by the Seabird Group and ICES (Reid 1997). We have seized the chance, however, to publish a selection of papers in this special issue of *Atlantic Seabirds*, issueing from the conference in Wilhelmshaven above and beyond the Abstract Booklet available (Tasker 2000). The generosity of the sponsors of the conference, especially of the main supporters of this special issue, the organisations "Bürger für Wilhelmshaven" and the "Gerd-Möller-Stiftung", have made possible this much appreciated service both to the participants of the meeting and to the members of the Seabird Group and the Dutch Seabird Group, whose official journal *Atlantic Seabirds* is.

The present special issue contains five selected papers presented at the 7th International Seabird Group Conference which reflect the main themes of the conference programme.

Bernard Cadiou reports on the great interannual variation in the timing of breeding and the reproductive success of European Storm-petrels *Hydrobates pelagicus* in Brittany, which was probably due to changing food availability and has implications for census timing. Ingveig Langseth, Børge Moe and Claus Bech address the question of whether reductions in body mass and basal metabolic rate in Black-legged Kittiwakes *Rissa tridactyla* during chick rearing may be an adaptation aimed at reducing maintenance costs in favour of investing more energy in chick growth. The return rates of subadult Common Terns *Sterna hirundo* to their natal colony are not affected by parameters of the individuals' chick period such as hatching position or number of fledged siblings, as Tobias Dittmann, Jan-Dieter Ludwigs and Peter H. Becker show, using new techniques to record breeders and non-breeders remotely and automatically at the colony site. Bill Bourne and Ken Simmons present long-term data on population changes in seabirds breeding on the island of Ascension in the tropical Atlantic Ocean and on their distribution at sea, which may be linked with weather and oceanographic fluctuations such as the El Niño/Southern Oscillation, a problem complex which is bound to attract more attention in the future. In the final paper, Thorsten Krüger and Stefan Garthe focus on flight altitudes of seabirds migrating along the southern North Sea coast in relation to wind direction and speed; the results recorded by sea-watching are relevant to the current discussions on offshore windmill farms.

VOORWOORD

De zevende internationale Seabird Group Conferentie van 17 t/m 19 maart 2000 in Wilhelmshaven had zeevogelreproductie als hoofdthema. Het wetenschappelijk programma bestond uit 36 modnelinge en 33 poster presentaties, verdeeld voer vijf subthema's: a) reproductiestrategieën en ouderkwaliteit; b) reproductie en populatiebiologie; c) broedbiologie van zuidevogels van het Zuidelijk Halfrond; d) broedsucces en e) voedselvoorziening en foerageren. Hoewel het slechts een jaar na de conferentie is, zijn diverse artikelen al gepubliceerd in verschillende tijdschriften. Daarom kunnen geen volledige "proceedings" worden gemaakt, maar wordt, naast het boekje met Abstracts van alle presentaties (Tasker 2000), een selectie van artikelen in deze special van *Atlantic Seabirds* gepresenteerd.

ACKNOWLEDGMENTS

The editor is pleased to acknowledge the expert and efforts of the following referees to this special issue of *Atlantic Seabirds*: Mark Bolton, Monika Bukaczinska, Dariusz Bukaczinski, Kees Camphuysen, David Duffy, Jan Durinck, Eric Stienen, Robert W. Furness, Ommo Hüppop, Ellen Kalmbach, Ian C.T. Nisbet, Norman Ratcliffe, and Arie Spaans. James B. Reid and Ken Wilson checked the English. Steve Geelhoed made the final efforts to realize this special.

REFERENCES

Heubeck M. 2000. 7th International Seabird Group Conference, Wilhelmshaven, Germany, 17-19th March 2000. The Seabird Group Newsletter 85: 1 – 5.

Reid J.B. (ed) 1997. Seabirds in the Marine Environment. Proceedings of an ICES International Symposium, Glasgow 1996. ICES J. Marine Science 54: 503 – 739.

Tasker M. (ed) 2000. 7th International Seabird Group Conference “Seabird Reproduction”: Programme and Abstracts. Institut für Vogelfoschung, Wilhelmshaven.

This Special Issue of *Atlantic Seabirds* was edited by guest editor Peter H. Becker.

The 7th International Seabird Group Conference, Wilhelmshaven 2000, was supported by:

- Bürger für Wilhelmshaven
- Deutsche Forschungsgemeinschaft, Bonn
- Wilhelmshaven-Projekt-GmbH
- Stiftung Kulturkreis Wilhelmshaven-Friesland
- Franz-Kuhlmann-Stiftung, Wilhelmshaven
- Gerd-Möller-Stiftung, Wilhelmshaven
- Sparkasse Wilhelmshaven
- Oldenburgische Landschaft, Oldenburg
- Friesisches Brauhaus zu Jever
- Jacques' Weindepot, Oldenburg
- Friesische Gastlichkeit, Jever
- Joint Nature Conservation Committee, Aberdeen
- The Seabird Group, Thetford
- Institut für Vogelforschung „Vogelwarte Helgoland", Wilhelmshaven

THE BREEDING BIOLOGY OF THE EUROPEAN STORM-PETREL *HYDROBATES PELAGICUS* IN BRITTANY, FRANCE

BERNARD CADIOU

Cadiou B. 2001. The breeding biology of the European Storm-petrel *Hydrobates pelagicus* in Brittany, France. Atlantic Seabirds 3(4): 149-164. *In recent years (1996-1999), data have been collected on European Storm-petrel* Hydrobates pelagicus *colonies on the coast of Brittany, France, in order to investigate various breeding parameters, especially laying period, hatching success and breeding success. Data were obtained by regular examination of breeding sites and by estimating chick age at the time of ringing. Adults first returned to colonies in March or April. The laying period extended from the end of April to the beginning of August and showed high annual variability, with the date by which 50% of eggs had been laid ranging from mid May to early July. Annual variability in the timing of laying was probably due to variations in oceanographic conditions and food resources just before laying and had important implications for accurate censuses of breeding colonies. Data obtained from single visits at the same time in different years should be interpreted carefully, especially when using tape-playback methods only, as the proportion of attended nest sites may vary according to the interannual variation in the timing of laying. Estimates of hatching and breeding success were about 65% to 95% (over three years) and 0.53 (one year) respectively. The first chicks fledged in mid August, whereas the latest fledged in late October, or even sometimes November.*

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INTRODUCTION

In the southern part of their European range along the Atlantic coast, European Storm-petrels *Hydrobates pelagicus* breed in Brittany, France, on at least sixteen islands and islets. The population estimate was about 500 apparently occupied sites (AOS) in 1997-1998 (Cadiou 1998), and 700 AOS in 1999, after a marked increase in the two largest colonies (B. Cadiou unpubl. data). Mainly due to the nocturnal habits and the underground breeding of the species, its biology still remains poorly known, with only a few published data for colonies in the north-east Atlantic (Davis 1957; Scott 1970; Bolton 1996) or elsewhere. The timing of laying has important implications for accurate censuses of breeding colonies and for the development of standardised census methods to obtain better estimates of breeding population size (Mainwood *et al.* 1997; Ratcliffe *et al.* 1998a, 1998b).

Since 1996, more accurate censuses of breeding colonies have been

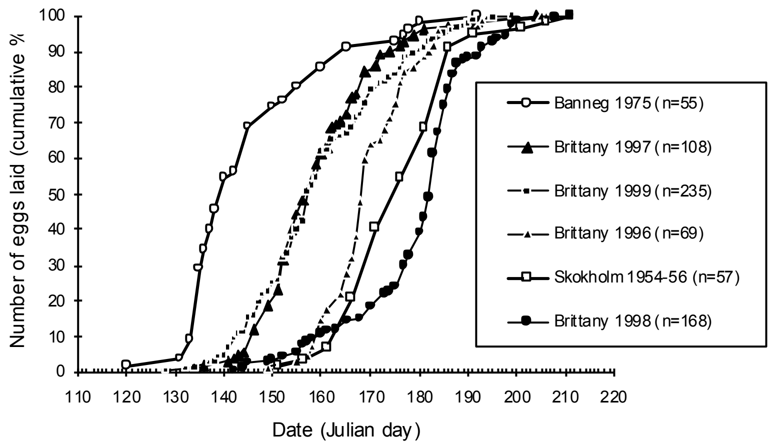

Figure 1. Laying period of European Storm-petrels in Brittany. Date in Julian days: 121 = 1 May, 152 = 1 June, 182 = 1 July and 213 = 1 August. Sample size in brackets.

Figuur 1. Legdatum van Stormvogeltjes in Bretagne. 121 = 1 mei, 152 = 1 juni, 182 = 1 juli, 213 = 1 augustus. Steekproefgrootte tussen haakjes.

made in Brittany and data on breeding biology have been collected simultaneously. The aim of this study is to investigate various breeding parameters that are poorly known in France and, indeed, in other parts of the breeding range, especially laying period, hatching success and breeding success. Before this study, the only available data on laying periods in Brittany came from a study conducted in 1975 on Banneg Island in the Molène archipelago (Henry & Monnat 1981). Laying ranged from early May to mid July, with 50% of laying around mid May (Fig. 1). Comparison with the data from Skokholm in Wales (Davis 1957) showed an earlier breeding period in Brittany (Fig. 1).

METHODS

Most of the work was carried out in the Molène archipelago, and especially on three of the five colonies: Banneg Island (48°25'N, 05°0'W) and two neighbouring islets, Enez Kreiz and Roc'h Hir. About 600 AOS (85% of the regional population) were counted in 1999 in the archipelago. Data were also obtained from other smaller colonies in Brittany, which were visited less often

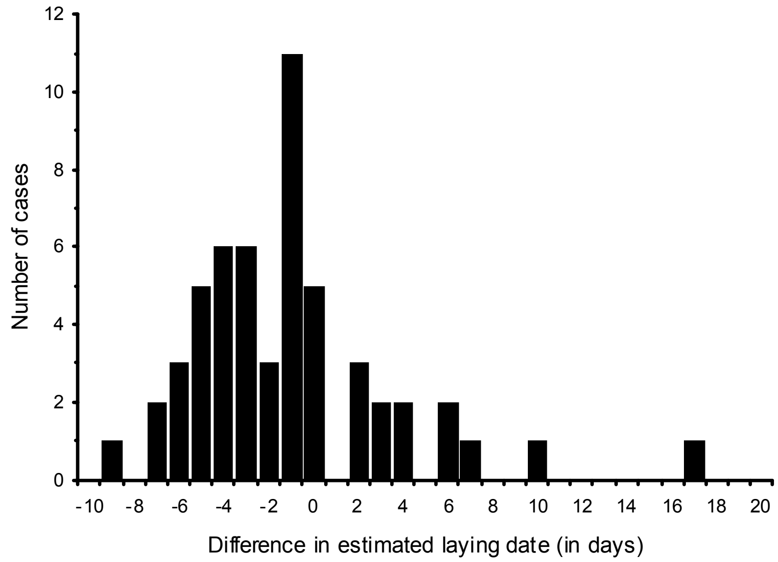

Figure 2. Accuracy of repeated ageing of European Storm-petrel chicks. The value on the x-axis is the difference between the estimated laying dates back-calculated from chick age determined on the second visit and age determined on the first visit in 1999 (or between third and second visit for the 3 chicks aged three times; n = *51 chicks and 54 cases).*

Figuur 2. Nauwkeurigheid van herhaalde leeftijdsbepalingen van stormvogelkuikentjes. Het getal op de x-as geeft het verschil aan tussen de geschatte legdatum berekend op basis van de kuikenleeftijd tijdens een tweede controle vergeleken met de schatting op basis van de eerste controle in 1999 (of tussen het derde en tweede nestbezoek bij kuikens waarvan de leeftijd drie maal werd bepaald; n= *51 kuikens, 54 gevallen).*

each year (especially Camaret islets and Sept-Iles archipelago). In the Molène archipelago, most of the petrels breed in old burrows of rabbits *Oryctolagus cuniculus*. The rabbit population became extinct in 1993 after a virulent myxomatosis epidemic. In all surveyed colonies, breeding sites were numbered and mapped.

Adults first returned to colonies in March or April. Early in the season, from the end of April, previously known sites were both regularly and randomly inspected in order to determine the beginning of the laying period. Intensive census of the colonies was made after the peak of egg laying, mainly from July to September. All visits were conducted by day. Combinations of different methods were used for census: direct observation with a torch, direct investigation by hand and tape-playback method. Direct investigation by hand was made very carefully to limit disturbance and to avoid nest desertion, without taking out the adults, and by slipping the two longer fingers delicately under the bird to search for an egg or a chick. In most cases when using this technique, adults did not move away. For the playback method, a male purr call recorded on Banneg Island in 1989 by V. Bretagnolle was played for about 20 s, once or twice, using a standard tape recorder (Tamashi C-671). Occupied and attended nest sites refer, respectively, to sites with at least one proof of occupancy over the whole breeding season and to sites with at least one adult present at a given visit.

Laying phenology At the different colonies, all accessible chicks were ringed (except in 1996), and their age was estimated to the nearest five days using data on plumage development (Davis 1957). Other visible chicks were also aged in the same way. Estimation of the laying date was made by back-calculation, considering the chick's age and an average incubation period of 41 days (Davis 1957; Scott 1970). All sites with incubating birds or unhatched eggs on one day were as far as possible checked once again later in the season until hatching or failure was recorded.

There are at least three potential biases that can affect the estimate of the laying date from chick ageing. In the first place, the incubation duration is variable, ranging from 38 to 50 days, with a mean value of 41 days (Davis 1957; Scott 1970), used to back-calculate the laying date. Secondly, late laid eggs have lower hatching success (Scott 1970), and therefore all of them can not be taken into account. Thus, laying periods obtained from chick age are always partially truncated and slightly underestimated (see also Ratcliffe *et al.* 1998a). Thirdly, laying date may be overestimated for retarded chicks. But such chicks are generally easy to identify as they are lighter and smaller, sometimes unhealthy, and can be excluded from the analyses. The older the chick, the greater the effect of retarded or accelerated growth on the estimation of laying date. As discussed by Scott (1970), accuracy of ageing on plumage development can be very low in poor seasons, but in the present study, chick growth, based on weight and wing length at ringing, was very similar in 1997, 1998 and 1999 (B. Cadiou unpubl. data).

In 1999, 51 chicks were aged at least twice in the season within approximately 4 weeks, of which three were also aged a third time. The difference (mean ± SE) in the estimate of the laying date between the second and the first observation, or between the third and the second one, was -1.1 ± 0.6

days (Fig. 2). The chick with 17 days of difference was assumed to be about 10 days old on 20 August, based on plumage features, but only 11-15 days old on 9 September, and unhealthy; the corpse was found on a subsequent visit on 27 September. Thus, with the exception of obviously retarded chicks, the difference for chicks aged twice in the season was generally less than 5 days (79.6% of the cases), and estimated laying dates for the older chicks were generally more advanced (negative values on Fig. 2). But the difference between these estimates and the true laying date remains unknown. For eight empty nests on the first visit, there was no discrepancy between the estimated laying dates and the field observations on subsequent visits (i.e. last day with empty nest and first day with an adult incubating an egg).

The terminology '50% (or 90%) of laying' refers below to the date, and not to the period, by which 50% (or 90%) of eggs had been laid in a given year.

Breeding parameters At the end of the season, some unhatched and abandoned eggs were measured to the nearest 0.1 mm using callipers. More regular visits were made to the small islet of Enez Kreiz to obtain data on hatching and breeding success (1997: 4, 5 July, 21 August and 24 September; 1998: 4 June, 23 July, 19 August and 23 September; 1999: 11, 22 June, 6, 20, 23 July, 18 August and 9, 27 September). Numbers of AOS on this islet increased from 61 in 1997, to 70-72 in 1998 and 122-125 in 1999. The increase from 1998 to 1999 was real and not a result of the more frequent visits to the islet or to changes in census methods. Out of these identified AOS, only the sites with breeders and chicks always easily visible or accessible, and found during the incubation or brooding period, were included in analyses of breeding parameters (i.e. 46, 55 and 94 nest sites for the three years respectively). Nests found late in the season at the chick stage were excluded to avoid an over-estimation of hatching and fledging success. Chicks come closer to the entrance of their burrows as they get older, and thus become more observable (pers. obs.). Breeding failure at the egg stage included all cases of broken, cracked, addled or desiccated eggs or intact unhatched eggs more than 50 days after initial observation. As breeding failure occurred at an unknown stage for some sites each year (nine in 1997, eight in 1998, eleven in 1999), two calculations were made for hatching and fledging success (number of chick fledged per egg hatched), assuming that all failures occurred before or after hatching respectively (i.e. at the egg stage or at the chick stage). Minimum (or maximum) hatching success = minimum (or maximum) number of eggs hatched / total number of eggs laid; minimum (or maximum) fledging success = total number of chicks fledged / maximum (or minimum) number of eggs hatched. This uncertainty has no influence on the calculation of overall breeding success (total number of chicks fledged / total number of eggs laid). Chicks were considered to be fledged if, based on ageing by plumage features, they were potentially at least 50 days old on the date when the empty nest was recorded.

RESULTS

Laying period In 1995, the few available data, for 9 chicks at one colony only, indicated a similar temporal pattern of laying to that in 1975. In 1996, more data were collected and the results indicated a delay in the laying period. Laying ranged from the end of May to the end of July, with 50% of laying around mid June (Fig. 1). This pattern of laying is closer to that recorded on Skokholm, Wales. In 1997, laying was more advanced than in the previous year and ranged from mid May to the end of July, with 50% of laying around early June. In 1998, a long delay in breeding was recorded. As in 1996, laying ranged from the end of May to the end of July, but 50% of laying was around early July (Fig. 1), i.e. 6 weeks later than in 1975. It appeared that a problem for the birds occurred in early June, with a temporary break in laying from 5 to 17 June. In 1999, the pattern of egg laying was very similar to that in 1997. Laying ranged from early May to mid July, with 50% of laying around early June. Field observations suggested that some eggs were probably laid during the first ten days of August, and perhaps even later. For example, on Banneg Island, one bird was found incubating an egg on 20 August 1999 and his partner on 9 September. Two weeks later, the egg was abandoned. Furthermore, from 1996 to 1999, the pattern of egg laying in Brittany appeared to be very similar between northern, western and southern colonies.

Attendance patterns A simple attendance model, assuming continuous attendance of one parent during the 41 days of the incubation period and the 7 first days of the chick's life (Ratcliffe *et al.* 1996), allows investigation of a potential effect of interannual variation in laying patterns on census results (Fig. 3). The results indicate that observers could sometimes easily underestimate a large change in breeding numbers using tape-playback methods in early July for example (Fig. 3). Depending on the year and the laying phenology, the theoretical proportion of nests attended can vary between about 90-95% and 60-65% or even less if the census is made a few days earlier or later in years with late or early breeding respectively (Fig. 3).

Breeding parameters A sample of 49 eggs was measured in 1999 in the Molène archipelago colonies. The mean size was 27.9 × 20.6 mm (± SE: 0.2 × 0.1; range: 25.6-30.1 × 18.3-22.3 mm).

Data obtained from Enez Kreiz islet showed that hatching success ranged from 63.6% to 95.7% (Table 1); the uncertainty was due to some sites

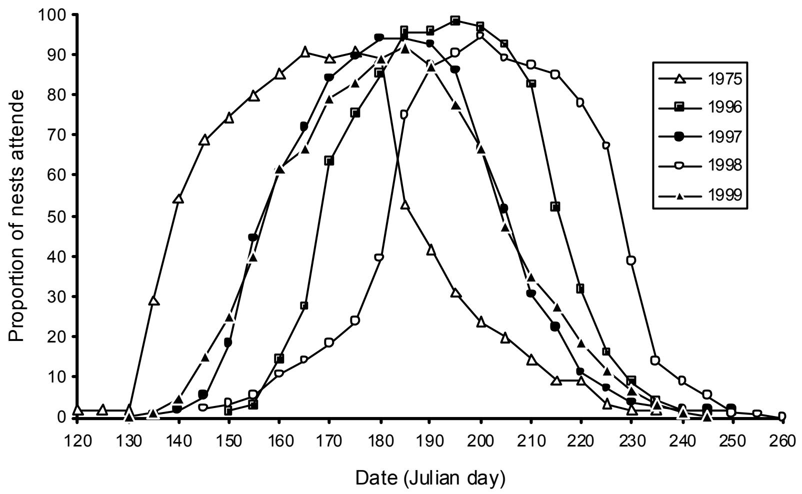

Figure 3. Theoretical proportion of European Storm-petrel nests attended by an adult. The curves are based on data from Fig. 2 and the model assumes a continuous attendance of one parent from laying to the seventh day of the chick's life (Ratcliffe et al. *1996). Date in Julian days: 121 = 1 May, 152 = 1 June, 182 = 1 July, 213 = 1 August and 244 = 1 September.*

Figuur 3. Theoretische nestholtebezetting (%) door een volwassen vogel. De curves zijn gebaseerd op figuur 2 en op een model uitgaand van een voortdurende aanwezigheid van tenminste één ouder vanaf de eileg t/m de zevende levensdag van het kuiken (Rattcliffe et al. *1996). 121 = 1 mei, 152 = 1 juni, 182 = 1 juli, 213 = 1 augustus, 244 = 1 september.*

where breeding failure may have occurred either at the egg stage or at the chick stage. In some instances, eggs disappeared between two successive visits, no remains, eggshells or corpses of dead chicks being found. More regular visits in 1999 allowed calculation of the minimum and maximum incubation period for these eggs: (last day of observation of the egg - first day of observation of the egg) and (first day with empty nest-site - first day of observation of the egg) respectively. For some eggs, already laid on the first visit, the minimum incubation period was equal to 0 because the corresponding nests were not checked again before the third visit and were empty by that time. The mean duration (± SE) was 17.9 ± 4.8 days and 39.5 ± 4.7 days respectively (*n* = 11),

Table 1. Breeding parameters for European Storm-petrel in Brittany (data from Enez Kreiz islet, Molène archipelago). Sample size in brackets.

Tabel 1. Broedsucces van Stormvogeltjes in Bretagne (gegevens verzameld op Enez Kreiz eiland, Molène eilandengroep). Steekproefgrootte tussen haakjes.

Year	Sites [a]	Hatching success (%) [b]	Fledging success [b, c]	Breeding success [d]
1997	all	76.1-95.7 (46)	?	?
1998	all	63.6-80.0 (55)	?	?
1999	all	67.0-78.7 (94)	0.68-0.79 (74, 63)	0.53 (94)
	old	69.5-81.4 (59)	0.71-0.83 (48, 41)	0.58 (59)
	'new-old'	60.0-66.7 (15)	0.60-0.67 (10, 9)	0.40 (15)
	new	65.0-80.0 (20)	0.63-0.77 (16, 13)	0.50 (20)

[a] category of sites: old = sites with proof of occupancy at least in 1998 and 1999, 'new-old' = previously known sites but not occupied in 1998, new = sites unknown before 1999; [b] uncertainty for hatching and fledging success was due to some sites where breeding failure occurred either at the egg stage or at the chick stage (see Methods for the calculation of minimum and maximum values); [c] for hatched eggs only; [d] overall breeding success (young fledged per egg laid); ? = no precise data

indicating that breeding failure mainly occurred in the second part of the incubation period.

There was no between-year difference of hatching success for the minimum estimates ($\chi^2_2 = 1.56$, n.s.) but the difference was significant for the maximum estimates ($\chi^2_2 = 6.81$, $P < 0.05$), with a decrease from 1997 to 1998-1999 (Table 1). Precise data on fledging and breeding success were available only in 1999. Fledging success ranged between 0.68 and 0.79 for hatched eggs, and overall breeding success was 0.53 young fledged per egg laid (Table 1). Of the 13 nests where breeding failure occurred at the chick stage, the corpses were found in five cases (chick's age less than 1 week in four cases and less than 4 weeks in one case). In the eight remaining cases the chick disappeared between two subsequent visits; chick's age less than 3 weeks in one case, less than 4 weeks in six cases, and less than 6 weeks in one case. The value obtained for breeding success included an unknown number of older chicks depredated by Great Black-backed Gulls *Larus marinus*, before fledging when they left their burrows at night to exercise their wings or during the night of departure. At least two chicks were preyed upon on Enez Kreiz in 1999. The first one was 40-60 days old (feather remains were found nearby the entrance of the burrow), and the second one was 50-70 days old (the ring was found in a regurgitated gull pellet on the islet; the nest of this chick, found late, was not included in the study sample). The first chicks generally fledged around mid August, whereas

Table 2. Breeding parameters for European Storm-petrel in north-west Europe.
Tabel 2. Broedsucces van Stormvogeltjes in Noordwest-Europa.

Colony	Hatching Success (%)	Fledging success[a]	Breeding success[b]
Mousa, Shetland (Bolton 1996)	86	0.71	0.61
Skokholm, Wales (Davis 1957)	66	0.89	0.59
Skokholm, Wales (Davis 1970)	55-68	0.49-0.78	0.27-0.50
Enez Kreiz, Brittany (this study)	64-96	0.68-0.79	0.53
Biarritz, SW-France (Hémery 1980)	64	0.90-1.00	0.62
Benidorm, E-Spain (Minguez 1994)	70	0.90	0.63
Range	55-96	0.49-1.00	0.27-0.63

[a]for hatched eggs only; [b]overall breeding success

the latest fledged in late October, or even perhaps occasionally November in very late years (although no visits were conducted at this time of the year).

Given the marked increase in breeding numbers from 1997/98 to 1999, the potential effect of site history was also tested. There was no significant difference between new sites (discovered in 1999) and old sites (occupied at least in 1998), but 'new-old' sites (occupied before, but not in, 1998) showed the lowest estimates for each of the three breeding parameters (Table 1; hatching success: $\chi^2_2 = 0.53$, n.s., for minimum estimates and $\chi^2_2 = 1.57$, n.s., for maximum estimates, fledging success: $\chi^2_2 = 1.25$, n.s., for minimum estimates and $\chi^2_2 = 0.68$, n.s., for maximum estimates, breeding success $\chi^2_2 = 1.60$, n.s.).

DISCUSSION

Breeding parameters Recorded egg sizes in this study were in the same range as those noted by others (Cramp & Simmons 1977, Scott 1970). Data from elsewhere in north-west Europe indicate greater variability in hatching success and fledging success than in overall breeding success (Table 2). The estimates obtained in Brittany accord well with other data (Table 2). Regular observations made in 1999 have shown that, after breeding failure, unattended and unhatched eggs may remain for some weeks in the nest sites (up to at least 7 weeks), but that corpses of young chicks disappear more rapidly. Scott (1970) showed that most of the failures after hatching occurred within 48 hours, and most of the eggs that subsequently disappeared in 1999 were incubated for at least 3 to 6 weeks (see Results). Thus, the higher estimates for hatching success are probably closer to the actual figures (maximum: 79-96% in Table 1), ranging annually from about 75-80% to 90-95%. On Banneg and Roc'h Hir, and possibly on Enez Kreiz, there is a small population of shrews *Crocidura suaveolens*, and these small insectivorous mammals may perhaps eat and remove some dead young chicks (M. Pascal *pers. comm.*), further compounding the uncertainty about hatching success. The late breeding season in 1998 did not appear to have any impact on hatching success (Table 1).

Overall breeding success in 1998 seemed to be around 0.45 young per egg laid, but the data were far less accurate than in 1999. As a large increase in breeding numbers was recorded in 1999, potentially due to the recruitment of inexperienced birds, a global decrease in success could be expected (Scott 1970), but hatching success in 1999 was not lower than in the previous year (Table 1). Moreover, there was no significant difference in success between old sites (probably mainly reoccupied by experienced breeders) and new sites (Table 1), although the exact status of the breeders here was unknown. As hatching success tended to decrease from 1997 to 1998/99 (Table 1), a potential effect of disturbance due to intrusion in nest sites and the increasing number of visits cannot be excluded. There was no evidence of such an effect, which might be indicated by a high desertion rate, but it remained difficult to assess it in the absence of a sample of control nest sites receiving less disturbance. Another explanation of the higher hatching success in 1997 could be that only two main visits were conducted at an interval of 48 days, leading to an over-estimation as some sites with breeding failure would have not been detected. Due to the variability in incubation and rearing period duration (Davis 1957; Scott 1970), to the fact that all the nests taken into account were found during the incubation or brooding period, to the reduced numbers of visits on the study colony, and to the assumption that 'mortality rate is approximately even across each stage', the Mayfield method (Mayfield 1975) appeared not to be a feasible alternative approach to calculating the different breeding parameters.

Potential effects of variation in laying date on census results The attendance patterns based on estimated laying dates (Fig. 3) represent maxima as some breeders had already failed and deserted the colony and some eggs may have been left unattended, but non-breeders may also have responded to playback. On Mousa (Shetland), the observed proportion of nests attended peaked at 85-90% in late June (Ratcliffe *et al.* 1998a). Latitudinal extrapolation of the peak of laying, used in some studies to determine the optimum date for censusing colonies where there is no precise data on the breeding period (Mainwood *et al.* 1997; Gilbert *et al.* 1998), should be considered only as indicative. Nevertheless, early to mid July appears to be the recommended time for playback census at colonies, at least in Britain, Ireland and Brittany (Ratcliffe *et al.* 1998a; this study).

As chicks respond more frequently to playback than stated in Mainwood *et al.* (1997), especially when about 10 to 20 days old (pers. obs., but no quantitative data), the proportion of chicks heard during playback census could be an indicator of the laying phenology. Many responses of chicks would indicate that the peak of nest attendance by the adults, and thus the better census period, has been passed beyond. However, more precise data should be collected on response rate of European Storm-petrel chicks.

In conclusion, data obtained from single visits at the same time in different years should be interpreted carefully, especially when using tape-playback methods only, as the proportion of attended nest sites may be very different. It appears important to record, as much as possible, an adequate sample of nest contents and age of chicks when visiting European Storm-petrel colonies (using plumage features, Davis 1957, or tarsus length, M. Bolton *in* Ratcliffe *et al.* 1998a), in order to investigate the timing of breeding and discover any delays that could affect the results of the count. Inspecting nests in a study plot through the season would also be valuable.

European Storm-petrel on Banneg island Stormvogeltje op Banneg-eiland *(photo René-Pierre Bolan)*

Laying period and observed variability Despite the limitations of back-calculation of laying date from chick age (see Methods), the large sample sizes and consistency of methods in the current study indicate that the overall laying period extends from the end of April to early August and shows high interannual variability, with 50% of laying ranging over 6 weeks, from mid May to early July; 90% of laying appears to be less variable, ranging over 4 weeks, from mid June to mid July (Fig. 1). The situation between 1975 and 1996 is not known because very few chicks were ringed and aged. However, from samples of 17 and 22 chicks ringed and measured in August 1986 and 1990 respectively (J.-P. Cuillandre unpubl. data), it appears that the breeding period in both years occurred somewhere between that recorded in 1975 and 1997-1999 (Fig. 1), and seemed to be earlier in 1986 than in 1990.

The late 1998 breeding season in Brittany indicated a temporal pattern placed between the one recorded in Wales and the one recorded in northern Scotland (Davis 1957; Scott 1970; Ratcliffe *et al.* 1996; Mainwood *et al.* 1997). Such a great delay in a single colony seems not to have been recorded elsewhere for European Storm-petrels, and appears to be very uncommon for other seabirds, although one case of late breeding was reported for European Storm-petrels on Mousa (Ratcliffe *et al.* 1998b). Davis (1957) and Scott (1970), over seven breeding seasons on Skokholm, found that 50% of laying ranged over less than 10 days in an early year to other more typical periods. On Skokholm and Skomer, the Manx Shearwater *Puffinus puffinus* also exhibited a high constancy in laying (Brooke 1990), but one late season has been recorded on Rum, western Scotland (K. Thompson, pers. comm.).

Factors influencing the timing of laying Several factors can influence the duration of the breeding period in seabirds. Among European Storm-petrels, young, first-time breeders tend to breed later in the season than experienced breeders (Scott 1970), but population size in the Molène archipelago remained similar from 1997 to 1998, and the large increase in breeding numbers recorded in 1999 was not associated with a late breeding season (Fig. 1). Higher densities of breeders can induce an earlier breeding in seabirds (Danchin 1988; Harris & Wanless 1988), but in the present study all available data on laying, from different colonies and different areas within colonies, with different densities, were pooled together. Massive predation in consecutive years on eggs and chicks at some Black-legged Kittiwake *Rissa tridactyla* colonies in Brittany leads to a progressive delay in breeding from the end of April or early May (usual dates) to early June (J.-Y. Monnat & B. Cadiou unpubl. data). Predation by gulls, especially Great Black-backed Gulls, mainly on pre-breeding and breeding European Storm-petrels, has increased since the beginning of the 1990s in the Molène archipelago (Cuillandre *et al.* 1989; Cadiou 1998 and unpubl. data), but an effect on laying date appears improbable. In alcids, the timing of laying appears quite constant from year to year within colonies. However, there are some occasional late years, apparently resulting from climatic conditions that may influence abundance and availability of food resources (Birkhead & Harris 1985; Harris & Wanless 1988). A potential link between food and late breeding was also suggested for the Black-legged Kittiwake (Coulson & Thomas 1985; Harris & Wanless 1997). A study of the Fork-tailed Storm-petrel *Oceanodroma furcata* in Alaska showed high between-year variability both in laying period, with a mean hatching date ranging over more than one month, and in chick growth (Boersma & Parrish 1998). The authors suggested that this was a direct response to environmental variability.

Thus, year-to-year variability in the timing of laying recorded in the present study on European Storm-petrels, and the temporary break recorded in June 1998 (Fig. 1), may be attributable to variations in oceanographic conditions and food resources at sea just before laying, when females have to store energetic reserves for egg production. The event that led to a delay in laying in 1998 should have been severe but confined to May-June only and not afterwards. It seems highly probable that other colonies, at least in the Celtic Sea, can exhibit similar year-to-year changes. Breeders originating from these different colonies may feed in adjacent areas of sea (Pollock *et al.* 1997) and encounter similar food conditions, and may thus respond in the same way to variation in food resources before egg laying.

Several studies have reported the broad spectrum of prey eaten by European Storm-petrels, especially zooplankton (Scott 1970; Cramp & Simmons 1977, d'Elbée & Hémery 1998), but it may be possible that during the pelagic phase of the breeding cycle, females feed mainly on a few prey species (for example ichthyoplankton), and become more sensitive to changes in their availability or abundance.

The El Niño Southern Oscillation (ENSO) climatic event has global and multifarious effects (Trenberth *et al.* 1998) and 1998 was the strongest ever recorded (Sydeman *et al.* 1999). It is tempting to propose a potential effect of El Niño on the laying period of European Storm-petrels. However, major ENSO events are generally associated in seabirds with effects over the whole breeding season and decreases in breeding numbers and breeding success (nest desertion, reduced productivity, etc.) or lower growth rate of chicks (Valle *et al.* 1987; Anderson *et al.* 1999; Sydeman *et al.* 1999). Clearly, no such effects were recorded in the present study (see Results; unpubl. data for chick growth). Other climatic events such as the North Atlantic Oscillation (NAO) or the Gulf Stream have direct effects on plankton communities (Fromentin & Planque 1996; Gerten & Adrian 2000), and, consequently, potentially on seabirds also (Hass 1999). However, the relationships between climate and plankton appears difficult to generalise (Beaugrand *et al.* 2000). Indeed, annual changes in the abundance of plankton in the English Channel during 1979-1995 were correlated with the NAO index but variation in plankton abundance in the Celtic Sea and in the Bay of Biscay were not (Beaugrand *et al.* 2000). No published oceanographic data for Celtic Sea appear to exist for 1996-1999, and data on diet collected on Banneg Island from regurgitates of adults or chicks are not adequate to identify any change (J. d'Elbée comm. pers.).

Two questions remain; first, is the variability in laying period of European Storm-petrels a regular or occasional event and, secondly, whether it is a recent trend with a possible link to climate change. Only long-term studies on the laying phenology at different colonies, coupled with analyses of oceanographic and climatic data, will improve our knowledge. In this context, the European Storm-petrel might act as a potential indicator of changes in the marine environment.

ACKNOWLEDGEMENTS

Most of this work was carried out on the Iroise National Nature Reserve (Molène archipelago), land property of the 'Conseil Général' of Finistère, with funding from the 'Conseil Régional' of Brittany through a 'Contrat Nature' on seabirds in Brittany. I am very grateful to Jean-Yves Le Gall and David Bourles, wardens of the Reserve, and to all the volunteers involved in field work. Many thanks also to Kate Thompson for helpful comments on an earlier draft of the paper, to Norman Ratcliffe, an anonymous referee, Peter Becker and Jim Reid for improvement of the manuscript, and to Maïwenn Magnier for revision of the English version.

BROEDBIOLOGIE VAN STORMVOGELTJES *HYDROBATES PELAGICUS* IN BRETAGNE, FRANKRIJK

De afgelopen jaren (1996-1999), zijn gegevens verzameld over de broedbiologie van Stormvogeltjes Hydrobates pelagicus *in kolonies langs de Bretonse kust in Frankrijk. De belangrijkste onderzochte aspecten waren legdatum, uitkomstsucces en uitvliegsucces. De gegevens werden verzameld door regelmatige controles van bezette holen en door het schatten van de kuikenleeftijd tegen de tijd dat de vogels geringd konden worden. De broedvogels keerden in maart of april op de nestplaatsen terug. De periode van ei-leg strekte zich uit van eind april tot begin augustus (!) en het tijdstip verschilde van jaar tot jaar sterk (mediaan half mei tot begin juli). Deze jaarlijkse verschillen werden vermoedelijk veroorzaakt door oceanografische fluctuaties en schommelingen in het voedselaanbod kort voor de eileg. Het hoeft geen betoog dat de mate grote verschillen in het tijdstip van leggen (en de daarmee samenhangende aanwezigheid van broedvogels op de kolonie) belangrijke implicaties had voor de onderzoekers. Gegegevens die gebaseerd worden op een enkel koloniebezoek moeten met grote terughoudendheid worden geïnterpreteerd, vooral wanneer alleen bandrecorders gebruikt worden om de populatie-omvang vast te stellen, omdat het percentage bezette nesten bij uitgestelde eileg buitengewoon laag kan zijn. Schattingen van het uitkomst- en uitvliegsucces bedroegen respectievelijk 65%-95% (over drie jaren) en 0.53 (één jaar). De eerste jongen vlogen half augustus uit, de laatste eind oktober of soms zelfs pas in november.*

REFERENCES

Anderson D., Keith J., Palacios E., Velarde E., Gress F. & King K.A. 1999. El Niño 1997-98: seabird responses from the Southern California current and Gulf of California. Pacific Seabirds 26: 22-23.

Beaugrand G., Ibañez F. & Reid P.C. 2000. Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. Marine Ecology Progress Series 200: 93-102.

Birkhead T.R. & Harris M.P. 1985. Ecological adaptations for breeding in the Atlantic Alcidae. In: Nettleship D.N. & Birkhead T.R. (eds) The Atlantic Alcidae: 205-231. Academic Press, London.

Bolton M. 1996. Energy expenditure, body-weight and foraging performance of Storm Petrels *Hydrobates pelagicus* breeding in artificial nesting chambers. Ibis 138: 405-409.

Boersma P.D. & Parrish J.K. 1998. Flexible growth rates in Fork-tailed Storm-Petrels: a response to environmental variability. Auk 115: 67-75.

Brooke M. 1990. The Manx Shearwater. Poyser, London.

Cadiou B. 1998. Oiseaux marins nicheurs de Bretagne, 1995-1998. 'Contrat Nature' Report, Bretagne Vivante - SEPNB / Conseil Régional de Bretagne / DIREN Bretagne.

Coulson J.C. & Thomas C.S. 1985. Changes in the biology of the Kittiwake *Rissa tridactyla*: a 31-year study of breeding colony. Journal of Animal Ecology 54: 9-26.

Cramp S. & Simmons K.E.L. (eds) 1977. The Birds of the Western Palearctic, Vol. I. Oxford University Press, Oxford.

Cuillandre J.-P., Bargain B., Bioret F., Fichaut B., Hamon J. & Henry J. 1989. Le pétrel tempête à Banneg. Première partie : évolution de la colonie entre 1968 et 1989, impact de la prédation par les laridés. Penn ar Bed 135: 19-33.

Danchin E. 1988. Densité des nids dans des colonies de mouettes tridactyles en déclin ou prospère : relations avec les paramètres de reproduction. Alauda 56: 391-400.

Davis P. 1957. The breeding of the Storm Petrel. British Birds 50: 85-101, 371-384.

d'Elbée J. & Hémery G. 1998. Diet and foraging behaviour of the British Storm Petrel *Hydrobates pelagicus* in the Bay of Biscay during summer. Ardea 86: 1-10.

Fromentin J.-M. & Planque B. 1996. Calanus and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series 134: 111-118.

Gerten D. & Adrian R. 2000. Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. Limnology and Oceanography 45: 1058-1066.

Gilbert G., Hemsley D. & Shepherd M. 1998. A survey of Storm Petrels on the Treshnish Isles in 1996. Scottish Birds 19: 145-153.

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.

Harris M.P. & Wanless S. 1997. Breeding success, diet, and brood neglect in the Kittiwake (*Rissa tridactyla*) over an 11-year period. ICES Journal of Marine Science 54: 615-623.

Hass T. 1999. Oscillations in the North Atlantic and Southern Hemisphere: Gulf Stream lags and petrel pile-ups. Pacific Seabirds 26: 24-25.

Henry J. & Monnat J.-Y. 1981. Oiseaux marins de la façade atlantique française. SEPNB / MER Report.

Hémery G. 1980. Dynamique de la population basque française de Pétrels tempête (*Hydrobates pelagicus*) de 1974 à 1979. L'Oiseau et R.F.O. 50: 217-218.

Mainwood A.R., Ratcliffe N., Murray S. & Mudge G.P. 1997. Population status of Storm Petrels *Hydrobates pelagicus* on islands off north-west Scotland. Seabird 19: 22-30.

Mayfield H.F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456-466.

Minguez E. 1994. Censo, cronologia de puesta y exito reproductor des Paíño Común (*Hydrobates pelagicus*) en la Isla de Benidorm (Alicante E de España). Ardeola 41: 3-11.

Pollock C., Reid J., Webb A. & Tasker M. 1997. The distribution of seabirds and cetaceans in the waters around Ireland. JNCC Report, No. 267.

Ratcliffe N., Suddaby D. & Betts M. 1996. An examination of the census methods used for Storm Petrels *Hydrobates pelagicus* on Mousa and Skokholm. Unpublished RSPB Report.

Ratcliffe N., Vaughan D., Whyte C. & Sheperd M. 1998a. Development of playback census methods for Storm Petrels *Hydrobates pelagicus*. Bird Study 45: 302-312.

Ratcliffe N., Vaughan D., Whyte C. & Sheperd M. 1998b. The status of Storm Petrels on Mousa, Shetland. Scottish Birds 19: 154-159.

Scott D.A. 1970. The breeding biology of the Storm Petrel *Hydrobates pelagicus*. D. Phil. thesis, Oxford University.

Sydeman W.J., Parrish J.K., Martin P., Gress F., Hester M.M., Hastings K.K., Hebshi A.J., Thayer J.A., Buffa J. & Nur N. 1999. Spatial and temporal trends in reproductive dynamics of seabirds in the California Current Marine Ecosystem: response to El Niño and lower frequency marine climate change. Pacific Seabirds 26: 26.

Trenberth K.E., Branstator G.W., Karoly D., Kumar A., Lau N.-C. & Ropelewski C. 1998. Progress during TOGA in understanding and modeling global teleconnections associated with tropical sea surface temperatures. Journal of Geophysical Research 103: 14 291-14 324.

Valle C.A., Cruz F., Cruz J.B., Merlen G. & Coulter M.C. 1987. The impact of the 1982-1983 El Niño-Southern Oscillation on seabirds in the Galapagos Islands, Ecuador. Journal of Geophysical Research 92: 14 437-14 444.

REDUCTION IN BODY MASS AND BASAL METABOLIC RATE IN BREEDING FEMALE BLACK-LEGGED KITTIWAKES *RISSA TRIDACTYLA*: AN ADAPTATION TO REDUCE MAINTENANCE COSTS?

INGVEIG LANGSETH, BØRGE MOE & CLAUS BECH

Langseth I., Moe B. & Bech C. 2001. Reduction in body mass and basal metabolic rate in breeding female Black-legged Kittiwakes *Rissa tridactyla*: An adaptation to reduce maintenance costs? Atlantic Seabirds 3(4): 165-178. *We studied changes in body mass and basal metabolic rates (BMR) in breeding female Black-legged Kittiwakes* Rissa tridactyla *on Svalbard (79°N, 12°E) in 1997 and 1998. Measurements of body masses and BMR were obtained two weeks before hatching, at hatching, early in the chick-rearing period and late in the chick-rearing period. During incubation, body mass and mass specific BMR remained relatively stable. From hatching to late chick-rearing, body mass and mass specific BMR decreased by 12% and 26% respectively. However, from about two weeks up to about four weeks into the chick-rearing period, body mass and BMR did not change significantly. Whole body BMR scales with body mass$^{2.18}$. This exponent is greater than that expected for a homomorphic variation in BMR, and indicates that the reduction in BMR must involve properties other than an overall body mass reduction. The simultaneous reduction in body mass and BMR could result from a negative energy balance, leading to a reduction in the masses of metabolically active organs. Alternatively, a reduction in BMR could be an adaptation to compensate for an elevated activity level during the chick-rearing period. By a reduction in the adult's maintenance costs, more energy can be allocated for promoting chick growth.*

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INTRODUCTION

Most birds face an energetic challenge during reproduction because this period often involves an increase in activity and a reallocation of energy from self maintenance and survival to egg formation, incubation and chick growth. Since both time and energy may be limiting resources, the adult birds often experience a reduction in body mass, and consequently also in body condition, during reproduction (Moreno 1989). This reduction in body mass has generally been considered to be a consequence of energetic stress (Ricklefs 1974; Harris 1979; Drent & Daan 1980; Ricklefs & Hussel 1984; Monaghan *et al.*1989; Moreno 1989). However, some evidence exists that a reduction in body mass is part of a mechanism that compensates for the increased level of activity during reproduction, either by reducing the cost of flying (Freed 1981; Norberg 1981) or by reducing energy consumption at rest (Deerenberg *et al.* 1998).

The basal metabolic rate (BMR) is defined as the rate of energy transformation in an endothermic organism in a rested, awakened, fasting and thermoneutral state (IUPS Thermal Commission 1987), and is considered as an obligatory part of the total energy expenditure. Allometric relationships between BMR and body mass (BM) reveal mass exponents of 0.60-0.82, depending on taxonomic level (Elgar & Harvey 1987; Bennet & Harvey 1987). This partially reflects the relationship between body surface and volume, which roughly calibrates with $BM^{0.67}$. Heusner (1984) stated that when body mass changes while other properties that affect the metabolic rate (temperature, density, mass-specific enthalpy, chemical composition, form) remain unchanged, energy turnover should calibrate approximately with $BM^{0.67}$, also called a homomorphic variation. Considerable deviations are often noted from the allometric relationships and interspecific variation in BMR has been considered as an adaptation to environmental differences and ways of living (Bennet & Harvey 1987). There is also increasing evidence that even within single species BMR is a flexible parameter that changes with season, or with other external or internal factors (Daan *et al.* 1989; Piersma *et al.* 1996). Intra-individual mass-exponents in excess of 1.0 have been found in birds (Daan *et al.* 1989; Deerenberg *et al.* 1998). This indicates that change in body mass also may include a change in other properties that can alter metabolic intensity.

The possible impact of an alteration in BMR on total energy expenditure is not clear. Some argue that since BMR represents the cost of keeping the metabolic machinery operative, the BMR-level should reflect the total capacity of this machinery. BMR and the maximal sustained metabolic rate should then be closely linked (Drent & Daan 1980; Daan *et al.* 1990; Hammond & Diamond 1997). In this case it would be advantageous to have a high BMR in periods with elevated energetic demands in order to be able to increase the total energy turnover, and a reduction in BMR would consequently reflect a reduced maximal metabolic capacity. Other studies have failed to find any relationships between BMR and the maximal metabolic rate within a species (Hayes *et al.* 1992; Konarzewski & Diamond 1994; Meerlo *et al.* 1997). This would argue in favour of a possible benefit of a decrease in BMR during energy demanding periods, since a reduction in BMR will enable more of the available energy to be allocated into other activities, such as reproduction (Gadgil & Bossert 1970).

Black-legged Kittiwakes *Rissa tridactyla* lose mass during chick rearing (Moe *et al.* 2001), a period in which both their activity level and total energy expenditure increases (Fyhn *et al.* 2001). The aim of the present study was to investigate whether a change in body mass of breeding female Black-legged Kittiwakes corresponds with changes in their BMR and to discuss what possible impact this would have on their energy balance.

MATERIALS & METHODS

The study was performed in a Black-legged Kittiwake colony at Kongsfjorden (78°54'N 12°13'E), 7 km west of Ny-Ålesund on Svalbard. In this colony about 600 Black-legged Kittiwake pairs breed with 50-100 Brünnich's Guillemots *Uria lomvia* and five to ten pairs of Black Guillemots *Cepphus grylle* (Mehlum & Fjeld 1987). The birds experience continuous daylight throughout the breeding season.

In two breeding seasons, 11 June-13 August 1997 and 19 June-29 July 1998, the colony was visited on a regular basis in order to record nest contents and hatching dates. Females used in the experiments were randomly selected after their sex, based on biometric measurements, had been confirmed. They were all breeding but no consideration was taken of their clutch or brood size (mainly because of an insufficient number of single egg/chick nests). The adult birds were captured when sitting on their nests, using a fishing pole fitted with a terminal noose. On the first capture, measurements of head+bill (skull) length were obtained to the nearest 0.1 mm, using a flexible ruler. Body masses were obtained to the nearest 1.0 g on every capture occasion, using a spring balance. For pairs for which data from both adults were obtained, the sexes were differentiated according to their relative size, the smaller (in both body mass and size) being the female. This method gave 98% correct determination when sexing Black-legged Kittiwakes on Hornøya, 70°N (Pichl 1997). When only one individual in a pair was captured, the females were assumed to have a skull length of less than 92.1 mm, and males were assumed to have a skull length of more than 92.1 mm. This method gave 87% correct determination when sexing Black-legged Kittiwakes on Hornøya (Barrett *et al.* 1985). We managed to capture the partner of all but one of the experimental birds. This female had a skull length of 91.4 mm, which is well beyond (0.7 mm) the limit of 92.1 mm, and we are therefore trusting that all the experimental birds were females.

Altogether we obtained 67 measurements of BMR in 40 female Black-legged Kittiwakes, of which 24 measurements were made during the incubation period (in 1997), 10 just around hatching time (in 1998), 17 about two weeks after hatching (in 1997) and 16 late during the chick-rearing period (7 in 1997 and 9 in 1998). Metabolic rates were measured indirectly as the rates of oxygen consumption in resting post-absorptive individuals, using open flow-through respirometry. After capture in the field, the Black-legged Kittiwakes were placed in a cage and transported to a laboratory in Ny-Ålesund for BMR-measurements. Within 7 hours (on average) the Black-legged Kittiwakes were placed in a metabolic chamber of approximately 25 l, in which the ambient temperature (T_a) was measured using a copper-constantan thermocouple (California Fine Wire Co., type 0.005). Dry outside air was drawn through the chamber at a rate of *ca.* 2.2 l min^{-1}. The actual flow-rate was constantly measured by a flow-meter (Bronkhorts Hi-tek, type 201C-FA). Effluent air was dried over silica-gel and a fraction of the dry effluent air was directed into an oxygen analyser (Servomex, type 244A) for measurement of oxygen concentration. Readings of T_a and the voltage output of the flow-meter and the oxygen-analyser were recorded every minute by a data-logger (Grant Squirrel, type 1203) and transferred to a computer for further analysis. The birds were weighed to the nearest 1.0 g immediately before and after each experiment, which on average lasted for 10 hours. A linear decrease in body mass was assumed when calculating the body mass, from which the mass-specific BMR was calculated. The birds (except 16, which were sacrificed and used in studies of body composition) were released outside the laboratory. All were observed back on their nests within a couple of hours afterwards.

Rates of oxygen consumption were calculated using formula 3A in Withers (1977) and assuming a respiratory quotient of 0.8. We used the method described by Niimi (1978) in order to correct for washout delay and to obtain instantaneous rates. The minimum 25 minutes running mean was considered to represent the basal metabolic rate (for further details on method see Bech *et al.* 1999). Oxygen consumption values were converted into Watts (W) using a factor of 20.1 kJ per litre of oxygen.

A number of nests, 48 in 1997 and 55 in 1998, were randomly selected as controls. Hatching rates, chick growth and chick survival were similar for the experimental nests and the control nests (pers. obs.). Hence, removal of the females from their nests during the BMR measurements did not seem to have any deleterious effect on reproduction. The mean body mass and BMR values obtained during the incubation period did not differ significantly between the two seasons (1997 and 1998), nor did the means obtained during the chick rearing period. Hence, we have not analysed the data for the two seasons separately in this study. All statistical analyses were performed using SigmaStat software (SPSS Inc., v. 2.03). Values are presented as means ± 1 standard deviation (SD) and the results were considered statistically significant at values of $P \leq 0.05$. The National Committee for Animal Research (Forsøksdyrutvalget) in Norway approved the experimental protocol for the experiments. Permissions to work in the colony and the collection of individuals for analyses of body composition were obtained from the Governor of Svalbard (ref. 96/00569-2 and 98/00469-5).

RESULTS

The body masses of female Black-legged Kittiwakes recorded in the field two weeks prior to hatching and around hatching time did not differ significantly (on average 387 ± 24 g, $n = 33$), nor did the body mass values obtained early and later on in the chick-rearing period (on average 342 ± 16 g, $n = 31$). However, the latter mean is significantly lower (about 12%) than the incubation period mean value (t-test, $t = 8.663$, df = 62, $P < 0.001$). The body masses of the female Black-legged Kittiwakes recorded in the laboratory at the same time as the BMR values were recorded (hereafter called the lab body masses) are lower than the body masses recorded earlier in the field due to the intervening fasting period. There was no significant difference in relative body mass decrease between the five groups (Kruskal- Wallis one way ANOVA on ranks, $H = 6.87$, $P = 0.076$) and the reduction was on average 9.1 ± 3.2% ($n = 64$, we failed to obtain field body masses for three individuals.).

The mean lab body masses for the females two weeks prior to hatching, around hatching, two weeks into the chick rearing period and late in the chick rearing period were 347 ± 20 g ($n = 24$), 360 ± 24 g ($n = 10$), 312 ± 20 g ($n = 17$), 313 ± 11 g ($n = 7$) and 312 ± 13 g ($n = 9$) respectively (Fig. 1). The two body mass means obtained during the incubation period were not significantly different from each other, nor were the three body mass means obtained during the chick-rearing period. However, the mean values obtained during the incubation period were significantly different from the three mean values for the chick-rearing period (one-way ANOVA followed by a Student-Newmann-Keul procedure for pairwise comparisons, $F_{4,62}$, $P < 0.0001$). This suggests that body mass declined from incubation to the chick-rearing period.

The ambient temperatures recorded during the BMR measurement periods ranged from 7 – 24 °C. There was no significant relationship between T_a and the metabolic rates measured either in the incubation period or in the chick-rearing period. Thus we considered all the measurements to lie within the thermoneutral zone for Black-legged Kittiwakes on Svalbard, which has previously been found to include temperatures from 5°C up to at least 20°C (Gabrielsen *et al.* 1988).

The time from capture in the field to the actual BMR measurement ranged from 5-24 hours. The minimum time of 5 hours may seem insufficient for the birds to become post-absorptive since 5 hours is the approximate retention time of Black-legged Kittiwakes (Hilton *et al.* 1998). However, the time from capture to the end of the experiment was never less than 10 hours. The minimum metabolic rate recorded as little as 5 hours after capture may indicate that the birds had already been fasting before capture. In addition, Hawkins *et al.* (1997) showed that in Brünnich's Guillemots the effect of heat

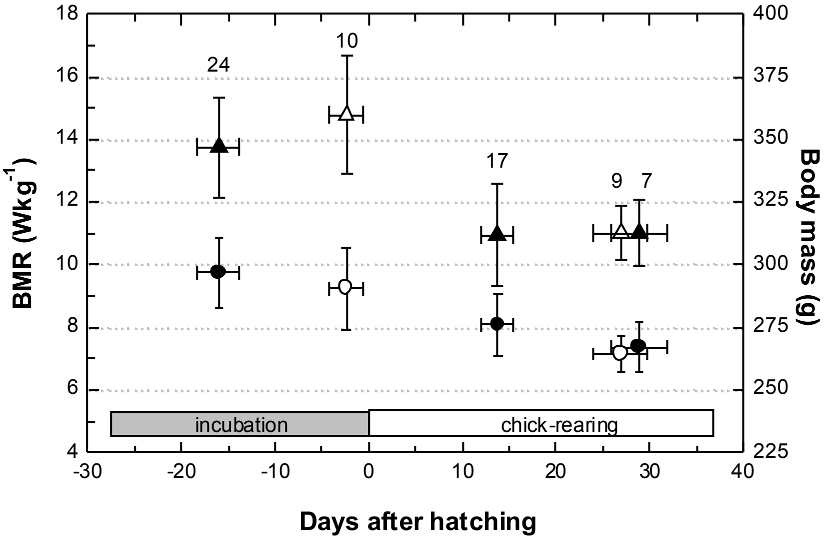

Figure 1. Mass specific BMR (circles) and corresponding body masses (triangles) of breeding female Black-legged Kittiwakes in 1997 (filled symbols) and 1998 (open symbols). Data are presented as mean values ± 1 SD, with numbers of individuals shown above the symbols. Time of hatching of the first chick in a clutch indicated by 0 on the x-axis.

Figuur 1. Massa-specifieke BMR (cirkels) en de bijbehorende massa (driehoeken) van broedende wijfjes Drieteenmeeuwen in 1997 (zwarte symbolen) en 1998 (open symbolen). De gegevens zijn weergegeven als gemiddelden ± 1 SD, met het aantal individuen boven de symbolen. Het moment van uitkomen van het eerste kuiken is als 0 op de x-as weergegeven.

increment of feeding (HIF) lasted for 85 minutes after intake of Polar Cod (*Boreogadus saida*). Assuming a similar effect of HIF on Kitiwakes, a period of 5 hours from last feeding opportunity to measurement should not affect the BMR-values.

Mass specific BMR changed in line with change in body mass (Fig. 1). For the two recordings made during the incubation period BMR values were 9.75 ± 1.14 W kg^{-1} (n = 24) and 9.23 ± 1.33 W kg^{-1} (n = 10) respectively.

These values are not significantly different from each other. Two weeks into the chick rearing period mean BMR was 8.08 ± 1.01 W kg^{-1} (n = 17) and late in the chick rearing period the means were 7.16 ± 0.57 W kg^{-1} (n = 7) and 7.38 ± 0.77 W kg^{-1} (n = 9) (Fig. 1). These last three mean values are not significantly different from each other, but they are all significantly different from the mean values obtained during the incubation period (one-way ANOVA followed by a Student-Newmann-Keul procedure for pairwise comparisons, $F_{4,62}$, $P < 0.0001$).

Since mass-specific BMR decreases with body mass, a reduction in body mass will have an even stronger effect on the whole-body BMR. The relationship between whole-body BMR and lab body mass of breeding female Black-legged Kittiwakes is described by the equation:

$$(1) \qquad BMR = 9.1 * 10^{-6} BM^{2.18}$$

(least square linear regression, $R = 0.80$, $n = 40$, $df = 38$, $P < 0.001$) where BMR is in W and BM is body mass in g. Only one BMR measurement of each individual is included in the analysis, giving $n = 40$. Equation 1 can further be used to eliminate body mass as a determining factor and to calculate residual values of BMR

$$(2) \qquad BMR_{residual} = BMR_{measured}/BMR_{predicted\ by\ eq.\ 1} * 100$$

A regression between $BMR_{residual}$ and the corresponding stage of breeding gives a significant, negative relationship:

$$(3) \qquad BMR_{residual} = 104.7 - 0.4 * \text{days after hatching}$$

(least square linear regression, $R = -0.47$, $n = 40$, $df = 38$, $P = 0.002$) where $BMR_{residual}$ is in percent (Fig. 2).

DISCUSSION

The Black-legged Kittiwake has a biparental care system, both sexes taking an equal share in both the incubation period, which normally lasts for 27 days, and the chick-rearing period (Mehlum 1990). The chicks attain thermal independence about one week after hatching (Barrett 1978), but are constantly brooded for another 10 days (Gabrielsen *et al.* 1992). They are dependent on food provisioning until fledging time, 5-6 weeks after hatching (Mehlum 1990). Moe *et al.* (2001) studied the body mass dynamics of breeding male and female Black-legged Kittiwakes in the same colony as in the present study. Their findings showed that body mass change closely followed the changes in activity levels during different stages of the breeding cycle. During the incubation period, when activity levels are low, body mass remained stable or showed a slight increase. After hatching, the parents must provide both food and heat to their fast growing chicks and consequently less energy and time will be

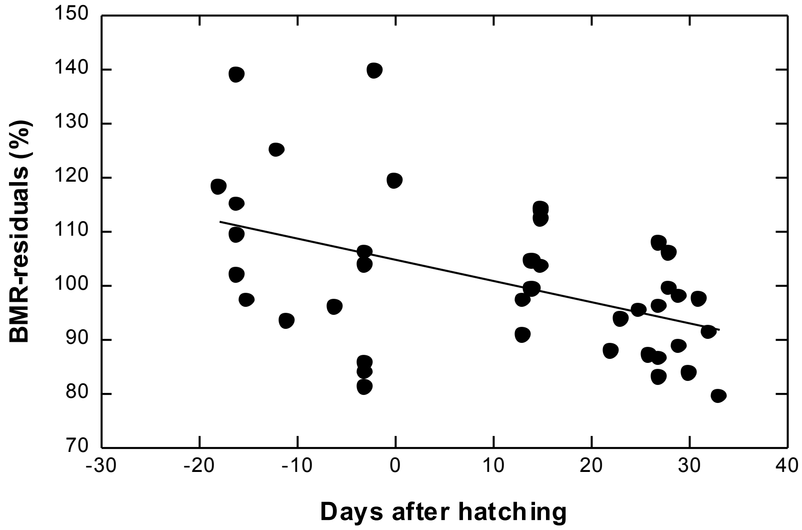

*Figure 2. Relationship between the residuals of the regression of whole-body BMR and body mass (equation 1) and days after hatching of breeding female Black-legged Kittiwakes (*n *= 40, linear regression:* R *= -0.47,* df *= 38,* P *= 0.002).*

*Figuur 2. Het verband tussen de residuen van de regressie van BMR en massa (formule 1) en het aantal dagen na het uitkomen van de jongen bij broedende wijfjes Drieteenmeeuwen (*n *= 40; lineaire regressie* R *= -0.47,* df *= 38,* P *= 0.002).*

available for self-maintenance. The result is a decrease in parental body mass. During the last part of the chick-rearing period the chicks can be left alone for longer periods and, even though their total energy demand increases, more time is available to provide for the adults' own maintenance requirements. The result is that the adult body masses level off. The body mass changes of the female Black-legged Kittiwakes observed in the present study agrees with the findings of Moe *et al.* (2001) and of Wendeln & Becker (1996) in Common Terns *Sterna hirundo*.

From the time of capture in the field until the BMR measurements were made in the laboratory, the body masses of the females decreased by approximately 9%. This was mainly due to emptying of the gut during the fasting period. The degree of body mass reduction was similar in all five groups and the changes in the lab body masses, in consequence, showed the same pattern of change as the field body masses.

Gabrielsen *et al.* (1988) measured the oxygen consumption of 16 adult Black-legged Kittiwakes, of both sexes, on Svalbard in June/July and found a resting metabolic rate (RMR) of 1.64 ml O_2 $g^{-1}h^{-1}$ (= 9.16 W kg^{-1}, mean body mass 365 g). Even though the precise reproductive stage for these individuals was not reported, we assume, based on the dates, that the measurements were made during the incubation period. In four Black-legged Kittiwakes in Scotland, mean BMR was found to be 1.62 ml O_2 $g^{-1}h^{-1}$ (= 9.05 W kg^{-1}, mean body mass 305 g, Bryant & Furness 1995). Neither the sex nor the reproductive stage of these individuals was stated. Our own values of BMR from the incubation period (9.75 and 9.23 W kg^{-1}) lie within the range of these previous measurements of BMR in Black-legged Kittiwakes, but our values from the chick-rearing period (8.08, 7.16 and 7.38 W kg^{-1}) are lower.

The mass specific BMR of female Black-legged Kittiwakes decreases in line with body mass during the chick-rearing period. This implies that the whole body BMR is reduced by more than would have been expected from an effect of a decrease in body mass alone. Accordingly, BMR changes in proportion to $BM^{2.18}$ (see eq. 1). This mass exponent exceeds the exponent expected for a homomorphic variation in BMR (0.67), and it indicates that lightweight individuals have a relative, as well as an absolute, lower BMR than heavier individuals, and that a small change in body mass will have a profound effect on the BMR. This is further demonstrated by the relationship between the residuals of BMR and the days after hatching (Fig. 2), which shows that during incubation females even have relatively higher BMR than would be expected by their high body masses.

High mass-exponents have also been found in other birds in situations that may resemble those experienced during the chick-rearing period. In female Kestrels *Falco tinnunculus*, with varying nutritional conditions, the exponent was 1.6 (Daan *et al.* 1989). In a study of Zebra Finches *Taeniopygia guttata*, with experimentally increased workloads, the intra-individual mass exponent of the metabolic rate was 2.30 (Deerenberg *et al.* 1998). Obviously, in these studies, including our own, the change in metabolic intensity must have involved mechanisms other than an overall body mass change.

A growing understanding exists as to how an inter- and intra-specific variation in BMR reflects variations in body composition (Daan *et al.* 1990; Weber & Piersma 1996). Different organs and tissues vary in their intrinsic metabolic rates (Krebs 1950). Organs such as the liver, heart, kidney and intestine have high metabolic rates, whereas fat and muscle tissues have low metabolic rates. In this way, BMR level may reflect the relative sizes of different organs (Daan *et al.* 1990). Within an individual, a rearrangement of body composition may be an adaptation or a response to different situations according to a use/disuse principle (Piersma & Lindström 1997) and this may in turn lead to changes in BMR. In individual Kestrels that were kept on either high maintenance regimes (*ad libitum* food intake) or low maintenance regimes (resembling body condition during the late chick-rearing period), Daan *et al.* (1989) found that nocturnal BMR was lower during the low maintenance regime than during the high maintenance regime. This was partly due to a greater depression of the nocturnal body temperature. In addition, analyses of body composition revealed a disproportionate reduction in heart and kidney lean mass, and the authors surmised that the variation in BMR reflected variation in the masses of these metabolically highly active organs. A study of the changes in body composition of breeding female Black-legged Kittiwakes has produced similar results (Langseth *et al.* 2000). From incubation to chick-rearing there was a mass reduction in most of the internal organs in the chick rearing period, but a disproportionate decrease in the liver and kidney masses. These organs are both metabolically highly active and a positive relationship between liver mass and mass-specific BMR has been reported in small mammals (Konarzewski & Diamond 1994; 1995) and some birds (Bech & Østnes 1999; Chappell *et al.* 1999). However, one cannot ignore that the mass of the skeleton and the plumage probably will remain relatively constant with a change in body mass. Thus, with a reduction in body mass, the relative mass of skeleton and plumage will increase. Since these tissues have low, or even zero, metabolism this could also lead to a reduction in mass-specific BMR with a reduction in total body mass.

In small mammals there seems to be a mobilisation of the supply organs (e.g. intestine and liver) in connection with reproduction (Hammond & Diamond 1997). The metabolic machinery must apparently be upgraded in order to be able to support the extra energy demands faced during pregnancy and lactation. This may also cause a rise in BMR. In breeding female Brown Long-Eared Bats *Plecotus auritus* BMR increased from pregnancy until after parturition, despite a decrease in body mass (McLean & Speakman 2000). For the Black-legged Kittiwakes it would thus seem unlikely that a reduction in BMR, as a consequence of a reduction in the kidney and liver masses, represents an adaptation to a period during which the energy demands are considered to increase. In small mammals atrophy of the liver is found to be a response to starvation and to a negative energy balance (Goodman & Ruderman 1980; Burrin *et al.* 1988). This could also be the case for Black-legged Kittiwakes during the chick-rearing period, when limitations in both time and food intake may render the birds unable to maintain a positive energy balance.

The field metabolic rate (FMR) of breeding Black-legged Kittiwakes on Svalbard increases throughout the chick-rearing period (Fyhn *et al.* 2001). Hence, it does not seem that a reduction in the masses of internal organs, which occurs in parallel to a reduction in BMR, affects their ability to increase their total energy expenditure. Thus, it is tempting to speculate that a reduction in BMR during the chick rearing period may be a mechanism that minimises maintenance costs, which in turn enables the adult birds to allocate more energy to chick-growth without greatly increasing their total energy consumption. Such a mechanism will be advantageous in situations where both food and time are limiting resources and costs are associated with increasing the food intake. In some species of birds, a reduction in RMR has been found to compensate for increased activity. Deerenberg *et al.* (1998) manipulated the workload of individual Zebra Finches by experimentally increasing the amount of activity (number of hops) required to get access to food. They found that for individuals with a high workload daily energy expenditure and daily food intake were lower than for individuals with a low workload. The difference was larger than could be explained by a reduction in the body mass of the high-workload individuals. Deerenberg *et al.* (1998) concluded that the high-workload individuals compensated (or even over-compensated) by behaviourally increasing their efficiency and by decreasing their RMR, both during the night and the inactive hours of the day. Although this study did not explain the physiological mechanisms underlying the reduction in RMR, it did show that even though the birds had *ad libitum* access to food they compensated for the increased activity by reducing their body mass and RMR rather than increasing their food intake. A similar change in RMR was found in male White-crowned Sparrows *Zonotrichia leucophrys gambelii* with varying testosterone levels (Wikelski *et al.* 1999). Males (both intact and castrated) with testosterone implants showed an increased activity level, but a decrease in both body mass and RMR, compared with pre-implantation values.

These findings of a body mass related reduction in RMR in Zebra Finches and White-crowned Sparrows in connection with an increase in activity, resemble our finding of a reduction in BMR in female Black-legged Kittiwakes during the chick-rearing period. One can speculate that whereas female mammals must mobilise the metabolic machinery in order to support the growing foetus and later the endogenous milk production, birds, in contrast, seem to be able to slow down their metabolic intensity at rest as a compensation for the increased workload during reproduction. However, the question still remains as to whether Black-legged Kittiwakes lose body mass because of limited food and time resources, or whether there are costs associated with increasing food intake, such as increased predation risk, which exceed the costs of losing weight. Obviously there must also be costs associated with reducing metabolic rate at rest, otherwise it would have been energetically advantageous to maintain a constant low metabolic rate. A reduction in body mass may involve a depletion of body reserves that normally serve as insurance against starvation (Lima 1986), and a reduction in BMR may result in damage to the immunological defence mechanism (Deerenberg *et al.* 1997). In order to further elucidate whether free-living Black-legged Kittiwakes really do compensate for increased activity during the chick-rearing period by reducing their body mass and BMR, or whether this is merely a consequence of energetic stress, manipulative experiments are called for, either by increasing food availability or by increasing the workload.

ACKNOWLEDGEMENTS

The study was supported by a grant (no 112871/720 to C. Bech) from the Norwegian Science Research Council. Thanks are due to the staff at the Kings Bay Company and the Research Station of The Norwegian Polar Research Institute in Ny-Ålesund. We also thank Ingrid Næss, Marianne Fyhn, Geir W. Gabrielsen, Geir Magne Pedersen and May Britt Tessem for help during the field work.

TERUGLOPEND LICHAAMSGEWICHT EN BASAALMETABOLISME BIJ BROEDENDE WIJFJES DRIETEENMEEUWEN *RISSA TRIDACTYLA*: EEN AANPASSING OM ONDERHOUDSKOSTEN TE BEPERKEN?

Veranderingen in lichaamsgewicht en basaalmetabolisme (BMR) werden onderzocht bij broedende wijfjes Drieteenmeeuwen Rissa tridactyla *op West-Spitsbergen (79°NB, 12°OL) in 1997 en 1998. Massabepalingen en metingen van het BMR werden verricht tijdens het broeden (twee weken voor het uitkomen van de eieren), rondom het uitkomen van de eieren, in de eerste dagen van jongenzorg en vlak voor het uitvliegen van de jongen. Gedurende het bebroeden van de eieren waren massa en BMR beide tamelijk stabiel, maar vanaf het moment van uitkomen tot het moment van uitvliegen namen massa en BMR respectievelijk met 12% en 26% af. Vanaf twee weken tot ongeveer vier weken in de periode van jongenzorg werden er echter geen veranderingen gevonden. Het BMR gemeten voor het gehele lichaam verhoudt zich als lichaamsmassa*$^{2.18}$*. Deze exponent is groter dan verwacht voor een homomorfe variatie van het BMR en dit suggereert dat er andere factoren een rol spelen dan alleen een afnemend lichaamsgewicht. Het tegelijkertijd afnemen van massa en BMR zou het resultaat kunnen zijn van een negatieve energiebalans met als gevolg daarvan een teruglopende massa van de metabolisch actieve organen. Aan de andere kant zou een teruglopend BMR een aanpassing kunnen zijn om de verhoogde activiteit samenhangend met de jongenzorg op te vangen. Een reductie van de onderhoudskosten van de volwassen vogels zorgt ervoor dat meer energie kan worden gestoken in de jongenzorg waardoor de kuikens sneller kunnen groeien.*

REFERENCES

Barrett R.T. 1978. Adult body temperatures and development of endothermy in the Kittiwake (*Rissa tridactyla*) Astarte 11: 113-116.

Barret R.T., Fieler R., Anker-Nilssen T. &. Rikardsen F 1985. Measurements and weight changes of Norwegian adult puffins *Fratercula arctica* and Kittiwakes *Rissa tridactyla* during the breeding season. Ringing Migr. 6: 102-112.

Bech C. & Østnes J.E. 1999. Influence of body composition on the metabolic rate of nestling European shags (*Phalacrocorax aristotelis*). J. Comp. Physiol. B 169: 263-270.

Bech C., Langseth I. & Gabrielsen G.W. 1999. Repeatability of basal metabolism of breeding female Kittiwakes (*Rissa tridactyla*). Proc. R. Soc. Lond. B. 266: 2161-2167.

Bennet P.M. & Harvey P.H. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. J. Zool. Lond. 213: 327-363.

Bryant D.M. & Furness R.W. 1995. Basal metabolic rates of North Atlantic seabirds. Ibis 137: 219-226.

Burrin D.G., Britton R.A. & Ferrel C.L. 1988. Visceral organ size and hepatocyte metabolic activity in fed and fasted rats. J. Nutr. 118: 1547-1552.

Chappell M.A., Bech C. & Buttemer W.A. 1999. The relationship of central and peripheral organ masses to aerobic performance variation in house sparrows. J. Exp. Biol. 202: 2269-2279.

Daan S., Masman D., Srijkstra A.& Verhulst S. 1989. Intraspecific allometry of basal metabolic rate: relations with body size, temperature, composition and circadian phase in the Kestrel, *Falco tinnunculus*. J. Biol. Rhythms 4: 267-283.

Daan S., Masman D. & Groenewold A.1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. Am. J. Physiol. 259: R333-R340.

Deerenberg C., Overkamp G.J.F., Visser G.H. & Daan S. 1998. Compensation in resting metabolism for experimentally increased activity. J. Comp. Physiol. B. 168: 507-512.

Deerenberg C., Apanius V.A., Daan S. & Bos N. 1997. Reproductive effort decreases antibody responsiveness. Proc. R. Soc. Lond. B. 264: 1021-1029.

Drent R.H. & Daan S.1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.

Elgar M.A. & Harvey P.H. 1987. Basal metabolic rates in mammals: allometry, phylogeny and ecology. Funct. Ecol. 1: 25-36.

Freed L.A. 1981. Loss of mass in breeding wrens: Stress or adaptation? Ecology 62: 1179-1186.

Fyhn M., Gabrielsen G.W., Nordøy E.S., Moe B., Langseth I. & Bech C. 2001. Individual variation in field metabolic rate of kittiwakes (*Rissa tridactyla*) during the chick-rearing period. Physiol. Biochem. Zool. 74: 343-355.

Gabrielsen G.W., Mehlum F. & Karlsen H.K. 1988. Thermoregulation in four species of arctic seabirds. J. Comp. Physiol. B. 157: 703-708.

Gabrielsen G.W., Klaassen M. & Mehlum F.1992. Energetics of Black-legged Kittiwakes *Rissa tridactyla* chicks. Ardea 80:29-40.

Gadgil M. & Bossert W.1970. Life history consequences of natural selection. Am. Nat. 104: 1-24.

Goodmann M.N. & Ruderman N.B. 1980. Starvation in the rat. I. Effect of age and obesity on organ weights, RNA, DNA and protein. Am. J. Physiol. 239: E269-276.

Hammond K.A. & Diamond J. 1997. Maximal sustained energy budgets in humans and animals. Nature 386: 457-462.

Harris M.P. 1979. Measurements and weights of British Puffins. Bird Study 26: 176-196.

Hayes J.P., Garland J.R. & Dohm M.R. 1992. Individual variation in reproduction metabolism and reproduction of *Mus*: are energetics and life history linked? Funct. Ecol. 6: 5-14.

Hawkins P.A.J, Butler P.J., Woakes A.J. & Gabrielsen G.W. 1997. Heat increment of feeding in Brünnich's guillemot *Uria lomvia*. J. Exp. Biol. 200: 1757-1763.

Heysner A.A. 1984. Biological similitude: Statistical and functional relationships in comparative physiology. Am. J. Physiol. 246: R839-R845.

Hilton G.M., Houston D.C. & Furness R.W. 1998. Which components of diet quality affect retention time of digesta in Seabirds? Func. Ecol. 12: 929-939.

IUPS Thermal Commision 1987. Glossary of terms for thermal physiology. Pflügers Arch. 410: 567-587.

Konarzewski M. & Diamond J.1994. Peak sustained metabolic rate and its individual variation in cold-stressed mice. Physiol. Zool. 67: 1186-1212.

Konarzewski M. & Diamond J. 1995. Evolution of basal metabolic rate and organ masses in laboratory mice. Evolution 49: 1239-1248

Krebs H.A. 1950. Body size and tissue respiration. Biochim. Biophys. Acta. 4:249-269.

Langseth I., Moe B., Fyhn M., Gabrielsen G.W. & Bech C. 2000. Flexibility of Basal Metabolic Rate in Arctic breeding Kittiwakes (*Rissa tridactyla*). In: Heldmaier G. & Klingenspor M. (eds) Life in the Cold, 471-477. Springer-Verlag, Heidelberg and New York.

Lima S.L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. Ecology. 67(2): 377-385.

McLean J.A. & Speakman J.R. 2000. Effects of Body Mass and Reproduction on the Basal Metabolic Rate of Brown Long-Eared Bats (*Plecotus auritus*). Physiol. Biochem. Zool. 73: 112-121.

Meerlo P., Bolle L., Visser G.H., Masman D. & Daan S.1997. Basal metabolic rate in relation to body composition and daily energy expenditure in the field vole, *Microtus agrestis*. Physiol. Zool. 70: 362-369.

Mehlum F. 1990. Birds and Mammals of Svalbard. Norsk Polarinstitutt, Oslo.

Mehlum F. & Fjeld P.E. 1987. Catalogue of seabird colonies in Svalbard. Norsk Polarinstitutt Rapportserie. 35: 90.

Moe B., Langseth I., Fyhn M., Gabrielsen G.W. & Bech C. 2001. Changes in body condition in breeding Kittiwakes (Rissa tridactyla). J. Avian Biol. (submitted).

Monaghan P., Uttley J.D., Burns M.D., Thaine C. & Blackwood J. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic Terns (*Sterna paradisaea*). J. Anim. Ecol. 58: 261-274.

Moreno J. 1989. Strategies of mass change in breeding birds. Biol. J. Linn. Soc. 37: 297-310.

Niimi A.J. 1978. Lag adjustment between estimated and actual physiological responses conducted in flow-through systems. J. Fish. Res. Bd. Can. 35: 1265-1269.

Noreberg R.Å. 1981. Temporary weight decrease in breeding birds may result in more fledged young. Am. Nat. 118: 838-850.

Nur N. 1984. The consequences of brood size for breeding Blue Tits. I. Adult survival, weight change and the cost of reproduction. J. Anim. Ecol. 53: 479-496.

Pichl H. 1997. The life-history trade-offs constraining clutch size in the Kittiwake. Cand. Scient thesis. Inst. Biol. Univ. Tromsø.

Piersma T. & Lindstrøm Å. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. Trends Ecol. Evol. 12: 134-138.

Piersma T., Bruinzeel L., Drent R., Kersten M.. Van der Meer J. & Wiersma P. 1996. Variability in basal metabolic rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. Physiol. Zool. 69: 191-217.

Ricklefs R.E. 1974. Energetics of reproduction in birds. In: Paynter R.A. (ed) Avian energetics, 152-292. Nuttal Ornithological Club, Cambridge.

Ricklefs R.E. & Hussell D.J.T. 1984. Changes in adult mass associated with the nestling cycle in the European Starling. Ornis. Scand. 15: 155-161.

Weber P.C. & Piersma T. 1996. Basal metabolic rate and the mass of tissues differing in metabolic scope: migration-related covariation between individual knots *Calidris canutus*. J. Avian. Biol. 27: 215-224.

Wendeln H. & Becker P.H. 1996. Body mass change in breeding Common Terns (*Sterna hirundo*). Bird Study 43: 85-95.

Wikelski M., Lynn S., Breuner C., Wingfield J.C. & Kenagy G.J. 1999. Energy metabolism, testosterone and corticosterone in white-crowned sparrows. J. Comp. Physiol. A. 185: 463-470.

Withers P.C. 1977. Measurements of $V\mathrm{O}_2$, $V\mathrm{CO}_2$ and evaporative water loss with a flow-through mask. J. Appl. Physiol. 42: 120-123.

THE INFLUENCE OF FLEDGLING NUMBER AND HATCHING ORDER ON RETURN RATES OF COMMON TERNS *STERNA HIRUNDO*

T. DITTMANN, J.-D. LUDWIGS & P. H. BECKER

Dittmann, T., Ludwigs J.-D. & Becker P.H. 2001. The influence of fledgling number and hatching order on return rates of Common Terns *Sterna hirundo*. Atlantic Seabirds 3(4): 179-186. *Natal characteristics of Common Terns* Sterna hirundo *that returned as prospecting pre-breeders to their home colony in a coastal brackish water lake in North-western Germany were compared with those that did not return. No influence of either fledgling number or hatching order on return rates (mean 41%) could be found. These findings indicate that during the stage of post-fledging care, individual parental quality becomes less important for the survival of the offspring.*

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INTRODUCTION

In semi-altricial seabirds, including the Common Tern *Sterna hirundo*, both hatching order and number of siblings within a brood have proved to be important factors affecting chick survival until fledging (e.g. Parsons *et al.* 1976; Spear & Nur 1994; Nisbet *et al.* 1995; Royle & Hamer 1998). In contrast, knowledge about the influence of both factors on post-fledging survival is limited, mainly due to methodological problems. Young Common Terns depend entirely on being fed by their parents until fledging and are still provided with food for some weeks thereafter, and possibly also during autumn migration as in larger tern species (Burger 1980). Hence, siblings within a brood may compete for food even for some time after fledging. Nisbet (1996) investigated the influence of hatching order on post-fledging survival of Common Terns, based on a small sample size, and found no effect. Most surviving Common Terns explore their home colony site as subadults when 2 years old, arriving several weeks later than breeding birds (Becker *et al.* 2000) and breed for the first time at an age of 3 years (Wendeln & Becker 1998; Becker *et al.* 2000). Return rates to their natal colony site of Common Terns in Wilhelmshaven, Germany, vary between 22% and 46% among different year classes (Wendeln & Becker 1998). The aim of the present study was to investigate effects of both hatching order and number of siblings fledged on individual survival from fledging until return to the natal colony using a large sample.

Common Tern feeding young, Banter See study colony, 13 July 2000 *Adulte Visdief voert jong, Banter See onderzoekskolonie, 13 juli 2000* (J-D. Ludwigs)

STUDY AREA AND METHODS

In 1992-1999 studies were conducted in a Common Tern colony situated in the *Banter See*, a brackish water lake on the German Wadden Sea coast in the harbour area of Wilhelmshaven, Lower Saxony (53°27'N, 08°07'E). The colony site consisted of six rectangular concrete islands each measuring 10.7 x 4.7 m. All of these islands were surrounded by a low wall (60 cm high) with 42 elevated places for landing and resting (resting platforms, Becker 1996; Becker & Wendeln 1997). During the study period the colony increased from 90 to 250 breeding pairs.

All nests were visited at intervals of 2-3 days to record the fate of eggs and chicks. After hatching, chicks were ringed with steel rings from the ringing centre "Vogelwarte Helgoland". If two or three siblings were found in a nest on the same day the hatching order was determined from the size of the remains of the yolk sac on the chick's belly, which becomes smaller with age (Wagener 1998). In this paper the hatching order is denoted by A (first), B (second) and C (third chick). Chicks were considered to have fledged if they were encountered alive for the last time at least 18 days old and not found dead later in the same season. Mean fledging age was 26 days.

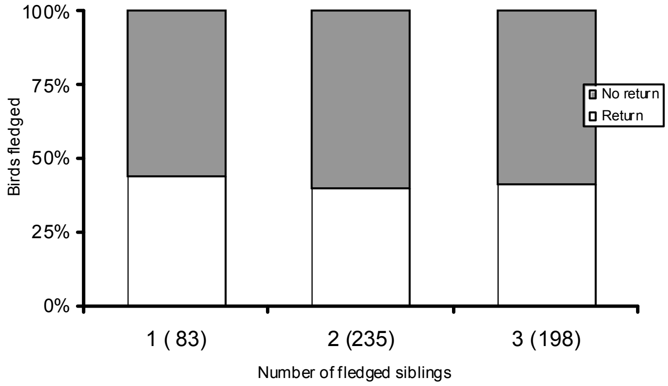

Figure 1. Proportion of fledged Common Terns with known number of fledglings per brood that were resighted in the natal colony (absolute numbers of returned and non-returned birds in brackets).

Figuur 1. Percentage uitgevlogen jonge Visdieven met bekend aantal uitgevlogen nestgenootjes dat na verloop van tijd terugkeerde als hoopvolle broedvogel in de kolonie (totale aantallen teruggekeerde en niet-teruggekeerde aantallen vogels).

From 1992 onwards, all chicks were marked with subcutaneously injected passive transponders before fledging (Becker & Wendeln 1997). These transponders sent an individual alphanumeric code when activated by special antennae placed on resting platforms (see above) around the colony, thereby allowing identification of birds for their whole life without retrapping (Becker & Wendeln 1997). The antennae were active continuously throughout the seasons. All antennae (1993-94: 12; 1995-96: 22; 1997-98: 30; 1999-2000: 35) were distributed equally among the platforms and their positions were changed regularly at intervals of 2-3 days in order to record the presence of marked birds at all platforms. Using these methods we recorded with a high probability all marked birds that returned to their home colony. Only chicks from broods in which three chicks hatched were used for the analysis, so that the number of chicks raised to fledging would serve as an index of parental quality. In this study, 215 fledglings from the years 1992-1997 with known information about hatching position or the number of fledged siblings and re-encountered up to the end of the breeding season in 2000 were compared with 307 fledglings that did not return to date. To test for an influence of either hatching order or of number of fledged siblings on return rates we performed two-tailed Chi-square tests. For testing for combined effects on return rates of both hatching order and number

Table 1. Proportion of fledged Common Terns of known hatching order in broods of different sizes that returned to the natal colony.

Tabel 1. Percentage uitgevlogen jonge Visdieven met bekende volgorde van uitkomst in broedsels van verschillende grootte dat na verloop van tijd terugkeerde als hoopvolle broedvogel in de kolonie.

Fledglings	Hatching order						Total	
	A		B		C			
	%	*n*	%	*n*	%	*n*	%	*n*
one	48.8	20	48.0	12	100	1	49.2	33
two	41.5	37	41.8	33	47.6	10	44.1	80
three	44.2	23	43.1	22	42.1	24	43.1	69
Total	44.0	80	46.2	67	44.3	35	43.8	182

of fledged siblings with and without respect to the study year we used a multiple logistic regression because outcomes were binary (the birds either returned or not) and binomially distributed. All statistics were performed using SPSS 8.0 (level of significance $P \leq 0.05$). All fieldwork was conducted under licences of the Niedersächsisches Landesverwaltungsamt, Hannover, and of the Bezirksregierung Weser-Ems, Oldenburg (Nationalparkverwaltung; Tierschutzangelegenheiten).

RESULTS

From 516 chicks with known fledgling brood size that fledged between 1992 and 1997, 212 (41%) were recorded again at the colony up to 2000 (Fig. 1). Return rates of young birds were independent of the number of siblings that had survived to fledging in the same brood ($\chi^2_2 = 0.910$, n.s.). From 442 chicks with known hatching order that fledged between 1992 and 1997, 185 (42%) birds were re-encountered in their natal colony (Fig. 2). No effect of hatching order on post-fledging survival could be found ($\chi^2_2 = 0.032$, n.s.).

For 416 birds fledged between 1992 and 1997 both the number of fledged siblings and hatching order were known. 182 (44%) of them returned to their home colony as subadults. Return rates varied only slightly between the chick groups (Table 1): lowest return rate was found in A-chicks of broods with two fledglings (41.5%), highest rate (48.8%) in A-chicks fledged without siblings. The only C-chick fledged alone returned to the colony. In total, in a logistic regression analysis, whether or not including year class as a factor, no combined effects of both number of fledged siblings and hatching order on return rates were detectable (Table 2).

*Table 2: Test for combined effects of hatching order HO, number of fledged siblings NFS and study year SY (Logistic regression models, likelihood ratio statistic LRS (-2 log likelihood) (*n *= 416).*

Tabel 2. Test voor de gecombineerde effecten van uitkomstvolgorde (HO), het aantal uitgevlogen nestgenootjes (NFS) en het jaar van onderzoek (SY).

Term	Adjusted for:	LRS	df	*P* value	Regression coefficient	SE
NFS	HO	570.06	1	0.723	-0.0014	0.004
NFS	SY	698.78	1	0.552	-0.0003	0.0013
HO	SY	578.59	1	0.952	0.0000	0.0001

DISCUSSION

In the Common Terns studied, neither hatching order nor number of fledglings per brood influenced return rates of prospecting individuals. This is in accordance with the findings of Nisbet (1996) whose study was based on a much smaller number of birds that returned. In this study we also found no evidence that potential effects of hatching order and sibling number on fledgling survival might mask each other. But why do both natal characteristics lose their importance after fledging?

In the pre-fledging stage, many studies document the importance for survival of intrinsic factors such as body weight at hatching and of extrinsic factors such as hatching order or brood size (Parsons 1970; Becker & Finck 1985; Rhymer 1988; Sydeman & Emslie 1992; Nisbet *et al.* 1995). In several seabird species last-hatched chicks suffer higher mortality (e. g. Parsons 1970; Becker & Finck 1985; Sydeman & Emslie 1992). However, the importance of these factors for pre-fledging survival depends strongly on parental quality, as shown by studies of Bolton (1991), Nisbet *et al.* (1998) and Wendeln & Becker (1999). During the post-fledging stage, some studies show effects of hatching position or brood size on survival (Nisbet & Drury 1972; Coulson & Porter 1985; Viksne & Janaus 1993). Other investigations, including this study, found that these factors are no longer important after fledging (Spear & Nur 1994; Nisbet 1996).

In species whose young depend on being fed by the parents for a long time after fledging, as in the Common Tern (Burger 1980), parental quality is expected to be of particular importance also for post-fledging survival. At our study site, fledglings are fed by their parents up to an age of at least 64 days, that is about six weeks after fledging (Kühn & Becker, unpubl. data). Watson & Hatch's (1999) data support the idea that parental care in the Roseate Tern *Sterna dougalli* may extend through the migration period as documented for the

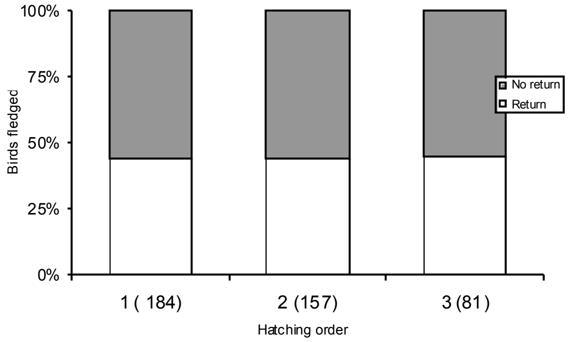

Figure 2. Proportion of fledged Common Terns with known hatching order that were resighted in the natal colony (absolute numbers of returned and non-returned birds in brackets).

Figuur 2. Percentage uitgevlogen jonge Visdieven met bekende volgorde van uitkomst dat na verloop van tijd terugkeerde als hoopvolle broedvogel in de kolonie (totale aantallen teruggekeerde en niet-teruggekeerde aantallen vogels).

large tern species (Burger 1980). In the Common Terns studied, a higher number of fledged siblings did not result in increased mortality after fledging despite the possibility that competition for food might continue into the post-fledging period. Viksne & Janaus (1993) even found greater survival of fledglings from large broods of Black-headed Gulls. Similarly, after fledging, hatching position of the Common Terns studied had no effect on survival. This is in contrast to the findings of Coulson & Porter (1985) in the Black-legged Kittiwake *Rissa tridactyla,* and may indicate that effects of hatching position on Common Tern chick survival that are known to occur in the first days of life have been balanced already at the age of fledging by other factors.

As in other seabird species, recent investigations have shown that Common Tern adults differ greatly in quality, with consequences for their reproductive performance (Wendeln & Becker 1999). Many authors studying long-lived seabirds report that older birds have a higher breeding success (Coulson & Thomas 1985; Ollason & Dunnet 1988; Clutton-Brock 1988; Forslund & Pärt 1995). In the Common Tern, reproductive success seems to increase with age only during the early years of reproduction (Nisbet *et al.* 1984). Besides age, individual body condition may reflect bird quality, and the breeding success of Common Terns strongly depends on the parents' body masses, a constant individual trait with low intra-individual variation between years and mostly independent of age (Wendeln & Becker 1999; Becker *et al.* 2000).

Consequently, hatching order and sibling number may be important factors during the first days in the life of a chick. But the number of chicks that can be reared successfully under the prevailing environmental conditions mainly depends on the quality of the parents. At fledging, possible effects of hatching order have been balanced by parental quality, and brood size has been adapted to the parental capacity for rearing chicks (see also Becker *et al.* 2000). The lack of influence of both hatching order and sibling number on post-fledging survival of Common Terns indicates that the quality of a pair that is reflected already in the number of fledglings, loses much of its importance after their young fledge. Probably post-fledging care is much less demanding than pre-fledging care because the fledglings accompany their parents to the feeding grounds within a few days after fledging (Nisbet 1976; own unpubl. data). Furthermore, parents are able to exploit additional feeding resources that are situated beyond the feeding range during the pre-fledging stage. Both factors might minimise the competition between siblings.

ACKNOWLEDGEMENTS

We are indebted to M. Wagener and H. Wendeln for their help in the field as well as with data management. Many thanks to many other voluntary fieldworkers. We thank H. Wendeln and the reviewers I.C.T. Nisbet and N. Ratcliffe for commenting on the manuscript. This study was supported by the Deutsche Forschungsgemeinschaft (Be 916/3 and 916/5).

DE INVLOED VAN DE VOLGORDE VAN UITKOMEN EN UITVLIEGEN OP HET PERCENTAGE TERUGKERENDE JONGEN BIJ DE VISDIEF *STERNA HIRUNDO*

Bij dit onderzoek werden uitgevlogen Visdieven die als hoopvolle broedvogels terugkeerden op de onderzoekskolonie in de Banter See (havengebied Wilhelmshaven, Duitsland), vergeleken met vogels die niet terugkeerden. Bij ieder legsel werden de jongen gemerkt en werd bepaald in welke volgorde de eieren uitkwamen. Vervolgens werd gekeken in welke volgorde de jongen de kolonie als vliegvlugge juvenielen verlieten. Er bleek geen enkel verband te bestaan tussen de volgorde van uitkomen en uitvliegen en de kans dat een dergelijk jong in de kolonie werd teruggezien. De gegevens suggereren dat gedurende de jongenzorg ná het uitvliegen van de jongen (rond de kolonie en onderweg naar de overwinteringsgebieden) de individuele verschillen in kwaliteit van de ouders een ondergeschikte rol spelen op de overlevingskansen van het jong.

REFERENCES

Becker P.H. 1996. Flußseeschwalben (*Sterna hirundo*) in Wilhelmshaven. Oldenb. Jahrbuch 96: 263-296.

Becker P.H. & Finck P. 1985. Witterung und Ernährungssituation als entscheidende Faktoren des Bruterfolgs der Flußseeschwalbe (*Sterna hirundo*). J. Ornithol. 126: 393-404.

Becker P.H. & Wendeln H. 1997. A new application for transponders in population ecology of the Common Tern. Condor 99: 534-538.

Becker P.H., Wendeln H.& González-Solís J. 2000. Population dynamics, recruitment, individual quality and reproductive strategies in Common Terns marked with transponders. Ardea: 89: 241-252.

Bolton M. 1991. Determinants of chick survival in the Lesser Black-backed Gull: relative contributions of egg size and parental quality. J. Anim. Ecol. 60: 949-960

Burger J. 1980. The transition to independence and post-fledging parental care in seabirds. In: Burger J., Olla B.L. & Winn H.E. (eds) Behaviour of marine animals, 4; marine birds: 367-447. Plenum Press, New York.

Clutton-Brock T.H. 1988. Reproductive success. University of Chicago Press, Chicago.

Coulson J.C. & Thomas C.1985. Differences in the breeding performance of individual Kittiwake Gulls, *Rissa tridactyla*. In: Sibly R.M. & Smith R.H. (eds.): Behavioural Ecology: 489-503. Blackwell Science, Oxford.

Coulson J.C. & Porter J.M. 1985. Reproductive success of the Kittiwake *Rissa tridactyla*: The roles of clutch size, chick growth rates and parental quality. Ibis 140: 315-322.

Forslund P. & Pärt T.1995. Age and reproduction in birds–hypotheses and tests. TREE 10: 374-378.

Nisbet I.C.T. 1976. Early stages in post-fledging dispersal of Common Terns. Bird-Banding 47: 163-164.

Nisbet I.C.T. 1996. Post-fledging survival in Common Terns in relation to brood order, hatching date and parental age. Col. Waterb. 19: 253-255.

Nisbet I.C.T., Winchell J.M. & Heise A.E. 1984. Influence of age on the breeding biology of Common Terns. Col. Waterb. 7: 117-126.

Nisbet I.C.T., Spendelow J.A. & Hatfield J.S. 1995. Variation in growth of Roseate Tern chicks. Condor 97: 335-344.

Nisbet I.C.T., Spendelow J.A., Hatfield J.S., Zingo J.M. & Gough G.A. 1998: Variation in growth of Roseate Tern chicks: II. Early growth as an index of parental quality. Condor 100: 305-315.

Nisbet I.C.T. & Drury W.H. 1972. Post-fledging survival in Herring Gulls in relation to brood-size and date of hatching. Bird-Banding 43: 161-172.

Ollason J.C. & Dunnet G.M. 1988. Variation in breeding success in Fulmars. In: Clutton-Brock T.H. (ed.) Reproductive success: Studies of individual variation in contrasting breeding systems: 263-278. Univ. Chicago Press, Chicago.

Parsons J. 1970. Relationship between egg size and post-hatching mortality in the Herring Gull (*Larus argentatus*). Nature 228: 1221-1222.

Parsons J., Chabrzyk G. & Duncan N. 1976. Effects of hatching date on post-fledging survival in Herring Gulls. J. Anim. Ecol. 45: 667-675.

Rhymer J.M. 1988. The effect of egg size variability on thermoregulation of Mallard (*Anas platyrhynchos*) offspring and its implications for survival. Oecologia 75: 20-24.

Royle N.J. & Hamer K.C.1998. Hatching asynchrony and sibling size hierarchies in gulls: effects on parental investment decisions, brood reduction and reproductive success. J. Avian Biol. 29: 266-272.

Spear L. & Nur N. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. J. Anim. Ecol. 63: 283-298.

Sydeman W.J. & Emslie S.D. 1992. Effects of parental age on hatching asynchrony, egg size and third-chick disadvantage in Western Gulls. Auk 109: 242-248.

Viksne J. & Janaus M. 1993. Post-fledging survival of the Black-headed Gull (*Larus ridibundus*) depending on hatching parameters. Ring 15: 387-389.

Wagener M. 1998. Praktische Hinweise für brutbiologische Untersuchungen an der Flußseeschwalbe *(Sterna hirundo)*. Vogelwelt 119: 279-286.

Watson M.J. & Hatch J.J. 1999. Difference in foraging performance between juvenile and adult Roseate Terns at a pre-migratory staging area. Waterbirds 22: 463-465.

Wendeln H. & Becker P.H. 1998. Populationsbiologische Untersuchungen an einer Kolonie der Flußseeschwalbe *Sterna hirundo*. Vogelwelt 119: 209-213.

Wendeln H. & Becker P.H. 1999. Effects of parental quality and effort on the reproduction of Common Terns. J. Anim. Ecol. 68: 205-214.

THE DISTRIBUTION AND BREEDING SUCCESS OF SEABIRDS ON AND AROUND ASCENSION IN THE TROPICAL ATLANTIC OCEAN

W.R.P. BOURNE[1] & K.E.L. SIMMONS[2]

Bourne W.R.P. & Simmons K.E.L. 2001. The distribution and breeding success of seabirds on and around Ascension in the tropical Atlantic Ocean. Atlantic Seabirds 3(4): 187-202. *Ascension was once one of the greatest seabird colonies in the world, comparable to the largest in the Pacific and Indian Oceans, the only one in the apparently barren centre of the tropical South Atlantic. The birds have been reduced by introduced rats and cats over the last three centuries, but early accounts, guano and bones suggest there were once more, most breeding in the north of the island. Observations from the shore and at sea indicate that while some seabirds may feed offshore and in an area of marine turbulence in the lee of the island to the west, many fly north towards the Equatorial Counter-current, where there are many more birds and cetaceans than to the south. Periodically there is increased rainfall which may be accompanied by seabird breeding failures, as in 1876, 1924, 1958-59, 1963, 1991-92 and 1997, possibly associated with fluctuations in the counter-current, similar to, but not always simultaneous with, El Niño-Southern Oscillation (ENSO) events elsewhere. There is a need for world-wide monitoring and attention to the implications of these fluctuations.*

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"We steered away SSE and SSE half East until in the Lat. of 7 deg. 50. min. we met with many Ripplings in the Sea like a Tide or strong Current, which setting against the wind caused such a rippling. We continued to meet these Currents from that Lat. until we came into the Lat. of 3 deg. 22 N. when they ceased. During this time we saw some Boneta's and Sharks; catching one of these."

William Dampier (1703)

INTRODUCTION

Ascension is a recent volcanic island some 10 km in diameter lying at 07°57'S 14°22'W, nearly 500 nautical miles south of the Equator in the central tropical Atlantic (Figs. 1, 2). Its climate is usually dry, with local orographic condensation where the prevailing SE trade-winds strike 500 m Green Mountain in the east, and with torrential rain mainly in March and April at irregular intervals of several years. It originally had a poor flora and terrestrial fauna, now reinforced by introductions, but when first discovered in 1501 many breeding seabirds

Table 1. Seabirds breeding on Ascension. Population size given in individuals (Moreau 1962-63 and Ashmole et al. *1994, corrected from later observations).*

Tabel 1. Broedvogels van Ascension (individuen; Moreau 1962-63, Ashmole et al. *1994, gecorrigeerd voor latere waarnemingen).*

Species	Subfossil bones	Recently
Audubon's Shearwater *Puffinus lherminieri*	*	(1?)
Madeiran Storm-petrel *Oceanodroma castro*	*	3000
Red-billed Tropicbird *Phaethon aethereus*	*	1100
Yellow-billed Tropicbird *Phaethon lepturus*	*	2200
Masked Booby *Sula dactylatra*	**	9000
Brown Booby *Sula leucogaster*	**	2000
Red-footed Booby *Sula sula*	**	30
Ascension Frigatebird *Fregata aquila*	**	<10 000?
Sooty Tern *Sterna fuscata*	**	350 000
Brown Noddy *Anous stolidus*	*	1000
Black Noddy *Anous minutus*		20 000
White Tern *Gygis alba*	*	5300

*- some bones, **- many bones found.

occurred (Stonehouse 1962; Packer 1968; Ashmole *et al.* 1994; Ashmole & Ashmole 2000).

By the time of the British Ornithologists' Union's Centenary Expedition to Ascension in 1957-1959 (Stonehouse 1960; Moreau 1962-63), seabirds were mostly confined to outlying stacks except for a vast colony of Sooty Terns *Sterna fuscata* breeding in the south every ten lunar months. Guano and subfossil bird bones are still widely distributed on the low ground, especially in the north, however. This showed that the original species were probably much the same as today (Table 1), with more Red-footed Boobies *Sula sula* and Audubon's Shearwaters *Puffinus lherminieri*, and an extinct endemic night-heron and rail, which may have exploited the seabird colonies (Ashmole 1963a; Olson 1977; Bourne *et al.* in prep).

During 1962-1997 Simmons made a series of visits to the island, latterly with R.J. Prytherch, largely to study the boobies, but also collecting various other information and bones (Simmons 1967a,b, 1970, 1990; Simmons & Prytherch 1994, 1997, 1998). Between 1982-1990 Bourne, W.F. Curtis and other members of the Royal Naval Bird-watching Society (RNBWS) made many voyages from Britain past Ascension to the Falklands, recording the birds seen at sea, and sometimes landing. Since 1987 there have also been visits by the Royal Air Force Ornithological Society (RAFOS) in February 1987 and November 1988 (Blair 1989; Osborn 1994), and Army Ornithological Society (AOS) with members of the other societies in March 1990, June-July 1992, and

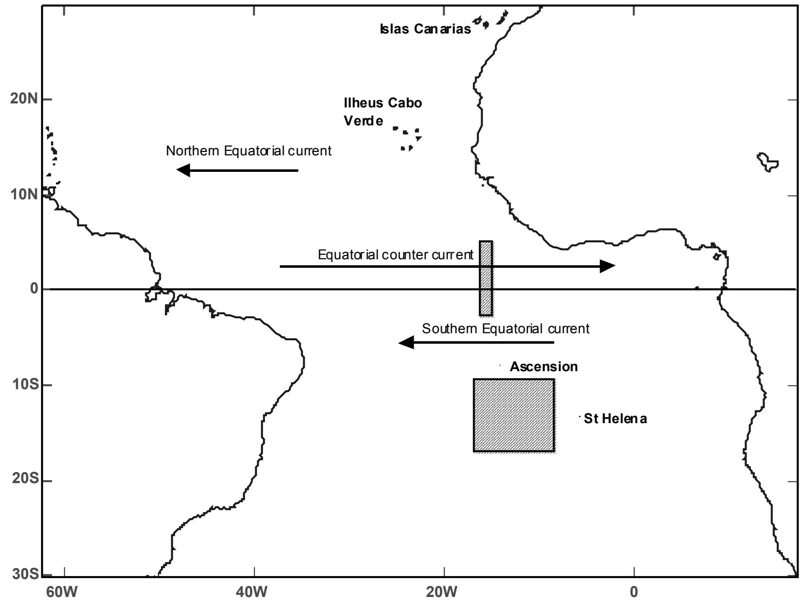

Figure 1. Location of Ascension and (shaded) areas of observation in Table 2.

Figuur 1. Ligging van Ascension en (gearceerd) de locaties waar de in tabel 2 weergegeven waarnemingen werden verricht.

April 1994 (Nash *et al.* 1991; 1992, Hughes *et al.* 1994; Dickey *et al.* 1997). These results are summarised by Bourne & Simmons (1998, Table 1), and we now draw some general conclusions about the seabirds on Ascension.

THE DISTRIBUTION OF SEABIRDS ASHORE

It remains debatable how many seabirds formerly bred on Ascension, which lies far from the continental shelves in an area of impoverished tropical surface water where birds are normally only seen at intervals of hours or days (Table 2 part 2). Large quantities of bird remains and guano are still found in areas where the birds must have gone over a century ago, however, with more in the north of the island (Fig. 2). Since such remains are very durable in such a dry climate it is possible that they were deposited over a long period. Populations no larger than the present ones may have moved around, perhaps to avoid the accumulation of parasites, as with Sooty Terns on Bird Island in the Seychelles (Feare 1976), since a similar tick *Ornithodoros denmarki* was also found in the Ascension Wideawake Fairs (colonies) in 1990.

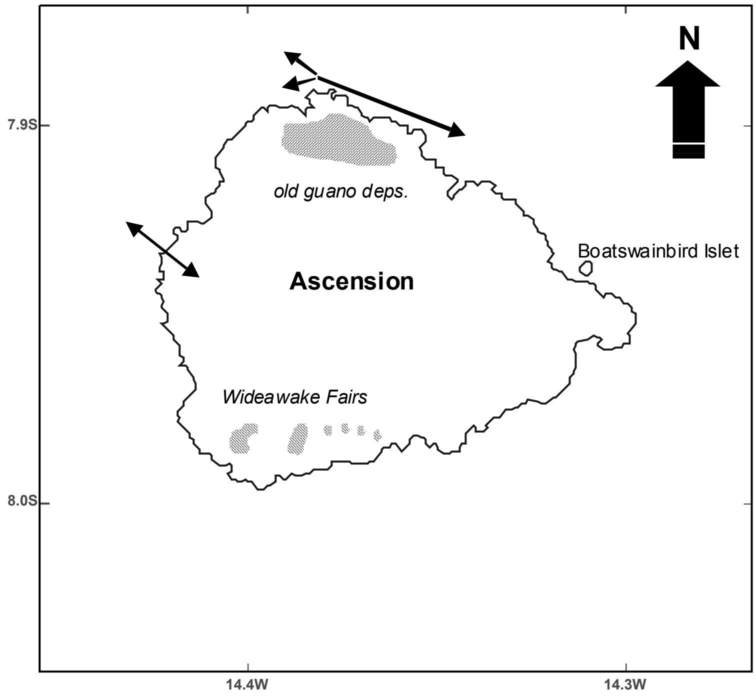

Figure 2. Ascension Island, location of greatest old guano deposits and modern Wideawake Fairs, and most important directions of movement of the birds.

Figuur 2. Ascension, locatie van oude vogelmestafzettingen en moderne Wideawake Fairs en de belangrijkste vliegrichtingen van broedvogels.

The possibility that seabirds were once more numerous is confirmed by a report by Van Linschoten in 1589. When they called at Ascension "birds of the bignesse of young geese... came by thousands flying about our ships, crying and making great noyse, and ran up and down in the ship, some leaping and sitting on our shoulders and armes, not once fearing us, so that we took many of them and rung their neckes, but they are not good to eate, because they taste morish (fishy)" (Tiede 1885), in a way now unknown anywhere. The large seabird seen most often by the RNBWS on ships in the tropics is the Red-footed Booby, which normally nests on trees and is now rare at Ascension. Its fossil remains are common there, however, and the lava-flows are stained with old guano in patterns suggesting it nested on them instead.

Table 2. Birds and cetaceans seen in ten-minute periods during ten voyages by Bourne, two by W.F. Curtis, two by B.W. Rowlands, and one by Cadée (1981), 1979-1990.

Tabel 2. Vogels en walvisachtigen in tien-minuten perioden tijdens 10 reizen van Bourne, twee van W.F. Curtis, twee van B.W. Rowlands en één door Cadée (1981), 1979-1990.

Birds and cetaceans seen per hour within 5° of the Equator between 15-17°W

Month	Aug	Oct	Nov	Jan	Feb	Apr	May	Total
Hours	2.8	12.7	4.7	4.7	22.7	5.8	12.8	66.2
Bulwer's Petrel *Bulweria bulwerii*						0.2	0.4	6
Cory's Shearwater *Calonectris diomedea*			8.1	3.1	7.2	3.4		229
Great Shearwater *Puffinus gravis*							2.7	26
Large shearwaters *Calonectris/ Puffinus*		0.2					1.0	12
Wilson's Storm-petrel *Oceanites oceanicus*			0.2					1
Leach's Storm-petrel *Oceanodr. leucorhoa*			3.6	5.1	12.0	0.2		313
Madeiran Storm-petrel *Oceanodroma castro*?	0.7		0.6	3.2	0.3	1.0	1.3	50
Storm-petrel *Hydrobatidae* sp		3.6		1.3	0.2	0.2		58
Masked Booby *Sula dactylatra*					0.04		0.5	8
Large skua *Catharacta* sp				0.4				2
Small skua *Stercorarius* sp			3.4		0.7	1.9		43
Sooty Tern *Sterna fuscata*	0.4			5.1	10.0	42.9	0.1	495
Arctic Tern *Sterna paradisaea*						3.6		21
Terns *Sterna* sp		6.1				10.2		138
Noddies *Anous* sp					0.4	8.6		54
Large whale sp				1.7	0.4			16
Pilot whale sp				6.4	0.04			31
Dolphin sp					>0.4	8.6		>60
Total	1.1	9.9	16.1	22.7	31.6	80.8	10.7	1563

[Table 2 continued]

Birds and cetaceans seen per hour between 10-20°S and 8-21°W

Month Hours	Aug 3	Sep 5	Nov 4	Jan 5	Feb 11	Apr 2.8	May 11.5	Total 42.3
Bulwer's Petrel *Bulweria bulwerii*			0.25		0.09			2
Great Shearwater *Puffinus gravis*							0.09	1
Madeiran Storm-petrel *Oceanodroma castro*?					0.09			1
Black-bellied Storm-petrel *Fregetta tropica*							0.09	1
Yellow-billed Tropicbird *Phaethon lepturus*			0.25					1
Large whale sp		0.40						2
Total	0	0.40	0.50	0	0.18	0	0.17	8

Some identifications may be uncertain; thus Wilson's and Madeiran Storm-petrels may have been identified as Leach's, which certainly come on board ships much more often (Bourne 1992). It is also uncertain if the few large skuas *catharacta* sp. were *C. skua*, *C. antarctica* and its allies, or *C. maccormicki*, but all three smaller skuas *Stercorarius* sp. have been reported, *S. parasiticus* in November and February, *S. pomarinus* in February, and *S. longicaudus* in April. Arctic and possibly other terns also appear to stage in this area on migration. The cetaceans included Sperm Whales *Physeter catodon* in January, a Sei Whale *Balaenoptera borealis* and other unidentified rorquals in February, a Bryde's Whale *B.edeni* in October, and unidentified smaller species, none seen around Ascension.

THE DISTRIBUTION OF THE BIRDS AT SEA

The long incubation shifts found for several Ascension seabirds (Moreau 1962-63) imply that they travel far to feed. Stonehouse (1962) suggested they may exploit enriched water to lee of the south-west African upwelling. This might be reinforced by the passage of mesoscale eddies of upwelling water raising nutrients and food from the thermocline along the northern border of the Benguela Current where it passes west out to sea around 20°S to become the South Equatorial Current (Diester-Haass 1985), in the way found along the Gulf Stream (Haney 1986). However, Rowlands (1992) and Barritt (1992) among others have failed to find many birds here.

Oceanographic investigations, the presence of more bones and guano in the north, and the main direction of flight of the birds (Fig. 2) and their density at sea (Table 2) indicate that most birds may feed instead to the north of Ascension. Bourne (1955) has postulated that the Atlantic equatorial current system (Fig. 1), apparently first described by Dampier (1703, quoted above) may provide food for seabirds here. Basically the easterly trade-winds drift surface water to the west in the tropical oceans, and compensatory counter-currents then return east, often below the westward surface drift. The change in the direction of Coriolis' force also leads to a divergence in westbound currents near the equator, causing local turbulence and upwelling. This leads to increased biological productivity, attractive to tuna which drive their prey to the sea surface where it becomes available to birds (Khanaychenko 1965; Neumann 1965; Longhurst & Pauly 1987; Scullion 1990 in Ashmole *et al.* 1994).

The RNBWS have reported flocks of seabirds occur here (annual reports in *Sea Swallow*), but there have been few detailed accounts, possibly because most activity occurs over a narrow, fluctuating belt which is liable to be crossed in a few minutes, half the time by night, when the birds can only be heard calling in the darkness. Where counts were made, the vicinity of the equator was frequented by over a hundred times more birds than a comparable area to the south (Table 2), and Jesperson (1930) reported equally few birds to the north.

In general, Ascension seabirds go out to sea in the morning, and few can be seen feeding from the shore except when there is an influx of pelagic prey fish. Flocks of hundreds of Ascension Frigatebirds *Fregata aquila*, Masked and Brown Boobies *Sula dactylatra* and *S. leucogaster*, Sooty Terns, noddies *Anous* sp. and White Terns *Gygis alba* feed in declining numbers for at least a hundred miles out to sea during the day. When a flock formed the first birds to appear were adult Ascension Frigates which came down out of the sky, after which Sooty Terns, Black Noddies *Anous minutus* and Masked Boobies, with a few Brown Boobies and small skuas *Stercorarius* sp. joined them over the sea. Although the skuas often chased the other birds, the Ascension Frigates did not hover over the rest and parasitise them as Magnificent Frigatebirds *Fregata magnificens* do around the West Indies, but led the feeding frenzy, though they rob other birds at other times.

These fish shoals might be feeding in eddies passing along the South Equatorial Current as already mentioned. Alternatively, when naval exercises were carried out west of Ascension on 11 Feb 1985 most birds were seen where the sea surface temperature fell from the usual 27.8° to 26.8°C eight miles offshore, implying turbulence and upwelling to the lee of the island. A thousand Black Noddies with fewer Brown Noddies *Anous stolidus*, Brown Boobies and an immature Red-footed Booby occurred here again on l6 April 1986, when although some breeding Sooty Terns dispersed in all directions, most went NW. In 1976-1977, 1993 and 1996-1997 Simmons and Robin Prytherch also saw many birds, mainly boobies and Black Noddies, return from the NW along the north coast of Ascension in the evening to roost in the vicinity of Boatswainbird

Islet (Simmons 1990; Simmons & Prytherch 1994, 1997), as also reported by Blair (1989) and Hughes *et al.* (1994). The main flight-line of Sooty Terns returning to the south of the island is also from the north-west (Simmons & Prytherch 1997; Bourne pers. obs.), so most seabirds may feed in this direction.

Further out to sea the SE trade-wind usually extends north across the equator in the northern spring and summer, doubtless drifting the birds west, which may explain why more were seen returning from the north-west at dusk than departing in that direction in the morning. While some birds were seen along the equator at this season, the numbers were higher, with feeding flocks of many Sooty Terns and fewer shearwaters, where the equatorial counter-current is marked on the chart far to the west off northern South America. Incidentally, although Sooty Terns are alleged to remain on the wing for months on end (Ashmole 1963b), on 22 May 1985 Bourne saw about thirty briefly fold their wings and sit together on the water in the middle of a feeding flock of about 500 birds at 08°13'N 52°20'W. In the autumn and winter the vicinity of the equator north of Ascension was more often calm ('the doldrums'), and birds were then more noticeable there, with shearwaters and even storm-petrels also often resting on the water in flocks.

Bourne also saw scattered Sooty and other terns, Cory's Shearwaters *Calonectris diomedea*, Leach's *Oceanodroma leucorhoa* and other storm-petrels, skuas, a Masked Booby, several rorquals, and many dolphins, at 04°S 15°W on 10 Feb 1985, when the sea showed the clear lanes separated by lines of ripples aligned north and south caused by internal waves where opposed currents occur at different levels (Longhurst & Pauly 1987). Presumably this patterned water surface marked the narrow eastward flow sometimes submerged below the westward drift of surface water before the trade winds reported within the westerly South Equatorial Current at this latitude by Mazeika (1968). The birds fed over the lines of ripples in the way described by Haney (1987), and settled to rest in the calm lanes in between. Their numbers reached a climax where a long drift-net, presumably set for tuna, was aligned east and west along the southern boundary of the patterned water, and declined to the south. Many birds have also been found further east along the equator where there is a fertile 'dome' in the thermocline at the end of the counter-current in the Gulf of Guinea (Mazeika 1967) during the northern winter by Cadée (1981), and in April by Lambert (1988).

The equatorial counter-current also appears to provide an important winter-quarters for Sooty Terns (Robertson 1969) and storm-petrels. In addition to numerous northern Leach's Storm-petrels *Oceanodroma leucorhoa* (Bourne 1992) the type of the Black-bellied Storm-petrel *Fregetta tropica*, thought to be 'confined to the equatorial regions, being most abundant in the vicinity of the line' (Gould 1844), but now known to breed to the south, was taken here at

06°33'N 18°06'W in July 1838, with "*Rhynchops*" (presumably Sooty Terns?) and frigates (Gould 1840). There is another old *F. t. tropica* from 00°12°S 30°W, a Tristan White-bellied Storm-petrel *F. grallaria leucogaster* from 07°05'S 03°30'W on 11 Apr 1950, and a Tristan White-faced Storm-petrel *Pelagodroma m. marina* from 05°S 4°W on 23 Apr 1957, all in moult, and an Antarctic Tern *Sterna vittata* said to come from between Ascension and St. Helena (Saunders 1876) in the (British) Natural History Museum, and two *F. g. leucogaster* from 03°02'S 03°W on 31 May 1916 at Leiden.

POTENTIAL ENSO-RELATED EVENTS

St Helena was included among the areas affected by droughts during a major El Niño-Southern Oscillation or ENSO due to global fluctuations in the atmospheric pressure as early as 1791 (Grove 1998). Similar events have been identified again in the Atlantic as well as the Pacific during more recent major ENSOs (symposium in *Nature* 322: 236-253; Longhurst & Pauly 1987; Glantz 1996; Davis 2001). These include a long series of records of fluctuations in the Humboldt Current affecting breeding seabirds at the time of the arrival of El Niño at Christmas along the west coast of South America, and more recently the Benguela Current off SW Africa and the Christmas Island which occupies a comparable position to Ascension on the north side of the equatorial current system in the central Pacific (Duffy & Schreiber1988; Schreiber & Schreiber 1989). While there are few regular records of tropical seabird breeding performance on oceanic islands elsewhere except recently for Roseate Terns showing a similar pattern in the Seychelles in the Indian Ocean (Ramos 1998), on Ascension there are also records of exceptional rainfall (Duffey 1964; Walmsley 1997), also be related to ENSOs, as follows:

1876-1877 On 5 September 1876 a local naturalist, Unwin, reported to Howard Saunders that the Sooty Terns had "remained months longer than usual, due to a very unusual downpour of rain, which flooded their breeding ground, and killed thousands of young birds. They left about May, and were back in August" (Penrose 1879). It seems debatable if the mortality was necessarily due to the downpour, which Duffey (1964) reports occurred on 26 March 1876. Gill (1878) reports the terns returned on time two breeding cycles later in October 1877. By this time an ENSO had caused droughts and famines throughout the world (Nicholls & Katz 1991; Davis 2001).

1924-1925 Three days of heavy rain were also associated with poor breeding success for the Sooty Terns in February and March 1924 (Huckle 1924; Duffey 1964), and subsequently interfered with the collection of guano in 1925-1928

(Packer 1968). There were exceptional Niño conditions in both the Humboldt and Benguela currents in 1925 (Murphy 1936: 103), and a very severe ENSO in SE Asia in 1925-1926 (Davis 2001).

1957-1959 The BOU Centenary Expedition found that first the chicks of the Masked and Brown Boobies and Black Noddies starved while the Sooty Terns were away in July-October 1958, and then when the Sooty Terns returned their young also starved in January-February 1959, though the other seabirds appeared unaffected (Moreau 1962-63; Ashmole *et al.* 1994). There was an ENSO in the Pacific, Brazil and China in 1957-1958 and disturbance of the marine biology of the tropical Atlantic in 1958-1959 (Longhurst & Pauly 1987; Davis 2001).

1963 There was 295 mm of rain on Ascension in March, when the annual mean between 1962 and 1987 was 176mm (RAF records, Simmons 1967b; Packer 1968). At the two Brown Booby colonies studied in 1962-1964 by Simmons (1967b, 1970), laying ceased from 7 February-15 July 1963, the males lost the breeding colour of their bare parts, the birds made unusually long hunting trips out to sea, nine of eleven dependent juveniles returned to be fed for much longer than usual, and the other two almost certainly died. In late February and March 1963 some Sooty Terns also deserted their eggs, and at least one fair was abandoned. The birds were about a month late in returning to breed (Simmons and John Packer, personal observations). There was an ENSO in the Pacific (Jordan 1991).

1972-1974 An ENSO in the Pacific, Brazil, Africa and Asia in 1972-1973 was also followed by 104 mm of rain in Ascension in March 1974, but there were no observations on the birds then.

1982-1984 There was a major world-wide ENSO in 1982-1983 (Davis 2001), with a massive disruption of seabird populations in the Pacific (Schreiber & Schreiber 1984), followed by a prolonged decline in Great Frigatebirds *Fregata minor* in particular during Christmas Bird Counts at Hawaii (Vandenbosch 2000). 152 mm of rain fell on Ascension in March 1984, and 339 mm in April 1985, but there were no observations on the birds. The Sooty Terns may have been away, since when Bourne passed through the island in October 1984 they had eggs and young, though Brown Boobies on the Stacks had no large chicks.

1986-1988 There was seabird mortality off SW Africa in 1985-1986 (Crawford *et al.* 1986) and a Niño in the Pacific in 1986-1987. The Sooty Terns started breeding on Ascension in December 1986 (Islander 12 December), and two

RAFOS Expeditions found them completing cycles in February and November 1987, but nothing unusual was noticed (Blair 1988; Osborn 1994) except 135 mm of rain on Ascension in April 1988. The Roseate Terns on Aride Island in the Seychelles had poor success in the northern summers of 1985-1988 (Ramos 1998).

1991-1992 There was a Niño in Peru and severe drought in Africa and Mexico between September 1991 and March 1992 (Davis 2001). The Sooty Terns returned to Ascension in late October 1991 and were incubating by December, but the eastern Mars Bay Fairs were then abandoned, and some 23 600 and 20 700 eggs deserted, though reduced breeding continued at the Waterside Fair and at Pillar Bay to the west. They laid again at the Waterside Fair in September (N.J. Sylverwood Brown, Islander 31 January, 14 February, 16 April and 18 September, and with B.J. Hughes in Nash *et al.* 1992). After two good years the Roseate Terns in the Seychelles failed to breed in 1991 and had poor success in 1992 (Ramos 1998).

1997 Simmons and Prytherch (1998) visited Ascension in October and November during an ENSO with world-wide repercussions (Davis 2001). They found that the Pelecaniformes and Black Noddies were exploiting a coastal influx of fish, but a Sooty Tern breeding cycle had failed with massive desertion of eggs and small young (including 97 000 in one 'fair'), and there were many non-breeding birds. The Roseate Terns on Aride Island in the Seychelles also had poor breeding success again after four better seasons (Ramos 1998).

Thus as occurs with the variable timing of ENSOs elsewhere (Davis 2001) ornithological effects of oceanic and climatic fluctuations in the tropical Atlantic often appear to occur within months of, but not always simultaneously with, the more prominent events in the Pacific (Longhurst & Pauly 1987), and also Indian Ocean (Ramos 1998). Part of the breeding population of Sooty Terns on Ascension with their short breeding cycle may then be washed out, fail to lay, desert their eggs or lose their chicks, though they maintain their normal 10 lunar month breeding cycle afterwards. The Brown Boobies, on the other hand, which breed continually with a longer cycle, may try to rear existing young with reduced success, but lay no more eggs. It is not yet clear what happens with the other seabirds, but the Masked Boobies and Black Noddies may also be affected, while the tropicbirds and frigates may not (Ashmole *et al.* 1994). These events do not appear so closely related to seabird breeding failures in higher latitudes, as in the North Atlantic in recent years, and to the south in 1977-1978, 1983-1984 and 1985-1986 (Bourne 1987, Croxall *et al.* 1988), which may be affected by local factors.

CONCLUSION

It appears Ascension once formed the only breeding-station for a large, distinct community of seabirds, including the endemic Ascension Frigatebird and many more Red-footed Boobies than are found now, exploiting a biologically-enriched area along the equatorial counter-current about 500 nautical miles to the north in the tropical Atlantic. Its numbers have been reduced over the last 500 years as a result of human activity, especially the introduction of cats (Ashmole *et al.* 1994).

It appears that while Ascension Sooty Terns breed very regularly every ten lunar months (Chapin 1954), there are also variations in the weather and seabird breeding success in this area comparable with those elsewhere. This may help explain the poor breeding success of some seabirds found by the BOU Expedition on Ascension in 1958-1959 (Asmole *et al.* 1994). It is however notable that AOS censuses of Sooty Terns breeding on Ascension indicated a population of 176 000 in March 1990 before a breeding failure, 202,000 in November 1996, and 207 000 in June 1998 after a breeding failure the previous year (Hughes 1999). Thus these events do not appear to have affected the adult population of these and other seabirds, who can presumably if necessary disperse until conditions improve.

Such events make it increasingly necessary to exercise care in interpreting such factors as breeding seasons, cycles and success and adult survival of seabird populations, since they may also have other more complex effects, including for example not only a change in the food supply, but in the weather, the vegetation, and the number of predators or competitors at the breeding places, cascading up and down the food-chain afterwards (Holmgren *et al.* 2001). Therefore it seems desirable that attempts to rehabilitate the damaged ecology of oceanic islands should be accompanied by a long-term, but perhaps low intensity, international monitoring programme, as discussed in Symposium 29 at the 19th International Ornithological Congress in 1986 (Schreiber & Duffy 1988) and by Schreiber & Schreiber (1989).

While there are records from western South America for a long period, and they are now made more widely in the eastern Pacific, there are still very few from elsewhere in the tropics. If possible in addition to Ascension they should be obtained from at least the islands in the Gulf of Guinea to the east and Fernando de Noronha and Rocas Reef to the west in the Atlantic, on Christmas Island (Schreiber & Schreiber 1984) and Henderson Island (Brooke 1995) where reduced seabird breeding success has occurred during ENSOs, but in the latter case was attributed to rats, among many other places in the Pacific, and on Christmas Island with another endemic frigatebird, *Fregata andrewsi*, and endemic Abbott's Booby *Papasula abbotti*, and other island groups in the Indian Ocean, to discover more about the fluctuation in breeding success.

ACKNOWLEDGEMENTS

In addition to those listed by Ashmole *et al.* (1994) we are indebted to Philip and Myrtle Ashmole, Marion Simmons, Robin Prytherch, John Holmes, Hilary Nash, John Walmsley and the Army Ornithological Society for assistance on Ascension, Bill Curtis, Beau Rowlands and other members of the Royal Naval Bird-watching Society for records of birds at sea, Mike Blair, David Osborn and the RAF Ornithological Society for assistance and meteorological records supplied by the RAF Senior Meteorological Officer, Ascension Island, Betty Anne Schreiber for advice about ENSOs, and Jaime A. Ramos for information about the Roseate Terns of the Seychelles.

DE VERSPREIDING OP ZEE EN HET BROEDSUCCES VAN DE ZEEVOGELS VAN ASCENSION IN DE TROPISCHE ATLANTISCHE OCEAAN

Omvangrijke afzettingen van vogelmest, grote hoeveelheden subfossiele en fossiele vogelbotten en historische verslagen van zeevarenden laten zien dat vroeger op Ascension belangrijke zeevogelkolonies moeten zijn geweest. Geïntroduceerde ratten en katten hebben daaraan gedurende de afgelopen drie eeuwen effectief een einde gemaakt. De vroegere zeevogelkolonies zijn naar alle waarschijnlijkheid vergelijkbaar geweest met de grootste kolonies in de tropische Grote en Indische Oceanen en het was de enige geschikte broedplaats in dit afgelegen, op het eerste gezicht voedselarme gedeelte van de Atlantische Oceaan. Op grond van waarnemingen ten noorden en ten zuiden van Ascension, aangevuld met gegevens over vliegrichtingen bij vertrek- en aankomst van de zeevogels die hier nu nog steeds broeden,en de ligging (het noorden) van de nu verdwenen en zonder meer meest belangrijke kolonies uit eerdere jaren wordt afgeleid dat veel zeevogels van Ascension op grote afstand van het eiland foerageren. De verzamelde aanwijzingen suggereren dat het vooral de Equatoriale tegenstroom is (een naar het oosten gerichte waterbeweging; Fig. 1) waar de meeste zeevogels en zeezoogdieren gezien worden. Behalve de broedvogels van Ascension foerageren hier ook soorten die elders broeden en hier als doortrekkers of tijdelijke pleisteraars voorkomen. Op Ascension wordt soms exceptioneel veel neerslag gemeten, soms leidend tot het afbreken van het broedseizoen van de grondbroeders (1876, 1924, 1958/59, 1963, 1991/92 en 1997). Deze regenval lijkt samen te hangen met fluctuaties in de kracht van de Equatoriale tegenstroom en is vergelijkbaar met, maar niet altijd simultaan optredend met de El Niño/Southern Oscillation (ENSO) in de Grote Oceaan. De auteurs geconstateren dat er een grote behoefte bestaat aan een wereldwijd monitoringprogramma waarin de effecten van dergelijke fluctuaties in de voornaamste golfstromen worden gedocumenteerd.

REFERENCES

Ashmole N.P. 1963a. Subfossil bird remains on Ascension island. Ibis 103b: 382-389.
Ashmole N.P. 1963b. The biology of the Wideawake or Sooty Tern *Sterna fuscata* on Ascension Island. Ibis 103b: 297-364.
Ashmole N.P., Ashmole M.J. & Simmons K.E.L. 1994. Seabird conservation and feral cats on Ascension Island, South Atlantic. Birdlife Conservation Series l: 94-121.
Ashmole N.P. & Ashmole M.J. 2000. St Helena and Ascension Island: a natural history. Anthony Nelson, Oswestry.
Blair M. 1989. The RAFOS Expedition to Ascension Island, 1987. Royal Air Force Orn. Soc. J. 19: 1-35.

Barritt M.L. 1992. Some observations in winter in the tropical South Atlantic. Sea Swallow 41: 4-10.

Bourne W.R.P. 1955. The birds of the Cape Verde Islands. Ibis 97: 508- 556.

Bourne W.R.P. 1992. Leach's Storm-petrels visiting ships at sea. Brit. Birds 85: 556-557.

Bourne W.R.P. 1987. Penguin breeding failure and mortality. Oryx 21: 112.

Bourne, W.RP., Ashmole N.P., Ashmole M.J. & Simmons, K.E.L. in prep. The distribution of guano and bird bones in Ascension Island, South Atlantic Ocean, with descriptions of a new night heron and new genus for the Ascension rail. Ardea (submitted).

Bourne W.R.P. & Camphuysen C.J. 2000. Seabirds. In: Sheppard C. (ed) Seas at the Millennium: 105-115. Elsevier Science, London.

Bourne W.R.P. & Curtis W.F. 1985. South Atlantic Seabirds. Sea Swallow 34: 18-38.

Bourne W.R.P. & Simmons K.E.L. 1998. A preliminary list of the birds of Ascension Island, South Atlantic Ocean. Sea Swallow 47: 42-56.

Brooke M. de L. 1995. The breeding biology of the gadfly petrels *Pterodroma* spp. of the Pitcairn Islands: characteristics, population sizes and controls. Biol. J. Linn. Soc. 56: 213-231.

Cadée G.C. 1981. Seabird observations between Rotterdam and the Equatorial Atlantic. Ardea 69: 211-216.

Chapin J.P. 1954. The calendar of Wideawake Fair. Auk 71: 1-15.

Crawford R.J.M., Williams A.J. & Crawford P.B. 1986. A note on mortality of seabirds off western South Africa, October 1985- February 1986. S. Afr. J. Mar. Sci. 4: 119-123.

Croxall J.P., McCann T.A., Prince P.A & Rothery P. 1988. Reproductive performane of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976-1987: implications for Southern Ocean monitoring studies. In: Sahrhage D. (ed.) Antarctic Ocean Resources Variability: 261-285. Springer-Verlag, Berlin.

Dampier W. 1703. A Voyage to New Holland. Part 1. James Knapton, London.

Davis M. 2001. Late Victorian Holocausts- El Niño Famines and the Making of the Third World. Verso, London & New York.

Dickey R.C., Hughes B.J., Etheridge C., Wearn C. & Walmsley J.G. 1997. Exercise Booby V, Ascension Island, 28 Oct. - 9 Nov. 1996. Adjutant 26: 4-9.

Diester-Haass L. 1985. Late quaternary upwelling history off southwest Africa. (DSDP Leg 75, HPC 532). In: Hsu K.J. & Weissert H.J. (eds) South Atlantic Paleoceanography: 47-55. Cambridge Univ. Press, Cambridge.

Duffey E. 1964. The terrestrial ecology of Ascension Island. J. Appl. Ecol. 1: 219- 251.

Feare C.J.1976. Desertion and abnormal development in a colony of Sooty Terns *Sterna fuscata* infested by virus-infected ticks. Ibis 118: 112-115.

Gill I.S. 1878. Six months on Ascension. London: John Murray.

Glantz M.H. 1996. Currents of Change: El Niño's impact on climate and society. Cambridge Univ. Press, Cambridge.

Glantz M.H., Katz R.W. & Nicholls N. 1991. Telecommunications linking worldwide climatic anomalies. Cambridge Univ. Press, Cambridge.

Gould J. 1844. On the family Procellariidae, with descriptions of ten new species. Proc. Zool. Soc. Lond. 1844: 360-368.

Grove R.H. 1998. Global impact of the 1789-93 El Niño. Nature 393.

Haney H.C. 1986. Seabird segregation at Gulf Stream frontal eddies. Mar. Ecol. Prog. Ser. 28: 279-285.

Haney H.C. 1987. Ocean internal waves as sources of small-scale patchiness in seabird distribution on the Blake Plateau. Auk 104: 129-133.

Holmgren M., Scheffer M., Exequiel E.,. Gutiérrez J.R & Godefridus M.J.M. 2001. El Niño effects on the dynamics of terrestrial ecosystems. TREE 16: 89-94.

Huckle C.H. 1924. Birds of Ascension and St Helena. Ibis (11) 6: 818- 821.

Hughes B.J. 1999. The status of Sooty Terns *Sterna fuscata* on Ascension Island, South Atlantic. Adjutant 28: 4-13.

Hughes B.J., Thompson R.G., Walmsley J.G. & Varley M.J. 1994. Exercise Booby IV: Ascension Island, 12-28 April 1994. Adjutant 24: 4-31.

Hutchinson G.E. 1950. The biogeochemistry of vertebrate excretion. Bull. Amer. Mus. Nat. Hist. 96: 1-554.

Jesperson P. 1930. Ornithological observations on the North Atlantic Ocean. Danish Dana Exp. Rep. 1920-22, Oceanogr. Rep. 7: 1-36.

Jordàn S.R. 1991. Impact of ENSO events on the southeastern Pacific region. In: Glantz M.H., Katz R.W. & Nicholls N. (eds) Telecommunications linking worldwide climatic anomalies: 401-430, Cambridge.

Khanaychenko H.K., Khlystov N.Z. & Zhidkov V.G. 1965. (The System of Equatorial Countercurrents in the Atlantic Ocean). Oceanology Acad. Sci. USSR 5(2): 24-32. (Russian, English transl.).

Lambert K. 1988. Nächtliche Zugaktivität von Seevögeln im Golf von Guinea. Beitr. Vogelkd. 34: 29-35.

Longhurst A.R. & Pauly D. 1987. Ecology of Tropical Oceans. Acad. Press, London.

Mazeika P.A. 1967. Thermal Domes in the Eastern Tropical Atlantic Ocean. Limnology & Oceanography 12: 537-539.

Mazeika P.A. 1968. Eastward flow within the South Equatorial Current in the Eastern South Atlantic. J. Geophys. Res. 73: 5819-5828.

Moreau R.E. (ed.) 1962-63. Centenary Expeditions Volume. Ibis 103b(2-3).

Murphy R.C. 1936. The Oceanic Birds of South America. American Museum of Natural History, New York.

Nash R.H.J., Hughes B.J. & Walmesley J.G. 1991. Exercise Booby II: ABWS Expedition to Ascension Island, March 1990. Adjutant 21: 4-25.

Nash R.H.J., Hughes B.J., Thompson R.G. & Walmesley J.G. 1992. Exercise Booby III: Ascension Island, 30 Jun- 7 Jul 1992. Adjutant 22: 4-40.

Neumann G. 1965. Oceanography of the Tropical Atlantic. Anais Acad. Bras. Cienc. 37 (Suppl.): 63-82.

Nicholls N. & Katz R.W. 1991. Teleconnections and health. In: Glantz M.H., Katz R.W. & Nicholls N. (eds) Telecommunications linking worldwide climatic anomalies: 493-510. Cambridge Univ. Press, Cambridge.

Olson S.L. 1977. Additional notes on subfossil bird remains from Ascension Island. Ibis :37-43.

Osborn D.1994. Royal Air Force Ornithological Society Expedition to Ascension Island, 15-30 November 1988. Royal Air Force Orn. Soc. J. 23: 19-29.

Packer J.E. 1968. The Ascension Handbook. Georgetown. (revised edition, 1983).

Penrose F.G. 1879. Notes on a collection of birds' skins and eggs made by Mr. D. Gill, F.R.A.S. on Ascension Island. Ibis 4(3): 272-282.

Raimos J.A. 1998. Unpublished report to the Royal Society for Nature Conservation. London.

Robertson W.B. Jr. 1969. Transatlantic migration of juvenile Sooty Terns. Nature 222: 632-634.

Rowlands B.W. 1994. Seabird observations between Ascension, St Helena and Tristan da Cunha in the central South Atlantic. Mar. Ornithol. 20: 25-40.

Schreiber R.W. & Duffy D.C. 1988 (convenors). Symposium 29: Birds and the El Niño Southern Oscillation. Proc. Intern. Ornith. Congr. 19: 1738-1775.

Schreiber E.A. & Schreiber R.W. 1989. Insights into Seabird ecology from a Global "Natural Experiment". Nat. Geogr. Res. 5(1): 64-81.

Schreiber R.W. & Schreiber E.A. 1984. Central Pacific seabirds and the El Niño Southern Oscillation: 1982 to 1983 perspectives. Science 225: 713-716.

Scullion J. 1990. Review of the fish resources, fisheries and oceanography within the exclusive fishing zone of Ascension Island. Latin America, Caribbean and Atlantic Department of the Overseas Development Administration, London.

Simmons K.E.L. 1967 a. Ecological adaptations in the life of the Brown Booby at Ascension Island. Living Bird 6: 187-212.

Simmons K.E.L. 1967 b. The role of food supply in the biology of the Brown Booby at Ascension Island. M.Sc.-thesis, Bristol Univ., Bristol.

Simmons K.E.L. 1970. Ecological determinants of breeding adaptations and social behaviour in two fish-eating birds. In: Crook J.H. (ed.): Social Behaviour in Birds and Mammals. London.

Simmons K.E.L. 1990. The status of the Red-footed Booby at Ascension Island. Bull. Brit. Orn. Cl. 110: 213-222.

Simmons K.E.L. & Prytherch R.J. 1994. (Report on visit to Ascension in September/October 1993). Ibis 136: 258-259.

Simmons K.E.L. & Prytherch R.J. 1997. Ascension Island 1996. Ibis 139: 433-434.

Simmons K.E.L. & Prytherch R.J. 1998. Ascension Island 1997. Ibis 140:725-727.

Stonehouse B. 1960. Wideawake Island. The story of the B.O.U. centenary expedition to Ascension Island. London.

Stonehouse B. 1962. Ascension Island and the British Ornithologists' Union centenary expedition 1957-59. Ibis 103 b: 107-123.

Tiede P.A. 1885. The Voyage of John Huyghen van Linschoten to the East Indies, 2. Hakluyt Soc. Publ. (1) 71: 259-265.

Vandenbosch R. 2000. Effects of ENSO and PDO events on seabird populations revealed by Christmas Bird Count data. Waterbirds 23: 416-422.

Walmsley J.G. 1997. Feral cat predation and other predators on the seabirds of Ascension. Adjutant 26: 11-17.

FLIGHT ALTITUDES OF COASTAL BIRDS IN RELATION TO WIND DIRECTION AND SPEED

THORSTEN KRÜGER[1,3] & STEFAN GARTHE[2,3]

Krüger, T. & Garthe S. (2001): Flight altitudes of coastal birds in relation to wind direction and speed. Atlantic Seabirds 3(4): 203-216. *During systematic sea watches carried out between 1 September and 15 November 1999 on the East Friesian island of Wangerooge, observations were recorded of the flight altitude of coastal birds in relation to wind direction and speed. In Red-throated Diver* Gavia stellata, *Common Eider* Somateria mollissima *and Common Scoter* Melanitta nigra *the proportion of birds flying into the wind low over the water (0-1.5m) increased with wind speed. On the other hand, in the same species, the number of low-flying birds decreased in inverse proportion to the speed of a tail wind and the ratio of birds flying at greater altitudes increased (1.5-12m and 12-25m respectively). Irrespective of wind speed, the proportion of individual birds flying low into the wind was highest in Red-throated Diver, Shelduck* Tadorna tadorna, *Common Eider and Common Scoter. This pattern is repeated at a higher level in Sandwich Tern* Sterna sandvicensis *and Common/Arctic Terns* S. hirundo/paradisaea. *In contrast, in tail winds, the greatest proportion of birds of these species invariably flew at the highest levels. Comparisons of flight altitudes reveal that these species fly noticeably higher in tail winds. This behaviour can be explained in terms of economy of effort on migration. The present study also reveals that diurnal movement of the observed species takes place mainly at a low flight altitude (up to 25m, occasionally up to 50m, rarely higher) above sea level. This demonstrates potentially adverse effects on birds from construction of proposed offshore wind farms. The data indicate that, to be of any value in the assessment of the potential disturbance of the wind farms to North Sea migrants, flight altitude records must be viewed against the background of the meteorological situation as a whole.*

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INTRODUCTION

Little is known about the flight altitudes of coastal birds migrating through the southern North Sea, and even less about their relation to meteorological parameters. Statements about flight altitudes based on sea-watch observations have generally been vague; scattered information about species migrating at a particular height may be found in Berndt & Drenckhahn (1974), Camphuysen & van Dijk (1983), Nehls & Zöllick (1990) and Temme (1995). Although radar observations have improved our understanding of bird migration over the North Sea substantially (Lack 1963; Jellmann 1979; Buurma 1987), they have not been able to provide clear information on low-level migratory movement until very recently; radar equipment used to date is mostly accurate only at heights above (50) 100-300 m, and it is often not possible to identify birds to species level using radar (Williams & Williams 1990; Berthold 2000). For a long time the intensity of low-level migratory movements over the sea generally were thought - aside from the moult migration of Shelduck *Tadorna tadorna*- to be of minor importance (*cf.* Jellmann 1979, 1987, 1989). Major improvements in radar technology now enable exact measurements of flight altitudes (e.g. Dirksen *et al*. 1996, 1998). However, such studies have been carried out so far only at selected locations, usually to inform environmental issues such as wind energy utilization.

The purpose of the study described here was to examine the flight altitudes of the most common coastal birds and seabirds by field observations of visible migration and to identify the influence of the meteorological parameters wind direction and speed.

METHODS

Visible migration of coastal birds and seabirds was studied on 52 days between 1 September and 15 November 1999 on Wangerooge Island, Germany. Wangerooge is located in the southern North Sea (German Bight; 53°47'N 07°54'E) and constitutes the easternmost of the East Frisian islands. Observations followed common sea watching methods (Camphuysen & van Dijk 1983) using a telescope (Swarovski, AT 30x80 HD). We excluded all common gull species from the observations (*Larus argentatus, L. fuscus, L. marinus, L. canus, L. ridibundus*) because it was impossible to distinguish between true migration and frequent local movements between resting and feeding sites. The method of sea watching has been proved suitable for describing and analysing migratory behaviour (e.g. phenology, influence of wind) of birds along the coast and at sea (e.g. Camphuysen & van Dijk 1983, Platteeuw *et al*. 1994). It is not the purpose of this study to assess all birds flying during day and night, which could be done much more comprehensively by radar studies.

In order to study whether wind direction and wind speed influence directly the flight altitude of migrating birds, all individuals passing Wangerooge were allocated to one of several pre-arranged flight levels. Because the estimation of flight altitude is difficult in general and because "observers nearly always overestimate the height of migrating birds" (Thienemann 1931, see also Gätke 1900, Lucanus 1923), a simple but accurate schema had to be devised (Fig. 1):

- Birds flying low over the water were allocated to the lowest level *(low)*. The upper limit of this level was about 1.5 m. In light winds and relatively calm seas it was easy to identify this level. In these conditions, the birds often flew so low over the

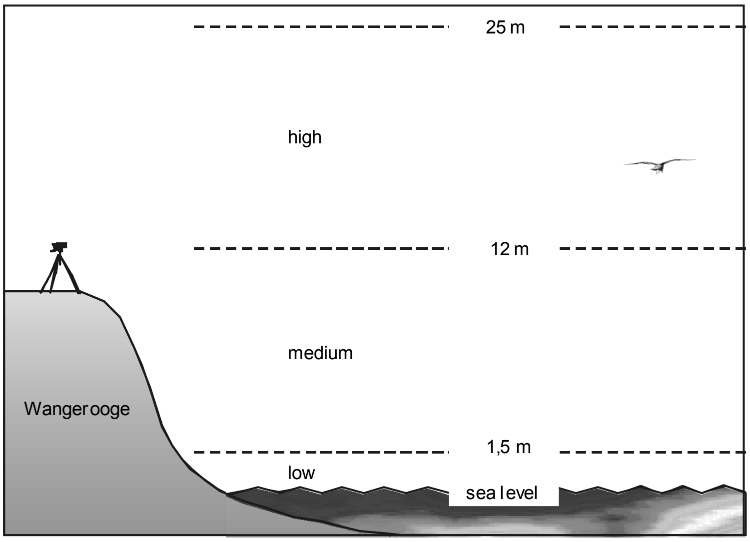


Figure 1. Allocation of flight altitude above the sea surface to various pre-determined levels.
Figuur 1. Verdeling van vlieghoogte in hoogteklassen ten opzichte van het zeeoppervlak.

surface that the reflection of their wingtips in the water was clearly visible at considerable distances. In rougher or stormy seas, high waves frequently forced the birds to leave their low trajectories for at least part of the time. To be sure of a correct flight altitude allocation, the observers were obliged to follow the flight paths over longer distances in order to distinguish between a *medium* flight altitude and a tendency towards a *low* trajectory.

- The upper limit of the next higher level *(medium)* was at eye-level for the observers and thus encompassed the space from about 1.5 m to 12 m a.s.l. This categorised all those birds that were not clearly flying "low" and yet not flying above eye-level (= side view). Birds in flight above eye-level, and thus viewed at an angle from below, were allocated to a third level *(high)*, whose upper limit was assigned to about 25 m.
- A further category *(very high)* was established for birds flying even higher, at flight altitudes > 25 to 100 m.
- The levels low, medium and high lay all within the telescope's field of vision. The observations were regulary interrupted by searching the sky for very high-flying birds with a binocular (Zeiss 10x40). As a rule, birds passing >3 km away were excluded from flight altitude assessments as these could not be estimated accurately.

Table 1. The correlation (r) between the percentage of birds passing Wangerooge in autumn 1999 and wind speed, grouped according to wind direction and flight altitude. Correlation coefficient r is in italics where p< 0.05 (cf. Fig. 2).
Tabel 1. Correlatie (r) tussen het aandeel vogels dat Wangerooge in het najaar van 1999 passeerde en de windsnelheid, gegroepeerd naar windrichting en vlieghoogte. Correlatiecoëfficiënt r is cursief indien p < 0.05 (cf. Figuur 2).

	Headwind	**Tail wind**
	Low	Low
Red-throated Diver	0.295	*-0.720*
Common Eider	0.550	*-0.770*
Common Scoter	0.223	*-0.668*

To minimise distortion of the results through other meteorological factors, rainy, hazy and foggy days during the period of the investigation were excluded from the evaluation (*cf.* Bruderer 1971). In order to correlate the observed migration with the wind, measurements of wind speed and wind direction were taken from a meteorological station on Minsener Oog (8 km E of Wangerooge; Wasser- und Schiffahrtsamt Wilhelmshaven, Abt. Gewässerkunde). During the study, the main migration direction was west. Consequently, winds from SW-NW are defined as headwinds, those from SE-NE as tail winds.

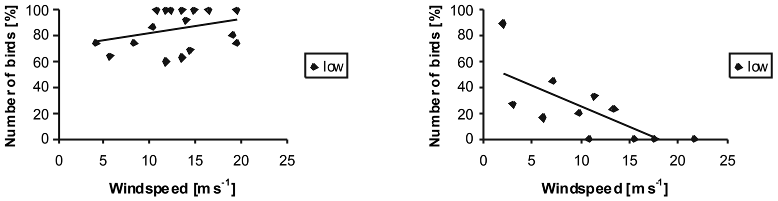
RESULTS

Flight altitudes in relation to wind speed and direction

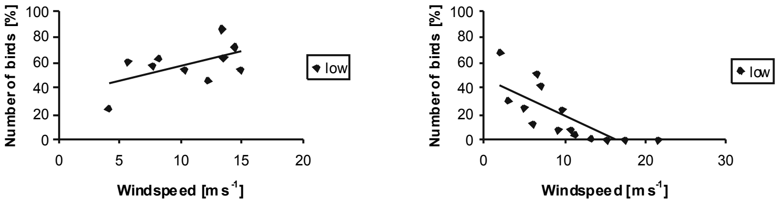
Red-throated Diver *Gavia stellata* During headwinds, most Red-throated Divers migrated low over the water (range: 60-100%; Fig. 2). The proportion of low-flying birds increased with increasing wind speed, and was up to 100% beyond speeds of 10.8 m s^{-1}. High-flying individuals were seldom recorded in headwinds and even then the breezes were only light.

During light tail winds, the greatest percentage of Red-throated Divers were still low-flyers, even though this decreased significantly with increasing wind speed (Table 1, Fig. 2). No low flying Red-throated Divers were recorded in tail winds of over 15.4 m s^{-1}. Thus, the proportion of birds flying at medium height became greater with increasing wind speed. High-flying Red-throated Divers – rarely observed in headwinds – made up as much as 90% of the individuals in tail winds. Their proportion increased in general with wind speed.

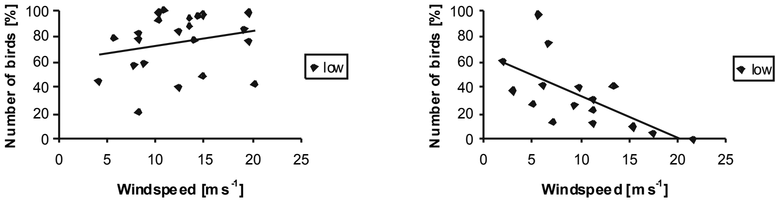
Headwind Tail wind



Red-throated Diver (n = 147) Red-throated Diver (n = 111)



Eider (n = 4,241) Eider (n = 10,164)



Common Scoter (n = 4,030) Common Scoter (n = 2,724)

Figure 2. Flight altitude of westward migrating coastal birds in headwinds (NW-SW) and in tail winds (NE-SE). Lines = linear regression per flight level; correlation coefficient r: see Table 1.

Figuur 2. Vlieghoogte van westwaarts vliegende kustvogels bij tegenwind (NW-ZW) en bij meewind (NO-ZO). Lineaire regressielijn per vlieghoogte; zie tabel 1 voor waarden van correlatiecoëfficiënt r.

Common Eider *Somateria mollissima* The low flight path was the most frequently chosen by this species (46-72%; Fig. 2), increasingly so with stronger headwinds. The medium level was used most frequently at wind speeds of 4.1 m s^{-1} (42%), this proportion decreasing with stronger winds. The percentage of high-flying Common Eider dropped from 34% at 4.1 m s^{-1} to 0% at 13.4 m s^{-1} and more.

In light tail winds Common Eiders mainly flew low over the surface of the water (2 m s^{-1}: 68%; Fig. 2). The low level was used less with increasing wind speed, and was not used at all in winds in excess of 13.3 m s^{-1}. Instead, the proportion of high-flying Common Eider increased, reaching 86% at wind speeds of 13.3 m s^{-1}. The proportion of Common Eiders flying at medium height tended to remain constant with increasing wind speeds.

Common Scoter *Melanitta nigra* The percentage of Common Scoters flying low into the wind increased with increasing wind speed, reaching values of over 90% at speeds of 10.3 m s^{-1} and above (Fig. 2). Correspondingly, the stronger the wind, the smaller the number of Common Scoters migrating at medium level. Only 1-9% of the Common Scoters observed flew high into the wind. In tail winds of increasing strength, Common Scoters became increasingly reluctant to fly low over the surface of the water (Fig. 2). Instead, the percentage of birds migrating at medium height rose and eventually predominated. 5-39% of the Common Scoters passed at the high level but increasing wind speeds did not result in a clear trend.

Flight altitudes in relation to wind direction Considered without reference to prevailing wind speeds, westward moving Red-throated Divers used most frequently the low level in winds from the NW-SW sector (headwind; 83%; Fig. 3). They rarely flew higher (medium: 15%, high: 2%). In winds from the NE-SE sector (tail winds), the two (or three) higher flight levels were used more often: low = 34%, medium = 27%, high = 38%, very high = 1%. The pattern of flight altitude allocation in headwind conditions differed significantly from that in tail winds (Table 2).

When flying against the wind, approximately 75% of Shelduck passed low over the water and 23% selected the next higher level (Fig. 3). In tail winds, a preference for the high and very high levels was detected (51% and 3% respectively); the percentage of low-flying birds was 15%. In headwinds, the majority (58%) of Common Eider migrated low over the water, but large numbers also chose the medium level (34%; Fig. 3). In tail winds, the greatest number of Common Eiders flew past at medium height (38%), but almost as many (31%) – certainly much more than in Red-throated Divers and Common Scoters – migrated at high level. Westward migrating Common Scoters mostly

*Table 2. The numbers of coastal migrants passing Wangerooge in autumn 1999, grouped according to wind direction and flight altitude. χ^2 = significance of the 2*3 contingency tables for differences between headwinds and tail winds. $p < 0.001$.*

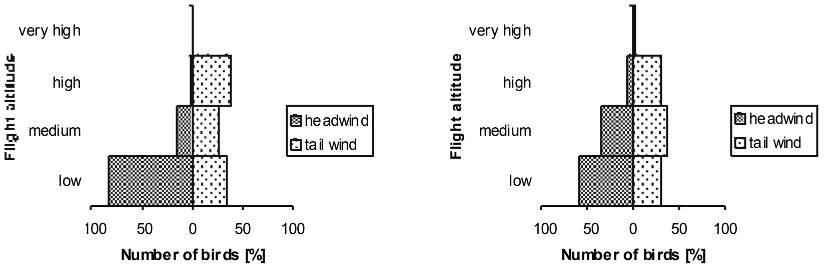
Tabel 2. Aantal trekvogels dat Wangeroog najaar 1999 passeerde, gegroepeerd naar windrichting en vlieghoogte. $p < 0.001$.

	Headwind			**Tailwind**			
	low	medium	high	low	medium	high	χ^2
Red-throated Diver	113	21	2	38	30	43	74.4
Shelduck	218	70	17	107	221	380	349.9
Common Eider	2442	1428	371	2998	3850	3316	1305.9
Common Scoter	3286	711	33	1022	1389	308	1429.8
Sandwich Tern	179	560	40	0	63	117	392.1
Comm/Arctic Tern	5	117	26	0	33	90	85.8

flew low over the water during headwinds, whereas the medium level was used most often during tail winds (51%; Fig. 3).

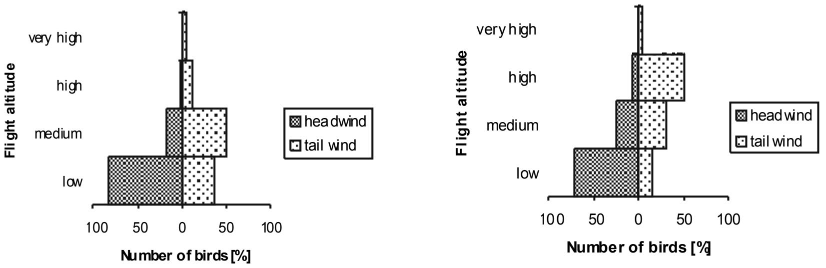
Most Sandwich Terns *Sterna sandvicensis* flying into the wind clearly preferred the medium level (72%) and a further 23% selected the low level (Fig. 3). In tail winds the high level was most frequently used (65%); 35% flew at medium height, and there were no records of low-flying migrating Sandwich Terns. 79% of Common/Arctic Terns *S. hirundo/paradisaea* migrated in headwinds at medium levels and another 18% flew high (Fig. 3). Headwinds saw the bulk (73%) of the birds in the high flight path, whereas only 23% were to be found at medium height.

Even within a single observation day it became evident that flight altitude was influenced by the direction of the wind. During the autumn migration period, Common Eiders off Wangerooge regularly moved in both easterly and westerly directions (see also Camphuysen & van Dijk 1983, Platteeuw *et al.* 1994). On days during which migration took place in both directions, one of the routes – eastward or westward – had headwinds. On nine headwind days (only days with more than 1,000 individuals were considered), Common Eiders migrated for the most part low in a westerly direction. Conversely, birds moving east on those days mostly had a medium or high flight altitude (Fig. 4). In same-day comparisons, they always moved one or two levels higher up. On nine tail wind days, however, the mass of the birds migrated medium or high levels in a westerly direction. The birds moving east for the most part flew low over the water (Fig. 4).



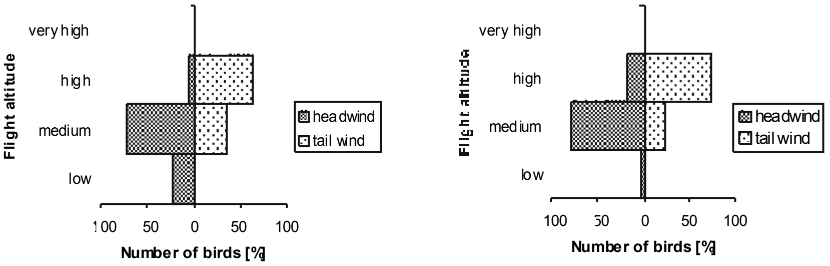
Red-throated Diver (n = 247)

Eider (n = 14,405)



Common Scoter (n = 6,754)

Shelduck (n = 1,013)

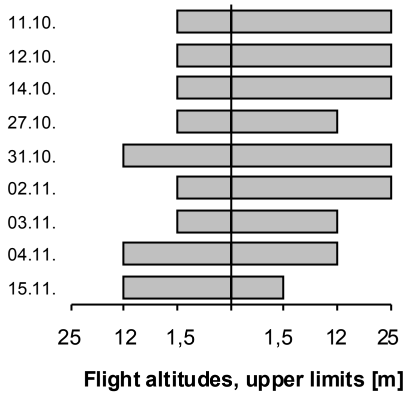


Sandwich Tern (n = 959)

Common/Arctic Tern (n = 271)

Figure 3. Relative frequency of westward moving coastal birds, grouped according to flight altitude and wind direction.

Figuur 3. Relatieve verdeling van westwaarts vliegende kustvogels, gegroepeerd naar vlieghoogte en windrichting.



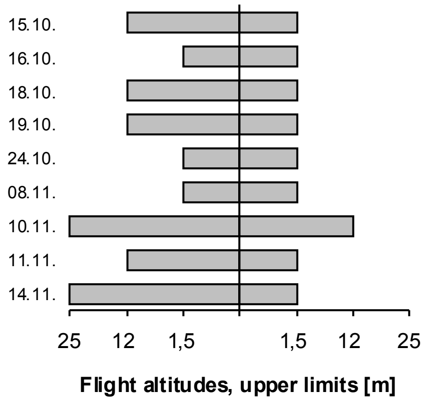


Figure 4 . Common Eider flight altitudes on days with NW-SW winds off Wangerooge (upper) and Common Eider flight altitudes on days with NE-SE winds off Wangerooge (lower), autumn 1999. The bars show in each case the most frequent level; westerly migrants to the left, easterly to the right of the central axis.

Figuur 4. Vlieghoogtes van Eiders op dagen met NW-ZW-winden langs Wangerooge (boven) en vlieghoogtes op dagen met NO-ZO-winden (onder), najaar 1999. De staven geven voor iedere dag de meest frequente vlieghoogte weer; westwaarts vliegende vogels links, oostwaarts vliegende vogels rechts van de y-as.

Black-throated Divers Parelduikers *(Frits-Jan Maas)*

DISCUSSION

According to Bruderer (1971), migration altitude is influenced – always within the limits set by the aerodynamic and physiological characteristics of the species – by secondary (external) factors, principally meteorological factors such as wind, fog, cloud conditions and precipitation, and changes in overall weather conditions. Among these, wind is of greatest importance (Alerstam 1979a). The horizontal speed of wind over the sea increases with height; directly above the water surface there is a zone of lower wind speed caused by the breaking effect of the water. Jameson (1960) describes a case where the wind speed just 15 m above sea level was at force 8 Bft, twice that immediately above the water surface. Wind reaches its full force only above 500 m (Alerstam 1979b; Nachtigall 1987; Stein & Schultz 1995).

Assuming that the radar ornithological results apply, the observations of the present study confirm those of numerous investigations showing that the height of migration in tail wind conditions is greater than that in headwinds, and that where wind direction is opposed to the migration direction, in general lower flight altitudes with attendant lower wind speeds are selected (Bruderer 1971; Karlsson 1976; Kumari 1983; Bruderer 1997; Bruderer & Liechti 1998).

The reason for the migratory behaviour observed off Wangerooge is probably that birds need to save time and energy when on migration (cf. Berthold 2000). In general, active flying costs birds much energy per unit of time. In order to minimise these costs, some bird species have developed flight techniques that enable them to cover long distances with less energy expenditure (e.g. gliding and soaring, formation flying; see reviews by Rüppel 1980; Norberg 1996). Still other species employ alternating flight techniques, such as the shearwaters, which flap-glide, alternately beating their wings and sheering through the wave-troughs. These means of saving energy are not available to all species. Some species have unfavourable wing area to body mass ratios (wing loading) and find it impossible to glide or soar long distances over water; such species are obliged to propel themselves forward by continuous wing-beating (swans, geese, ducks, auks etc., Rüppel 1980; Pennycuick 1987 a, b). The species under investigation in this paper belong mostly to the latter group. The most efficient way for these birds to minimise energy costs of migrating up-wind in terms of optimal migration (Alerstam & Lindström 1990) is to fly low – the stronger the headwind, the lower the flight level. In tail winds, they migrate more efficiently at greater heights (see also Gatter 2001). The present study suggests, that this pattern is also valid for migration across the North Sea at low(er) altitudes.

Behaviour like this makes it possible for birds in some cases almost to double their flight speed and to halve their energy costs (Liechti & Bruderer 1998; Liechti & Schaller 1999; Liechti *et al.* 2000). These relationships have already been found by Bellrose (1967) who summarised the findings of his radar studies: "[...] demonstrate that birds have a phenomenal understanding of winds. They select [...] altitudes having favourable directional winds and favourable wind speeds." The data on flight altitudes presented in this paper are predominantly based on migration flights (Krüger 2001). It is, however, not possible to quantify the extent to which they have been influenced by compensating movements or have been caused by disturbances. Those shorter flights could be performed in a different manner (e.g. lower flight altitudes) and under different energy saving strategies as real migration flights.

An interesting result of this study is that the visible, diurnal movements of the species investigated take place mainly at low heights above the water surface (up to 25 m, occasionally up to 50 m, rarely higher). This accords with other observations of bird migration in coastal areas. Thus 75% of migrating Red-throated Divers in the Fehmarn Belt (Baltic Sea) in the winter of 1956/57 were observed between 6 and 15 m (mean flight altitude: 10.5 m, maximum: 45 m). In other years also, flight altitudes of 60-100 m were registered during tail wind conditions (Drenckhahn *et al.* 1974). Temme (1974) found that the majority of Common Eiders off Norderney (southern North Sea) migrated between 1 and 3 m over the water surface, in rare occasions up to 20-25 (45) m. Common Scoters off Rügen (Baltic Sea) were recorded migrating usually at altitudes of 1-2 m; in strong tail winds they reached 10-100 m (Nehls & Zöllick 1990).

The findings of this study are not only interesting in terms of coastal bird ecology but also with respect to current environmental issues in the southern North Sea. Extensive plans to construct windmill farms in offshore areas of the German Bight and other areas may create a substantial risk for migrating birds at sea. In order to study the potential risk with regard to collision (which causes mortality) and flight route disturbance, comprehensive environmental impact assessments need to be carried out (e.g. Garthe 2000). Such studies should consider flight altitudes of birds also in relation to the prevailing meteorological situations.

ACKNOWLEDGEMENTS

K. Wilson helped with the English language. P.H. Becker, C.J. Camphuysen, W. Gatter and an anonymous referee gave valuable comments on the manuscript. The *Mellumrat e.V.* made it possible to stay on Wangerooge. The *Wasser- und Schiffahrtsamt Wilhelmshaven* provided meteorological data. M. Feuersenger, R. Lottmann, J. Dierschke and M. Heckroth helped with the fieldwork and discussed the method.

VLIEGHOOGTES VAN KUSTVOGELS IN RELATIE TOT WINDRICHTING EN WINDSNELHEID

Tijdens systematische zeetrektellingen tussen 1 september en 15 november 1999 op het Oost-Friese eiland Wangerooge, werden waarnemingen verzameld over de vlieghoogte van kustvogels in relatie tot windrichting en -snelheid. Bij Roodkeelduiker *Gavia stellata*, Eider *Somateria mollisima* en Zwarte Zee-eend *Melanitta nigra* nam het aandeel laag (0-1.5 m)tegen de wind in vliegende vogels toe met toenemende windsnelheid. Het aandeel laag vliegende vogels nam met meewind omgekeerd evenredig af met de windsnelheid, terwijl het aandeel hoger vliegende vogels (1.5-25 m) toenam. Het aandeel individuen dat tegen de wind invloog was, ongeacht de windsnelheid, het hoogst bij Roodkeelduiker, Bergeend *Tadorna tadorna*, Eider en Zwarte Zee-eend. Grote Stern *Sterna sandvicensis* en Noordse Dief *S.hirundo/paradisaea* vertonen een zelfde beeld, zij het op grotere hoogte. Met meewind vloog het merendeel van deze soorten in de bovenste hoogteklassen. Vergelijking van de vlieghoogtes laat zoen dat alle soorten met meewind aanmerkelijk hoger vliegen. Dit gedrag kan verklaard worden uit energetisch oogpunt. Deze studie laat tevens zien dat dagtrek van de waargenomen soorten met name op lage hoogtes (tot 25 m, soms tot 50 m, zelden hoger) boven zee plaatsvindt. De gegevens wijzen op potentiële, schadelijke effecten op vogels van de bouw van voorgestelde offshore windmolenparken. Om van enig nut te zijn bij risico-analyse van potentiële verstorende effecten van windmolenparken op door de Noordzee trekkende vogels moeten waarnemingen van vlieghoogtes tegen de achtergrond van de gehele metereologische situatie beschouwd worden.

REFERENCES

Alerstam T. 1979 a. Wind as selective agent in bird migration. Ornis Scand. 10: 76-93.

Alerstam T. 1979 b. Optimal use of wind by migrating birds: combined drift and overcompensation. J. Theor. Biol. 79: 341-353.

Bellrose F.C. 1967. Radar in orientaion research. Proc. 14th Int. Ornithol. Congr., Oxford 1966: 281-309.

Berndt R.K. & Drenckhahn D. 1974 (eds). Vogelwelt Schleswig-Holsteins, Vol. 1. Neumünster.

Berthold P. 2000. Vogelzug. Eine aktuelle Gesamtübersicht, Darmstadt.

Bruderer B. 1971. Radarbeobachtungen über den Frühlingszug im Schweizerischen Mittelland (Ein Beitrag zum Problem der Witterungsabhängigkeit des Vogelzugs). Ornithol. Beob. 68: 89-158.

Bruderer B. 1997. The study of bird migration by radar. Part 2: Major achievements. Naturwiss. 84: 45-54.

Bruderer B. & Liechti F.1998. Intensität, Höhe und Richtung von Tag- und Nachtzug im Herbst über Südwestdeutschland. Ornithol. Beob. 95: 13-128.

Buurma L.S. 1987. Patronen van hoge vogeltrek boven het Noordzeegebied in oktober. Limosa 60: 63-74.

Camphuysen C.J. & van Dijk J. 1983. Zee- en kustvogels langs de Nederlandse kust, 1974- 79. Limosa 56: 83-211.

Dirksen S., Spaans A.L. & van der Winden J. 1996. Nachtelijke trek en vlieghoogtes van steltlopers in het voorjaar over de noordelijke havendam van IJmuiden Sula 10: 129- 142.

Dirksen S., Spaans A.L., van der Winden J. & van den Bergh L.M.J. 1998. Nachtelijke vliegpatronen en vlieghoogtes van duikeenden in het IJsselmeergebied. Limosa 71: 57- 68.

Drenckhahn D., Gloe P. & Heldt R. 1974. Sterntaucher *Gavia stellata*. In: Berndt R.K. & Drenckhahn D. (eds). Vogelwelt Schleswig-Holsteins, Vol. 1. Neumünster.

Gätke F. 1900. Die Vogelwarte Helgoland, Braunschweig.

Garthe S. 2000. Mögliche Auswirkungen von Offshore-Windenergieanlagen auf See- und Wasservögel der deutschen Nord- und Ostsee. In: Merck T. & von Nordheim H. (eds.): Technische Eingriffe in marine Lebensräume. Workshop of the "Bundesamt für Naturschutz, Internationale Naturschutzakademie Insel Vilm", 27 - 29 October 1999. BfN-Skripten 29: 113-119.

Gatter W. 2001. Vogelzug und Vogelbestände in Mitteleuropa. 30 Jahre Beobachtung des Tagzugs am Randecker Maar. Wiesbaden.

Jameson W. 1960. Flight of the Albatross. Natural History 69: 62-69.

Jellmann J. 1979. Flughöhen ziehender Vögel in Nordwestdeutschland nach Radarmessungen. Vogelwarte 30: 118-134.

Jellmann J. 1987. Radarbeobachtungen zum nächtlichen Mauserzug der Brandgans (*Tadorna tadorna*) an der Nordseeküste. Seevögel 8: 63-64.

Jellmann J. 1989. Radarmessungen zur Höhe des nächtlichen Vogelzuges über Nordwestdeutschland im Frühjahr und im Hochsommer. Vogelwarte 35: 59-63.

Karlsson J. 1976. Radar measurements of migration altitudes of Eiders (*Somateria mollissima*) over southernmost Sweden. Fauna Flora, Uppsala 71: 152-157.

Kumari E. 1983. Characteristics of seaduck movements in the Baltic. Ornis Fennica Suppl. 3: 39-40.

Krüger T. 2001. Untersuchungen zum Zugverhalten ausgewählter See- und Küstenvögel in der südlichen Nordsee. Diplomarbeit. Universität Oldenburg.

Lack D. 1963. Migration across the southern North Sea studied by radar. Part 4. Autumn. Ibis 105: 1-54.

Liechti F., Klaassen M. & Bruderer B. 2000. Predicting migratory flight altitudes by physiological optimal migration models. Auk 117: 205-214

Liechti F. & Schaller E. 1999. The use of low-level jets by migrating birds. Naturwissenschaften 86: 549-551.

Lucanus F. v. 1923. Die Rätsel des Vogelzugs, Langensalza.

Nachtigall W. 1987. Vogelflug und Vogelzug, Hamburg.

Nehls H.W. & Zöllick H. 1990. The moult migration of the Common Scoter (*Melanitta nigra*) off the coast of the GDR. Baltic Birds 5: 36-46.

Norberg U. 1996. Energetics of Flight. In: Carey C. (ed). Energetics and nutritional ecology. New York.

Pennycuick C.J. 1987a. Flight of seabirds. In: Croxall J.P. (ed). Seabirds: feeding, ecology and role in marine ecosystems. Cambridge, New York, Melbourne.

Pennycuick C.J. 1987b. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: Ornithodolite observations. J. Exp. Biol. 128: 335- 347.

Piersma T. & van de Sant S. 1992. Pattern and predictability of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. Ornis Svecica 2: 55-66.

Platteeuw M., van der Ham N.F. & den Ouden J.E. 1994. Zeetrektellingen in Nederland in de jaren tachtig. Sula 8, Spec. Issue: 1-203.

Rüppell G. 1980. Vogelflug, Reinbek.

Stein W. & Schultz H. 1995. Wetterkunde für Segler und Motorbootfahrer, Bielefeld.

Temme M. 1974. Zugbewegungen der Eiderente (*Somateria mollissima*) vor der Insel Norderney unter besonderer Berücksichtigung der Wetterverhältnisse. Vogelwarte 27: 252-263.

Temme M. 1995. Die Vögel der Insel Norderney, Cuxhaven.

Thienemann J. 1931. Vom Vogelzuge in Rossitten, Melsungen.

Williams T.C. & Williams J.M. 1990. The orientation of transoceanic migrants. In: Gwinner E. (ed.) Bird Migration: The Physiology and Ecophysiology, Berlin.