Rise and fall of the nesting population of the Common Eider *Somateria mollissima* in the Netherlands since 1906: a demographic reconstruction distinguishing between catastrophic mortality events and non-breeding

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Abstract

In the Netherlands, Common Eiders Somateria mollissima successfully established a breeding colony in 1906 on the coastal barrier Wadden Sea Island of Vlieland. The size of the colony increased rapidly from 350 breeding females in 1940 to 4000 in 1960, but declined to 800 breeding females in 1968 due to a large-scale pollution peak in coastal waters with organochlorides and recovered slowly. By 1980, the colony had regained stability but at a lower level with a long-term average (1980-2003) of 2150 (1050 – 2700) breeding females. Declines in the number of breeding females were observed anew between 1988 and 1993 and since 2000, and it is the purpose of this paper to examine the causes in demographic terms (making use of the results of a ringing programme at this colony).

The number of fledglings produced has been highly variable (0-3000) with two periods with low productivity (resp. 70 and 29 fledglings-year in 1966-1977 and 1989-1994) coinciding with the first two declines in breeding numbers. Since 1994 production of fledglings has been comparable to the 1980s.

Beach surveys of carcasses (systematic data since 1978) substantiate increased mortality of adult eiders in the Dutch Wadden Sea during the periods of colony decline (1988-93 and since 2000) but these figures include migrants from other populations and non-breeders.

Estimates of annual survival in females from the Vlieland colony were calculated using MARK based on females caught and ringed as fledgling or as breeding adult at the nest. For females caught as fledgling (1975-1985), long-term average survival was 0.926 ± 0.028 for juveniles, 0.971 ± 0.010 for immatures and 0.921 ± 0.002 for adults. Long-term (1974-2003) survival of breeding females was on average 0.927 (± 0.008 S.E.) with a constant reporting rate of 0.241 (± 0.019 S.E.). Survival was reduced during the 10 ‘kill-years’ (1984, 1988-92, 2000-03) identified by the beach carcass surveys and averaged 0.872 (± 0.006 S.E.), in contrast to 0.955 (± 0.006 S.E.) in normal years.

Survival of breeding females, juveniles and immatures derived from the ringing programme at Vlieland were negatively and highly significantly related to total mortality assessed by the survey of beached carcasses along the Dutch coast. Adult females caught at the nest were primarily reported dead during the breeding season (April-June, in the ‘kill-years’ especially May). The beached surveys of dead eiders (which include losses from the abundant wintering population) revealed extensive pre-breeding mortality in late winter and spring.

Annual estimates of survival were extrapolated since 1985 for the population trajectory using total annual mortality as a predictor of juvenile, immature and adult female survival. Adult females caught at the nest were primarily reported dead during the breeding season (normal years: April – June; ‘kill-years’: May), while total annual mortality peaked prior to breeding in March. The propensity of breeding (probability of an individual in the age group to breed) for immatures
Non-breeding (or intermittent breeding) is one of the major determinants of fitness at the individual level (Newton 1989). Non-breeding has been frequently reported in many species especially for long-living species, such as raptors (Newton 1985), gulls (Bradley et al. 2000, Hatch 1987), geese (Rockwell et al. 1985), cormorants (Boekelheide & Ainley 1989), auks (Jones & Montgomerie 1992), flamingos (Cezilly et al. 1996) and sea ducks (Coulson 1984). In order to survive individuals may decide to skip current reproductive effort if insufficiently recovered from the previous breeding attempt and/or when the current circumstances were not sufficient to allow sustainable reproduction. Intermittent or skipping reproduction can be interpreted as an adaptive strategy to avoid the potential costs

(2nd and 3rd year old birds) was estimated at respectively 0.188 (± 0.072) and 0.696 (± 0.138).

Population trajectories were calculated for the colony on Vlieland in order to predict the total pool of breeding females and calculate the expected annual fraction of non-breeding in the population. This model exercise relied on actual data on the number of breeding females and fledglings (assuming equal sex ratio at fledging) and estimations data for the probability of breeding in 2nd and 3rd year old females and the annual survival of juvenile, immature, all adult and only breeding adult females. Comparison of the empirical census data revealed the existence of widespread non-breeding in adult females of the Vlieland population (up to 60%) during two periods which coincided with mass-mortality in the beach surveys and colony declines (1988-1992, 2000-2003).

The rapid recovery of the Vlieland colony between 1991 and 1994 can be accounted for by re-entry from the extensive pool of non-breeding adult females originating in 1988-1990 as revealed by the population modelling. The current decline (starting 2000) has not yet been reversed.

This study shows that long-lived breeding bird species such as the Common Eider can qualify as a quality indicator of an entire ecosystem, i.e. Wadden Sea, providing they are the subject of long-term ecological investigations. A simple enumeration of the total number of breeding females is an inadequate measure of the underlying processes, and study must include total mortality estimated from ringed individuals, estimates on the annual production of young, and the annual rate of non-breeding.

Introduction

Non-breeding (or intermittent breeding) is one of the major determinants of fitness at the individual level (Newton 1989). Non-breeding has been frequently reported in many species especially for long-living species, such as raptors (Newton 1985), gulls (Bradley et al. 2000, Hatch 1987), geese (Rockwell et al. 1985), cormorants (Boekelheide & Ainley 1989), auks (Jones & Montgomerie 1992), flamingos (Cezilly et al. 1996) and sea ducks (Coulson 1984). In order to survive individuals may decide to skip current reproductive effort if insufficiently recovered from the previous breeding attempt and/or when the current circumstances were not sufficient to allow sustainable reproduction. Intermittent or skipping reproduction can be interpreted as an adaptive strategy to avoid the potential costs
of breeding and to increase the Residual Reproductive Value and maximize Lifetime Reproductive Success (Aebischer & Wanless 1992, Wooler et al. 1989).

At the population level, non-breeding affects the growth rate of a population and is potentially an important regulatory mechanism (Hémery et al. 1986). The importance of non-breeding has been undervalued in population biology and evolutionary ecology (Cam et al. 1998). Extensive non-breeding has been reported for a breeding population of Common Eiders Somateria mollissima in England with non-breeding varying up to 65% in some years (Coulson 1984). Coulson studied an individual colony over a twenty-five year period and relied on an ongoing ringing programme to elucidate the demographic factors that might explain the changes in numbers of breeding eiders he observed (increasing trend 1958–82). Common Eiders are capital breeders and females use body condition relative to a fixed threshold as a cue for breeding (Drent & Daan 1980). Females rely completely on stored reserves for breeding (Thomas 1988), which are stored prior to breeding in the vicinity of the breeding colony (Christensen 2000, Parker & Holm 1990). In the Dutch breeding colony on Vlieland, female eiders are non-migratory and extremely philopatric to the natal and breeding colony throughout their annual cycle (Swennen 1991a), and are dependent on food availability near the breeding colony for survival and reproduction.

In this paper we investigated the temporal decline (1988–1993) in the number of breeding females, and the subsequent recovery up to 2000 which was observed in the total Dutch breeding population and individual colonies. Detailed information on breeding reproduction and survival of the breeding colony on Vlieland (1974–2003) was used to calculate a reconstruction of the population trajectory of the potential breeders in order to distinguish whether the observed declines in breeding numbers relate to reduced survival and/or non-breeding.

First, how did the size of the breeding population on Vlieland develop since the re-establishment in 1906? And, how did the colony develop with respect to total number of fledglings produced? Long-term data on the number of breeding females was based on an historic reconstruction until 1962 (c.f. Swennen 1976a, 1991a). Since then, the number of breeding females and fledglings produced were estimated annually.

Second, did total annual mortality vary between years and within years? Did patterns in total mortality differ in years with mass-mortality? Mortality was estimated for each month using beach surveys of carcasses (1977/78 – 2002/03) in order to calculate annual (November to October) and seasonal (winter: November – April) estimates.

Third, how did annual survival of females vary in time? Did survival vary with age and breeding? Estimates of annual female survival were calculated using MARK. Annual survival of juvenile, immature and all adult females was estimated using the females caught and banded with steel rings as fledgling (1975–1985), while survival of adult breeding females (representing a sub-sample of the total
pool of adult females) was estimated using breeding females caught at the nest (1974–2003). This independent data set allowed comparison with the mortality estimated from the beach carcass survey 1978–2003.

Fourth, what was the probability of first breeding in 2nd and 3rd year old females? The probability of first breeding in 2nd and 3rd year old females was based on females ringed as fledgling and subsequently reported as breeding in the colony in the following years using all data females ringed as fledglings (aluminium: 1962–1973; steel: 1974–85).

Finally, population trajectories for the breeding colony on Vlieland were calculated in order to explain whether the observed declines in the observed number of breeding females (1988–94 and since 2000) were related to reduced survival and/or increased non-breeding?

**Methods**

**Study area**

The Dutch section of the Wadden Sea (N 52° 45' – N 53° 33' and E 6° 43' – E 6° 56') is a large tidal area (2409 km²) in the northern part of the Netherlands and is characterised by tidal mud- and sand flats with gullies, and natural beds of Atlantic Blue Mussels Mytilus edulis and Edible Cockles Cerastoderma edule occurring in the tidal and sub-tidal parts of the Wadden Sea. Vlieland is one of the six coastal barrier islands and is located in the western part of the Wadden Sea (1618 km²).

**Data collection**

**Breeding biology of the colony on Vlieland**

**Breeding females and fledglings**

The development of the size of the breeding colony (expressed as the number of breeding females) on Vlieland since the beginning of the 20th century was based on previous reviews (Swennen 1976a, Camphuysen 1996) and extended up to the breeding season of 2003. Since 1962, annual surveys on the number of breeding females are indirect and derived from counts of birds on the water around the colony (Duiven & Zuidewind 2001) conducted prior to the hatching of the first nest, which was in general observed in the second week of May. This count is based on a complete survey of males (where juvenile and adult can be distinguished) and female eiders taken all together due to difficulties in aging females in the field. The number of breeding females was calculated as follows on the assumption that the breeding females are all on the nest and that the ratio of breeding females to adult males is 1:1:
Breeding females = Adult males – (all females – juvenile males) \hspace{1cm} (1)

Missing data (1992, 1996 – 1999) was imputed using monitoring data of a fixed plot in the Vlieland colony (Vallei van het Veen, unpublished data Peter de Boer) using those years when data of both types of survey were available (breeding females = 1752*Log(Vallei van het Veen) – 825, n = 7, R^2 = 0.76, p = 0.011).

The number of successful fledglings of 5 – 7 weeks old was assessed in the first week of July during surveys at high tide, because mortality among ducklings peaked during the first weeks after hatching and créches of fledglings rested near the natal island at high tide (Swennen 1991b). For Vlieland, fledgling data was available for 1947 and since 1962 with no data during two periods (1989-93, 1998-99). Swennen (1989) carried out experiments on the role of food and predation on the survival of fledglings and increased the number of successful fledglings at the Vlieland colony with in total 1895 fledglings in 1975 (93), 1976, (826) and 1978 (976). These experimentally raised birds were ringed so their fate can be traced.

SURVIVAL, FIRST BREEDING AND TOTAL MORTALITY OF THE VLIELAND CONTINGENT

Estimating time and age dependent female survival and reporting rates of a local population followed standard procedures as applied to ringed individuals. Survival (Φ) and recovery rates (ρ or probability of a marked bird being reported dead) were estimated for live capture and dead reporting data using MARK (White & Burnham 1999). The NIOZ (1963–1996) and Alterra/RuG teams (2001–2003) caught Eiders in the Wadden Sea during a long-term banding program with dead birds being reported to the Dutch Bird Banding Scheme (Vogeltrekstation Heteren). The analysis was restricted to females due to their extreme philopatric nature of breeding, i.e. life-time dependence on the colony of hatching and breeding (Coulson 1984, Swennen 1991a). In the Netherlands, Eiders were caught since 1963 and ringed with steel rings starting in 1974, which were used in this analysis. Ringing data was available for breeding adult females caught at the nest (1974–2003: between the end of April and the end of May) and for females caught as 6 to 8 week old fledglings near the colony (1975–1985: the beginning of July). Fledglings were caught around the age of 6–8 weeks, because mortality among juveniles was predominantly observed during the first 4 weeks since hatching (Swennen 1989). Time-dependent survival was analysed with a year running from 1 November until 31 October.

Time dependent-survival of females in the breeding pool was estimated for adult breeding females (caught at nest: n = 2109), and for juvenile, immature and adult females (caught as fledgling: n = 2238). The inclusion of time and age-dependent survival and reporting rates in the models was determined by the lowest value of the Akaike Information Criterion (AIC), which selects the most parsi-
monious model explaining the data best with the smallest number of parameters. In MARK, the fit of the model to the data (H0: model not different from data) was tested by means of a bootstrap Goodness of Fit (running 100 simulations). Significant individual model hypothesis, only if nested, were tested by likelihood ratio test (LRT) and were considered significant at p < 0.05 (White & Burnham 1999). The degree of over-dispersion was given by the variation inflation factor \( c \).

Models were corrected for over-dispersion at values of \( c \geq 2 \) using the adjusted over-dispersion factor \( c \), which was calculated as the ratio between the models deviance and the average boot-strapped deviance, and the most parsimonious corrected model was subsequently selected by the lowest value of QAIC.

**Age of first breeding**
The probability of first breeding in relation to age was calculated using the following model:

\[
E[x_{ij}] = n_j \cdot p_{ij} = n_j \cdot \{(m_i \cdot b(j-i) \cdot s(j-i)) / (\sum k<j) m_k b(j-k) s(j-k)\},
\]

with \( x_{ij} \) the number of female birds, recovered in year \( j \), which were ringed in year \( i \), \( n_j \) the number of female birds, recovered as breeding in year \( j \), \( p_{ij} \) the probability that a bird recovered in year \( j \) was ringed in year \( i \), \( m_i \) the number of females ringed as fledgling \( m \) in year \( i \), \( b(j-i) \) the breeding fraction of birds of age \( j-i \), \( s(j-i) \) the probability of annual survival of birds of age \( j-i \). Hence, \( x_{ij} \) followed a multivariate hypergeometric probability distribution, but since \( m \gg n \) this can be approximated by a multinomial distribution. So the log-likelihood \( L = -\sum x_{ij} \log p_{ij} \) was minimised in order to obtain parameter estimates. It was assumed that \( b(j-i) \) equals 0 when \( (j-i) \leq 1 \); \( b(j-i) \) equals \( b_2 \cdot b \) when \( (j-i) = 2 \); \( b(j-i) \) equals \( b_3 \cdot b \) when \( (j-i) = 3 \); and \( b(j-i) \) equals \( b \) when \( (j-i) > 3 \). Furthermore for \( (j-i) > 1 \), the survival rate \( s(j-i) = s_0 s_1 j^i \) when \( i < 1974 \) (aluminium rings) and \( s(j-i) = s_0 s_2 j^i \) when \( i \geq 1974 \) (steel rings). Hence \( s_1 \) includes the rate of ring loss.

**Total mortality derived from beach surveys of the Dutch coast-line**
Total annual mortality of Common Eiders (or the total estimated number dead birds) in the Wadden Sea area was assessed by numerous volunteers (participating in the long-term national Beached Bird Survey or BBS along both North Sea and Wadden Sea shorelines) as reported by Camphuysen et al. (2002). BBS were conducted by walking along the high-tide line while counting and describing all encountered dead corpses with respect to age, sex, oil and freshness of the corpse, and double counts were avoided by clipping the primaries of both wings. The total estimated number of dead Eiders was calculated using log-linear models with a Poisson distribution, a log-link and over-dispersion. Data was corrected for effort and length of the transect, and the number of dead Eiders encountered during BBS was assumed to be equal to the effort (Ens & Kats 2004, Kats et al. 2007a).
The data was best explained by a model with transect, year and month as factors and the month by year interaction. One has to realise that the current estimates of the total annual mortality are an underestimation representing the minimum total mortality, because corpses were transported by currents outside the Wadden Sea area, and sometimes Eiders have been removed from coastal areas prior to our surveys to avoid complaints from tourists, which was observed on Texel (pers. obs. RK). For the temporal patterns in mortality, total mortality was separated for winter (1 November – 30 April) and summer (1 May – 31 October).

**Modelling the expected size of the breeding colony on Vlieland**

The variation in the size of the breeding population was modelled for the colony of Vlieland (1978–2002) in order to determine whether the low numbers of breeding females (1988–94 and since 2000) related to increased mortality and/or due to periodic non-breeding. Population trajectory of the total pool of breeding females (PBF) was calculated from estimated breeding and survival parameters using the following equations:

\[
P_{BF(t+1)} = N_{BF(t)} * S_{ad(t)} + R_{(t+1)} \]  

\[
R_{(t+1)} = + (N_{F(t)} * SRF * S_{juv(t)} * A_{B_{juv}}) \]  

\[
+ (N_{F(t-1)} * SRF * S_{juv(t-1)} * S_{imm(t)} * A_{B_{imm1}}) \]  

\[
+ (N_{F(t-2)} * SRF * S_{juv(t-2)} * S_{imm(t-1)} * S_{imm(t)} * A_{B_{imm2}}) \]  

\[
+ (N_{F(t-3)} * SRF * S_{juv(t-3)} * S_{imm(t-2)} * S_{imm(t-1)} * S_{ad(t)} * A_{B_{ad}}) \]

where \( t = \) time, PBF = total pool of breeding females, \( R = \) the number of new recruited females, \( N_{BF} = \) actual number of breeding females (Figure 9.2), \( N_{F} = \) total number of fledglings or at age of 6–8 weeks old (Figure 9.2), SRF = sex ratio of 1 at fledging (Swennen 1991a), \( S = \) survival, ad = adult, juv = juvenile or 1\(^{st}\) year old, imm = immature or 2\(^{nd}\) and 3\(^{rd}\) year old, \( A_{B} = \) probability of age dependent breeding, imm1 = 1\(^{st}\) year immature or 2\(^{nd}\) year old, imm2 = 2\(^{nd}\) year immature or 3\(^{rd}\) year old. Trajectories were calculated using annual survival estimates of juvenile, immature and adult breeding females, the probability of breeding in 2\(^{nd}\) and 3\(^{rd}\) year old females, the total number fledglings produced, and the sex ratio at fledging, and were compared with the observed number of breeding females. The total pool of breeding females in the first year of the population trajectory, i.e. 1974, was varied by increasing the proportion of the non-breeding for this year from 0\% to 50\%. Trajectories were calculated using the observed number of fledglings, constant and time-dependent survival of juveniles, immatures and (1) all adult females, (2) only adult breeding females. Calculations were done separately with (3) the actual number of experimentally increased number of fledglings (1976–1978) or alternatively the number of “natural” fledglings estimated for those three years (without the experimental supplement).
Recruitment of the colony on Vlieland was assumed to depend solely on local reproduction (i.e. the number fledglings produced in previous years in the same colony), because only a small fraction (9 out of 641) of the breeding females were recaptured at the neighbouring island indicating negligible exchange (Swennen 1991a). No data was available for the number of fledglings produced in 1989, 1998 and 1999, but fledgling estimates were calculated using the number of breeding females as predictor since 1983 (Fledglings = 0.4626*(Breeding females) – 575, \( R^2 = 0.393 \), \( F = 10.4 \), d.f. = 17, \( p = 0.005 \)) and were estimated at respectively 456, 783 and 881. Two population trajectories were calculated with a constant or long-term average survival and a time-dependent survival of juveniles, immatures (2nd and 3rd year old birds) and adults (older than 3 years and breeding females).

Results

Settlement, colony size and fledglings
The first breeding female on Vlieland was found in 1906 and the colony increased from 21 nests in 1928 to 350 nests in 1940, which was also the size of the total Dutch breeding population. The colony grew rapidly to 4000 in 1960 representing 70\% of the total breeding population. A steep decline to 800 nests in 1968 was observed, but the size of the breeding colony recovered slowly to approximately 2200 around 1980 (representing 45 \% of total breeding population). Since then, the colony approached stability around an average colony size of 2135 fluctuating between 1035 in 1991 and 2716 in 1999, but declined steeply thereafter (Fig. 9.1).

The long-term data on number of fledglings produced in the breeding colony of Vlieland extends with some gaps from 1962 to 2003 and averages 533 fledglings-year but inter-annual fluctuations were large (0 – 3230) (Figure 9.1). The number of fledglings was low between 1966 and 1977 (70 fledglings-year), but recovered in the period 1978-1988 (mean 753 fledglings-year). Between 1990 and 1993 the annual output was less than 10 fledglings with respectively 6, 3, 0 and 0 fledglings.

Total mortality
The total mortality from the beach carcass survey fluctuated widely (Figure 9.2: estimated annual total 922 – 22527) and was predominantly observed in winter (22 out of 26 years) between November and April. Over all years winter mortality (November through April) accounted for 65\% of the annual carcass finds. Mortality predominating in summer (May through October) was only observed twice (1996: 49.6\%; 1998: 48.7\%) in years with low overall losses, but in three consecutive years clustering around a major mortality event (1989: 49.3\%; 1990: 22.4\%; 1991: 44.1\%). For further analysis we have classified ten years as “kill-years” of heightened mortality (1985, 1989–1993, 1995, 1996, 2000–2002) and display the monthly totals in Figure 9.3 as contrasted to the “non-kill years”. The
total number of Eiders reported dead per month in the beach surveys was on average 2.9 times higher in kill years (peaking in spring and early summer, Figure 9.3). These seasonal trends can be compared with the number of adult female breeders ringed at the nest (Vlieland) subsequently reported dead, sorted according to the same classification of years. Mortality of the local resident breeding females peaked in spring and early summer, with a pronounced May peak in the “kill-years”

**Female survival**

Female survival of three age classes (juveniles, immatures, adults) using females caught at fledglings (1975–1985) and of adult breeding females (age unknown) caught at the nest (1974–2003) were based upon estimates of the most parsimonious model, which included time-dependent survival and constant reporting rates for both datasets. Long-term average female survival increased from 0.926 ± 0.028 in juveniles (Figure 9.4A) to 0.971 ± 0.010 in immatures (Figure 9.4B) and to 0.981 ± 0.002 in adults (Figure 9.4C) for females caught as fledgling. Variation was large between years within each age-class, but decreased with age-class (Figure 9.4A-C). Long-term annual survival of breeding females caught as breeding females at the nest averaged 0.927 ± 0.008, but averaged 0.872 during 10 ‘kill’-years
Figure 9.2 Beach survey of total mortality of Common Eiders *Somateria mollissima* in the Wadden Sea area (1977/78 – 2002/03) during winter (November – April: white bars) and summer (May – October: black bars). Years commence in November, and winter 77/78 is booked as 1978. Years with increased mortality of nesting female eiders (see Figure 9.4D) marked with asterisks (*).

Figure 9.3 Seasonal patterns of mortality (expressed as the monthly average number of birds reported dead with ± s.e.) in adult breeding female Common Eiders *Somateria mollissima* ringed at the nest (1974–2003) in the colony of Vlieland in (A) non-kill years and (B) kill-years (1984, 1988–1992, 2000–2003), and the total estimated number of Eiders reported dead in the Wadden Sea area in (C) non-kill years and (D) kill-years (1984, 1988–1992, 2000-2003). Years run from November through October and were defined as kill-years when survival in adult breeding females was reduced (< 0.90) and total mortality was above average (>5000). Females ringed as juveniles were not included.
Annual survival estimates of adult females of both datasets were positively correlated (see text Figure 9.4 and Tables 9.1A, 9.1B and 9.2).

Female survival for adults ringed at the nest was best explained by total mortality in winter ($F=32.51$, $P<0.001$), but was not improved by including mortality in summer ($F=2.19$, $P=0.15$). Female survival was negatively related to total annual mortality as determined from the beach surveys, both for individuals originally ringed as fledgling and recovered as juvenile, immature, or adult as well as those ringed as adult on the nest (Figure 9.5). The tight relationship between the data for nesting females from Vlieland with the general beach surveys dominated by eiders from other populations argues for accepting a common and local cause behind variation in mortality in these disparate groupings.
Table 9.1A Results of annual or time-dependent survival models based on recoveries of dead breeding female Eiders caught at the nest and banded in the breeding colony on Vlieland, The Netherlands. (t = time, S = survival rate, r = reporting rate, c = constant).

<table>
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<th>Model</th>
<th>AIC</th>
<th>AIC Weight</th>
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Table 9.1B Results of the Common Eider survival and recovery models based on recoveries of dead eiders ringed as female fledgling of 6 – 8 weeks old in the colony of Vlieland, the Netherlands: testing age dependence in annual survival and reporting rates with the models listed ranked by the Akaike Information Criterion (AIC) with the most parsimonious model at the top.

<table>
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<th>Delta AICc</th>
<th>AICc Weight</th>
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Model notation:
S = Φ = survival,
r = ρ = reporting rate,
t = time or annual dependent parameter,
c = constant parameter,
JUV = juvenile or 1st year,
IMM = immature or 2nd year,
AD = adult,
XX age = number of age classes
Age of first breeding
The first model was considered to be the best model (Table 9.3A) and resulted in the estimated probability of breeding in the second year at 0.188 (± 0.072 S.E.) and in the third year at 0.696 (± 0.138 S.E.) (Table 9.3B). Breeding was expected to be absent during the first year with the probability set at 0, but females of 4 years and older are able to breed with a probability of 1.

Modelling the breeding population on Vlieland: separating mortality from non-breeding
Several population trajectories were calculated to estimate the total pool of breeding females in order to investigate the observed declines or suppressions in the number of breeding females and finally to distinguish mortality from non-breeding. Therefore, the total pool of breeding females in the colony of Vlieland was estimated using the number of breeding females, number of female fledglings, and the probability of breeding in 2nd and 3rd year old females, survival of juveniles,
Non-breeding

Figure 9.5 Total annual mortality in the Wadden Sea area and female survival in the colony of Vlieland. Survival of females (A) ringed as fledgling (1975-1985): juvenile ($S_{\text{juv fem}} = -0.000041\times\text{Mortality} + 1.03$, $R^2 = 0.73$, d.f. = 7, $p = 0.007$; black squares, thin solid line), immature ($S_{\text{imm fem}} = -0.00002\times\text{Mortality} + 1.01$, $R^2 = 0.56$, d.f. = 8, $p = 0.020$; open circles, dashed line) and adult females ($S_{\text{ad fem}} = -0.0000012\times\text{Mortality} + 0.9867$, $R^2 = 0.34$, d.f. = 25, $p = 0.0019$; grey triangles, solid line), and (b) ringed as breeding female (1974-2003): breeding female ($S_{\text{breeding fem}} = -0.0000059\times\text{Mortality} + 0.957$, $F = 46.0$, $R^2 = 0.42$, d.f. = 25, $p = 0.0002$; grey squares, bold solid line). Years of heightened mortality (arbitrary boundary of survival of breeding females less than 0.900) highlighted in lower panel.

Table 9.3 Model results for estimating the probability of breeding for females only in the second and third year after fledgling: A) log-likelihood (L) of the models, and B) parameter estimates for the first model.

<table>
<thead>
<tr>
<th>A) Model</th>
<th>L</th>
<th>Parameters</th>
<th>B) Parameter</th>
<th>Estimate</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full</td>
<td>803</td>
<td>86</td>
<td>$b_2$</td>
<td>0.188</td>
<td>0.072</td>
</tr>
<tr>
<td>First</td>
<td>870</td>
<td>4</td>
<td>$b_3$</td>
<td>0.696</td>
<td>0.138</td>
</tr>
<tr>
<td>b(1)=0</td>
<td>883</td>
<td>2</td>
<td>$s_1$</td>
<td>0.860</td>
<td>0.013</td>
</tr>
<tr>
<td>null</td>
<td>1046</td>
<td>0</td>
<td>$s_2$</td>
<td>0.956</td>
<td>0.034</td>
</tr>
</tbody>
</table>
immatures and adult breeding females. Two types of trajectories were calculated using long-term averages or annual estimates of survival. Annual survival estimates of juvenile and immature females were predicted using the significant dependence on total annual mortality (Figure 9.6).

The breeding and survival estimates used for the calculation of the population trajectory of the breeding colony on Vlieland were based on the number of breeding females (Figure 9.1), the total number of fledglings (Figure 9.1), the equal sex ratio at fledging (Swennen 1991a), propensity to breed depending on age (Table 9.3), survival of adult breeding females (Figure 9.4d), and survival of juvenile and immature females caught as fledgling (Figure 9.6). Although the model was run with constant survival to begin with, a second version with time-dependent survival is considered an improvement and the outcome is displayed in Figure 9.7.

The breeding population on Vlieland recovered until the middle of the 1980’s, underwent a large decrease between 1988 and 1991 followed by a rapid upsurge and then since 1999 the number of breeding females again declined (Figure 9.1 and 9.7). When the model outputs predicting the number of breeding females available in the population are compared to the observed colony counts (Figure 9.7) discrepancies emerge concerning both phases of rapid change. In the period 1988–1992 far fewer females nested than were alive in the population according to the model outputs (both with and without accounting for the extra input of fledglings in 1975–77) The models with fixed propensity to breed depending on age and time-dependent survival point to the existence of a considerable pool of non-breeding females during periods of lowered survival or mass-mortality (1988-1992, 2002–2003). The overall pattern did not change drastically within both models when the fraction of non-breeding arbitrarily set in the first year (1974) was increased from 0% to 50% non-breeding. The size of the total pool of breeding

![Figure 9.6](image-url) Predicted annual survival of juvenile and immature females using significant relationships in Figure 9.5. Years run from November through October.
females averaged 9 (25% non-breeding in initial year) and 18 % (50% non-breeding in initial year) higher compared to the model without non-breeding in 1974. The maximum proportion of non-breeding was predicted to be observed in 1991 and estimated between 0.64 and 0.67 for the time-dependent survival model, which was 10% lower for the constant survival model with non-breeding between 0.58 and 0.62 (Figure 9.7). These values are well within the range reported by Coulson (1984) for an eider colony in England. Further, the models predicted non-breeding in 1989 to vary between 17–26% for the constant survival models and 41–47 % for time-dependent survival models, which was in agreement with the estimate of 35 % non-breeding in 1989 reported for this population by Swennen (1991a). We conclude that the observed recovery of the Vlieland population following the decline in the late 1980s could be explained by birds from the non-

Figure 9.7 Population trajectory of the predicted pool of potential breeding female Common Eiders Somateria mollissima on Vlieland with the observed number of breeding females shown for comparison. The predicted pool of breeding females is derived from the population model (see text) using fixed propensity of breeding females in 2nd, 3rd and ≥ 4th year (Table 9.3) and time-dependent estimates of survival (St) of juveniles and immatures (Figure 9.6) and adult survival of breeding females (Figure 9.4D). For the starting year of 1974, the effect of non-breeding (nb) was varied and calculated for 0.00, 0.25 and 0.50 non-breeding. Panel (A) includes the fledglings released experimentally (1975-77, see text) and panel (B) excludes them.
breeding pool returning to nest, and does not require the postulation of an extraordinary input of fledglings from former years, or the influx of adult breeders from elsewhere. If and when the Vlieland population will recover from the decline that set in after 2001 is still unknown at present. According to the modelling a considerable proportion of the females alive in 2003 refrained from breeding so there is potential for rapid recovery.

To determine which parameters have the greatest impact on the model predictions, a sensitivity analysis was applied on both models and each parameter was lowered with 10 % and subsequently the new population trajectory was calculated. For the constant survival model, long-term (1974–2003) survival reductions of 10 % within each pre-adult (1st – 3rd year) class resulted in a total decline of 9 % of the total pool of breeding females between 1974 and 2003, but 10 % reductions in the long-term survival of breeding adult females resulted in dramatic reductions of 54 % as expected in a long-lived species.

Discussion

Explaining abrupt changes in size of the breeding colony on Vlieland
In 1906, a breeding colony of Common Eiders was established on Vlieland and after a slow start, the colony grew rapidly between 1940 and 1960 (Figure 9.1). The colony nearly crashed during the 1960s due to the pollution of coastal waters with chlorinated hydrocarbons (Swennen 1972). The colony recovered during the 1970s and entered a new plateau period in the late 1980s when the size of the colony approached 2700 breeding females. A catastrophic depression in breeding numbers was observed in 1988 with a low of only 1000 nesting females in 1990-1991 and recovery setting in from 1992 on (Figure 9.1). The collapse in breeding numbers has been related to severe reductions in the stocks of shellfish on which the eiders feed (Camphuysen 1996). The unanswered question in this scenario was to elucidate the role of non-breeding in driving these numerical changes as distinct from mortality of the nesting females. The rapid recovery from 1992 onwards could hardly be explained by entry of new recruits and hinted that non-breeding was involved in this population as had earlier been established for a nesting colony in England (Coulson 1984). Recently (2002) a sudden fall in nesting numbers at Vlieland has again been observed but the course of recovery is still unknown.

Fortunately vital parameters (breeding propensity dependent on age, mortality) can be derived from recoveries of female eiders ringed in the breeding colony on Vlieland (either as fledgling or caught on the nest). Survival of female eiders increases with age from juvenile to adults (Table 9.4), which was also reported for female eiders in Scotland (Bailie & Milne 1982). Mortality of female eiders was predominantly reported around the breeding season (Figure 9.3) and survival of adult breeding females was lower compared to all adult females (Figure 9.4C+D).
Both of these findings point to a survival cost of breeding. Survival of all age groups in the Vlieland material was negatively related to total mortality for the eider population as a whole along the Dutch coast assessed from beach carcass surveys (Figure 9.5). The Vlieland data are thus representative for more than simply a local event. The survival of all adult female eiders (0.981: Figure 9.4C) and adult breeding females (0.927: Figure 9.4D) in the Netherlands was high compared to the values of 0.80 (Paludan 1962) and 0.90 (Noer & Hansen 1990) in Denmark, 0.895 in England (Coulson 1984), but closely similar to the value of 0.96 for Scotland (Baillie & Milne 1982).

Evidence and causes of non-breeding among Eiders in the Netherlands

Life history aims to unravel the lifetime management and timing of reproduction based on the assumption that trade-offs exist between various components of fitness (Drent & Daan 1980, McNamara & Houston 1996, Stearns 1992). Managing energy between functions within the individual becomes important when the amount of energy is limited resulting in a physiological trade-off between those functions. Reproduction and survival compete for the same resources and the costs of reproduction are described by a trade-off between current and future reproduction (Reznick 1985, Stearns 1989).

The decision to breed or not to breed is controlled by the physiological or conditional state of the parent (i.e. amount of stored energy) and local environmental conditions (Drent & Daan 1980). Condition of the parent relate to territory quality (Daan et al. 1990, Lunn & Boyd 1993), fat (Witter & Cuthill 1993) and protein reserves (Houston et al. 1995), foraging skills (Heinsohn 1991), parasite load (Norris et al. 1994, Möller 1993) and immune function (Gustafsson et al. 1994). Differences in individual (Curio 1983) and/or phenotypic quality (Harris & Wanless 1995) are also involved.

Non-breeding is a widespread phenomenon and may relate to age (Forslund & Pärt 1995), body condition and individual quality (Caladine & Harris 1997), weather (Quakenbush & Suydam 1999, Rönkä et al. 2005), predators (Bertram et al. 1934, Bird & Bird 1940), dispersal (Danchin & Cam 2002), pair bond (Mougin et al. 1997, Orell et al. 2004), and food, population density and/or previous activities (Danchin & Cam 2002). Non-breeding has been reported among long-living seabirds including several species of eiders, such as Common Eider (Coulson 1984), Steller’s Eider Polysticta stelleri (Quakenbush & Suydam 1999) and King Eider Somateria spectabilis (Bertram et al. 1934, Bird & Bird 1940).

In the previous study on the breeding population of Common Eiders on Vlieland, non-breeding was assumed to be negligible, but some evidence suggested that non-breeding did occur to some extent (Swennen 1991a). Non-breeding was suspected for 1968 and estimated to involve 35% of the breeding female stock in 1989 compared to 1988. Drawing on an additional fifteen years of ring recoveries the present study using a population trajectory with time dependent estimates of
female survival confirmed that non-breeding did indeed occur and was extremely prominent around 1990 (Figure 9.7). This result was also found employing constant female survival (graph not shown). Coulson (1984) suggested that density dependent processes play an important role in the occurrence of non-breeding. This can be clarified by considering non-breeding during the phase of population growth and at population stability at our colony.

First, the population trajectory showed that non-breeding was low during population growth (1974–1980) and the size of the predicted pool of breeding females was similar to the number of breeding females (Figure 9.7). In a British breeding population of Common Eiders on Coquet Island (1968–1981), non-breeding during population growth was on average less than 10% (average: 6.3%) accompanied by larger clutches and higher survival and recruitment (Coulson 1984).

Second, the incidence of non-breeding can be considered in a breeding population approaching stability in the late 1980s (Figure 9.2). The breeding colony on Vlieland reached stability, when the colony size entered the range of 2700 breeding females coinciding with the observed long-term decline in clutch size and fecundity (expressed as the average number fledglings produced per breeding female) (Kats et al. 2007c). Similar patterns were also observed in the English breeding population, which was close to reaching stability (Coulson 1984).

Now the question remains: What demographic factors account for the observed decline in the number of breeding females on Vlieland between 1988 and 1992? Although survival of the breeding females was reduced in the years of the dip in nesting numbers, the decline set in prior to the observed declines in breeding and a recovery in survival was already observed during the years of massive non-breeding (Figure 9.4). Second, the estimated fall in survival of the breeding females is quantitatively insufficient to account for the fall in nesting numbers (compare Figure 1 with Figure 9.4D). We conclude from the population model (Figure 9.7) that a large pool of adult breeding females was in existence which adequately explains the strong and quick recovery in the number of breeding females in the following years (Figure 1). The pool of adult females was large due in part to the presence of large number of fledgling eiders released after experimental feeding trials (1975–77: Swennen 1991a, 1991b) which can be seen by comparing Figure 9.7A with 9.7B. That these experimental releases contributed to these patterns in recovery since 1992, is likely because some of those experimental females were later reported breeding (1994–96: n = 20, unpublished data Kats) and some were recovered dead as late as 2002 (unpublished data Kats). Local production during the years of the population low (1990-1993) could not affect the pool of breeding females, because the production of fledglings was nearly absent (Figure 9.1). We exclude the possibility of immigration since breeding females show a high degree of natal philopatry (Swennen 1991a). These considerations are set out in the overview (Table 9.4)

We conclude that non-breeding was the main cause of the observed decline in the breeding population between 1988 and 1992, and as argued elsewhere was
caused by a reduction in the food supply available to the eiders in the Wadden Sea (see Chapter 10). The size of the breeding colonies in the Netherlands is limited by the area mudflat near the colony and year-to-year variations in breeding were related to variation in local food supply (Kats et al. 2007c). The observed declines in breeding with increased non-breeding coincided with years when food stocks were in general low in the whole Wadden Sea (Beukema 1993, Beukema & Cadée 1996). The number of breeding females was positively related to local stock of mussels and the presence of small cockles (Kats et al. 2007c). We assume that in seasons of low food stocks, a large proportion of breeding females was not able to store locally sufficient energy in order to breed successfully. As a consequence, breeding females skipped breeding on the short term in order to survive in the long run. In the colony on Vlieland, the incidence of non-breeding is related to the density of profitable food in the vicinity of the colony, which consisted of mussels and small cockles (Figure 9.8).

However, the recent decline in the size of the breeding colony on Vlieland population since 2000 has not yet been reversed and deserves attention. The available evidence assembled in our population model suggests that the total pool of adult breeding females has declined steadily since the mid 1980s (Figure 9.7A) or at least since 1992 (Figure 9.7B). The pool at our latest estimate (2003) had fallen to the level of the mid 1970s (Figure 9.7, holds true for both models). This is an indication that the Vlieland eiders are currently faced with the accumulated impact of lower fledgling production (Figure 9.1) with lowered survival of the nesting females (Figure 9.4d). It should be noted that at the most recent survey (2003) the food stocks around Vlieland were again as low as in the year 1990 and almost as depleted as in 1991 (the all-time low in the 14-year data set, see Figure 9.8). It is a matter of great urgency to continue the study at this critical juncture.

**Table 9.4** Overview of demographic parameters implicated in collapse and recovery of the breeding population on Vlieland 1988-1993.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Conclusions</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) mortality of nesting females</td>
<td>increased but losses insufficient to explain decline (Figure 9.4d)</td>
</tr>
<tr>
<td>(b) recruitment failure</td>
<td>fledging output through 1988 adequate (Figure 9.1) despite increased mortality of juveniles and immatures (Figure 9.6) pool of potential breeders does not fall until 1991 (model, Figure 9.7)</td>
</tr>
<tr>
<td>(c) “non-breeding” or skipping breeding</td>
<td>modelling pool of potential breeding females (Figure 9.7) reveals massive non-breeding during decline (up to 2/3 of pool) and re-entry during colony recovery; degree of non-breeding is negatively related to the local food supply (Figure 9.8)</td>
</tr>
</tbody>
</table>
Implications for monitoring programs

In long-lived birds, such as Common Eiders, periodic non-breeding has been observed before and in our study coincided with unfavourable conditions for breeding. Non-breeding could be interpreted as a prudent-parent-strategy (Drent & Daan 1980) in order to survive and invest in future breeding attempts, and to increase lifetime reproductive success. As shown in this study, the occurrence and the large variation in non-breeding can have serious consequences for monitoring programs when populations of long-living birds are concerned. Monitoring specific target bird species as indicators of an entire ecosystem has its drawbacks, because monitoring programs usually rely only upon the annual count of the number of breeding females. This is not sufficient for science-based decision making, especially in long-lived species. Therefore, we strongly encourage future monitoring programs of long-lived species, such as the eider, to include the assessment of non-breeding (in addition to the assessment of the total number of breeding females) and the number of fledglings produced. It is essential to include a long-term ringing program to generate annual input of survival estimates for population modelling, which has been demonstrated in this study to be a fruitful tool for science-based decision making. In addition, further knowledge on the spatial and temporal use of the local mudflats and the extent of its dependence on these tidal food stocks near the breeding colony is needed in order to predict the effects on food shortage on breeding performance of a monitoring species.

Figure 9.8 The proportion non-breeding female Common Eiders *Somateria mollissima* in the breeding colony on Vlieland (1990-2003) in relation to the food stocks (expressed as the density of fresh weight/km²) of profitable prey (mussels *Mytilus edulis* and small cockles *Cerastoderma edule*) sampled on the mudflats near the breeding colony. The regression is shown, Non-breeding = -0.46*Log(Total profitable density) + 1.95, n = 14, R² = 0.37, p = 0.020 (taken from *Kats et al. 2007c*).
Acknowledgements
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