Population dynamics of black-tailed godwits in the light of heavy metal pollution

Roodbergen, Maja

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2010

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.
5 Diagnosing declining grassland wader populations using simple matrix models

Chris Klok
Maja Roodbergen
Lia Hemerik

Animal Biology 59 (2009): 127-144
Chapter 5

Abstract

Many populations of wader species have shown a strong decline in number in Western-Europe in recent years. The use of simple population models such as matrix models can contribute to conserve these populations by identifying the most profitable management measures. Parameterization of such models is often hampered by the availability of demographic data (survival and reproduction). In particular, data on survival in the pre-adult (immature) stage of wader species that remain in wintering areas outside Europe are notoriously difficult to obtain, and are therefore virtually absent in the literature. To diagnose population decline in the wader species; Black-tailed Godwit, Curlew, Lapwing, Oystercatcher, and Redshank, we extended an existing modelling framework in which incomplete demographic data can be analysed, developed for species with a pre-adult stage of one year. The framework is based on a Leslie matrix model with three parameters: yearly reproduction (number of fledglings per pair), yearly pre-adult (immature) and yearly adult (mature) survival. The yearly population growth rate of these populations and the relative sensitivity of this rate to changes in survival and reproduction parameters (the elasticity) were calculated numerically and, if possible, analytically. The results showed a decrease in dependence on reproduction and an increase in pre-adult survival of the population growth rate with an increase in the duration of the pre-adult stage. In general, adult survival had the highest elasticity, but elasticity of pre-adult survival increased with time to first reproduction, a result not reported earlier. Model results showed that adult survival and reproduction estimates reported for populations of Redshank and Curlew were too low to maintain viable populations. Based on the elasticity patterns and the scope for increase in actual demographic parameters we inferred that conservation of the Redshank and both Curlew populations should focus on reproduction. For one Oystercatcher and the Black-tailed Godwit populations we suggested a focus on both reproduction and pre-adult survival. For the second Oystercatcher population pre-adult survival seemed the most promising target for conservation. And for the Lapwing populations all demographic parameters should be considered.
Introduction

In the second half of the 20th century, widespread changes in European land use resulted in drastic declines in many farmland bird populations (Gregory et al. 2005; Donald et al. 2006). Agricultural intensification has been identified as the main driver behind this biodiversity loss (e.g. Tucker and Heath, 1994; Gregory et al. 2005). The Common Agricultural Policy of the European Union (EU) played a large role in land use change, and is expected to have similar dramatic effects in former eastern European countries that are now joining the EU (Van Strien et al. 2001).

An important group of farmland bird species characteristic of European agricultural meadows are grassland waders, including species such as Black-tailed Godwit (*Limosa limosa*), Lapwing (*Vanellus vanellus*), Redshank (*Tringa totanus*), Oystercatcher (*Haematopus ostralegus*), and Curlew (*Numenius arquata*). These wader species are characterized by a long life-span and a low rate of reproduction. The average age at which these species start breeding varies from one (Redshank) to about five years (Oystercatcher) (Cramp and Simmons, 1983). Per year they can raise only one brood with a maximum of four chicks to fledging (Cramp and Simmons, 1983).

In Western-Europe in the last decade of the 20th century, populations of the Black-tailed Godwit and Lapwing showed a large decline in number (>30%), while numbers of Redshank, Oystercatcher and Curlew showed a more moderate decline (10-29%). All species except the Oystercatcher are classified as declining or vulnerable according to the EU25 threat status (BirdLife International, 2004).

In the Netherlands, agricultural meadows have become an important, if not vital, breeding habitat for wader species (Beintema, 1986). Their dependence on man-made habitat makes this group vulnerable to agricultural intensification. Many different conservation measures have been taken in the form of agri-environment schemes, but their effectiveness has been much debated (e.g. Kleijn et al. 2001; Wilson et al. 2007). For effective conservation, a good understanding of the population dynamics of a species is essential (Caswell, 2001). However, good data on demographic parameters (survival and reproduction) of species are often missing. All meadow birds are (semi-)precocial, indicating that they leave the nest when hatched. This complicates reliable estimation of the number of fledglings per pair. In addition, sub-adult survival (from post fledging age to age of first reproduction) is hard to estimate as immature individuals show lower site fidelity than adults and may remain in the wintering areas during their first year(s) of life. To overcome this data-scarcity problem, Hemerik and Klok (2006) developed a population model in which a single missing demographic parameter from the full set can easily be estimated visually if the population trend is known. Their model is applicable for species with a pre-adult stage of one year.
Chapter 5

The aim of this paper was to estimate the population viability of five wader species: Redshank, Black-tailed Godwit, Curlew, Lapwing and Oystercatcher, using a population model in which incomplete demographic data can be analysed. To analyse wader species with a pre-adult stage of more than one year (Black-tailed Godwit, Curlew, Lapwing and Oystercatcher), we first extend the population model developed by Hemerik and Klok (2006). The model gives information on the yearly population growth rate and its elasticity (the proportional change in the yearly population growth rate given an infinitesimal proportional change in one of the demographic parameters). Secondly, data from literature on population status and demographic parameters of the five wader species are assembled and projected in the resulting plots of the applicable model, in order to analyse the yearly population growth rate and to infer information on the missing demographic parameter. The available data on wader species generally lack information on pre-adult survival. Therefore, we relate adult survival to both pre-adult survival (as in Hemerik and Klok, 2006) and to reproductive output.

Material and methods

Model development
We extended the general stage structured model of Hemerik and Klok (2006) for species that start breeding at an age older than one year, such as Black-tailed Godwit (3rd calendar year), Curlew (probable 3rd calendar year), Lapwing (3rd calendar year), Oystercatcher (5th calendar year) (Cramp and Simmons, 1983). In our model only females are explicitly taken into account, and we assumed that (a) the sex ratio is 1:1, (b) the population growth rate is independent of density, (c) the survival of females is equal to that of males, and (d) breeding takes place in a short period in spring (in technical terms a pulse, Caswell, 2001 p25-27). We sampled (censused) the model yearly just after juveniles have fledged (post-breeding). Figure 1 shows a simplified life cycle graph used for the model.

Yearly population growth rate
The life cycle graph in Fig. 1 can conveniently be described in mathematical form. Here, we exemplify our model with a Leslie matrix for a life cycle with a pre-adult stage of two years. A general description for life cycles with a pre-adult stage of one to \( T \) years is given in the appendix.
Figure 1. Simplified life cycle graph as used for the models with a two or four year pre-adult life stage ($T=2$ or $4$). With a pre-adult life stage of two years individuals spend one year in the juvenile and one in the sub-adult stage, whereas with a pre-adult life stage of four years, one year is spent in the juvenile and three in the sub-adult stage.
Chapter 5

The change in number of individuals in the three stage classes over the years can be assessed with equation 1 (this is an extension of eqn. 4 in Hemerik and Klok, 2006),

\[
\begin{pmatrix}
  j_{t+1} \\
  s_{t+1} \\
  g_{t+1}
\end{pmatrix} = \begin{pmatrix}
  j_t \\
  s_t \\
  g_t
\end{pmatrix} = Z_3
\]

with

\[
Z_3 = \begin{pmatrix}
  0 & q & m \\n  q & 0 & 0 \\n  0 & q & a
\end{pmatrix}
\]

Here \( q \) equals yearly survival of individuals from the age of fledging until the age of adulthood (\( T, \) here 2), \( a \) yearly survival of adult birds and the subscript 3 indicates a Leslie matrix with 3 age classes. The number of fledged young per pair per year is represented by \( m \). When the census of the model is just after juveniles fledged (post-breeding), \( j_t \) represents the number of juveniles (aged 0⁺; birds in their first year), \( s_t \) the number of sub-adult birds (aged 1⁺) and \( g_t \) the number of adult birds in year \( t \) (aged 2⁺).

Given an initial population in the different age classes, the change over the years can be assessed by iterating matrix \( Z_3 \). Under non-changing environmental conditions the population eventually grows at a yearly factor that equals the dominant (i.e. absolute largest) eigenvalue of matrix \( Z_3 \). This dominant eigenvalue (\( \lambda \)) is directly related to the intrinsic population growth rate \( r = \ln \lambda \) (Caswell, 2001). We calculated the dominant eigenvalue for values of \( q \) and \( a \) (from 0.001 to one, step 0.001) and relevant values of \( m \) for the Leslie matrix with a pre-adult stage of two years (Eq. 1) and show the line where the population growth rate equals zero (dominant eigenvalue \( \lambda = 1 \)), which separates parameter combinations where the population goes extinct (\( r < 0, \lambda < 1 \)) from the combinations where the population is viable (\( r > 0, \lambda > 1 \)). Furthermore, we show this line as a function of \( a \) and \( m \) for Leslie matrices with a pre-adult stage of one, two and four years (see appendix for the general matrix with a pre-adult stage of \( T \) years).

**Elasticity analysis**

Caswell (2001) gives formulas for defining the elasticity of matrix entries \( (z_{ij}) \) and underlying parameters of a matrix \( Z_3' \), by calculating explicitly the right and left eigenvectors for the dominant eigenvalue of the matrix. These eigenvectors have biological meaning; the right eigenvector (a column vector \( x \) for which \( Z_3' x = \lambda x \)) represents the stable age distribution, i.e. the composition of the population in age classes that the population can attain in the long run. The left eigenvector (a row vector \( y \) for which \( yZ_3' = \lambda y \)) gives the reproductive values, i.e. the expected relative reproductive output of the different age classes. We derived the elasticities of the lower level parameters \( a, q \) and \( m \) of \( Z_3 \) using implicit differentiation of the characteristic equation \( \det(Z_3 - \lambda I) = 0 \). The characteristic equation \( f_3(\lambda) = 0 \) of this
matrix is given in Eq. (2). For convenience, the derivative with respect to $\lambda$ is denoted $f_3'(\lambda)$

$$f_3(\lambda) = \lambda^3 - a\lambda^2 - \frac{mq^2}{2} \lambda = 0$$ (2)

The elasticity of a general lower level parameter $h$ (here $m, a, q$) of matrix $Z_3$ is defined as:

$$e_3(h) = \frac{h \partial \lambda}{\lambda \partial h}$$ (3)

From implicit differentiation of Eq. (2) we can derive $\frac{\partial \lambda}{\partial h}$. Multiplying the result with $\frac{h}{\lambda}$ yields the elasticities:

$$e_3(a) = \frac{a\lambda}{f_3'(\lambda)}, e_3(q) = \frac{mq^2}{f_3'(\lambda)}$$ respectively $e_3(m) = \frac{mq^2}{2f_3'(\lambda)}$ (4)

The derivation of the elasticity of the underlying parameters of a Leslie matrix with a pre-adult stage of $T$ years is given in the appendix.

The elasticity of an underlying parameter has biological meaning: it quantifies the effect of relative change in a parameter value in terms of a relative change in the population growth rate.

**Literature-derived demographic data for five wader species**

We selected population studies on the five species of meadow birds from published literature, based on the completeness of the presented set of demographic parameters. We selected only those studies that reported data on at least two of the following parameters: pre-adult survival, adult survival, and/or reproduction, complemented with data on population trends.

**Results**

**Yearly population growth rate**

The largest eigenvalue ($\lambda$) for the 3x3 Leslie matrix Eq. 1 was analytically derived as

$$\lambda = \frac{a}{2} + \frac{\sqrt{a^2 + 2q^2 m}}{2}$$
Lines in the adult ($a$), and pre-adult ($q$) survival plane, where the largest eigenvalue equals one (implying an intrinsic rate of population growth equal to zero) for the 3x3 Leslie matrix, are drawn in Figure 2a for a number of fledglings produced per pair ($m$) equal to 0.4, 0.6,.., 1.6. The parameter space to the right and above the lines indicates combinations of $a$ and $q$ where the population is viable ($\lambda>1$). With a higher value of $m$, the part of the parameter space where a population is viable increased (Fig. 2a). From the perspective of conservation of a species, not only $\lambda =1$ but also the parameter space around it is of interest. In Figure 2b and 2c we therefore indicated the combinations of $q$ and $a$ for which $\lambda \in (0.95, 1.05)$ (between thin dotted lines). This illustrates the uncertainty in $\lambda$ from the demographic parameters for $m$ values of 0.4 (Fig. 2b) and 1.6 (Fig. 2c). The elasticities of the three lower level parameters $a$, $q$, and $m$ were indicated (see Table 1).
q and m are proportional with ratios $\frac{2a\lambda}{mq^2} : 2 : 1$. This is illustrated in Figs. 2bc, which shows that, for the larger value of m (1.6; Fig. 2c), the area where pre-adult survival (q) has the largest elasticity, is small compared to the same area in Fig 2b (m = 0.4).

Figure 3 is similar to Fig. 2 but now the lines with $\lambda = 1$ (Fig. 3a) are depicted in the adult survival (a) and number of fledglings per pair (m) plane, for values of sub-adult survival (q) varying from 0.4, 0.5,..., 0.8. As in Fig. 2a, the population is viable $\varepsilon(\lambda > 1)$ above and to the right of the lines. Figs. 3bc show the line $\lambda = 1$ (thick dashed) and the space around this line where $\lambda(0.95, 1.05)$ (between thin dotted lines) for q
values equal to 0.4 (Fig. 3b) and 0.8 (Fig. 3c), moreover, the ranking of elasticities is depicted. A larger value of \( q \) resulted in a larger area of the parameter space in which the population is viable. In addition, the area where \( q \) has the highest elasticity increased, whereas the area where the elasticity of \( a \) is higher decreased (compare Fig. 3c with 3b).

The derivation of the characteristic equation for an \( n \times n \) Leslie matrix with the same general structure is given in the appendix. For Leslie matrices larger than 4x4 the analytical derivation of the largest eigenvalue resulted in a complicated form, and therefore can easier be solved numerically. The derivation of the elasticities of the underlying parameters is also given in the appendix. Elasticities of the parameters
Meadow bird population models

\[ \frac{2a\lambda^{n+1}}{mQ^{n+1}} : n + 1 : 1 \]

with \( n \) the duration of the pre-adult stage. This equation indicates that the elasticity of \( m \) is always smaller than the elasticity of \( q \) and \( a \) (with the exception of life-histories with a pre-adult stage of one year, where \( e(m) = e(q) \)).

To illustrate the model for the Oystercatcher and Redshank we also depicted the yearly population growth rate and elasticity results of a 5x5 (Fig. 4) and 2x2 Leslie matrix (Fig. 5) in the \( a, m \) plane similar to Figure 3.

As can be inferred from Fig. 5a, 3a and 4a (respectively pre-adult stage of one,

![Figure 5. As in Fig. 3 but for species with a pre-adult stage of one year (after Hemerik and Klok, 2006). For pre-adult survival (\( q \)) ranging anticlockwise from 0.4, 0.5,..., 1.0.](image)
two and four years), an increase in the duration of the pre-adult stage results in more steep lines $\lambda=1$, showing lower dependence on $m$ values. This implies that the pre-adult survival ($q$) must increase for a population to remain viable for a certain combination of $a$ and $m$. This is also apparent from the “equal” elasticity lines in Fig. 3b,c to 5b,c: the area, where $q$ has the highest elasticity, increased with the duration of the pre-adult stage, while the area, where $a$ has the highest elasticity, decreased.

**Inference on missing demographic parameter**

Table 1 summarizes the available data on the population status, survival and reproduction in the five wader species in western Europe. Data on pre-adult survival are missing for three species, and data on reproduction are absent for the Lapwing. For the two Oystercatcher populations and one Black-tailed Godwit population, full data on demographic parameters were reported (Harris, 1967; Schnakenwinkel, 1970; Groen and Hemerik, 2002). Most survival estimates are based on live resightings based on return rate only (Table 1).

The demographic data (Table 1) of the five wader species are plotted in Figs. 2 to 5 and the inference from these graphs on the missing demographic parameter is given in Table 1. For example it can easily be inferred graphically from the figures that populations cannot be viable for two reported datasets on Curlew (Fig. 3a) and Redshank (Fig. 5a). For all data sets adult survival has the highest elasticity suggesting that this demographic parameter is an important target for management.

**Discussion**

Most data on survival (Table 1) are based on live resightings, and estimates are not corrected for resighting probability. In resighting studies, dispersal from the study site cannot be separated from mortality, and therefore survival in these studies tends to be underestimated (Lebreton et al. 1992). Not correcting for resighting probability will further depress survival estimates, which indicates that survival values of the populations in Table 1 are probably higher than reported.

For the two Lapwing populations, the model suggests a number of fledglings per pair ($m$) of 0.69 and 1.36 respectively, which is higher than the average of wader productivity estimates reported in the literature, which falls below 0.5 (Roodbergen et al. in prep). With a number of fledglings per pair ($m$) $<$0.5, the population can only be viable ($\lambda$>1) if both pre-adult and adult survival reaches values of 0.8 or more (read from Fig. 2a), whereas the reported estimates for adult survival in waders range from 0.6-0.83 (Roodbergen et al. in prep). Based on these data we suggest future management of these declining populations to focus on adult and pre-adult survival (inferred from the elasticity pattern Fig. 2c) and reproduction.

Our model result on pre-adult survival ($q$) for the Black-tailed Godwit population
Table 1. Estimates of demographic parameters reported in the literature for Redshank (Tringa totanus), Lapwing (Vanellus vanellus), Black-tailed Godwit (Limosa limosa), Curlew (Numenius arquata) and Oystercatcher (Haematopus ostralegus). Not all authors give the standard deviations and therefore just the means are given. Population trend is coded as −/0/+ for declining, stable and increasing populations respectively.

<table>
<thead>
<tr>
<th>Species</th>
<th>Country</th>
<th>Period</th>
<th>Fledgling production (m)</th>
<th>1st year survival</th>
<th>Adult survival (a)</th>
<th>Method</th>
<th>Population trend</th>
<th>Conclusion based on calculations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redshank</td>
<td>Sweden</td>
<td>1997-2003</td>
<td>0.125</td>
<td>nr</td>
<td>0.797</td>
<td>L</td>
<td>o</td>
<td>λ&lt;1 for all possible values of q</td>
</tr>
<tr>
<td>Lapwing²</td>
<td>Great-Britain</td>
<td>1963-1998</td>
<td>nr</td>
<td>0.63</td>
<td>0.82</td>
<td>D</td>
<td></td>
<td>λ&gt;1 if m&gt;0.69 (based on q = √(0.63 0.82))</td>
</tr>
<tr>
<td>Lapwing³</td>
<td>Great-Britain</td>
<td>1930-1988</td>
<td>nr</td>
<td>0.6</td>
<td>0.71</td>
<td>D(Haldane)</td>
<td></td>
<td>λ&gt;1 if m&gt;1.36 (based on q = √(0.6 0.71))</td>
</tr>
<tr>
<td>Black-tailed Godwit⁴</td>
<td>Netherlands</td>
<td>1984-1987</td>
<td>0.81</td>
<td>0.19</td>
<td>0.81</td>
<td>L(r)</td>
<td></td>
<td>λ&gt;1 if q&gt;0.68</td>
</tr>
<tr>
<td>Black-tailed Godwit⁵,⁶</td>
<td>Netherlands</td>
<td>2002-2005</td>
<td>0.24</td>
<td>nr</td>
<td>0.93</td>
<td>L</td>
<td>o</td>
<td>λ&gt;1 if q&gt;0.77</td>
</tr>
<tr>
<td>Black-tailed Godwit⁵,⁶</td>
<td>Netherlands</td>
<td>2002-2005</td>
<td>0.52</td>
<td>nr</td>
<td>0.81</td>
<td>L</td>
<td></td>
<td>λ&gt;1 if q&gt;0.86</td>
</tr>
<tr>
<td>Black-tailed Godwit⁷</td>
<td>Netherlands</td>
<td>1960-2000</td>
<td>nr</td>
<td>0.36</td>
<td>0.77</td>
<td>D</td>
<td></td>
<td>λ&gt;1 if m&gt;1.66 (based on q = √(0.36 0.77))</td>
</tr>
<tr>
<td>Curlew⁸</td>
<td>N-Ireland</td>
<td>1993-1995</td>
<td>0.235</td>
<td>nr</td>
<td>0.85</td>
<td>L(r)</td>
<td></td>
<td>λ&lt;1 for all possible values of q</td>
</tr>
<tr>
<td>Curlew⁹</td>
<td>Sweden</td>
<td>1985-1992</td>
<td>0.25</td>
<td>nr</td>
<td>0.82</td>
<td>L(r)</td>
<td>+</td>
<td>λ&lt;1 for all possible values of q</td>
</tr>
<tr>
<td>Curlew¹⁰</td>
<td>Germany</td>
<td>1973-1980</td>
<td>0.3</td>
<td>nr</td>
<td>0.885</td>
<td>L(r)</td>
<td></td>
<td>λ&gt;1 if q&gt;0.88</td>
</tr>
<tr>
<td>Oystercatcher¹¹</td>
<td>Germany</td>
<td>1949-1962</td>
<td>0.36</td>
<td>0.5</td>
<td>0.937</td>
<td>L(r)</td>
<td>+/-</td>
<td>λ&lt;1 if q&gt;0.77</td>
</tr>
<tr>
<td>Oystercatcher¹²</td>
<td>Wales</td>
<td>1963-1965</td>
<td>1.2</td>
<td>0.6</td>
<td>0.89</td>
<td>L(r)</td>
<td>o</td>
<td>λ&lt;1 if q&gt;0.65</td>
</tr>
</tbody>
</table>

nr = not reported, q = pre-adult survival, L = live resightings, (r) = return rate only, not corrected for resighting probability, D = dead recoveries, (Haldane) = Haldane’s method, not corrected for reporting probability (see Roodbergen et al. in press).¹: Ist & 2nd year.
reported by Groen and Hemerik (2002) is far higher than their reported minimum value. With their data (assuming that average pre-adult survival equals the mean of first year and adult survival \( q = \sqrt{0.19 \cdot 0.81} \)) our model estimates a yearly population growth rate of 0.88 which implies a yearly decline of about 12%, which is unrealistically strong. Survival data reported by Groen and Hemerik (2002), however, are based on resightings in a local population and the estimate for the survival from fledging to first year is a real minimum as juveniles show lower site fidelity than adults. Published estimates of survival in Black-tailed godwits range from 0.36-0.44 in the first (two) year(s) of life and 0.77-0.95 for adult birds (Roodbergen et al. in prep). With average pre-adult survival equal to the mean of first year and adult survival, which range from 0.53-0.65 (based on the data above), and an adult survival value of 0.82 (average of values in Table 1) the number of fledglings per pair \( (m) \) required to reach a viable population must range from 0.68-0.83. This value equaled 1.66 when calculated with the survival estimates reported by van Noordwijk and Thomson (2008); this far higher value results from their low adult survival estimate (Table 1). Their survival estimate is, however, based on dead-recovery data only. Survival estimates based on combined dead-recovery and re-sighting data are generally higher because census data on re-sightings contain information that birds had not died (Bressers et al. 1991; Klok et al. 2006). Given the relatively low values of \( m \) reported by Roodbergen and Klok (in press) and adult survival values which are already reasonably high (this value equals 0.93 for the 2nd study; Table 1), we suggest for the declining Black-tailed Godwit populations to focus future management more on reproductive output and pre-adult survival than on adult survival. This suggestion is strengthened by the decline in reproductive output of the species in The Netherlands over the last three decades (Schekkerman et al. in press).

Two of the reported data sets for the Curlew suggest population decline for all possible values of pre-adult survival. This is supported by the negative trend in one of the Curlew populations (Grant et al. 1999), but not the Curlew population reported by Berg (1991) for which the trend was positive (Table 1). The model estimate for pre-adult survival of the German Curlew population is relatively high compared to published estimates which range from 0.34-0.47 in the first year of life and 0.33-0.63 in the second (Roodbergen et al. in prep). Moreover, again adult survival is relatively high in all three populations, therefore we evaluate the elasticity pattern by suggesting a focus of future management on reproduction.

Interestingly, our model results for pre-adult survival in the two Oystercatcher populations, for which complete demographic data and a population trend are given, were higher than those reported in the studies (Table 1). This may partly be a consequence of the fact that our estimate of pre-adult survival \( (q) \) is actually the average survival of fledged individuals over the pre-adult lifespan. Reported data in general give estimates of survival in the first year of life (Table 1). If we calculate the
average survival for the pre-adult period assuming that survival of the third to fifth year is equal to the reported adult survival of 0.937, the resulting average pre-adult survival equals $0.729 = (0.5^{0.5}*0.937^{0.5})^{1/5}$ which is nearer to our result of 0.77. Based on the elasticity pattern and the scope for increase in the demographic data we suggest a focus on pre-adult survival and reproduction in the case of the population reported by Schankenwinkel (1970) and a focus on adult survival in the case of the population reported by Harris (1967).

The model result for the Redshank implies that either the reported reproduction is an underestimate, or this value stems from a sink population supplemented by immigration. The latter was suggested by (Ottvall, 2005). Given the fact that even if survival of pre-adult and adult individuals is unrealistically high (both > 0.9), populations cannot be viable for the given values of $m$, thus reproduction is a better target for management of this population despite the fact that adult survival has highest elasticity.

In our model we differentiate survival of immature individuals into pre- and post-fledging; pre-fledgling survival is included in the fertility factor $(m)$ determining the number of fledglings produced per pair and post-fledging survival appears as $(q)$ pre-adult survival in the model. Such a distinction may be violated since chicks are usually ringed at varying ages before fledging, such that reported data on pre-adult survival may partly include pre-fledging survival. If published estimates indeed report both fecundity (as the number of fledged chicks), and pre-adult survival (that includes pre-fledging mortality), the resulting population growth rate estimated with our model can be an underestimate.

Furthermore, we assumed that both pre-adult and adult survival are constant with age. Survival rates may gradually increase over time, both during the immature and the adult stage (Bainbridge and Minton, 1978; Insley et al. 1997). The model can be improved by including age-dependent survival. However, data on age-dependent survival rates are largely absent in literature; only three out of 40 literature references on grassland waders reported age-dependent survival (Roodbergen et al. in prep.).

**Conclusions**

As already indicated by Hemerik and Klok (2006) the model framework makes it relatively easy to graphically deduce incomplete demographic data for species. This is a valuable first step for informative management of threatened species, since the framework shows in which part of the parameter space the population is viable ($\lambda \geq 1$). Furthermore, the elasticity graphs show which demographic parameter has the largest influence on the intrinsic rate of population increase. This parameter is the most promising target for management aiming to mitigate population declines, given that this parameter has scope for increase. For the data of the five wader
species, adult survival has the highest elasticity which is a general result for long-lived species (e.g. Heppell et al. 1996). Although the demographic parameter with the highest elasticity can in principle be the best target for management (Heppell et al. 2000), improvement of this parameter may be restricted if it already has a high value (Norris and McCulloch, 2003). This is illustrated by the published data we report here, which indicate that adult survival is already above 0.8 for nine populations (Table 1). Our result that the elasticity of pre-adult survival \( q \) increased with time to first reproduction has not been reported previously.

Matrix population models that suggest management decisions by perturbation analysis (sensitivity and elasticity patterns) have been developed for many species, usually case-based and targeting a single species (e.g. Crouse et al. 1987; Klok et al. 2006). Because endangered species are present in different phylogenetic groups, more general frameworks for setting management priorities are required (Caughley, 1994; Groom and Pascual, 1998). General frameworks have been developed for mammals (Heppell et al. 2000) and birds (Sæther and Bakke, 2000; Stahl and Oli, 2006). These compare elasticities between species and show considerable variation in elasticity patterns of closely related species. Our current extension of an earlier model framework (Hemerik and Klok, 2006) differs from the existing ones in that it focuses on the practical applicability for management. It can be used as a diagnostic tool tailored to the available information on groups of species that differ in their age at first breeding.

In our model framework we assumed relatively simple dynamics; all individuals participate in breeding, no density dependence and constant environments (e.g. no stochasticity included). Obviously in the real world not all individuals breed and density dependence and stochasticity can play a role. All these factors tend to depress the yearly population growth rate (Tuljapurkar, 1990; Hemerik and Klok, 2006) which indicates that the missing demographic values inferred from our time-invariant Leslie matrix models are minimal estimates for viable populations. Elasticity patterns, however, seem robust to large changes in parameter values (Caswell, 2000; de Kroon, 2000).

**Acknowledgements**

This research was inspired by the Annual Conference of the Wader Study Group in Falsterbo, Sweden, 2006. The research of MR was supported by NWO-SSEO. We thank Johan Grasman and Jennifer Gill for their valuable comments which improved our paper.
References


Chapter 5


Roodbergen, M., Hötker, H. & Van der Werf, B. How survival and reproduction in meadow-breeding waders contribute to Europe-wide population changes: review and meta-analysis. (submitted).


Chapter 5

Appendix

For a life cycle with a pre-adult stage of $T$ years the Leslie matrix has $n \times n$ dimensions (where $T+1=n$):

$$Z_n = \begin{pmatrix}
0 & 0 & 0 & \cdots & 0 & \frac{mq}{2} & \frac{ma}{2} \\
q & 0 & 0 & \cdots & 0 & 0 & 0 \\
0 & q & 0 & \cdots & 0 & 0 & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\
0 & 0 & 0 & \cdots & 0 & 0 & 0 \\
0 & 0 & 0 & \cdots & q & 0 & 0 \\
0 & 0 & 0 & \cdots & 0 & q & a
\end{pmatrix} \quad (A.1)$$

The characteristic equation $f_n(\lambda)$ is determined by:

$$\det(Z_n - \lambda I) = 0 \iff f_n(\lambda) = 0 \quad \text{with} \quad f_n(\lambda) = \lambda^n - a \lambda^{n-1} - \frac{mq^{n-1} \lambda}{2} \quad (A.2)$$

The elasticities of the underlying parameters $a$, $q$ and $m$ of matrix $Z_n$ are easily calculated using implicit differentiation as:

$$e_n(a) = \frac{a \lambda^{n-2}}{f_n'(\lambda)} \quad (A.3)$$

$$e_n(q) = \frac{m(n-1)q^{n-1}}{2f_n'(\lambda)} \quad (A.4)$$

$$e_n(m) = \frac{mq^{n-1}}{2f_n'(\lambda)} \quad (A.5)$$

Where $f_n'(\lambda)$ is used to denote the derivative with respect to $\lambda$.

For $n=2$ it holds that $e(m)=e(q)$ and for $n>2$ $e(m)<e(q)$.

To be able to draw the figures 2bc to 5bc we have to determine where the elasticity of the adult survival $e(a)$ equals one of the other elasticities.
First consider $e(a)=e(q)$: this happens when
\[
f_n(\lambda)/\lambda = 0 \iff \lambda^{n-1} - a \lambda^{n-2} = 0 \quad \text{and} \quad \lambda n^2 = \frac{m(n-1)q^{n-1}}{2}.
\]
This results in
\[
a q^{n-2} \left( \frac{m n}{2} \right)^{n-1} = \frac{m(n-1)q^{n-1}}{2} \quad \text{(A.6)}
\]
Now we consider $e(a)=e(m)$: this happens when
\[
f_n(\lambda)/\lambda = 0 \iff \lambda^{n-1} - a \lambda^{n-2} = 0 \quad \text{and} \quad \lambda n^2 = \frac{m q^{n-1}}{2} , \text{this results in}
\]
\[
a q^{n-2} \left( m \right)^{n-1} = \frac{m q^{n-1}}{2} \quad \text{(A.7)}
\]
Rewriting equations (A.6) and (A.7), we thus have $e(a)=e(q))$ respectively $e(a)=e(m)$ in the $(a,q)$ plane if
\[
q = \frac{2}{m(n-1)} \left( \frac{m n}{2} \right)^{n-1} a \quad \text{respectively} \quad q = m^{n-1} a
\]
For particular values of $m$ and $n$, both equations are straight lines through the origin. Rewriting equations (A.6) and (A.7) in another way, we have $e(a)=e(q)$ respectively $e(a)=e(m)$ in the $(a,m)$ plane if $a$ as a function of $m$ equals:
\[
m = \left( \frac{2a}{q(n-1)} \right) \left( \frac{n}{2} \right)^{n-2} \quad \text{respectively} \quad m = \left( \frac{2a}{q} \right)^{n-1}
\]
Both equations represent curves through the origin for particular values of $q$ and $n.$
Chapter 5