

Survival, reproduction, and immigration explain the dynamics of a local Red-backed Shrike population in the Netherlands

Lia Hemerik · Marten Geertsma · Stef Waasdorp ·
Robert P. Middelveld · Hein van Kleef · Chris Klok

Received: 30 October 2013 / Revised: 22 August 2014 / Accepted: 15 September 2014
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Abstract Populations of many bird species strongly declined in Western Europe in the late twentieth century. One such species is the Red-backed Shrike in the Netherlands. In one of the last strongholds of this species, the Bargerveen Reserve, the breeding population flourished in the 1990s due to rewetting management. However, further development of the area has led to a

decline in breeding numbers such that the population is now less than half the size it was in the 1990s. Here, we analyze the vital rates of the Red-backed Shrike population in the Bargerveen. In 2001–2008, nestlings in this population were individually marked, and resighting data was collected during the breeding seasons of 2002–2009. We used estimates of vital rates based on monitoring in 2001 until 2009 to diagnose the population dynamics. Mark–recapture data were analyzed with the program MARK. The most parsimonious model gave age- and gender-specific survival probabilities of 0.12 for first-year females, 0.64 for older females, 0.20 for first-year males, and 0.54 for older males (with overlapping confidence intervals for the gender-specific adult survival values). The estimated yearly resighting probabilities were gender specific, with a higher probability observed for males (0.81) than for females (0.53). For 2001–2009, we computed an average number of offspring per breeding pair of 2.91 (with 72 % of the pairs breeding successfully). Using these vital rates, we parameterized a simple matrix model. The resulting yearly growth was 0.80. Adult survival had an elasticity of 0.83, while juvenile survival and reproduction both had an elasticity of 0.20. Because the population numbers have stabilized since 2005, the observed yearly population growth suggests that 20 % of the Red-backed Shrikes breeding in the Bargerveen are immigrants. Comparison with data on other Red-backed Shrike populations indicates that juvenile and adult survival rates can be improved in the Bargerveen Reserve. Appropriate management measures to accomplish this are discussed.

Communicated by C. Barbraud.

Electronic supplementary material The online version of this article (doi:10.1007/s10336-014-1120-2) contains supplementary material, which is available to authorized users.

L. Hemerik (✉) · R. P. Middelveld
Biometris, Department of Mathematical and Statistical Methods,
Wageningen University, P.O. Box 100, 6700 AC Wageningen,
The Netherlands
e-mail: lia.hemerik@wur.nl

M. Geertsma · S. Waasdorp · R. P. Middelveld · H. van Kleef
Bargerveen Foundation, Radboud University Nijmegen,
P.O. Box 9010, 6500 GL Nijmegen, The Netherlands

H. van Kleef
Department of Animal Ecology and Ecophysiology,
Radboud University Nijmegen, P.O. Box 9010,
6500 GL Nijmegen, The Netherlands

C. Klok
Department of Ecology and Environment, ALTERRA,
Droevendaalsesteeg 3, P.O. Box 47, 6700 AA Wageningen,
The Netherlands

C. Klok
IMARES, Ambachtsweg 8A, P.O. Box 57, 1879 AB Den Helder,
The Netherlands

Keywords Survival analysis · MARK · Juvenile survival · Adult survival · Immigration · Apparent survival · Population dynamics · Matrix model · Elasticity

Zusammenfassung

Überleben, Reproduktion und Einwanderung erklären die Dynamik einer lokalen Neuntöter-Population in den Niederlanden

Die Populationen vieler Vogelarten in Westeuropa haben sich im späten zwanzigsten Jahrhundert stark verkleinert, was auch für den Neuntöter in den Niederlanden gilt. In einer der letzten Hochburgen dieser Art, dem Bargerveen Schutzgebiet, florierte die Brutpopulation in den 1990ern infolge von Wiedervernässungsmaßnahmen. Eine weitere Entwicklung dieses Gebiets allerdings führte zu einer Abnahme der Brutzahlen, und inzwischen sind es weniger als die Hälfte. Mit dieser Studie untersuchten wir die Vitalitätsdaten in der Neuntöter-Population in Bargerveen. Zwischen 2001 und 2008 wurden Nestlinge in dieser Population individuell markiert, und Sichtungsdaten wurden während jeder Brutsaison von 2002 bis 2009 gesammelt. Zur Untersuchung der Populationsdynamik verwendeten wir Schätzungen der Populationsdaten aus dem Monitoring zwischen 2001 und 2009. Mark-Recapture (Markierung–Wiederfund) Daten wurden mit dem Programm MARK analysiert. Das beste Modell ergab alters- und geschlechtsabhängige Überlebenswahrscheinlichkeiten, die 0.12 betragen für erstjährige Weibchen, 0.64 für ältere Weibchen, 0.20 für erstjährige Männchen und 0.54 für ältere Männchen (mit überlappenden Konfidenzintervallen bei den geschlechtsabhängigen Überlebensraten der adulten Vögel). Die geschätzten jährlichen Wiederfundwahrscheinlichkeiten waren geschlechtsabhängig, mit einer höheren Wahrscheinlichkeit für Männchen (0.81) als für Weibchen (0.53). Für 2001–2009 berechneten wir eine durchschnittliche Zahl von Nachkommen pro Brutpaar von 2.91 (wobei 72 % der Paare erfolgreich brüteten). Diese Populationsdaten verwendeten wir zur Parametrisierung eines einfachen Matrix-Modells. Das resultierende jährliche Wachstum beträgt 0.8. Das Überleben der adulten Tiere hat eine Elastizität von 0.83, während sowohl das Überleben der Juvenilen als auch die Reproduktion eine Elastizität von 0.20 haben. Weil sich die Populationszahlen seit 2005 stabilisiert haben, deutet das zu beobachtende Wachstum der Population darauf hin, dass 20 % der Brutpopulation in Bargerveen aus Zuzüglern besteht. Ein Vergleich mit Daten aus anderen Neuntöter-Populationen hat gezeigt, dass das Überleben von juvenilen und adulten Vögeln im Bargerveen Schutzgebiet verbessert werden kann. Angemessene Management-Maßnahmen um das zu erreichen, werden diskutiert.

Introduction

Many bird species strongly declined during the 1970s in Western Europe (Berendse et al. 2004; Gregory et al.

2005). While the conservation of rare bird species has gained much attention (e.g., in Britain and Ireland; Baillie and Schaub 2009), declining populations of common species have received much less attention (e.g., of the House Sparrow *Passer domesticus*; Klok et al. 2006). These declining populations are generally assumed to be the consequence of agricultural practices such as mechanical cultivation or the use of pesticides and herbicides (Donald et al. 2006). Present-day farming practices negatively affect the size and quality of feeding and the breeding habitats of birds, and may also directly reduce nesting success and food availability (Cade and Temple 1995).

This is also the case for the Red-backed Shrike (*Lanius collurio*), a passerine that was once widespread throughout Europe but has since declined in many European countries (Bani et al. 2009; Hagemeyer and Blair 1997; see Esselink et al. 1995 for an overview). That said, the European breeding population is still relatively large (4.8–8.0 million pairs; Burfield and Van Bommel 2004) and has remained stable since 1995 (http://www.ebcc.info/index.php?ID=380&one_species=15150). However, in the Netherlands (at the edge of its range), the Red-backed Shrike population declined dramatically during the twentieth century, from approximately 5,000–15,000 to about 200 breeding pairs in the 1990s (Hustings and Bekhuis 1993). This decline was even more pronounced in coastal dune areas, where Red-backed Shrikes almost completely disappeared (Kuper et al. 2000).

Breeding success, survival, and immigration or emigration are essential parameters for understanding the constraints acting on demographic processes which contribute to yearly population growth (Sæther and Bakke 2000; Hemerik and Klok 2006). The fecundity and nest survival of the Red-backed Shrike have been studied throughout Europe, and many of those studies have been published (e.g., Ash 1970; Lefranc 1979; Kuzniak 1991; Olsson 1995; Leugger-Eggimann 1997; Bijlsma 2000; Geertsma et al. 2000; Simek 2001; Jakober and Stauber 2004; Golawski 2006; Jørgensen et al. 2013). Survival estimates can only be obtained by large-scale marking and monitoring of individually recognizable birds over an extended period (Lebreton et al. 1992). Only a few studies of both adults and juveniles after fledging have estimated survival (Geertsma et al. 2000; Rytman 1996; Schaub et al. 2011, 2013). Interpretation of survival estimates is complicated, as mark–recapture data are simultaneously influenced by survival as well as migration. However, studies of this species are often performed as part of a continuum. For comparison, Schaub et al. (2013) wrote that “red-backed shrikes occur more or less continuously across the landscape; the boundaries of the study population were based mainly on logistic rather

than on biological grounds.” Undetected birds must be considered dead or to have settled outside the study plot. More individuals can be assumed to settle outside the study plot in a population continuum than in an isolated local population. This implies that the estimated survival may be biased by study plot size in a population continuum. Such a bias in the apparent survival in a population continuum caused by study plot size is illustrated by Marshall et al. (2004), who found an increase in apparent survival with study plot size. Schaub et al. (2013) realized that not adopting natural boundaries for the study site has implications. They stated: “This has important consequences when making inferences. The smaller the spatial units, the stronger dispersal contributes to the regulation of the local population and the less other demographic processes contribute. As the spatial scale increases, dispersal contributes progressively less to the dynamics, thus, it might even be claimed that dispersal is a scale effect or an artefact of finite study area size (Lambrechts et al. 2000).”

In this paper, we solve this problem by studying a relatively isolated population of Red-backed Shrikes. The population is mainly surrounded by unsuitable breeding habitat (see also Geertsma et al. 2000), and only a few other “core” populations (>10 pairs) at distances of 20 km or more are present in the surroundings. As a result, the estimated emigration of our study population in the Dutch Bargerveen Reserve is very low (only 7 % of resighted marked birds have been resighted outside the reserve). Therefore, our apparent survival estimates are only barely biased by the size of the study area, and are expected to be relatively high. The high site fidelity in the reserve provides a unique opportunity to interpret survival estimates precisely. We have used this opportunity to study vital rates for the local population of Red-backed Shrikes in the Bargerveen with the intention of identifying management options for stimulating population growth. Therefore, we analyzed resighting data with mark–recapture techniques to study the survival and resighting (recapture) probability of Red-backed Shrikes marked as nestlings in the period 2001–2008. Moreover, we combined those survival estimates with reproductive data to parameterize a matrix model (Caswell 2001). In the present work, the yearly population growth factor was assessed together with the relative contributions of the different parameters to this growth factor. By comparing the yearly population growth with count data on the number of breeding pairs, we were able to infer the role of migration. Best options for increasing vital rates were identified by performing an elasticity analysis and by comparing our reproduction values and estimated survival values with those of other published studies. Management options for stimulating population growth are discussed.

Table 1 The total number of pairs (P), the number of successful pairs with known numbers of fledglings followed ($P(\text{known})$), the total number of fledglings (F), the fraction of successful pairs in the full population as estimated from observed unringed fledglings at the end of the breeding season (“Successful”), and the average number of fledglings per successful pair ($F/P(\text{known})$) and per breeding pair (F/P) followed for the period 2001–2009

Year	P	$P(\text{known})$	F	Successful	$F/P(\text{known})$	F/P
2001	78	27	105	0.50	3.89	1.95
2002	59	39	165	0.75	4.23	3.16
2003	37	24	108	0.78	4.50	3.53
2004	52	33	131	0.67	3.97	2.67
2005	47	30	115	0.77	3.83	2.93
2006	47	29	126	0.75	4.34	3.23
2007	45	29	118	0.76	4.07	3.07
2008	48	22	79	0.69	3.59	2.47
2009	48	23	96	0.77	4.17	3.22

$F/P(\text{known})$ is calculated by dividing the total number of fledglings (F) by the number of successful pairs with known numbers of fledglings ($P(\text{known})$), a subset of the total number of pairs. F/P is calculated by multiplying $F/P(\text{known})$ by the fraction of the total estimated number of pairs that were successful (“Successful”) in Bargerveen, the Netherlands

Methods

Study area

The Bargerveen Reserve is a raised bog of approximately 2,000 hectares situated in the northeast of the Netherlands, near the border with Germany (52°42'N, 7°01'E). It is one of the last remnants of a much larger raised bog, the Bourtanger Moor, and a rather isolated habitat for the Red-backed Shrike. Prior to its drainage and exploitation, which were initiated in medieval times, this bog extended over 300,000 hectares along the northern Dutch–German border. Since 1972, the reserve has been managed by the Dutch State Forestry Service, and all breeding birds have been monitored annually since that time. Bird management focuses on regrowth of the original peat-moor vegetation by rainwater retention (van Berkel 1993).

Initially, rainwater retention created an open landscape and enhanced the insect diversity and thus improved food availability for the Red-backed Shrike. This resulted in an increase in its population (Esselink et al. 1995). However, the population started to decline in the late 1990s due to habitat loss caused by further development of the area (Bargerveen Foundation, unpublished data). The decline stopped in 2005, and the population is currently stable (Table 1, Fig. S.1 of the Electronic supplementary material, ESM). The Bargerveen is rather isolated; the closest relatively large population (approximately 50 breeding pairs) is between 20 and 30 km away in Germany (in

Table 2 Total numbers of nestling Red-backed Shrikes ringed and resighted in Bargerveen, the Netherlands, during the breeding seasons in the years 2001–2009 (the number of resighted females is given in parentheses)

Ringing year	Number of nestlings ringed and fledged	% of all nestlings ringed and fledged	Cumulative number of resighted birds in all years	Resighted in year									
				2002	2003	2004	2005	2006	2007	2008	2009		
2001	98	69	7 (5)	5 (3)	2 (1)	1 (0)	1 (1)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	
2002	162	92	18 (4)		15 (2)	4 (0)	6 (1)	8 (2)	1 (0)	1 (0)	0 (0)	0 (0)	
2003	103	84	22 (12)			16 (6)	12 (5)	6 (4)	2 (2)	1 (1)	1 (1)	1 (1)	
2004	134	94	16 (4)				15 (3)	6 (4)	6 (3)	3 (1)	0 (0)	0 (0)	
2005	110	86	19 (5)					16 (5)	11 (3)	6 (1)	2 (1)	2 (1)	
2006	128	86	23 (7)						18 (5)	12 (3)	9 (2)	9 (2)	
2007	118	79	10 (3)							9 (2)	6 (2)	6 (2)	
2008	73	66	7 (2)									7 (2)	

It should be noted that some individuals are resighted in more than one year (the number of resighted birds is less than the cumulative number of resightings)

Tinner and Stavener Dose). Within the Netherlands, the closest population (about 10 pairs) is about 20 km away, while the second nearest population (also about 10 pairs) is over 40 km from the Bargerveen. Additionally, a few scattered pairs are found breeding within 5–10 km of Bargerveen each year.

Collection of reproductive and ringing data

Red-backed Shrikes are able to reproduce from their second year of life on. In Western Europe, the species produces only one brood per year, resulting in 3–6 (occasionally 7) fledglings per pair. Nestlings were usually counted and color-ringed at the age of 7–9 days. Ringing was done with a unique combination of inscribed color and metal rings. Subsequently, the nests were checked regularly for survival until fledging. A nest was considered successful when at least one young fledged. Reproductive success was defined as the number of fledglings per female. Due to the inaccessibility of the swampy terrain, we were not able to find all nests prior to fledging. Consequently, not all offspring could be counted and ringed. Therefore, we estimated the total number of fledglings by extrapolation, using the mean number of fledglings per nest found. This also allowed us to calculate the yearly percentage of ringed fledglings (Table 2). On average, 82 % of all young birds fledged with rings.

Searches for breeding pairs and nests and checks for ringed individuals took place as soon as the first Red-backed Shrikes arrived in the Bargerveen (usually in early May). This carried on until mid-August, when the last shrikes left for their African wintering areas. Over the study period, for at least three days a week, the area was searched by two observers (MG and SW). In addition to the

core area of Bargerveen, many of the surrounding populations and single breeding pairs were checked for ringed birds each year, but less effort was expended on them than in the core area.

Whereas adults can easily be sexed based on their plumage, nestlings cannot be sexed based on visual characteristics. In the absence of data on the primary sex ratio of the Red-backed Shrike, we assumed a 1:1 sex ratio for nestlings. To see whether estimates would vary if other sex ratios were used, we also performed analyses with sex ratios of 2:3 and a 3:2 (see below). This enabled us to use the data on gender of resighted individuals to compare sex-specific survival in the survival analysis. Over the period 2001–2008, the total number of ringed and fledged nestlings equaled 926 (Table 2). Resightings in the Bargerveen amounted to 82 males and 41 females.

Data analysis: survival and resighting estimation

Based on the resightings summarized in Table 2, we constructed a matrix with individual encounter histories. Likelihood estimates of survival and resighting probabilities of the Red-backed Shrike were estimated with program MARK version 5 (White and Burnham 1999). This program computes parameter estimates for the Cormack–Jolly–Seber (CJS) model, which has been especially developed for analyzing mark–recapture data, as well as for other survival models (Lebreton et al. 1992). When analyzing resighting data from birds with known ages (i.e., marked as nestlings), age-dependent CJS models can be used to assess the effect of age on survival (starting with a model that differentiates survival over the years, which equaled 8 years in our case based on Table 2). We used the R (R Development Core Team 2012) package

RMark (Laake 2008) to construct models for program MARK.

The most general model $\varphi(g^*S3)p(g^*t)$ was tested with the bootstrap GOF test in MARK and was found to fit adequately to the data ($P = 0.10$). In this model, survival (φ) is estimated for both females and males (“g” denotes gender) in the age classes “first year,” “second year,” and “3 years and older” (“S3;” MARK notation $(a0,a1,a2)$), and resighting probability (p) is gender dependent (“g”) and time dependent (“t”). Simultaneously, overdispersion of the data (i.e., greater variability in the data than would be expected based on a given simple statistical model) is estimated. This is indicated by the variance inflation factor \hat{c} . For the general model that fitted the data, the correction for extra-binomial variation in the data was performed as conservatively as possible by using the largest estimate of \hat{c} out of three different estimates (Cooch and White 2010). Akaike’s information criterion corrected for a small sample size (AICc) was used in model selection (Lebreton et al. 1992). When overdispersion was detected in the data, the AICc had to be corrected with \hat{c} , and models were selected by the quasi-likelihood AICc (QAICc) (Cooch and White 2010). The model with the minimum AICc was considered to be the most appropriate, and differences in AICc between models ($\Delta AICc$) were used to identify the most likely models. Models with $\Delta AICc < 2$ cannot be distinguished since these are all strongly supported by the data (Burnham and Anderson 2002).

The estimated survival values were subsequently used to parameterize our matrix model. The survival analysis was based on resighted birds at the beginning of the breeding season (approximately mid-May) and birds ringed as nestlings, just before fledging (approximately mid-July). Therefore, the estimated survival of juveniles (φ_0) is the average survival of juveniles across 10 months, and the survival of adults (φ_1) is the average yearly survival of birds aged 10 months and older. For most bird species, first-year survival is lower than survival later in life. As we did not know in advance whether this is also true for second-year survival, we started with a model for three age classes, $\varphi(g^*S3)p(g^*t)$. We used standard models for analysis (“logit” link functions and variance estimation using “2ndpart”). The models for both survival φ and resighting probability p can be gender dependent (denoted by “g”) or not. Moreover, they can distinguish between two age classes (denoted by “S2” = first-year and adult survival; MARK notation $(a0, a1)$), three age classes (“S3” = first-year, second-year, and adult survival; MARK notation $(a0, a1, a2)$), be constant for all groups (“.”), and be time dependent (“t”). Thus, a total of 64 ($=2^6$) different models (age-dependent and time-dependent models for φ and p included) were fitted to the data. Model

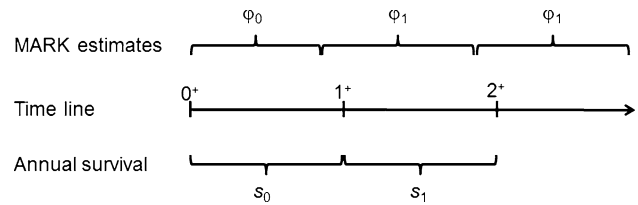


Fig. 1 Conversion of MARK survival estimates to annual survival estimates for the post-breeding matrix model. It should be noted that most Red-backed Shrikes return to the Netherlands in May (the starting point of the upper curly brackets for φ_1) and that the fledglings normally leave their nests in July (at time points 0^+ , 1^+ , and 2^+)

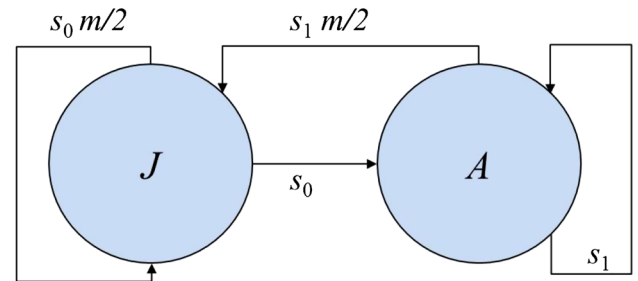


Fig. 2 Life cycle graph with two age classes of the Red-backed Shrike (*Lanius collurio*). Annual survival of fledglings (J) indicated by s_0 , s_1 the annual survival of adults (A). Yearly survival multiplied by the number of female fledglings produced per female ($m/2$) represents the fecundity of each class

selection for the survival of the Red-backed Shrike was based on a variance inflation factor \hat{c} of 1.20.

The matrix model used to calculate the yearly population growth requires annual survival estimates. The annual juvenile survival (s_0 , see Eq. 1) was calculated by multiplying the survival from ringing until resighting (10 months) by the adult survival for the remaining 2 months ($=1/6$ year) (Fig. 1). The annual survival of adults remains the same (s_1). This results in the following annual survival probabilities: $s_0 = \varphi_0 \varphi_1^{1/6}$ and $s_1 = \varphi_1$.

Matrix model

The population dynamics of the Red-backed Shrike can be modeled with a matrix model using survival estimates and the observed mean reproduction. The structure of the matrix model used to model the annual population dynamics of the Red-backed Shrike population of Bargerveen is based on the results of the MARK analysis (a two-stage model). In this model, the census moment is just after fledging (post-breeding), and only females are considered, as is standard practice in matrix modeling (Caswell 2001). The life cycle graph (Fig. 2) describes the probability of surviving 1 year (for juveniles this means

maturing and entering the adult stage) and the contributions of each stage to the juvenile stage. Both the juvenile and adult stages of year t contributed to the juveniles of year $t + 1$ since the census occurred 1 year after the juveniles were ringed. The life cycle graph (Fig. 2) can be translated into mathematical notation as a stage-structured matrix model (Eq. 1). The model describes the population composition in year $t + 1$ as a function of the composition in year t . It is crucial to choose the appropriate time step for this kind of model (van Groenendael et al. 1988).

Transitions from one stage to another in the projection matrix C can be calculated when survival and reproduction are known. For both stages, reproduction (the number of female fledglings produced per female) is denoted in the first row of C , and yearly survival of the two stages is denoted in the second row of C . Data on reproduction did not allow stages (age groups) to be differentiated. Therefore, we used the mean number of fledglings per pair (m) for both stage groups. Thus, the number of female fledglings from a female is $0.5 m$ (assuming a 1:1 sex ratio; see also the first row of the matrix in Eq. 1). The actual per capita reproduction is the product of $0.5 m$ and the survival probabilities of different stages (s_0 and s_1), as birds must first survive the year before they can produce offspring.

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = C \cdot \begin{pmatrix} J(t) \\ A(t) \end{pmatrix} = \begin{pmatrix} s_0 \frac{m}{2} & s_1 \frac{m}{2} \\ \dots & \dots \end{pmatrix} \cdot \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}. \tag{1}$$

To determine the population growth factor or the dominant eigenvalue of matrix C , the characteristic equation must be solved (Caswell 2001). For further details of the calculation, see the ESM.

Elasticity analysis

The contribution of the vital rates m , ϕ_0 , and ϕ_1 to the population growth factor can be determined with an analytical tool called elasticity analysis (see the ESM). The elasticities can be derived analytically for the current model because the dominant eigenvalue is easily expressed as a function of these three parameters, namely $\lambda_d = \phi_1 + \phi_0 \left(\phi_1^{1/6} \right)^{\frac{m}{2}}$ (see the ESM for details). The parameter with the largest elasticity ($e(\text{parm})$ in Eq. 2) makes the largest relative contribution to the population growth factor (λ_d):

$$\begin{aligned} e(m) = e(\phi_0) &= \frac{\phi_0 \left(\phi_1^{1/6} \right) m}{2\phi_1 + \phi_0 \left(\phi_1^{1/6} \right) m}, \quad e(\phi_1) \\ &= \frac{2\phi_1 + \phi_0 \left(\phi_1^{1/6} \right) \frac{m}{6}}{2\phi_1 + \phi_0 \left(\phi_1^{1/6} \right) m}. \end{aligned} \tag{2}$$

Table 3 Model selection for the survival (ϕ) and resighting probability (p) of Red-backed Shrikes ringed in Bargerveen, the Netherlands, based on a variance inflation factor (\hat{c}) of 1.20. The quasi likelihood AICc (QAICc), the difference in QAICc between the current model and the best model (Δ QAICc), the number of estimable parameters (k), and the deviance (Qdev) are given for each model

Model	QAICc	Δ QAICc	Weight	k	Qdev
$\phi(S2^*g)p(t^*g)$	964.796	0.000	0.316	18	125.056
$\phi(S2^*g)p(g)$	965.732	0.936	0.198	6	150.544
$\phi(S2)p(t^*g)$	966.842	2.047	0.114	16	131.232
$\phi(S2)p(g)$	967.889	3.093	0.067	4	156.741
$\phi(S3^*g)p(t^*g)$	968.204	3.408	0.058	20	124.320
$\phi(S3)p(t^*g)$	968.673	3.877	0.045	17	131.000
$\phi(.)p(.)$	1062.669	97.874	0.000	2	255.547

The models are listed in order of increasing QAICc. Notation used to define models (combinations of the following are possible): (.): a constant value is estimated for this parameter; two-stage (S2): distinction between “first year” and “second year or older;” three-stage (S3): distinction between “first year,” “second year,” and “third year or older;” g: distinction between females and males; t: each year is treated differently. The most general model is shown in bold

Estimating the accuracy of the yearly population growth

The standard error in the yearly population growth can be estimated by bootstrapping the data on the vital rates (Efron and Tibshirani 1993; Lande et al. 2003) or by taking the variance of a first-order Taylor expansion of the yearly population growth (Alvares-Buylla and Slatkin 1993; Lande et al. 2003; see, e.g., Klok et al. 2010 for an example relating to the Greylag Goose). As we have information on the distributions of the vital rates, we sampled the 95 and 50 % confidence intervals of the vital rates and simulated 10,000 matrices with values for m , ϕ_0 , and ϕ_1 drawn uniformly from these intervals.

Results

Reproduction and survival

The average percentage of successful pairs equaled 72 %, and the average number of fledglings (m) per pair was 2.91 ± 0.16 (S.E.) (Table 1). Table 3 shows the six best fitting models, including the most general model $\phi(g^*S3)p(g^*t)$ and the model that assumes constant resighting and constant survival probabilities $\phi(.)p(.)$ over the estimated time period (10 months for ϕ_0 and a year for ϕ_1). Models including age classes for survival (either two or three classes) fitted much better than those without. Among the models that describe survival in age classes, models with two age classes fitted better than those with three,

Table 4 Estimated parameter values for survival φ and yearly resighting p with their 95 % confidence intervals (CI) in the most parsimonious best-fitting model, φ (S2*g)p(g)

Parameter	Estimate	Lower bound of CI	Upper bound of CI
1st 10-month survival $\varphi_0 \text{ ♂}$	0.20	0.16	0.24
1st 10-month survival $\varphi_0 \text{ ♀}$	0.12	0.08	0.16
Adult yearly survival $\varphi_1 \text{ ♂}$	0.54	0.45	0.62
Adult yearly survival $\varphi_1 \text{ ♀}$	0.64	0.52	0.75
Resighting probability $p \text{ ♂}$	0.81	0.70	0.88
Resighting probability $p \text{ ♀}$	0.53	0.40	0.67

suggesting that survival probabilities for birds older than 2 years and birds with ages of between 1 and 2 years were similar. Within the subset of S2 models, models that accounted for gender in resighting probability fitted better than those that did not. Therefore, the two best-fitting models (Table 3) include survival estimates that are gender dependent and differ for two age classes. These models have approximately the same QAICc. We applied the principle of parsimony within the set of models that differ by <2 from the best fitting (=first) model. The parameters from the most parsimonious model within this set of models, i.e., $\varphi(g*S2)p(g)$, are given in Table 4. Using this model, we estimated the 10-month survival probabilities as 0.12 in first-year females and 0.20 in first-year males, but the 95 % confidence intervals overlap. Yearly adult survival probabilities were 0.64 for females and 0.54 for males; again the 95 % confidence intervals overlap. These survival probabilities were calculated under the assumption of a 1:1 sex ratio of fledglings. When the sex ratio was changed to 40 % females and 60 % males, male juvenile survival was 0.17 and female juvenile survival was 0.15, again with overlapping confidence intervals. With a sex ratio of 60 % females and 40 % males, juvenile survival probability was 0.25 for males and 0.10 for females. Adult survival probabilities did not change when the fledgling sex ratio was biased towards a 2:3 or 3:2 (male: female) ratio.

Population growth factor and elasticity analysis

Matrix C (Eq. 1 and Eq. A.1 in the ESM) was parameterized with the vital rates for females, resulting in the matrix $\begin{pmatrix} 0.16 & 0.93 \\ 0.11 & 0.64 \end{pmatrix}$. Solving this matrix for the dominant eigenvalue (λ_d) resulted in an estimate for the population growth of 0.80. When we analyzed the time series from Fig. S.1 of the ESM starting from the year 2000 using a generalized linear model with Poisson error, the estimated growth factor was 0.92. Equation 2 shows that the elasticity of λ_d with respect to the vital rate m is equal to

that with respect to φ_0 . Based on the estimates for juvenile female survival φ_0 and reproduction m , this equaled 0.20. For the adult female survival, $e(\varphi_1) = 0.83$. After analyzing 10,000 simulated matrices, the dominant eigenvalues were found to lie in the range (0.62, 0.99) if parameter values were drawn from their 95 % confidence intervals, and in the range (0.74, 0.87) if parameter values were drawn from their 50 % confidence intervals. When searching for the minimum value required for φ_0 for the population to be able to grow, given the current values of φ_1 and m , it is important to realize that the dominant eigenvalue should equal 1. This requirement yields $\lambda_d = 1$ or $1 = \varphi_1 + \varphi_0 \left(\varphi_1^{1/6} \right)^{\frac{m}{2}}$, so φ_0 can be solved using the formula $1 = 0.64 + \varphi_0 (0.64^{1/6})^{\frac{2.91}{2}}$. This procedure can also be performed for φ_1 given values for φ_0 and m , or for m given values for φ_0 and φ_1 . A stable Bargerveen population without immigration would require 6.5 fledglings per breeding pair, a juvenile survival of 0.27, or an adult female survival probability of 0.83.

Discussion

The Red-backed Shrike population in the Bargerveen Reserve went through a sequence of population increases, a period of stability with a high population density, a population decrease, and is currently a more or less stable population with a low density (Fig. S.1 of the ESM). Our data on vital rates were gathered in this final period. If the observed changes in the population in the reserve are not exclusively the result of temporal variability in immigration, it should be possible to stimulate population growth by maximizing key demographic vital rates within the reserve.

Population growth and migration

Based on our survival and reproduction estimates, a population growth rate of 0.80 (range 0.62, 0.99) was calculated, indicating a decline in the population. However, as is shown in Table 1 and in Fig. S.1 of the ESM, the number of breeding pairs in Bargerveen appears to be stable, suggesting that immigrants contribute to the local (stable) breeding population. With a population growth factor of 0.80, an inflow of immigrants to Bargerveen representing 20 % of the total population size or more is needed to stabilize the local population. Indeed, immigration seems to play an important role in the Bargerveen, as is suggested by the percentage of marked breeders, which was lower than expected considering that 82 % of all fledglings were ringed yearly: in 2007 we recorded 46 % marked breeders, and in 2008 and 2009 only 34 % of the breeders were ringed.

Table 5 Red-backed Shrikes native to Bargerveen, the Netherlands, that were resighted breeding elsewhere

Ring number	Year of birth	First resighting year	Gender	Distance (km)
H 253 489	2002	2003	♂	33
H 291 473	2003	2004	♂	8
H 291 540	2004	2005	♀	54
H 291 737	2004	2008	♂	8
*	2005	2006	♀	11
H 304 427	2005	2006	♀	57
H 309 503	2006	2009	♀	7
H 313 510	2007	2009	♀	55
H 313 890	2008	2009	♂	5

* Unknown number, identified as native to Bargerveen based on color ring code

A large number of Red-backed Shrike nestlings were color-ringed during 2001–2008 at many Dutch locations outside Bargerveen. The maximum observed natal dispersal distance in the Netherlands is 90 km (based on exchanges with other populations; Bargerveen Foundation, unpublished data). Within 90 km of the Bargerveen, about 1,300 young shrikes were marked with color rings. None of these were ever recorded in Bargerveen. We may therefore conclude that immigration mainly originates from nearby German populations (where there is no color-ringing scheme), as was also concluded by Geertsma et al. (2000) for the same area during 1993–1999. Schaub et al. (2013) also deduced that immigrants play a role in maintaining a southern German Red-backed Shrike population.

During the period 2001–2008, only 9 out of 132 ringed birds in the Bargerveen area that returned from their wintering areas were recorded outside the study area (Table 5). This suggests that emigration can be as low as 7 %, indicating that immigration occurs more often than emigration. However, monitoring was not performed as thoroughly outside the Bargerveen area as within the Bargerveen Reserve. Therefore, emigration may have been much higher. At present, given current vital rates and the estimated emigration, the Bargerveen population appears to act as an ecological sink, although it might also be a healthy population with a rather high juvenile emigration rate to nearby (monitored as well as unmonitored) populations.

Reproduction

Despite the high number of immigrants in the Bargerveen population, the reproductive success of Red-backed Shrikes in the Bargerveen lies within the range of other populations with stable or increasing populations (Table 6). The majority of studies of populations that are

known to be at least stable show a mean number of fledglings per pair of between 2.7 and 3.0 and a mean percentage of successful pairs of between 62 and 77 % (based on 9 of all 22 studies in Table 6). In decreasing populations, however, the number of successful pairs is often considerably lower (e.g., Sonnabend and Poltz 1979, Diehl 1995, Kuzniak and Tryjanowski 2003). Although only the percentage of successful pairs is given in most studies of declining populations, it is obvious that low breeding success goes hand-in-hand with a low mean number of fledglings per breeding pair, and thus a declining population.

Also, the reproductive success in the period 2001–2009 is comparable to that during the period 1993–1999, when the species was more abundant in the Bargerveen area. Hence, it is unlikely that the number of offspring or the number of successful breeding pairs can be significantly improved and become a management target for this species.

This conclusion is supported by our elasticity analysis. The analysis is a guide for research and management, particularly for poorly known species, and is a useful first step in a more extensive modeling effort to determine population viability (Heppell et al. 2000). Other parameters being equal, it holds that the population is viable (i.e., the yearly population growth factor $\lambda_d > 1$) if pairs on average produce at least 6.5 fledglings (m). As a comparable reproductive success rate has not been found in other studies, such a high rate of fledgling production is unrealistic. Therefore, improving survival is a more feasible target for management.

Adult survival

In survival analyses (CJS models) based only on resightings (recapture), true survival (S) cannot be separated from emigration ($1 - F$, where F is site fidelity), and the estimated survival in these models is referred to as “apparent survival.” Therefore, survival tends to be underestimated (Lebreton et al. 1992). In CJS models, the apparent survival is estimated as the product ($S \cdot F$) of true survival and site fidelity. As in most other studies of annual survival, our research fails to distinguish between true mortality and emigration. Therefore, survival estimates should be viewed as conservative. However, the observed emigration from our population appears to be low. This is probably a result of the fact that the study area is surrounded by unsuitable breeding habitat (see also Geertsma et al. 2000). Only two relatively small populations (>10 pairs) occur at a distance of approx. 20 km, with the next large population found more than 40 km away. So, in contrast to other European populations (Schaub et al. 2011, 2013), our study site hosts an isolated population, indicating that the calculated

Table 6 Reproductive success of the Red-backed Shrike in different populations in Europe (partly after Geertsma et al. 2000)

Country	Area	Period	Trend	F/P	Success	Authors
Poland	Leszno	1995–2001	–	1.6	46 %	Kuzniak and Tryjanowski (2003)
Great Britain	Hampshire	1954–1966	Strong decline	2.6	63 %	Ash (1970)
Poland	Leszno	1971–1979	±Stable	2.7	64 %	Kuzniak (1991)
Ukraine	(western part)	1973–1992	–	2.7	–	Gorban and Bokotej (1995)
Switzerland	Jura	1988–1991	±Stable	2.7	62 %	Leugger-Eggimann (1997)
Switzerland	Engadin	1988–1992	–	2.7	–	Pasinelli et al. (2007)
Hungary	Aggletek Nat. Park	1991–1996	±Stable	2.7	–	Horvath et al. (2000)
Denmark	Hulsig Hede	2003–2007	±Stable	2.7	76 %	Jørgensen et al. (2013)
Germany	Göppingen	1969–1985	±Stable	2.7	–	(Jakober and Stauber 1980, 1987)
Germany	Göppingen	1969–2003	±Stable	2.8	64 %	Jakober and Stauber (2004)
Germany	Göppingen	1971–2006	±Stable	2.8	66 %	Schaub et al. (2011, 2013)
Switzerland	Jura	1988–1989	–	2.9	66 %	Rudin (1990)
Netherlands	Drents-Friese Wold	1990–2000	Increase	2.9	64 %	Bijlsma (2000)
<i>Netherlands</i>	<i>Bargerveen</i>	<i>2001–2009</i>	<i>Decline then ± stable</i>	<i>2.9</i>	<i>72 %</i>	<i>This study</i>
Netherlands	Bargerveen	1993–1999	Increase then decline	3.0	77 %	Geertsma et al. (2000)
Czech Republic	South Bohemia	1990–1999	Increase then decline	<3.3	72 %	Simek (2001)
Sweden	Gryt	1956–1994	±Stable	3.4	80 %	Olsson (1995)
France	Elsace	1967–1975	–	3.5	83 %	Lefranc (1979)
Czech Republic	Moravia	1987–1992	–	3.7	80 %	Holan (1995)
Italy	Lombardia	1993–1995	–	–	42 %	Fornasari and Massa (2000)
Switzerland	Mindelsee	1948–1973	Strong decline	–	53 %	Sonnabend and Poltz (1979)
Poland	Kampinos Nat. Park	1964–1993	Strong decline	–	56 %	Diehl (1995)

The current study is highlighted in bold italics

F/P mean number of fledglings per breeding pair

– Indicates missing value

apparent survival estimates approach the actual survival rates. Nevertheless, our estimates of mean adult survival 0.59 (i.e., 0.54 and 0.64 for males and females, respectively) are similar to the survival estimates for dead recoveries in Sweden (Ryttman 1996), and are higher than the recent findings of Schaub et al. (2011, 2013) (Table 7). Although the mean adult survival in the isolated Bargerveen Reserve is higher than those seen in other open European populations, there is still room for improvement in the adult survival of Red-backed Shrikes in the Bargerveen. This appears to be supported by the elasticity analysis. The elasticity of adult female survival $e(\varphi_1)$ of 0.83 was the highest elasticity among all the vital rates.

This indicates that adult female survival potentially has the largest impact on λ_d . If φ_1 increases by 10 %, λ_d increases by 8.3 %. For a population to be viable ($\lambda_d > 1$), we need a 30 % increase in λ_d . If this increase depends solely upon adult survival, the adult female survival rate φ_1 should exceed 0.83. This makes adult survival a possible target for management. However, an increase in adult female survival of 0.19 is a daunting challenge, and managing a self-sustaining population probably also requires improvements in other vital rates.

A lower apparent survival in females than in males was found by Schaub et al. (2013), whereas our estimates pointed to a higher survival in females, but the confidence

Table 7 Survival estimates for the Red-backed Shrike in different populations in Europe

	Survival ♀ juveniles	Survival ♂ juveniles	Survival ♀ adults	Survival ♂ adults
Ryttman (1996) [†]	0.392 ^a	0.392 ^a	0.577 ^a	0.577 ^a
Geertsma et al. (2000)	0.18–0.33 ^a	0.18–0.33 ^a	0.49–0.63 ^a	0.49–0.63 ^a
Schaub et al. (2011) successful	–	–	0.48	0.58
Schaub et al. (2011) unsuccessful	–	–	0.32	0.32
Schaub et al. (2013)	0.06	0.10	0.37	0.44
This study	0.12	0.20	0.64	0.54

[†] Adult survival was calculated for birds aged 3 years or older. Survival of birds aged 2 years was estimated as 0.527; moreover, the birds were ringed as juveniles and there was a high mortality before ringing

– Indicates a missing value

^a Survival rates were calculated independent of sex

intervals overlap in both studies. Therefore, we speculate that the survival rate is the same for both sexes.

Juvenile survival

When we analyzed our data with 40 or 60 % females assumed for the fledglings, the estimates for juvenile survival shifted a bit. In our study, as also observed in the study of Schaub et al. (2013), we found a lower apparent survival for juvenile females than for males, although this may be caused by the assumed 1:1 sex ratio. The relatively high survival probability of juvenile males compared to females similarly suggests a higher natal fidelity in males than in females (Schaub et al. 2013). However, this hypothesis was not supported by our scarce emigration data, as the numbers of observed emigrating males and females were found to be almost equal (Table 5).

Mean juvenile survival in the Bargerveen Reserve was 0.16. This apparent juvenile survival is double that reported by Schaub et al. (2013) (Table 7). However, the authors state that they underestimated juvenile survival compared to adult survival, since juveniles were not color-ringed and had to be captured, which was “likely to result in lower reencounter probabilities.” In addition, Schaub et al. (2013) sampled from a less isolated population, which will have reduced the probability of resighting. Considerably higher juvenile survival rates have been reported in Sweden (Ryttman 1996). Also, higher probabilities of juvenile survival were reported from the Bargerveen Reserve when the density of Red-backed Shrikes was relatively high

(Geertsma et al. 2000). Although we have scant data to compare with, it appears that juvenile survival in the Bargerveen Reserve in the period 2000–2009 was low. Our elasticity analysis showed that a female juvenile survival probability of 0.27 is required for the population to be stable. This is in the range of juvenile survival probabilities reported by Ryttman (1996) and Geertsma et al. (2000). Thus, this seems to be a realistic target.

Management

The identification of plastic vital rates is the first step towards pinpointing suitable management actions. Based on our population model and a comparison of vital rates with other populations, the best targets for management are juvenile and adult (female) survival. In migratory birds, survival is influenced at the breeding grounds as well as at the wintering grounds and stopover sites. Practicality dictates that we start by improving the conditions at the breeding grounds. Unfavorable conditions at those grounds may result in the birds choosing different breeding sites, leading to emigration, or such conditions may increase mortality directly (predators) or indirectly (through body condition). Due to the low number of emigrants from the Bargerveen area, it is not very likely that increased emigration is the cause of suboptimal apparent juvenile or adult survival. Also, there has not been any indication of an increase in the on-site mortality rates of fledged or adult birds during the more than 20 years of research on this Red-backed Shrike population. That means that we must look for environmental drivers that increase the condition of the birds (fledglings as well as adults). The most plausible driver is food availability. The availability of shrike prey depends on different factors. First of all, the feeding habitat should produce sufficient prey biomass per unit area. These should preferably be relatively large prey, as the Red-backed Shrike collects and feeds individual prey to its young. At present, little is known of prey biomass production in raised bogs, so this is a topic that requires further research. According to Kuper et al. (2000), prey should be available regardless of the weather, time of day, and season. This requires a landscape with a patchwork of different habitat types and a large diversity of invertebrate prey species, leading to successional peaks in invertebrate activity throughout the season that are somewhat independent of the weather. Management should thus not focus on one target habitat with a large surface area but instead aim to create a variety of different abiotic conditions and gradual transitions between them in order to provide nesting opportunities and food. Finally, the Red-backed Shrikes should be able to reach their prey, so we should aim at half-open landscapes with sufficient perches from which the birds can hunt.

Acknowledgments Financial support was provided by the Prins Bernhard Fund to start this research in the Bargerveen Reserve. We are grateful to the State Forestry Commission, especially Jans de Vries and Piet Ursem, for permitting us to access the nature reserve and to use their accommodation. Hans Esselink is greatly acknowledged because he started the project and he performed a lot of field work on the Red-backed Shrike in the Bargerveen area before he unfortunately passed away on 30 August 2008. Hans van Berkel (who sadly died on 4 February 2013), as well as several students and volunteers, kindly assisted us in the field in the early years of the study period. Gerrit Speek of the Dutch Bird Ringing Station supplied us with licenses to ring Red-backed Shrikes. The Instrument-Making Department of Radboud University in Nijmegen allowed us to use their engraving machine to construct the bird rings. Henk Siepel and Rob Bijlsma are acknowledged for their comments on an earlier draft of this manuscript. Elizabeth van Ast-Gray is thanked for correcting the English used in this manuscript.

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