ARE HIGH FITNESS VALUES SUFFICIENT TO MAINTAIN A DUTCH POPULATION OF THE RED-BACKED SHRIKE (*Lanius collurio*)?

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ABSTRACT

Geertsma M., van Berkel H., Esselink H. 2000. *Are high fitness values sufficient to maintain a Dutch population of the Red-backed Shrike (Lanius collurio)?* Ring 22, 1: 79-88.

Red-backed Shrikes strongly decreased in the Netherlands during the past century. The only large population is found in the Bargerveen reserve, an isolated bog remnant in an intensively cultivated area. Here, the population increased from a few breeding pairs in the seventies to over hundred pairs in the nineties. Our previous studies indicate that improved food abundance by re-wetting management played an important role in the population development. However, immigrants must have reinforced the initial fast growth. Now, when the population seems to have stabilized, different scenarios can be made for the present behaviour of the population. Does it act as a source, from where nearby habitats get colonized? Do recruitment and adult survival maintain the population or is immigration still needed? To examine this, reproductive success and survival rates (by means of a ringing program) were determined during 1993-1999.

Reproductive success in Bargerveen lies within the range of other vital European Red-backed Shrike populations. Return rates of juveniles and adults were high compared to a German study on Red-backed Shrikes. This must be explained by absence of suitable habitats near Bargerveen, forcing short-distance dispersing birds to return to their native area. Almost all breeding pairs in the Netherlands have been checked for rings during the research period, but no successful settlements of ringed birds from Bargerveen were observed at greater distance from Bargerveen. Therefore, we consider survival rates equivalent to return rates in Bargerveen. Then immigration must have played an important role in at least three of the six examined seasons to maintain the present population level in Bargerveen, in spite of the high reproductive values and return rates. Nowadays suitable shrike habitats in the Netherlands have become very scarce and scattered. Probably the relative few long-distance dispersing birds from Bargerveen do not find these suitable remnants and so do not contribute at metapopulation level. If our findings are right, then immigration in Bargerveen and most new settlements in the Netherlands must be ascribed to long distance dispersing first-year birds of large populations from the German hinterland. From these results, we also have to conclude that in spite of the high fitness values Bargerveen acts as a sink for shrikes. It is imaginable that without the continuous supply of German birds the Red-backed Shrike would already have been extinct in the Netherlands. This phenomenon at the edge of the distribution of a declining species needs much more research attention and must have consequences for spatial restoration management to improve a close network of suitable habitats.

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Key words: *Lanius collurio*, population size, reproduction, survival, dispersal, immigration, sink

INTRODUCTION

In large parts of Europe, breeding numbers of Red-backed Shrikes have rapidly declined during the past century. In the Netherlands an estimated 5 000-15 000 pairs around 1900 fell down to at most 200 pairs in recent years (Hustings and Bekhuis 1993). Between 1970 and 1990, a decrease of more than 20% was reported in 21 of the 33 known populated European countries, including the Netherlands (Hagemeijer and Blair 1997). Today only a few local populations are stable or increasing on the long term, *e.g.* in Germany (Jakober and Stauber 1987a, Lübcke and Mann 1987) and in Belgium (Jacob 1999).

In the Netherlands, the only growing population is found in Bargerveen. Elsewhere, only a few small populations and some single pairs can be found. Here, the number of Red-backed Shrike territories increased from less than twenty between 1978 and 1987 to almost eighty in 1990 (Van Berkel 1993, Esselink *et al.* 1995). From 1991, a further increase took place to over 140 territories in 1996, after which the population seemed to have stabilized (Fig. 1). Here, peat-moor restoration has led to high variation in habitat types and high density and diversity of invertebrates. The high prey availability is reflected in marked differences between diet composition of nestlings in different habitats and during season and day (Esselink *et al.* 1994, Esselink *et al.* 1995, Hornman *et al.* 1998). Comparative research on Red-backed Shrikes breeding in coastal dunes demonstrates that lowered food availability may lead to extinction of this species (Kuper *et al.* 2000).

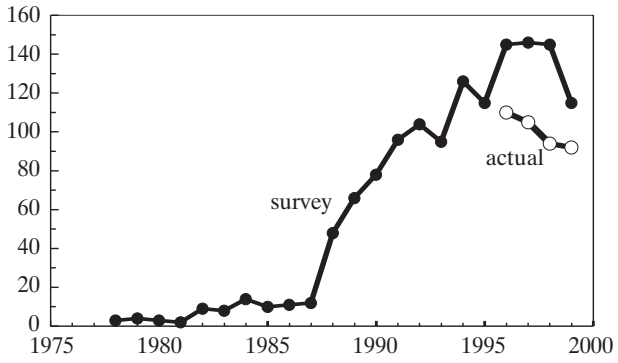

Fig. 1. Population development of Red-backed Shrikes in Bargerveen since 1978: survey – number of territories based on yearly integral census, actual – number of (potentially) reproducing pairs.

The favourable feeding conditions in Bargerveen are assumed to have played an important role in the development of the population. However, the initial fast growth of the population cannot solely be explained by recruitment. This is for example the case between 1987 and 1988, when an increase took place from 12 to 48 territories. Immigration thus must have played a role in certain years. In the nineties the increase of the population gradually stopped. This leads to questions about the present role of immigration in development of the Bargerveen population. Three scenarios can be expected for the present behaviour of the population (see also Pulliam 1988):

1. The population acts as a source from where other habitats are colonized (emigration > immigration).
2. Recruitment and adult survival maintain the present population size (immigration = emigration).
3. The population acts as a sink and immigration is needed to maintain the population (immigration > emigration).

During six consecutive years, starting in 1993, we tried to find out how the Bargerveen population was built up. For this purpose, we calculated expected population size based on reproductive success and survival rates of juveniles and adults. The yearly difference between expected and observed size should indicate which scenario is most probable.

STUDY AREA

Bargerveen is a peat-moor remnant of 2000 ha, situated in the northeastern part of the Netherlands near the German border (Fig. 2). Intensively cultivated fields

Fig. 2. Location of the research area, the peat-moor reserve Bargerveen

surround it. The area has been under influence of peat digging for centuries and large parts were fully dehydrated. In 1968, State Forestry started a program to rehabilitate the deteriorated ecosystem. The management is focused on regeneration of peat-moor vegetation by holding rainwater. For this purpose, about 40 km of dams were constructed throughout the reserve and most drainage ditches were blocked. The drier parts, mainly covered with heath, bramble-bushes and young birches, are prevented from ongoing succession by sheep grazing and selective removal of vegetation. Small part of the area consists of grasslands that are extensively used for sheep grazing and haymaking. Today the area is characterized by an enormous variation of structure-rich habitats. Many alternations between wet and dry parts and gradients, together with local abiotic differences have led to favourable circumstances for a great variety of invertebrate species. Due to the management, the distribution of suitable breeding habitats for Red-backed Shrikes changed during the research period, but total suitable area did not change obviously.

METHODS

Population size

Monitoring of Red-backed Shrikes was carried out by means of yearly integral census, to establish the number of territories. However, this method does not record breeding status of each pair or individual bird, which is necessary for calculating expected population size. Therefore, we used another method, solely based on the number of (potentially) reproducing pairs. Only sites, where a nest was found, a resident pair was observed or young fledglings were detected, were involved in the calculation of this number. In this way, the yearly numbers obtained gave the most reliable indication of the size of „actual breeding population". The actual breeding population was only reliably determined from 1996 onwards. For 1993, 1994 and 1995, the actual population size was estimated by using the mean difference between survey and actual numbers during 1996-1999.

Reproductive success

Reproductive success was expressed in terms of the mean number of fledglings per pair, based on yearly varying samples (Table 1) from the population. It was calculated by multiplying the proportion of the actual breeding population being successful (pairs producing at least one fledgling) with the mean number of fledglings per successful pair. Because precise number of young during fledging (normally after 14 days) could be determined only incidentally, reproductive success was mostly based on the number of nestlings at the age of ringing. This normally took place when nestlings were between seven and ten days old. Of 26 nests that were checked just before fledging, the mortality rate from the age of ringing was about two percent, so only slight correction was necessary for calculating reliable reproductive success.

Survival of juveniles and adults

For determining survival rates nestlings were colour-ringed yearly. An aluminum ring was attached on one leg, a colour-ring on the other leg. To distinguish between years of birth different colour-leg combinations were applied. Survival was calculated by dividing the number of returned juveniles by the total number of ringed and fledged nestlings in the preceding year. The number of returned ringed birds could not be determined exactly, because not all birds could be checked for rings. Therefore, return rates to Bargerveen were calculated by dividing the number of ringed recoveries by the proportion of birds checked for rings based on the total number of birds (Table 2). This total number was an estimation of the number of Red-backed Shrikes present during the season, considering all pairs, solitary birds and wanderers. To determine which part of the returned birds had settled outside the Bargerveen area (emigrants), most known Dutch breeding sites were checked yearly for colour-ringed individuals.

Survival of adults for different age-classes was calculated in the same way as in juveniles, but because of the low sample sizes (Table 2) ringing-recoveries were combined for all years together. Average adult survival was calculated with regard to relative distribution of all age-classes found. In cases, when year of birth could not be defined (*e.g.* when colour-ring was lost), bird numbers concerned were equally divided over possible age-classes. To give an example, the survival of four year old birds till their fifth year (63%) should be determined by calculating the total number of five year old returned ringed birds:

$$\text{in 1997: } \frac{0+1.7}{0.43}=4.0, \text{ in 1998: } \frac{0+0.3}{0.61}=0.5, \text{ and in 1999: } \frac{6+1.7}{0.80}=9.6.$$

So, the sum is: 4.0 + 0.5 + 9.6 = 14.1. The numbers of four year old birds are:

$$\text{in 1996: } \frac{1+2.0}{0.55}=5.5, \text{ in 1997: } \frac{4+0.5}{0.43}=10.5, \text{ and in 1998: } \frac{2+2.0}{0.61}=6.6$$

and give together the total sum: 5.5 + 10.5 + 6.6 = 22.5. To obtain the final result, 14.1 returned five year old birds should be divided by the original number of 22.5 four year old birds, what gives a survival of 63%.

In each fraction, the numerator is the number of ringing-recoveries plus the estimation of the number of unknown birds, while the denominator is the proportion of birds checked for rings.

RESULTS

The size of the actual breeding population between 1996 and 1999 appeared to be strikingly smaller than the size according to the survey method. The average difference was 27%, with a minimum of 20% and a maximum of 35% per year (Fig. 1). The average reproductive success during 1993-1998 (Table 1) was 3.0 young per pair, with extreme values of 2.5 (1993) and 3.5 (1994). These differences were due

to both variation in the proportion of successful pairs (67-88% yearly, mean 77%) and variation in the number of fledglings per successful nest (3.4-4.5 yearly, mean 3.9).

Table 1
Reproductive values of Red-backed Shrikes in Bargerveen during 1993-1998

	1993	1994	1995	1996	1997	1998	Mean
Successful pairs (%)	67	78	88	72	79	78	77
n pairs observed	15	23	17	44	38	36	
Fledglings per nest	3.7	4.5	3.4	4	3.8	3.8	3.9
n nests observed	10	18	15	36	29	28	
Fledglings per pair	2.48	3.51	2.99	2.88	3	2.96	2.97

Of more than 700 colour-ringed and fledged (Table 2) nestlings in Bargerveen (almost 40% of all fledged nestlings during 1992-1998), only one individual turned up outside the Bargerveen area during the research period. This concerned a first-year female, observed in 1996 at about 60 km distance from her natal grounds. However, this bird disappeared after one day. The return rates of juveniles to the Bargerveen area varied between 18 and 33% (Table 2). These rates were more or less stable until 1997, but lower in 1998 and 1999. The return rate of adults was on average 53% and seemed to increase with age (range 49-63%, Table 2). In most examined years adults of all possible age groups were observed. In 1999, we found a remarkably high number (6 – five males and a female) of five-year old birds. Birds of this age were not found in 1997 and 1998.

Table 2
Juvenile and adult survival rates of Red-backed Shrikes in Bargerveen based on colour-ringed nestlings. Unknown numbers refer to incomplete sightings (only aluminum rings seen) or to birds that had lost their colour-ring. These numbers were equally divided over the possible age-classes.

	Fledged[1] *y-1*	Checked[2] *y (%)*	Recoveries of different age-classes					Unknown numbers		Juv. surviv.
			1y	*2y*	*3y*	*4y*	*5y*	*1+3+5y*	*2+4y*	*y-1 → y*
1993	40	35	9	-	-	-	-	6	0	?
1994	50	46	7	10	-	-	-	1	0	33%
1995	128	56	16	7	4	-	-	8	0	28%
1996	120	55	20	12	0	1	-	4	4	33%
1997	141	43	16	6	4	4	0	5	1	29%
1998	127	61	19	8	7	2	0	1	4	25%
1999	105	80	13	7	4	2	6	5	0	18%
Ad. survival from age(*y*) to age+1:			-	49%	54%	58%	63%	⇒ weighed mean ad. surviv.: 53%		
Age distribution of adults:			0.50	0.24	0.13	0.08	0.05			

[1] corrected number of colour-ringed fledglings (see text); [2] estimated proportion of birds checked for rings (see text)

The calculated population size in 1994, 1996 and 1999 is markedly lower than the observed size when assuming a yearly adult survival between 40 and 60% (Fig. 3). This indicates that immigration must have taken place. In other years actual and expected size fitted well.

If the population changes were completely the result of recruitment, then with 40% adult survival a decrease would have taken place in all examined years (Table 3). With 50% adult survival the population would have been stable until 1997 and would have decreased afterwards. With an adult survival of 60% an increase until 1996, stability in 1997 and 1998 and a decrease in 1999 would have taken place.

Table 3
Expected population trend of Red-backed Shrikes in Bargerveen according to reproductive success and juvenile survival during 1993-1998 for adult survival rates of 40%, 50% and 60%, respectively.
0: 0-5% deviation, - or +: 6-20% deviation, --: > 20% deviation

	Average adult survival rate		
	40%	50%	60%
1993-1994	–	0	+
1994-1995	–	0	+
1995-1996	–	0	+
1996-1997	–	0	0
1997-1998	–	–	0
1998-1999	–	–	–

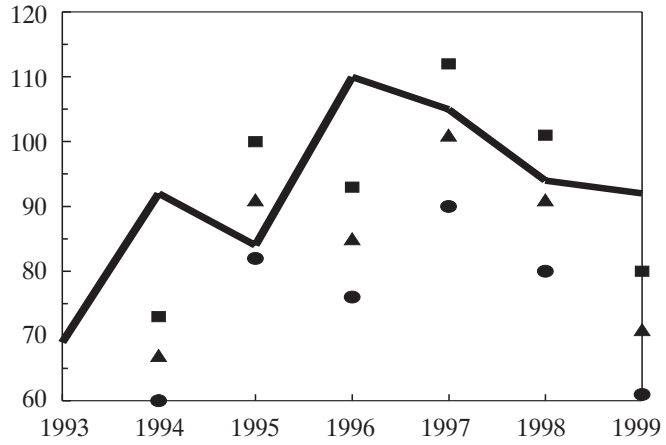

Fig. 3. Expected (symbols) against observed (line) population size (pairs) in Bargerveen from 1994 to 1999. Expected levels based on adult survival: squares – 60%, triangles – 50%, circles – 40%.

DISCUSSION

Reproductive success of the Bargerveen shrikes fitted well in the range of values of other long-term studies on Red-backed Shrikes in Europe (Table 4). Only in populations in France (Lefranc 1979) and in the Czech Republic (Holan 1995) values higher than 3.0 young per pair were found. Both the proportion of successful pairs and the number of fledglings per successful nest were higher in these countries. All populations used for comparison were stable or increasing, except England (Ash 1970), where the examined population was strongly declining. Therefore, it is striking that reproductive success of the British Red-backed Shrikes is of the same height as in Germany (Jakober and Stauber 1987a) and Switzerland (Leugger-Eggimann 1997). However, it is possible that methodological differences in the determination of the breeding parameters play a role here.

The average adult return rate of 53% in Bargerveen is about equal to the return rates of second-year (52.8%) and third-year (52.3%) males in a south-German study area (Jakober and Stauber 1987a). Much lower return rates were found for first- and fourth-year males and for females, which they assigned to age- and sex-dependent differences in site-fidelity. They concluded that the average adult yearly survival rate in their study area lies probably far above 50%. The return rates of adult birds in Bargerveen might be biased due to the small sample size, especially in the oldest birds. For future examinations it would be better to enlarge sample size by ringing the adults too.

Table 4
Reproduction of Red-backed Shrikes in various European long-term studies

Country - area (source)	Research period	Successful pairs	Fledglings/pair
Czech Republic - Moravie (Holan 1995)	1987-1992	80%	3.7
France - Elsace (Lefranc 1979)	1967-1975	83%	3.5
Netherlands - Bargerveen (this study)	1993-1999	77%	3.0
Germany - Baden-Württemberg (Jakober and Stauber 1987a)	1969-1985	64%	2.7
Switzerland - Jura (Leugger-Eggimann 1997)	1988-1991	62%	2.7
England - Hampshire (Ash 1970)	1954-1966	63%	2.6

The overall juvenile return rate of 6% found by Jakober and Stauber (1987b) is remarkably lower than the yearly return rates in Bargerveen. The examined German population, which is situated in a mountainous district of about 1800 ha, should however be regarded as part of metapopulation. Its close connection with adjacent populations facilitates dispersal of juvenile birds and thus lowers return

rates. Intensively cultivated fields surround the Bargerveen reserve, without suitable habitats in short-distance. Consequently, all juveniles in search for near habitats are forced to return to their native area. The yearly number of Red-backed Shrikes present in Bargerveen, which was hard to define, might bias the calculation of return rates in Bargerveen. To illustrate this, observations of ringed birds showed that other birds could replace territorial solitary birds and that unsuccessful pairs could settle elsewhere during the season.

In the last few years, we regularly recorded new settlements at many locations in the Netherlands, especially in the northern part, but none of the birds were born in Bargerveen. Because Red-backed Shrikes are rare elsewhere in the Netherlands, they are not supposed to be Dutch birds. Most probable these birds originate from the German hinterland. After Heckenroth and Laske (1997) 3 000-10 000 pairs are thought to breed in Niedersachsen – a German federal state neighbouring the northern part of Holland. This relatively high number compared to Bargerveen enlarges the chance for long-distance dispersing juveniles from this area to find the few remaining suitable Dutch habitats. Some native breeders may help these dispersing birds to settle, leading to clustered distributions (see also Van Nieuwenhuyse 2000). Probably each year a specific amount of juveniles from Bargerveen disperse at long-distance, but most of these emigrants are never seen again because they are in fruitless search of unoccupied habitats. The relatively high number of immigrants in Bargerveen in specific years may derive from the same German region. They probably do not derive from adjacent German areas, for most are heavily affected and consequently largely deserted.

To maintain a stable population, juvenile survival in Bargerveen should be at least 31% concerning the average calculated reproductive success of 3.0 young per pair and the average adult survival of 53%. This proportion touches the upper border of the juvenile survival range. This means that in years with low juvenile survival the population is not self-supporting anymore. To remain stable, the population has to act as a sink by increasing the immigration rate. Low juvenile survival rates were found in 1998 and 1999, probably due to lasting bad weather periods in the preceding seasons. However, only in 1999 the low recruitment seems to have been compensated by immigration. We can only speculate about yearly differences for immigration, but for certain years it may be of great importance in maintaining the population.

We can conclude that although fitness parameters of the Bargerveen shrikes are relatively high, the population seems to act as a sink. Immigration is taking place, but no successful emigration could be ascertained. In recent years immigration even seemed to be necessary to maintain the population. It is possible that without a continuous supply of German birds the Red-backed Shrike would already have been extinct in the Netherlands. This phenomenon at the edge of the distribution of a declining species needs much more research attention and must have consequences for spatial restoration management to improve close network of suitable habitats. In future research we will focus on tracing the origin of the immigrants by using genetic techniques. Also we must try to enlarge the number of ringed birds to get more detailed information on yearly survival rates of the Bargerveen Red-backed Shrikes.

ACKNOWLEDGEMENTS

We thank the staff of State Forestry department Drenthe-south: Jans de Vries, Frans Germes, Piet Ursem and Ep Smit for giving us the opportunity and the facilities to carry out our fieldwork. We are also very grateful to many students and volunteers that assisted in the fieldwork. Especially we would like to thank Ted Post, Sietske van Haren, Dick Visser and Jan Rocks for spending one or more seasons in searching for nests and in assisting with ringing. Many of our colleagues from Stichting Bargerveen helped to improve earlier versions of the manuscript.

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