

# DISPERSAL PATTERNS OF THE RED-BACKED SHRIKE (*Lanius collurio*) IN GAUME, BELGIUM

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## ABSTRACT

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In a study of dispersal pattern of the Red-backed Shrike in southern Belgium (Gaume), I tested the annual variance in proportional distribution for 10 years (1990-1999) in five distinct population clusters. The overall *chi*-square test showed no difference in proportional distribution ( $\chi^2 = 48.779$ ,  $df = 36$ ,  $p = 0.076$ ). Two-by-two tests gave mostly significant differences from 1990 to 1993 – after 1994, all following combinations were analogous. The annual population size elasticity on the annual average inter-territorial distance was calculated. The percent change in average distance for every percent increase in population size was -0.6 proving no real population independent optimal clustering behaviour. The yearly observed distribution was tested for complete spatial randomness yielding one year with a regular pattern and another with a clustered distribution. Site reoccupation was highly correlated with population size of the preceding year (reoccupation =  $0.31 \times$  population size year-1;  $p < 0.001$ ). The historical occupation of territories does not correlate with the average nearest neighbour distance or with the arrival date. The importance of site-fidelity on occupation probability was studied for 1997 and 1998 using a logistic regression of historical occupation of the sites with a multiplicative interaction term. Sites that were occupied in year-1 showed a lower occupation probability if the sites had a history of less than 5 years than unoccupied sites in year-1. The fidelity effect (occupation in year-1) only yielded higher probability in sites with a historical occupation of at least 5 years. Finally, the correlation of the annual distribution was only positively correlated in years with lower population levels for one or two consecutive years. Similarity in distributions got smaller in larger populations while the similarity of proportional distribution for different locations increased. Important fluctuations of shrike populations could be due to climatic changes on the long term while on the short term there might be an important exchange between regions. Shrike populations might target at a larger migration window. Apparent limited fidelity on the individual territory level becomes clear fidelity on a larger scale. Similarly, some local differential fluctuations might be explained by a redistribution of the same birds from one year to another. We find evidence for both the optimal habitat choice hypothesis and social preference hypothesis. It could be argued that the advantage of site fidelity is not necessarily induced by good habitat quality from a foraging and security point of view but rather socially induced. In that sense, the vicinity of conspecifics and opportunities for extra-pair copulations might be a very important determining factor for habitat quality.

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**Key words:** *Lanius collurio*, dispersal, site fidelity

## INTRODUCTION

Some striking observations about shrike dispersal and its controlling factors indicate that the processes that influence the dispersal patterns are much more complex than generally believed and crucial information for conservation. Shrike populations tend to fluctuate significantly – while increases are observed in some places (Van Den Brink 1996, Jacob 1999), populations in nearby localities are declining (Van Nieuwenhuysse 1999) at the same moment. Shrikes settle in high densities to exploit temporary habitat, *e.g.* forest clearings – the Great Grey Shrike (*L. excubitor*) and Red-backed Shrike (Söderström 1996); burnt forest, *e.g.* the Southern Grey Shrike – *L. meridionalis* (Lefranc and Worfolk 1997). From year to year, the pattern of settlement can be remarkably different (Jakober and Stauber 1983). Shrike territories occur regularly in a clustered dispersal pattern (Ash 1970, Jakober and Stauber 1987b, Van Nieuwenhuysse 1992), sometimes induced by habitat availability, sometimes by social preference and featured by extra-pair copulations and mate guarding behaviour. Shrikes show pronounced site fidelity either by the same individual birds (Red-backed Shrike – Jakober and Stauber 1989) returning every year, or different birds occupying favourite sites (the Lesser Grey Shrike *Lanius minor* – Krištin *et al.* 1999). Finally, own observations showed that the settlement of a shrike population in a given area changed considerably from year to year.

In order to understand the changes in the dispersal pattern of a Red-backed Shrike population in Gaume (southern Belgium) I use the theoretical framework of the optimal habitat choice hypothesis versus the hypothesis of social preference as the major factors governing settlement. A similar analysis has been done by Herremans (1993) on the Wood Warbler (*Phylloscopus sibilatrix*).

## MATERIAL AND METHODS

Since 1979, a yearly census was done of „integral survey” type (Hustings *et al.* 1985) taking up to one week at the end of June, beginning of July in the southern part of the Gaume (Belgian Lorraine – 49°30'N, 5°24'E).

The study area of approximately 50 km<sup>2</sup> has up to 25 km<sup>2</sup> of potentially suitable shrike habitat (obtained after the removal of all trivially unsuitable surfaces for the species *e.g.* forests, built-up areas). The principal land use is pastures and meadows for cattle grazing in the valleys and forests on hilltops. The altitude ranges between 190 and 365 m a.s.l. Five main population clusters are distinguished: Sommethonne valley (with mainly hayfields), Valley between Villers-la-loue and Couvreur (with pastures and hayfields), eastern slopes of Montquintin and Dampicourt (with hayfields, corn and other arable fields), the valley of the Vire (with meadows and pastures) and the slopes of the southern cuesta (with hayfields and pastures). These different zones are not only distinct zones in the landscape, they are also geographi-

cally isolated, and shrikes between the different clusters are not in visual or auditive contact. I assume that there are no physical or genetic interactions between the shrikes of different areas during a single breeding season. L. Fornasari and I consider a population cluster as a Pulliam's sub-population (1988) with physical and genetic interactions higher than random. Solitary males were identified as those males with specific advertising calling behaviour (rapid „ki-jet, ki-jet”-calls – Lefranc and Worfolk 1997) late in the season. At most, 2 solitary males were recorded each year (in July) and they are included in the analysis. A territory was considered as occupied as soon as at least one of the partners was observed foraging for at least 5 minutes in a given area or entered a shrub while carrying food.

All territories were mapped on digital maps of 1 : 10 000 resulting in a geographical reference with accuracy to about 20 m. The nearest neighbour distances were calculated in SAS. The tests for complete spatial randomness (Clark and Evans 1954) were carried out using ARC/INFO. The occupational probability was modelled using PROC LOGISTIC with a multiplicative interaction term (Friedrich 1982). Since birds could not be identified individually for each territory, I consider the reoccupation of a certain territory in a consecutive year without any assumptions about the territory holder. The historical occupation also makes no assumptions about the individual birds involved, or about the sequence of occupation and is measured as the number of times the site was occupied during the last decade. A *chi*-square test is used to investigate independence of the proportion of the population occupying the different subpopulations. The *Phi*-coefficient (Siegel and Castellan 1988) was calculated to test the correlation between the occupations of the respective sites year by year.

## RESULTS

During the last decade, there were no obvious changes in landscape and vegetation structure. Trimming and uprooting of hedges did not happen in a systematic way but rather randomly nor did the land use change dramatically. Detailed observations of prey availability are not available. The overall population was more or less stable by the end of the study period at about 130 territories, with exceptional 161 territories in 1996. In earlier years, the population fluctuated between 36 and 91 territories. The occupied territories are situated in 5 different clusters with possible intra-cluster physical and genetic contact and 6 additional small isolated zones with only 1-3 territories.

### Year-to-year agreement in proportional distribution

If the optimal habitats are used and no systematic impact in the habitat quality is seen, then there should be a year-to-year agreement in the proportional distribution of the population. After considering only the 5 clusters and ignoring the rest outside these areas, at least 89% of the yearly population was covered. The surface of the

clusters is 15.4 km<sup>2</sup> or about 63% of the potentially suitable shrike habitat. The relative surface per area ranges from 8 to 26%. The overall *chi*-square test showed no difference in proportional distribution ( $\chi^2 = 48.779$ ,  $df = 36$ ,  $p = 0.076$ ). Two-by-two tests of the proportional distributions gave mostly significant differences from 1990 to 1993, while from 1994 onwards all following combinations were similar as were most two years combinations (Table 1).

Table 1  
*Chi*-square values and probabilities of two-by-two tests of independence of the proportional distribution of a Red-backed Shrike population in Gaume (southern Belgium) in 5 population clusters

<i>p</i> -value	1990	1991	1992	1993	1994	1995	1996	1997	1998
1991	0.66								
1992	<b>0.03</b>	<b>0.02</b>							
1993	0.27	0.15	0.07						
1994	0.10	<b>0.01</b>	0.06	0.12					
1995	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	0.16				
1996	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.01</b>	0.33	0.79			
1997	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	0.07	0.78	0.85		
1998	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	0.15	0.69	0.92	0.92	
1999	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	0.07	0.76	0.79	0.96	0.97

$\chi^2$ , $df=4$	1990	1991	1992	1993	1994	1995	1996	1997	1998
1991	2.40								
1992	10.97	12.13							
1993	5.16	6.81	8.52						
1994	7.81	14.34	9.11	7.29					
1995	21.00	19.11	16.97	17.40	6.53				
1996	18.71	19.65	16.81	14.13	4.58	1.72			
1997	20.85	19.08	20.84	17.15	8.76	1.77	1.35		
1998	23.46	23.30	18.48	14.86	6.69	2.22	0.94	0.92	
1999	23.97	22.21	19.28	16.01	8.55	1.85	1.70	0.59	0.49

### Clustered distribution pattern

The distribution of the population was tested for complete spatial randomness (Clark and Evans 1954) year by year. The basis of this nearest neighbour method is the selection in turn of each individual in the population and the measurement of the distance between it and its nearest neighbour. The mean nearest neighbour distance for all the territories in a measured area, or a random sample of them, is com-

pared with the mean distance that would be expected if the individuals in a population of that density were randomly distributed. The resulting ratio is a measure of the departure from randomness. Two years had no spatial randomness *i.e.* 1995 had a regular distribution ( $R$ -value = 1.917,  $Z = 37.31$ ,  $p = 0.0005$ ) and 1996 had a clustered distribution ( $R$ -value = 0.902,  $Z = 2.35$ ,  $p = 0.0094$ ). Instead of finding clear clustering behaviour every year, I found an evolution in aggregation in function of the population size (Table 2) with a maximal average inter-territorial gap of 442 m (1991 –  $n = 36$ ) and a minimal gap of 177 m (1996 –  $n = 161$ ). The elasticity of the population size per year on the average inter-territorial gap:

$$\ln(\text{average gap}) = 8.26 - 0.602 \ln(\text{population size})$$

$$(p < 0.001, \text{Adj } R^2 = 0.924)$$

shows for every percent increase in population size a 0.6% decrease in average inter-territorial gap per year. The distribution of the inter-territorial gaps was very similar in the different years and positively skewed, confirming the lack of equal spread of the territories in favour of the maximisation of the territory size.

Table 2  
Population size, average inter-territorial distance and standard deviation per year  
of a Red-backed Shrike population in Gaume (southern Belgium) 1990–1999

	Mean gap	<i>SD</i> gap	<i>N</i>
1990	417.84	426.02	48
1991	442.27	411.38	36
1992	325.27	267.02	58
1993	244.64	253.94	85
1994	244.25	280.05	91
1995	217.27	170.19	133
1996	176.88	138.99	161
1997	224.10	160.59	134
1998	228.74	184.73	128
1999	182.30	139.98	130

### Reoccupation and historical occupation of sites

A low fidelity to the previous year's nesting site can be expected when a highly dynamic settlement would be present. The reoccupation of territories is highly depending on the population size of the preceding year while the proportion of reoccupied territories is rather constant (Table 3). For every unit increase in population size of the preceding year, the number of reoccupied territories increases with 0.317.

$$\text{reoccupied territories in year} = 0.317 \times \text{population size year-1}$$

$$(p < 0.001, \text{Adj } R^2 = 0.905)$$

An average yearly reoccupation of territories of around 26% is found. This means that at least some 74% of the population settles elsewhere compared to the

preceding year. The distribution of historical occupation shows that 56% of the ever used sites ( $N = 515$ ) is only used once, 22% – only twice and 10% – during 3 years. The location of sites with a high historical occupation is not necessarily in cluster centres since there is no relation of the average inter-territorial gap per site versus the historical occupation.

Table 3  
Population size per year, reoccupied territories and reoccupation rates of territories of Red-backed Shrike in Gaume (southern Belgium) 1990-1999

	Occupied territories			reoccupied %	Territories	
	in year yr	in yr-1	both yrs		new %	disappeared %
1991	36	48	12	0.33	0.67	0.75
1992	58	36	6	0.10	0.90	0.83
1993	85	58	22	0.26	0.74	0.62
1994	91	85	22	0.24	0.76	0.74
1995	133	91	29	0.22	0.78	0.68
1996	161	133	43	0.27	0.73	0.68
1997	134	161	52	0.39	0.61	0.68
1998	128	134	37	0.29	0.71	0.72
1999	130	128	31	0.24	0.76	0.76

The impact of the historical occupation on the occupational probability was analysed yearly and showed a non-linear relation (Fig. 1). The logistic regression with multiplicative interaction term using 10 years of historical occupation ( $n = 503$ ) results in 2 regression equations.

$$Z(O_{98}) = -1.9233 + 0.4787 \times HO - 1.4755 \times O_{97} + 0.2961 \times (HO \times O_{97})$$

$$O_{97} = 0: Z(O_{98}) = -1.9233 + 0.4787 \times HO \quad (1)$$

$$O_{97} = 1: Z(O_{98}) = -1.9233 + 0.4787 \times HO - 1.4755 + 0.2961 \times HO \quad (2)$$

where:

$O_{97}$  – occupation in 1997,  $O_{98}$  – occupation in 1998,  $HO$  – historical occupation.

The probability obtained after conversion of the Z-scores as calculated from the regression equations for all discrete values of historical occupations shows a difference in slopes of both curves which stresses the importance of site fidelity ( $> 5$  years occupation) and the importance of occupying new sites ( $< 5$  years occupation). Hence, a systematic part of the population tends to resettle while another part of the population seems to be opportunistic.

Finally, the analogy of the respective distributions between years was measured by the *Phi*-coefficient (Table 4) in two-by-two combinations. The correlation of the annual distribution was only positively correlated in years with lower population levels and only for one or two consecutive years. Similarity in distributions got smaller in larger populations while the similarity of the proportional distribution for different locations increased.

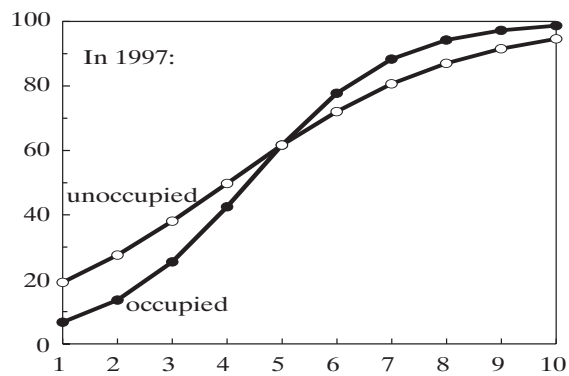


Fig. 1. Probability curves of occupation of Red-backed Shrikes territories in Gaume (southern Belgium) in 1998 using the historical occupation of the last decade and using the occupation in 1997 in a multiplicative interaction term.

Table 4

*Phi*-coefficients and respective *p*-values of two-by-two associations of the population distribution of Red-backed Shrike in Gaume (southern Belgium)

<i>p</i> -value for <i>Phi</i>	1990	1991	1992	1993	1994	1995	1996	1997	1998
1991	<b>0.00</b>								
1992	<b>0.00</b>	<i>n.s.</i>							
1993	<i>n.s.</i>	<i>n.s.</i>	<b>0.00</b>						
1994	<i>n.s.</i>	<b>0.01</b>	<b>0.00</b>	<b>0.03</b>					
1995	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<b>0.014</b>	<i>n.s.</i>				
1996	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>			
1997	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<b>0.03</b>		
1998	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	
1999	<i>n.s.</i>	<i>n.s.</i>	<b>0.09</b>	<i>n.s.</i>	<b>0.033</b>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>

<i>Phi</i> coefficient	1990	1991	1992	1993	1994	1995	1996	1997	1998
1991	0.226								
1992	0.160	0.047							
1993	0.073	0.022	0.206						
1994	0.062	0.133	0.173	0.096					
1995	-0.021	-0.005	0.056	0.106	0.064				
1996	-0.043	-0.037	0.078	0.039	0.061	0.014			
1997	-0.007	-0.006	0.041	0.034	-0.008	0.014	0.097		
1998	-0.061	-0.034	-0.020	-0.026	0.063	0.030	0.029	0.038	
1999	0.014	-0.019	0.090	-0.018	0.094	0.035	0.052	0.012	-0.014

## DISCUSSION

Herremans (1993) gave several arguments in favour of both the optimal habitat selection hypothesis and the social preference hypothesis (Table 5). The same arguments are taken into consideration to evaluate the importance of both hypotheses in the Red-backed Shrike.

Table 5  
Arguments in function of the optimal habitat choice hypothesis versus social preference hypothesis according to Herremans (1993)

Social preference hypothesis	Optimal habitat choice hypothesis
Exploitation of temporary habitats	Site fidelity with constant habitat
Heavy population fluctuations	Year to year agreement in proportional distribution
Highly dynamic population settlement	Clutch size depending on habitat quality
Aberrant territories are also occupied	Average inter-territorial gap decreasing on increasing population size
Constant average inter-territorial gap	
Population synchrony in clusters	
Breeding success increase in clusters	
Sneekers, helpers at nest	
<> distribution patterns for <> arrival patterns	

## Fluctuations in population numbers

Shrike population numbers can vary considerably from one year to another. Jakober and Stauber (1987b) observed the smallest population size as 49% of the maximal in 17 years time – in Gaume this is 22% for the last decade. Different causes for these variations have been suggested such as the weather – the Lesser Grey Shrike, food availability – the Great Grey Shrike and transformations of habitat by alterations in land use (Lefranc 1980). Long-term fluctuations might well be caused by climatic changes (Lefranc 1973). However, Jakober and Stauber (1987b) did not find any correlation between population numbers and the weather during the breeding cycle. Lack (1966) found that the reproductive success could not explain the changes in population size from one year to another. Therefore, the mortality was believed to determine the density. Ash (1970) also considered a high mortality rate as one of the main reasons for the decline and extinction of the species in UK, given by 68% juvenile loss and 84% loss the next year. Jakober and Stauber (1987b) found, however, only an adult mortality of 4-5%. Svårdson (in Lack 1971) noticed that in good years, the species could be found in unusual habitats, probably



because the suitable habitat is fully occupied. These increases do not mean that the whole population is actually increasing; reallocation of 1<sup>st</sup> year birds might give local increases (Lefranc 1973). Other evidence for influxes is found in extreme increasing local populations like Bargerveen (The Netherlands) going from 9 territories in 1982 to 145 in 1996 (Van Den Brink *et al.* 1996) and Gaume from 35 territories in 1991 to 161 in 1996 (pers. obs.) probably due to an influx. Ash (1970) studied three areas and found differential fluctuations; one area showed a decline while another area showed an increase. Birds were found to come back to former locations even after interruption of a few years, supporting the idea of dispersion over larger distances. Possible reallocation of birds between nearby areas could be seen in Belgium as well (Jacob 1999), where we see the population peak at Châtillon in 1995, in Virton and Marche-en-Famenne in 1996 and in Durby-Mormont in 1997. Fluctuations might very well be caused by exchange of birds over a wider area.

Ash (1970) found that ringed birds were found in consecutive years up to 10 and 14 km away. Jakober and Stauber (1987c) found that 72% of returning males settle between 0 and 200 m from their preceding breeding place, 18% – between 300 and 900 m and 10% – further than 1 km. Extreme cases were a male found breeding at 23 and respectively 200 km from the preceding year. This suggests that fluctuations might simply be due to dispersion of the local populations over larger distances supporting the social preference hypothesis. The situation could be similar to that in the Wood Warbler, which returns to a general area of a few thousand square kilometers without aiming precisely to the previous territory, even when they had bred there successfully (Herremans 1993).

#### **Dynamic versus constant distribution of the population according to habitat distribution**

If the habitat quality plays a major role in the settlement, the distribution should be rather constant, provided that the habitat in the cultivated areas did not alter considerably during the last decade. The Red-backed Shrike shows in Gaume a very homogeneous proportional distribution across the years, taking into account 5 major clusters. Even in years with small population numbers, similar proportions occurred in the 5 clusters. This is in contrast to the data of Jakober and Stauber (1987c) who found a clear difference in occupation of different landscapes. The variation coefficient (standard deviation divided by the average number of territories) was minimal in an area with the best habitats, while the occupation of less favourable habitats was much less constant. Jakober and Stauber state that in good habitats, it is habitat quality that plays the major role, while in less favourable habitat, it is the social aspect that has major importance, suggesting that the social preference hypothesis only plays role when all optimal habitats are taken, hence considering that this behaviour would be one of secondary importance.

### Dynamic settlement

In Gaume, however, the occupation of the territories is dynamic. Similarities between years are only found in one or two successive years, probably due to the resettlement behaviour of males and most in smaller density years. Ash (1970) observed breeding pairs in loosely colonial distributions, with intervening areas of suitable habitat unoccupied. Popular areas were sometimes deserted and new colonies formed. This dynamic settlement was also observed in Gaume and even tended to increase with increasing densities (only 1996-1997 and 1994-1999 correlate after 1994). This might be the consequence of closer settlement and heavier competition between individuals. The opportunism is clearly illustrated by low frequency of habitat use (78% of ever-used territories were used for maximally 3 years). Krištin *et al.* (1999) also found in *Lanius minor* about 50% of the ever used sites (103/207) used only once in a decade. The fact that the Red-backed Shrike inhabits mostly temporary habitats *e.g.* forest clearings (Lefranc and Worfolk 1997) illustrates the mobility of the species which allows the species to react rapidly to new opportunities.

### Reoccupation of territories

On the other hand, some birds might benefit from knowing the habitat when they reoccupy a territory. This might be reflected by an average reoccupation rate of 45% (or 51% for older males – Jakober and Stauber 1987b) or 26% in Gaume, and depending on the population of the preceding year. Since the density can still increase with an increasing population size in Gaume, there is still spare capacity for extra territories. What might be the case of Jakober and Stauber is that the optimal habitats are nearly all taken in the best area and that newcomers have to look for other sub-optimal habitat. In the same way the reoccupation rate might be higher because the amount of available territories is limited and hence the same are reoccupied. Brandl *et al.* (1986) found a difference in distribution of the historical occupation in different habitat types. Even though the curves of mixed habitat and pastureland are higher (compared to the rest), the same lognormal distribution is found in all habitat types. Krištin *et al.* (1999) found in the Lesser Grey Shrike a systematic reoccupation of specific territories but nearly always by different birds, without finding any real differences in habitat characteristics between nest sites in relation to historical occupation. Observed males resettled mostly within a range of around 600 m from the territory of the preceding year. Jakober and Stauber (1989) also found that 2-year-old birds breed at least 300 m away from the site of the preceding year. This confirms the idea of fidelity at cluster or even regional level.

### Site fidelity

The fidelity of species to territories is depending on sex, age and preceding breeding success. The highest fidelity rate to breeding places was found in those

males which had used their territories for two seasons or longer (Jakober and Stauber 1989, Massa *et al.* 1995). One-year-old males that disappear late in summer after unsuccessful attempts to breed, demonstrate a higher return probability than those that depart early. No comparison of the actual distribution patterns was done (Jakober and Stauber 1989). Site fidelity, however, is only common in adult birds since only 6% of young birds return to the place of birth in the following year or later; the majority of the surviving individuals settles outside the area (Jakober and Stauber 1987c). Data from winter quarters also suggest high return rate (23%) to non-breeding territories of previous winter (Herremans *et al.* 1995). *Lanius minor* displays very low site fidelity of individuals and low mate fidelity in Slovakia (Krištin *et al.* 1999).

### Historical occupation

If the habitats did not change, then the historical occupation of sites should be rather constant in optimal habitat choice models. If the optimal habitat choice hypothesis holds, then the historical occupation should correlate positively with habitat quality (best territories are most occupied) and negatively with the arrival date (best territories are first occupied). The average nearest neighbour distance of a site over the years should have very limited variance, since the same priority of occupation would exist under constant habitat quality. This is, however, not observed either in the Red-backed Shrike or in the Lesser Grey Shrike (Krištin *et al.* 1999). I found no relation between the historical occupation and the first occupation date for 1994 of 32 territories belonging to two different clusters. The variance showed a similar relation with population numbers, as did the average nearest neighbour gap and decreased with increasing densities. Hence, no real optimal inter-territorial gap exists (Table 2). A consistent behaviour towards habitat quality could neither be observed since there was apparently unsuitable habitat occupied and apparently suitable habitat that was not occupied. The occupation of apparently unsuitable habitat could be caused by increasing of population because of lack of additional territories (Svårdson after Lack 1971, Jakober and Stauber 1987c). However, if there is no saturation of available territories a trade-off between habitat quality and other parameters (e.g. vicinity of conspecifics) can be observed (Ash 1970, pers. obs.) since some apparently suitable territories are not necessarily occupied. Popular areas are sometimes deserted and new colonies formed. This confirms the importance of social aspects in habitat choice. Apparently, suitable habitat remains unoccupied and unsuitable habitat is taken. Territory composition of 1986 ( $n = 58$ ) was analysed using PCA ( $R^2$  of first two principal components: 37.2) (Van Nieuwenhuyse and Vandekerckhove 1992). The average of nearest neighbour distance (isolated territories removed) for 9 most aberrant territories in the first component (210 m) was on average smaller than the population mean (231 m), supporting the hypothesis that the vicinity of conspecifics is used as trade-off with habitat composition parameters.

### Crystal growth and clusters

Clustered distributions might result when early males in spring attract arriving conspecifics. Clusters might develop like growing crystals, starting with a random starting point and attaching additional molecules to the present ones. In the Wood Warbler habitat occupied was different in some years as a consequence of incidental settlement of a number of aggregated males at particular spots (Herremans 1993). Confirmation of similar behaviour in the Red-backed Shrike could be found in Gaume as well, *i.e.* between 1 May 1993 and 8 May 1993 (total population of 3 to 15 territories, respectively), a dense population cluster of 6 solitary males and one pair settled in one-week time, all merely 40 m from each other.

Differences in arrival patterns hence can also determine the formation of clusters. The arrival pattern within a population can differ remarkably from year to year and partly depends on the spring weather (Jakober and Stauber 1983). In some years, waves of arriving birds can be observed. Jakober and Stauber also found that there is correlation between the departure time of bird in given year and the arrival date in the consecutive year. In Gaume, I found for 1994 that the date of occupation of 32 territories showed no relation with historical occupation. Higher reoccupation rate for territories in the centre of clusters was not observed either. This confirms that the exact location of territories within clusters does not necessarily have to be identical from year to year. In increasing populations the shift of territories further tend to increase probably due to more intense competition between arriving males.

Lorek (1995) compared breeding biology in isolated and none-isolated pairs in the Great Grey Shrike and found breeding synchrony in pairs with neighbours (standard deviation: 7 days and 12 days for isolated pairs), a sooner clutch initiation (12 April and 22 April, respectively) and slightly better breeding results (average fledged young per breeding attempt 4.6 for none-isolated pairs, 4.5 – for isolated pairs). Opportunities for clustering behaviour hence could be important parameters in the assessment of habitat quality and used as trade-off with more general habitat parameters, in contrast to what Jakober and Stauber suggest (1987c).

In Germany, the number of solitary males varies between 3-6 individuals (5-12% of the male population) and seems to increase in decreasing population (Jakober and Stauber 1983). Our results only gave at maximum 1% of the population as solitary males. This might confirm again that conditions for shrikes, as seen in Gaume, are better. The relevance of the number of solitary males might, however, prove to become important in suboptimal conditions.

### Extra-pair copulations

Extra-pair copulations (EPC) have been reported in different shrike species (the Red-backed Shrike – Fornasari *et al.* 1994, Jakober and Stauber 1994; the Great Grey Shrike – Lorek 1993, Schön 1994; the Bull-headed Shrike *Lanius bucephalus* –

Yamagishi and Nishiumi 1994). Mate guarding has been considered as defence of males against EPC. Additionally, Jakober and Stauber (1989) found that the reaction of the Red-backed Shrike males against stuffed males was heavier during nest building and laying time than during incubation. The aggressive response of males may be a method to prevent extra-pair copulations. It is evident that EPC are easier in clustered populations than between isolated pairs. Own observations showed for 15 breeding pairs monitored for at least one hour per week during the breeding season, that all birds had some physical interactions with extra-parental birds (Van Nieuwenhuyse 1998).

It could be argued that the advantage of both clustered distribution and site or cluster fidelity is not necessarily caused by good habitat quality from foraging and security point of view, but rather socially induced. In that sense, the vicinity of conspecifics and opportunities for EPC might be very important determining factors for habitat quality and the assessment of the quality of a male.

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