

Breeding biology and breeding success of the Lesser Grey Shrike *Lanius minor* in a stable and dense population

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The Lesser Grey Shrike *Lanius minor* is highly endangered throughout Europe, having declined markedly in abundance and range. Long-term changes in climate and agricultural practices have been identified as the main reasons for its decline. To determine which factors influence short-term changes in breeding success, we examined several aspects of its breeding biology. Our investigation revealed that our study area bears a large and stable population of this species. In 1996 and 1997, we recorded 84 and 77 breeding pairs in an area of 20 km², with an average of 4.20 and 3.85 pairs/km² respectively. Data on breeding density, clutch size and fledging success from 1989 to 1997 (excluding 1992) indicate a stable breeding population with a constant high breeding success. Reproductive success declined through the season, mainly through seasonal variation in clutch size rather than chick mortality. However, breeding success was generally high (69% and 79% of the nests produced chicks), with low hatching failure and few nest losses. The main cause of breeding failure was nest predation (at least 50% of nest losses), mainly by magpies (at least 66% of depredated nests). Although in this population the Lesser Grey Shrike tends to aggregate in clusters, breeding density had no obvious effect on breeding success and nest predation.

The Lesser Grey Shrike *Lanius minor* has declined dramatically in the last 50 years (Lefranc 1993, 1995, Tucker & Heath 1994). Climatic changes and habitat deterioration due to changes in agricultural practice have been identified as the main causes for its decline (Niehuis 1968, Lefranc 1993, 1995, 1997), although the situation in the wintering grounds may have contributed to the population decline (Herremans 1997). However, there is almost no detailed information on which factors influence breeding behaviour and success in this species and which specific parameters (e.g. clutch size, hatching rate, or fledging rate) may be responsible for the decline. Nest predation and food availability are generally considered to be the two most important ecological factors determining breeding success, settlement strategies and hence population density in birds (Ricklefs 1969, Wiens 1989, Martin 1992). However, population density alone can be an important factor influencing breeding success through intraspecific competition for food and nest sites (Wiens 1989) or through 'apparent competition' (increased predator attraction with increasing

density; Hoi & Winkler 1994, Kleindorfer *et al.* 1996). In contrast, density could also reduce predation rate through better predator detection and more efficient defence and distraction (Wittenberger & Hunt 1985, Anderson & Hodum 1993).

Our study site comprises one of the last high-density populations of this species on the current northwestern border of its breeding distribution, thus providing a rare opportunity to understand its breeding biology in a stable dense population. We therefore reviewed the information already available from the study area and examined breeding performance in detail during two breeding seasons (1996 and 1997). We also investigated the role of ecological factors, such as unfavourable weather and nest predation, on reproductive success. The Lesser Grey Shrike is a social monogamous species that defends a large all-purpose territory around the nest (Cramp & Perrins 1993). Territories are usually not evenly distributed and pairs frequently settle in clusters of two to six territories, resulting in a high local variation in nest density in our study area (Kristin 1995). Therefore we also analysed the impact of breeding density on reproductive success.

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MATERIAL AND METHODS

The Lesser Grey Shrike is a long-distance migrant, overwintering in South Africa (8000–10 000 km from our study area). Pairs produce a single brood per season, although replacement clutches can be produced after nest failure. The species was studied in Central Slovakia (40°35′–38′N, 19°18′–22′E) from May to July 1996 and 1997. The study area comprises about 20 km² (450–850 m asl) in an extensively managed agricultural landscape characterized by a high diversity of habitats (meadows, pastures, fields, bare ground and orchards with plenty of tall trees). The nests are generally situated high above the ground (mean 8 m, range 3.2–17 m, $n = 138$) usually on the edge of the crown (mean 1.7 m, range 0–5 m from trunk axis, $n = 138$) of fruit trees (usually pear, apple, cherry and plum trees). Nest trees are frequently near farmhouses (mean 17.7 m range, 0–120 m, $n = 138$). For detailed habitat description, see Kristin (1995).

For comparative purposes we reviewed the information available (breeding density and breeding parameters) from our study area from 1989 to 1995 (except 1992), when a fixed area (10 km²) was surveyed with a low but comparable searching effort (for details see Kristin 1995). During 1996 and 1997 intensive monitoring was performed in a larger area (20 km²) including the former.

At the beginning of May, we started to check the study area at two-day intervals for the presence of adults. A territory was considered to be established when a pair was observed in the same place for more than five days. In all territories, we looked for nests in appropriate trees or tried to find them by watching birds during nest-building. Nests were checked at least once a week by climbing to them. Every check lasted no more than 10 minutes except when a ladder was used. These required about 20 min. We found no difference in the rate of nest failures (nest where no chick fledged) between visited and non-visited nests. For instance in 1996, 12 (12.5%) out of 47 visited and seven (31.8%) out of 22 non-visited nests failed (χ^2 test: $\chi^2 = 0.07$, $P > 0.7$) and in 1997 nine (20.5%) out of 44 visited and four (26.7%) out of 15 non-visited nests failed ($\chi^2 = 0.02$, $P > 0.8$). We recorded the number of eggs, number of chicks and unhatched eggs per nest, although not all parameters could be collected for all nests (for sample sizes see Tables 1 & 2). Nestlings were weighed and aged. We assumed fledging success to equal the number of chicks at the last check (chick age at least 10 days). Therefore, breeding success may be slightly overestimated

because chicks stay in the nest on average until 16 days old (Kristin 1995) and we cannot include losses happening in the last few days in the nest, although we believe these to be rare. Replacement clutches may compensate partly for nest predation as they occur at any stage of the breeding cycle, although clutch size is reduced and fledging success poorer (see also Glutz von Blotzheim & Bauer 1993, Cramp & Perrins 1993).

We distinguish first clutches (first egg laid until 25 May) from replacement nests. Most of the latter were replacement clutches and only few (none in 1996 and two out of 10 in 1997) resulted from nest desertion before laying.

We witnessed some cases of nest predation, but in some nests we could not ascertain the cause of failure and therefore inferred it from the tracks found in and around the nest. We recorded the location and density of potential nest predators, e.g. Black-billed Magpie *Pica pica* nests with nestlings in 1996, and the distance to the nearest shrike nest.

Tests are two-tailed and usually non-parametric (Zar 1984) except when they meet the requirements of normality. The study area was divided into 20 1-km squares on a regular grid. For each grid we determined: (i) the number of Lesser Grey Shrike nests; (ii) the number of Magpie nests; and (iii) the percentage of nest losses. For 1996 breeding data, a stepwise multiple regression analysis using a forward procedure was then performed to examine the effect of nest density, density of magpie nests, and season on reproductive success (percentage of unsuccessful nests). Partial correlation coefficients are given to examine the effect of each variable separately while controlling for the two others. Therefore, nest density/km² ($\log x + 1$ transformed), time in the breeding season as mean start of egg laying (Julian date)/km², and magpie density/km² ($\log x + 1$ transformed) were used as independent variables and nest loss rate/km² (arc sine transformed) as the dependent variable.

RESULTS

Population density and breeding parameters

From an examination of the data from 1989–95 and 1996–97, breeding density appears to be stable in our study area (Table 1). Moreover, across 1-km grid squares, we found a significant correlation in the number of nests between the 1996 and 1997 breeding season ($r = 0.76$, $P < 0.001$, $n = 17$) (Fig. 1). The slope of this correlation ($b = 0.905$) is near unity and the intercept near zero ($i = 0.3$) suggesting that breeding

Table 1. Breeding density of Lesser Grey Shrike in Central Slovakia from 1989 to 1997. During 1989–95 a fixed area (10 km²) was surveyed with a low but comparable searching effort (for details see Kristin 1991, 1995), whereas during 1996 and 1997 intensive monitoring was performed in a larger area (20 km²) including the former. For comparative purposes we offer data for the smaller area from 1989 to 1997 and additional data for our intensive study (1996 and 1997).

	1989	1990	1991	1993	1994	1995	1996	1997
Breeding pairs/10 km ²	26	23	18	24	18	26	42	39
Breeding pairs/20 km ²	–	–	–	–	–	–	84	77
Nests/10 km ²	20	16	11	18	13	19	42	37
Nests/20 km ²	–	–	–	–	–	–	73	65
Nests/km ² (range)	0–6	0–6	0–4	1–6	0–3	0–6	0–11	0–10
Replacement nests	4	–	5	3	3	4	11	10

density is constant across the two years. Nest density among grid squares varied widely in both years, with no nests in some and up to 11 nests in others (Table 1). For both years, the χ^2 value lies well above the upper 5% significance level (1996: 43.4, $df = 19$; 1997: 47.02, $df = 19$) for a Poisson series; therefore, agreement with a random distribution can be rejected ($P > 0.05$) and the high value of χ^2 indicates a contiguous spatial distribution of breeding shrikes (Fig. 2). In fact, we found a non-normal distribution when examining the distance to the nearest nest (Kolmogorov-Smirnov test, $P < 0.01$ for both years, $n = 55$ and 52 first clutches respectively), as a consequence of a marked skew to short distances. The shortest distance between active nests observed in dense breeding clumps was 25 m. In contrast, pairs tend to breed more isolated in replacement clutches, and the distance to the nearest nest is normally distributed (Kolmogorov-Smirnov, $P > 0.20$ for both years, $n = 9$ and eight replacement nests respectively). We

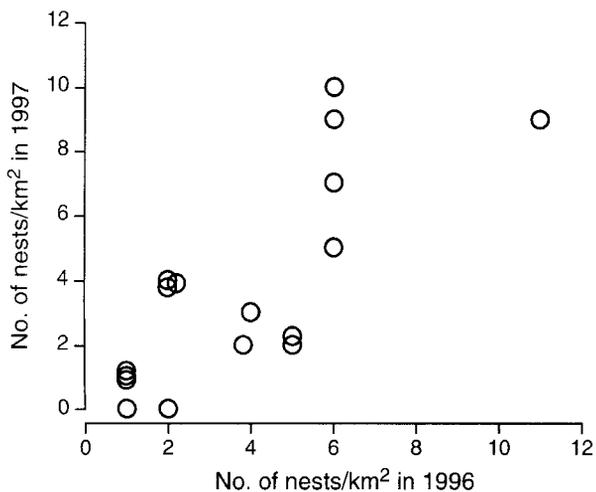


Figure 1. Relation between the number of Lesser Grey Shrike nests for each km² ($n = 17$) in two successive years (1996 and 1997). No. of nest/km² (1997) = $0.3 + 0.91$ nests/km² (1996).

found no variation in clutch size or fledging success for first clutches from 1989 to 1997 (excluding 1992) (Kruskal-Wallis test: $H = 7.51$, $df = 7$, $P > 0.38$; $H = 10.82$, $df = 7$, $P > 0.1$, respectively) (Table 2).

The median start of egg-laying for first clutches did not vary between 1996 and 1997 (17 May in 1996 vs 18 May in 1997) (Table 3). First eggs of replacement

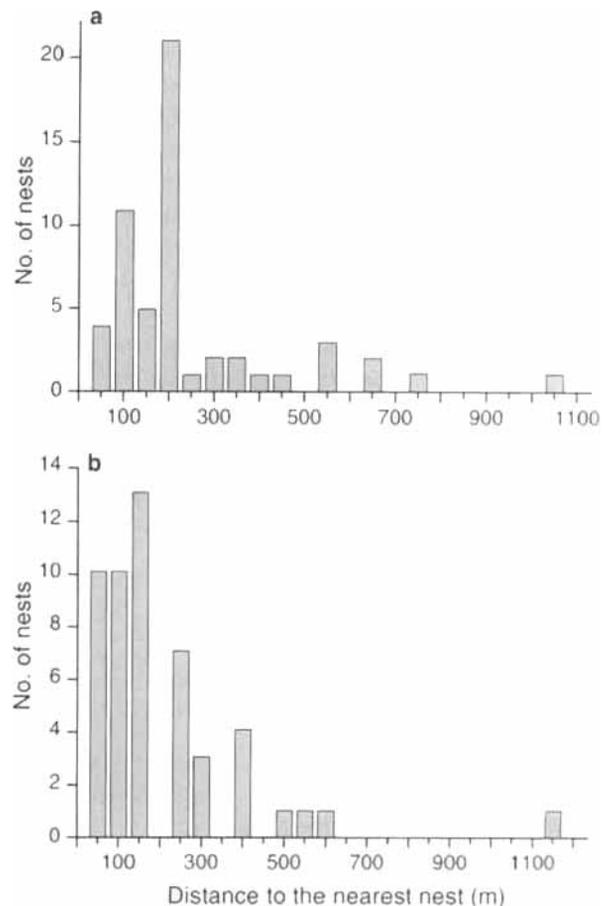


Figure 2. Frequency distribution of the distance to the nearest conspecific nest (first clutches only) for 1996 (a) and 1997 (b).

Table 2. Clutch size and fledging success (chicks at least 10 days old) for first clutches in Central Slovakia from 1989 till 1997. Given are the mean \pm se and sample size in brackets.

	1989	1990	1991	1993	1994	1995	1996	1997
Clutch size	6.0 \pm 0.12 (17)	6.0 \pm 0.01 (5)	5.66 \pm 0.33 (3)	6.18 \pm 0.23 (11)	6.0 \pm 0.01 (8)	6.28 \pm 0.19 (11)	5.8 \pm 0.14 (37)	5.7 \pm 0.14 (37)
Fledging success	5.11 \pm 0.24 (17)	5.2 \pm 0.22 (5)	5.33 \pm 0.33 (3)	6.0 \pm 0.27 (11)	5.75 \pm 0.16 (8)	5.44 \pm 0.33 (9)	5.3 \pm 0.18 (31)	4.9 \pm 0.20 (33)

clutches were laid later (approximately from end of May until mid-June, see Table 3) and there is almost no overlap between the clutch initiation of first and replacement clutches. Average clutch size for first broods was significantly greater than for replacement broods (Table 3) (Mann–Whitney *U*-test: 1996: $z = 2.94$, $P = 0.003$, $n = 37$, 9; 1997: $z = 2.46$, $P = 0.013$, $n = 37$, 7). Similarly, the mean number of fledglings in successful nests tended to be higher for first than for replacement nests (Table 3) (Mann–Whitney *U*-test: 1996: $z = 2.37$, $P = 0.017$, $n = 31$, 8; 1997: $z = 1.76$, $P = 0.07$, $n = 33$, 5).

Considering all nests, we found a seasonal decline in clutch size (for 1996: $r = -0.49$, $P < 0.001$, $n = 42$; for 1997: $r = -0.56$, $P < 0.001$, $n = 42$) and number of fledglings (for 1996: $r = -0.50$, $P < 0.003$, $n = 35$; for 1997: $r = -0.43$, $P < 0.007$, $n = 38$). This seasonal decline is also discernible when examining first and replacement clutches separately but not significant in every season (see Table 3, Figure 3, but note the low sample size of replacement clutches). However, after controlling for the seasonal decline of clutch size partial correlations revealed no significant seasonal reduction in number of fledglings (for 1996: $r_{\text{part}} = -0.18$, $P > 0.3$, $n = 35$, for 1997: $r_{\text{part}} = -0.16$, $P > 0.3$, $n = 36$).

Predation, breeding density and breeding success

Overall, hatching failure was low (mean percentage of unhatched eggs/nest \pm se: 9.15% \pm 1.98 for 40 nests in 1996 and 8.51% \pm 2.64 for 37 nests in 1997). It did not vary either between replacement nests and first clutches either within years (Mann–Whitney *U*-tests, $P > 0.10$ in both years) or between years (Mann–Whitney *U*-test, $P > 0.10$ for first and replacement clutches) (Table 3). Partial losses of chicks were also few (one chick in 1996 and the youngest individuals in five nests in 1997).

The nest failure rate was low: 19 (31%) out of 61 nests in 1996 and 11 (21.1%) out of 52 nests in 1997. Nest losses occurred significantly more frequently than expected (assuming a similar duration for incubation and nestling periods; Cramp & Perrins 1993) prior to hatching in 1996 ($\chi^2 = 6.36$, $df = 1$, $P = 0.01$), but there were no differences either in 1997 or when pooling years (χ^2 test, $df = 1$, $P > 0.1$ in both cases). Overall, nest failure did not differ between first and replacement broods in either year (two-sample proportion test: 1996: $z = -0.25$, $P = 0.80$, $n = 45$, 11; 1997: $z = 1.39$, $P = 0.16$, $n = 42$, 7). The main cause of nest failure was predation (Table 4), Black-billed

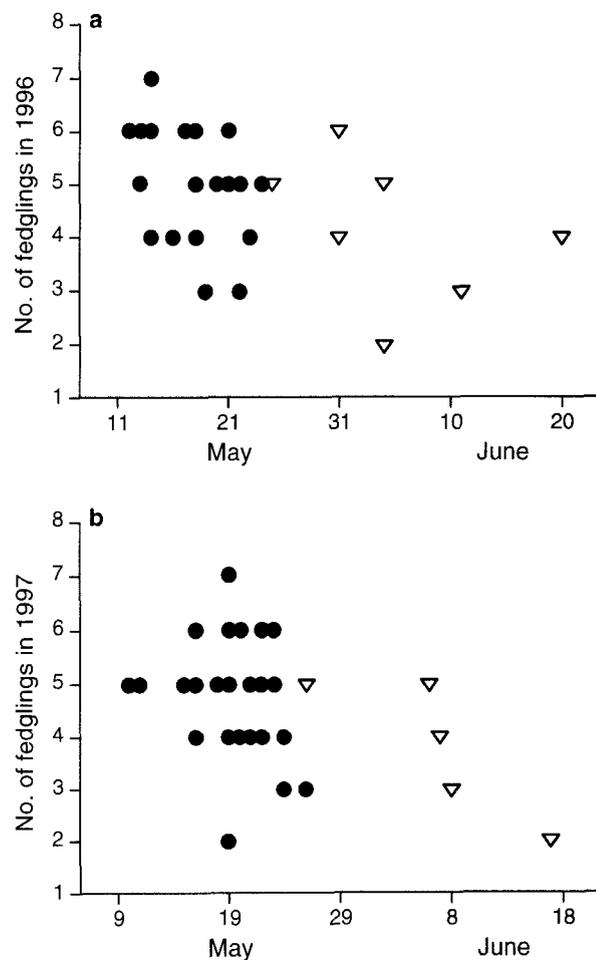
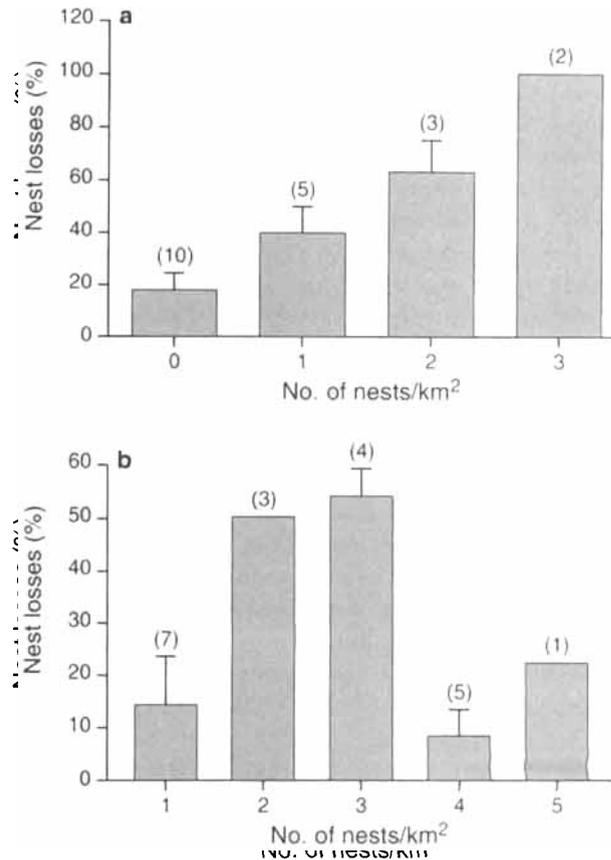
Table 3. Breeding parameters of Lesser Grey Shrikes breeding in Central Slovakia during two breeding seasons (mean \pm se and sample sizes in brackets) and seasonal effect on clutch size and fledging success (Spearman correlation coefficient, *P*-value and sample size).

	1996		1997	
	First clutches	Replacement clutches	First clutches	Replacement clutches
Range of start of laying (median for 1st clutches)	11–23 May (17 May) (39)	24 May – 19 June (11)	9–25 May (18 May) (41)	25 May – 16 June (5)
Clutch size	5.8 \pm 0.14 (37)	4.7 \pm 0.40 (9)	5.7 \pm 0.14 (37)	4.6 \pm 0.48 (7)
Hatching failure (mean % unhatched eggs/nest)	9.6 \pm 2.14 (32)	7.5 \pm 5.26 (8)	6.9 \pm 2.76 (32)	18.3 \pm 7.63 (5)
Fledglings	5.3 \pm 0.18 (31)	4.1 \pm 0.44 (8)	4.9 \pm 0.20 (33)	3.8 \pm 0.58 (5)
Seasonal effect				
Clutch size	-0.29 (ns) (33)	-0.33 (ns) (9)	-0.47 (< 0.01) (37)	-0.66 (ns) (5)
Fledglings	-0.41 (0.03) (27)	-0.51 (ns) (8)	-0.22 (ns) (33)	-0.97 (0.005) (5)

Table 4. Causes of breeding failure in the Lesser Grey Shrike in Central Slovakia during the breeding season 1996 and 1997.

Causes	1996	1997
Predation (nests surely predated by magpie)	7 (7)	8 (3)
Weather	1	2
Desertion	0	1
Human disturbance	2	0
Unknown	9	0
Total number of lost nests	19	11

Magpies being the main predators. In 1996, out of nine shrike nests with magpies breeding within 8–150 m, seven nests were depredated, which is significantly more than expected (one-tailed proportions test: $z = 1.6$, $P = 0.047$). The density of active magpie nests

**Figure 3.** Seasonal decrease of fledgling success in first (●) and replacement clutches (▽) during the 1996 (a) and 1997 (b) breeding seasons.**Figure 4.** Relation between nest losses (%) and number of nests/km²: (a) magpie and (b) Lesser Grey Shrike. Results are mean \pm se with the sample size above the bars.

averages 0.45 and 0.55/km² for 1996 and 1997, respectively, with a maximum of three nests/km².

We found no significant variation between shrike density/km² and nest losses (Kruskal–Wallis test, $H = 12.3$, $df = 4$, $P > 0.1$) (Fig. 4b), but nest losses increased with density of active magpie nests/km² (Fig. 4a) ($H = 9.01$, $df = 3$, $P = 0.028$). In a stepwise multiple regression analysis using breeding density/km², average start of egg laying/km² and magpie density/km² as independent variables and nest loss rate/km² as dependent variable only magpie density entered the regression model. Hence, only the density of magpies seems to explain shrike nest losses ($R^2 = 0.31$, $F = 8.26$, $P = 0.01$, $df = 1, 19$). The partial regression coefficient ($r_{\text{part}} = 0.56$) indicates that nest losses increased with density of magpie nests. Nest losses did not correlate with either shrike breeding density ($r_{\text{part}} = 0.12$, $P > 0.6$) or the date at the start of laying ($r_{\text{part}} = 0.28$, $P > 0.2$) and no relation was found between density of shrikes and magpie nests ($r_s = 0.03$, $P > 0.9$, $n = 20$ grids).

DISCUSSION

Our study area contains one of the largest continuous populations of Lesser Grey Shrike in the Western Palearctic with a very high breeding density (for comparison, 19 breeding pairs/12 km² in Aude in 1992, 3.8–6 breeding pairs/km² in Krim; Glutz von Blotzheim & Bauer 1993, Cramp & Perrins 1993). Additionally our long-term monitoring data (from 1989 to 1997) revealed that the population is more or less stable (see also Kristin 1991, 1995). The slightly lower numbers of breeding pairs for 1989 to 1995 are more likely a result of an underestimation due to lower monitoring effort than from an increase in population size in the years 1996 and 1997. Since the Lesser Grey Shrike has declined dramatically in the last 50 years (Lefranc 1993, 1997), it seems that our study area holds one of the last healthy populations at the current northwestern border of its breeding range. Clutch size and fledging success did not vary from 1989 to 1997 and both were high, but not obviously better than in previous studies (Hudec 1983, Glutz von Blotzheim & Bauer 1993).

We found a seasonal decline in clutch size and fledging success. Although this was not significant for all years, it seems to be a general rule that also holds for first and second clutches separately. Overall, nesting failure and hatching failure did not vary between first and replacement clutches and there was no seasonal decline in fledgling numbers when controlling for clutch size. Hence our analyses suggest that the decline in reproductive success arises from variation in clutch size, and from the fact that birds arriving earlier produced larger clutches and raised more offspring. Kristin *et al.* (in press) show that nutritional condition determines clutch size in this species. If clutch size reflects individual condition, our data suggest that either earlier-arriving birds are in better condition or that they occupy better territories.

Breeding failure in the Lesser Grey Shrike was low in this study compared with other shrike studies. For example Jakober and Stauber (1987) stated about 50% and Vanhinsbergh (pers. comm.) more than 70% of Red-backed Shrike nests failed due to nest predation. Earlier studies of the Lesser Grey Shrike have reported breeding failure rates of about 65% (Horvath 1959, Hantge 1957, Niehuis 1968). All these studies mentioned that nest predation was important, and Warncke (1958) and Horvath (1959) stated that nest predation by magpies, and human interference, may be the main cause of breeding failure. Breeding failure may be also caused by unfavourable weather (Hantge

1957, Niehuis 1968), although direct effects of weather were negligible in our study. There were only two nests destroyed by heavy rainfall (see also Kristin 1995). The main reason for nest losses in our study was nest predation by magpies. This is indicated by direct observations and indirectly by the strong effect of the nearest active magpie nest on shrike breeding success. Even controlling for breeding density and seasonal effects, nest losses correlated with magpie density.

Our results show a high variation in breeding density between squares. In contrast to other shrike species, the Lesser Grey Shrike is less territorial (Cramp & Perrins 1993) and shows a more clumped distribution (Kristin 1995). Hence it could be that to breed in clusters is beneficial in terms of reduced nest predation. Birds breeding in clusters may be more efficient in detecting and repelling intruding magpies by increased vigilance or communal defence. However, in our analysis of causes of nest losses, breeding density did not enter the regression model. In the Lesser Grey Shrike one individual usually guards the nest while the second (usually the male) chases the predator away. They only attack predators that pass through the territory or near the nest. Kristin (1995) observed that in rare cases, when territories overlapped, two shrike pairs would chase magpies simultaneously. Hence, breeding density is not obviously beneficial in terms of reduced nest predation due to communal predator defence. Vigilance may be increased, but is not obviously reflected in reduced breeding failure. Increased vigilance of breeding clusters may be outweighed by being more conspicuous for predators. Therefore, their obvious tendency to clump might be related to other factors like the availability of suitable nest sites or food.

The relatively low rate of nest predation in comparison to other studies (see above) may, in part, be due to the low breeding density of the Black-billed Magpie in our study area. For instance, only about one pair of Magpies breeds per 2 km² (see Results). Breeding density is more than ten times higher in many other parts of Europe (for review see Birkhead 1991). In fact, Magpies were absent in the study area until recently but did increase between 1988–97. Nevertheless, Magpies still have a very bad reputation among local farmers, because they take fruit (mainly cherries) and the eggs of poultry, and can attack livestock (Birkhead 1991). Consequently they intensively hunt Magpies and destroy their nests around farms. Only 5–10% of nests survive, due to human interference (pers. obs.). Lesser Grey Shrikes nest almost exclusively close to farmhouses (from 0 m to 120 m) and

consequently benefit from farmers destroying Magpie nests near the farm (Kristin *et al.* 1998). This association with humans is not obvious from other studies and is only described for one very early study (Glutz von Blotzheim & Bauer 1993).

To conclude, given the dramatic increase in population density of the Black-billed Magpie almost throughout Europe since the 1960s (Birkhead 1991), we think that nest predation by Magpies may be as important for the decline of the Lesser Grey Shrike as the changing environmental situation, namely habitat deterioration due to changes in agricultural practice resulting in the loss of appropriate food (Niehuis 1968, Lefranc 1993, 1995, 1997). Similarly, we think that the constantly high breeding success observed in our dense population cannot be explained solely by a low rate of nest predation. Rather, the combination of low predation and a suitable environment due to the maintenance of traditional, extensive farming (with almost no use of pesticides) resulting in a patchy environment, which probably provides greater food availability (unpubl. data) accounts for the high and stable density of this population.

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