

Philopatry, dispersal patterns and nest-site reuse in Lesser Grey Shrikes (*Lanius minor*)

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Abstract To nest in the same breeding area, territory or even nest-site in successive years may provide a possibility to look at mechanisms involved in breeding habitat selection and could also be an important tool for conservation, management and restoration attempts. In this study we examine site fidelity towards the breeding area as well as the nesting site in a dense and stable population of the Lesser Grey Shrike *Lanius minor*, a long-distance migrant and highly endangered passerine species, at its present northern border of its breeding range. Overall we recovered 48 out of 146 (32.8%) adults between 1996 and 2000. Recovery rate is significantly higher for males (31 of 77, 40.25%) than for females (17 of 69, 24.6%). Recovery rate of nestlings is much lower since only 51 of 790 (6.5%) were recovered and there is no significant sex difference. Furthermore, our results from 1989 to 2000 revealed that more than 30% (97/319) of the nests were built in the same nest tree in successive years and more than half (183/319 = 57.4%) of the nests in the same or neighboring trees (up to 20 m), but very seldom by the same individuals. The fact that nest reuse in successive years is almost exclusively done by different individuals suggests habitat copying and public information of individual birds. Due to optimal ecological breeding conditions other parameters like inbreeding avoidance or increased genetic variability could be important factors in nest-site selection strategies and consequently result in a “disperse over stay strategy”.

Keywords Nest-site selection · Philopatry · Habitat copying · Lesser Grey Shrike · Territory fidelity · Nest-site tradition

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Introduction

Many migratory birds return precisely to the same site for breeding attempts in successive breeding seasons which suggest fitness benefits over dispersal (Greenwood 1980; Gowaty and Plissner 1997). In fact, it has been shown that individuals experiencing a higher reproductive success in 1 year are more likely to return to the same territory in the following breeding season (Gavin and Bollinger 1988; Paton and Edwards 1996; Haas 1997, 1998), whereas individuals suffering a low reproductive success may more likely disperse (Robinson 1985). Site fidelity, however, may not only affect survival and reproductive success of individuals but also demography, dynamics (Brown and Kodric-Brown 1977; Freemark et al. 1995; Schmidt 2004) and genetic variability of a population (Lande and Barrowclough 1987). In small, isolated or fragmented populations female-biased dispersal can lead to male-biased sex ratios (Yosef 1992). Recent research has shown that females often have a limited ability to search for mates and may therefore effectively be lost from the breeding population if they disperse into areas empty of conspecifics (Dale 2001). Finally, the level of site fidelity could be a determinant for habitat quality and be used to (i) compare the state of different populations or (ii) evaluate the suitability of an area for a species. Thus site fidelity is an important argument for conservation, management and restitution attempts as well (Saunders et al. 1991; Fahrig and Merriam 1994). Dispersal patterns are still poorly known for most especially long distance migrant passerines (Holmes et al. 1996). In this study we focus on different parameters of site fidelity in the highly endangered Lesser Grey Shrike *Lanius minor*. We examined the return rates of (i) juveniles to the natal area, (ii) adults to the breeding area, and (iii) adults to the same territory. Furthermore, we analyzed sex specific differences (Lemon et al. 1996; Konczyk et al. 1997) and the role of mate fidelity (Harvey et al. 1979; Payne and Payne 1993) for site fidelity. We studied the frequency of nest-site reuse in several years and addressed the question whether this is due to the same or different individuals. We also investigated nest-site tenacity to the same tree, the core territory within 20 m and the territory within 100 m of adult birds.

The population density of Lesser Grey Shrikes (*Lanius minor*) has declined over large parts of its range and in some places there are only small isolated populations left (Lefranc and Worfolk 1997; Knysh and Pertsov 2003; Giralt and Valera 2003). This species performs one of the longest migratory movements among passerines, winters in South Africa and travels about 10,000 km (Lefranc and Worfolk 1997). Thus the Lesser Grey Shrike provides a possibility to study philopatry and fidelity to nest-sites not only for its own but also for conservation and management aspects.

A preliminary study on a dense breeding population indicates a high return rate of adults and a high nest tree tradition (Kristin et al. 1999). But otherwise there are only scarce and old data on philopatry, breeding site and mate fidelity of this species (Hantge 1957; Warncke 1958; Cramp and Perrins 1993; Glutz von Blotzheim and Bauer 1993). Our results suggest a constant high rate of breeding site fidelity which is highest for males and lowest for juveniles but, in contrast to many other shrike species, this does not result in nest-site (territory) fidelity. In fact, the reuse of the same nest-site or territory is mainly due to different individuals.

Methods

We conducted the study between May and July 1989–2000 (most intensively between 1996 and 2000) in Central Slovakia (40°35–38 N, 19°18–22 E). The study sites comprise 20 km² (450–850 m a. s. l.) of traditionally cultivated area characterized by high diversity of habitats (for detailed information and habitat description see Kristin et al. 2000; Wirtitsch et al. 2001).

A total of 146 adults and 790 nestlings were ringed in the breeding seasons of 1989–1999, most of them (143 adults and 612 nestlings) between 1996 and 1999. The number of investigated breeding pairs per season varied between 63 and 75 (1996–2000). The breeding population has been found to be stable for actually a whole decade (Kristin et al. 2000). Adult birds were trapped and re-trapped by means of bowl-traps with a cricket inserted as a lure. During the early hatchling period we used mist nets located close to the nests as well. Adults were provided with one or two color aluminum rings combined with standardized numbered alu-rings (Ringing Centre of National Museum Prague, ring series Z), which enabled individual identification also by visual observation. In a few cases rings and color combinations of recovered adult birds could only be identified with a telescope. We provided nestlings with a standardized alu-ring on the right leg when they were 6–10 days old. Identification was only possible by re-trapping.

Data on philopatry and reuse of nests were collected by checking all individuals, nests and territories used in previous breeding seasons in five successive years (1996–2000). For investigation of crucial factors influencing philopatry two distinct categories of adults were tested separately. We distinguished between individuals faithful to the breeding area (all those birds which were recovered in the study area in the following years) and individuals which were ringed in the study area, but could not be recovered by 2000.

Inter-nest distances were taken from a local map of a scale 1:25,000. For calculation of nest-site tenacity and territory fidelity we distinguished between: (i) nest-site faithful birds which returned to the same nest tree the following year, (ii) nest core territory faithful birds which returned to an area within a radius of 20 m around the original nest and (iii) territory faithful birds which returned to the same territory—an area within a radius of 100 m around the original nest. For the purposes of comparison we used territories with a radius of 200 m around the nest as well (for territory size see Wirtitsch et al. 2001).

Results

Fidelity towards the breeding area

In total, we recovered 48 out of 146 (32.8%) adults between 1996 and 2000. Recovery rate was higher for males (31 of 77, 40.3%) than for females (17 of 69, 24.6%) (χ^2 -test: $\chi^2 = 6.9$, $P = 0.008$). Six males (7.8%) returned twice in successive years and one female (1.5%) three times in successive years (1997–2000). Year to year philopatry varied from 11.7% to 28.9% among males, and from 5.8% to 15.8% among females. Twenty seven out of 31 males (87.1%) and 11 out of 17 females (64.7%) were already recorded in the first year after ringing, four males (12.9%) and six females (35.2%) were located later on (second to fifth year). Recovery rate of nestlings is much lower since only 51 out of 790 (6.5%) nestlings were recovered and there is no significant sex difference. About 24 nestlings were recovered as males and 27 as females, which does not deviate from by chance assuming an even sex ratio for nestlings (χ^2 -test: $\chi^2 = 0.16$, $P > 0.6$, $n = 790$). One female and one male ringed as nestling were recovered two times.

Fidelity towards nest-site and territory

Our results show that more than 30% (97/319) of all nests were built in the same nest tree in successive years and more than half (57.4%, 183/319) of the nests in the same or a neighboring tree (within 20 m) (Fig. 1). In fact, 11.0% ($n = 319$) of the nest-sites

(including a radius of 20 m around the original nest) were used in five successive years (1996–2000), 12.5% in four and 11.3% in three successive years. Including the period from 1989 to 1995 there are two nest trees, which were used for seven years. However, the high overall fidelity to the nesting site is not due to nest-site fidelity of individual birds. Males, in general, tend to return closer to the previous nest-site than females (Fig. 2), but male nest tree tenacity as well as nest core territory fidelity (including 20 m or even 100 m around the former nest tree) is very low when using the proportion of all males ringed. It is also low when using only the proportion of males which we actually recovered (Fig. 1). In fact, only two out of 31 (6.4%) returned males nested in the same nest tree twice. Three other males returned to the same territory within 20 m around the original nest, two others within 100 m (Fig. 1) and two within 200 m. In total, we recovered 9 out of 31 males (29%) within 200 m around the original nest. According to recoveries the maximum age of males was five years and of females six years. Both individuals were ringed as nestlings and found after five, respectively six years, 350 and 2800 m away from the natal site.

Female Lesser Grey Shrikes, however, ($n = 17$ females recovered) have never been found to breed in the same nest tree or its surrounding (within 100 m) again. The female breeding closest to the previous nesting place settled 130 m away. Other females were found more than 450 m away from previous nests. Nestlings ($n = 18$) never returned to the natal site or territory (within 100 or 200 m).

This, in general, low specific nest-site tenacity and its variation in relation to sex and age is reflected in the mean dispersal distance (Fig. 2). A two-way ANOVA (age and sex as independent factors) revealed that the distance from the previous nest tree, or natal site is significantly larger for nestlings than for adults (mean \pm SE: 2739.2 \pm 372.5 m, $n = 18$, vs. 1651.3 \pm 279.8 m, $n = 51$, respectively, $F = 4.9$, $P = 0.03$, $df = 69$). Neither differences among sexes are significant ($F = 2.16$, $P = 0.14$, $df = 69$) nor the interaction between age

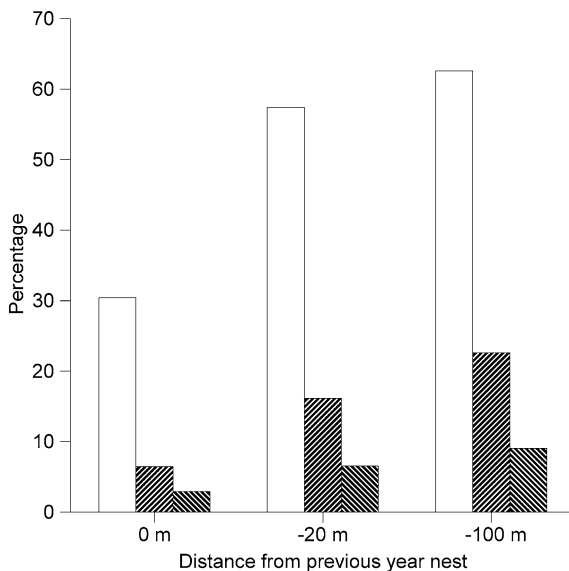
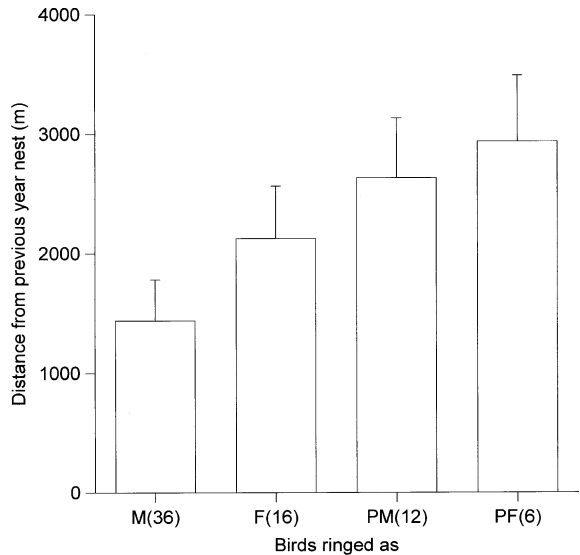


Fig. 1 Reuse of the same nest tree (0 m), the same nest core territory within 20 m around the original nests and the same nest territory within 100 m around the original nest by male Lesser Grey Shrikes in successive years (open bars, $n = 319$ nests), and reuse expressed as percentage of returned males (right hatched bars, $n = 31$) and percentage of all ringed males (left hatched bars, $n = 77$)

Fig. 2 Mean distances (\pm SE) between nests of recovered birds ringed as adult males (M), adult females (F) and nestlings (PM, PF) and their previous nest. Number of recovered individuals is given in parenthesis



and sex ($F = 1.00$, $P = 0.3$, $df = 69$), Males, however, tended to return nearer to the previous nest-site (Fig. 2). The most distant recovery for nestlings was made 5850 m (for males) and 4980 m (for females) off the natal site. For adults the most distant recovery was 5100 m (females) and 4950 m (male) away from a previous breeding site. However, these results are limited by the size of our study area. Birds which dispersed more than 9.000 m could not be detected because they were outside our study area.

Mate fidelity

The low nest-site fidelity of individuals is accompanied by their low mate fidelity. In the course of our study we ringed 64 complete pairs. However, in all cases, where we could re-sight both partners ($n = 5$), pairs divorced and had new mates and in two cases females paired with neighbors of the previous year.

Discussion

Our results demonstrate that adult Lesser Grey Shrikes have a comparatively high and significantly male biased return rate to the breeding area, which is in line with many other migratory passerines (Greenwood 1980; Clarke et al. 1997). About 40% of all male and 25% of all female Lesser Grey Shrikes returned to the breeding area. Similar results can be found in other closely related shrike species, i.e. in Woodchat Shrikes *Lanius senator* (Ullrich 1987), Red-backed Shrikes *L. collurio* (Jakober and Stauber 1987, 1989; Šimek 2001), Great Grey Shrikes *L. excubitor* (Yosef 1992), Loggerhead Shrikes *Lanius ludovicianus* (Collister and Smet 1997), or Brown Shrikes *L. cristatus* and Bull headed Shrikes *L. bucephalus* (Takagi 2003) but also in genetically more distant passerines (i.e. Barn swallow *Hirundo rustica*, Tree swallow *Iridoprogne bicolor*, Nightingale *Luscinia megarhynchos*, Willow warbler *Phylloscopus trochilus*, see review in Sokolov 1991). Studies on the Lesser Grey Shrike are rare and none of them mentioned any evidence of a

high return rate in this species (e.g. Hantge 1957; Warncke 1958; Lovász et al. 2000; Knysh and Pertsov 2003; Giralt personal communication). If past reproductive success of individuals increases breeding site fidelity (see Gavin and Bollinger 1988; Paton and Edwards 1996; Switzer 1997; Haas 1997, 1998; Hoover 2003; Sedgwick 2004), our results may indicate a healthy LGS population. This is, in fact, supported by the average high breeding success (see Kristin et al. 2000; Hoi et al. 2004) compared to other populations (Cramp and Perrins 1993; Lovász et al. 2000; Giralt and Valera 2004).

Secondly, we found that nest-site tradition was high in this species. About one third of all nest trees was used repeatedly and almost two thirds of the nests could be found in the same or a neighboring tree in successive years. In two cases we found a nest in the same nest tree in seven successive years and in some years even exactly at the same place at the tree. Such a long nest-site tradition is common in several long-lived, mainly non-passerine bird species (e.g. storks and raptors) and seems to be unusual in passerines (but see Yosef 1992). He found that some bushes were used as nest-site for about nine consecutive breeding seasons in the closely related Northern Shrike (*Lanius excubitor*). One would expect a frequent nest-site reuse due to high nest-site fidelity of individuals or conspecifics (see in Haas and Sloane 1989). But, in fact, the opposite is true in the Lesser Grey Shrike. The third and most surprising result is that returning males usually disperse less far than females (Fig. 2) but only 6% of all returning males reused the same nest tree and only 16% of the returning males used the same or a neighboring tree. This result suggests that most of this ‘nest-site tradition’ is due to different individuals. Together with the finding that Lesser Grey Shrikes always switched their mates in consecutive years (see results) mate switching could also be considered as an important factor responsible for the low nest site fidelity of individuals (see also Haas and Sloane 1989).

The question of how nest-site tradition can work across individuals remains. Conspecific attraction, for instance, could be one mechanism explaining cross individual nest-site tradition (Stamps 1988, 1991, Muller et al. 1997; Ward and Schlossberg 2004; Parejo et al. 2005). ‘Habitat copying’ which means that individuals use the reproductive performance of conspecifics to assess habitat suitability and choose their future breeding site might be another possible mechanism (Boulinier and Danchin 1997; Danchin et al. 1998; Doligez et al. 1999; Doligez et al. 2003). Furthermore, an innate preference for specific habitat features also would be sufficient to explain cross individual nest-site tradition, especially for our study population which lives in a very stable and predictable environment (Wirtitsch et al. 2001). However, at the moment we can only speculate about the exact mechanism behind nest-site choice and this topic has to be addressed in future investigations.

A second question related to cross individual nest-site tradition is why most individuals change nest-sites and territories between successive years. It is known that familiarity with the territory provides an advantage over intruders which might be greater for males than for females (Paton and Edwards 1996; Schjorring et al. 2000). Familiarity with foraging and nesting sites, for instance, may allow a quicker start of breeding or may, in general, improve the competitive abilities for breeding opportunities (Lozano and Lemon 1999). So why is changing of the breeding site the rule? In search of a better site, dispersal may be a consequence of breeding in a low quality habitat, or due to nest predation (Robinson 1985). In the Lesser Grey Shrike this explanation is contradicted by the fact that other individuals immediately replace the former, which will be unlikely if the habitat is poor and nest predation is in general very low (Kristin et al. 2000). Alternatively, one can assume that changing to a different breeding site must be beneficial or at least not more costly than reusing the same site. This would consequently mean that the benefits of familiarity with a territory may not be very important for individuals of our population. However, as already

mentioned, males do not disperse very far from the original site, so they may be familiar with the surrounding territories as well. When selecting a future breeding site, individuals might use ‘public information’, which means the local reproductive success of all conspecifics in a breeding patch. Patch reproductive success may even better integrate the effect of all environmental factors on breeding success (Boulinier and Danchin 1997; Danchin et al. 1998; Doligez et al. 1999, 2003). The open habitat in our study area (Wirtitsch et al. 2001) may simplify to gather information for future breeding attempts. Furthermore, habitat quality seems to be optimal for most sites of the study area (Wirtitsch et al. 2001). Breeding success is very high all over the study site (Kristin et al. 2000; Hoi et al. 2004). We could not identify habitat parameters influencing territory choice neither is there a settlement order across different years (Wirtitsch et al. 2001). All these arguments suggest, that habitat quality and resource availability might be very important for individuals to return to the breeding area (breeding site philopatry) but is probably of minor importance for territory choice. Due to the optimal breeding conditions other parameters like inbreeding avoidance or increasing of genetic variability (Pusey 1987) could turn into more important factors in nest-site selection strategies and consequently result in a “disperse over stay strategy”.

To conclude, our results revealed that on the one hand high nest-site tradition across individuals, which is probably due to habitat choice based on public information and the tendency to breed aggregated and on the other hand between year dispersal of individuals for reasons related to genetic variability (Lande and Barrowclough 1987; Pusey 1987; Weatherhead and Forbes 1994) may be important features when dealing with management concepts of the Lesser Grey Shrike (Ward and Schlossberg 2004). An ongoing study examining the mechanisms of territory choice may additionally shed light on habitat choice of this highly endangered bird species.

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