

Traditional versus non-traditional nest-site choice: alternative decision strategies for nest-site selection

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Received: 21 February 2011 / Accepted: 26 October 2011 / Published online: 16 November 2011
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Abstract In order to understand habitat selection, it is important to consider the way individual animals assess the suitability of a future reproductive site. One way of investigating mechanisms (such as those involved in nest site selection) is to examine breeding success and habitat characteristics in terms of animals returning to a place where they have already reproduced and using the same location over successive years or searching for new alternatives. This approach seems especially suitable for testing recent hypotheses suggesting that nest site selection is an integrative process that includes the use of social information (e.g. past breeding success of conspecifics). Determining the factors that elicit conservative or innovative behaviour regarding nest-site selection could be important for improving our understanding of habitat selection decisions in animals. More than half of the nests of the long-distance migratory lesser grey shrike *Lanius minor*, are built in the same or neighbouring trees. We found no evidence that habitat characteristics influence nest-site tradition. On the contrary, social information in

terms of the presence of conspecifics and past reproductive success in terms of complete nest failures due to nest predation (but not detailed information such as variation in fledgling number) influenced nest-site tradition. Hence, social information and past reproductive success may play a role in nest-site choice in this species. Our results further demonstrate that previous experience with a nest site does not appear to be beneficial.

Keywords Nest-site selection · Nest-site tradition · Use of social information · Past reproductive success · Lesser grey shrike

Introduction

In order to understand breeding-habitat selection, it is necessary to examine how individual animals assess environmental quality and the suitability of a future breeding site. Individuals may directly use environmental cues that reflect the intrinsic quality of the habitat (Orians and Wittenberger 1991; Shields 1984; Wiens 1989). In birds, for example, food availability around the nest site is beneficial for feeding offspring, and vegetation cover around the nest or its position above the ground may decrease the risk of nest predation (Hoi-Leitner et al. 1995; Ille and Hoi 1995). In line with this, even the research activity itself was found to induce a change in nest position in some species (e.g. in great grey shrikes; Antczak et al. 2005).

Alternatively, individuals may gain valuable information on habitat quality through habitat use of conspecifics and/or heterospecifics. Thus, tradition—defined as the transfer of any kind of information between individuals and species (Avital and Jablonka 2001; Danchin et al. 2004; Fragaszy and Perry 2003; Hromada et al. 2008)—may play

Communicated by Markku Orell.

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a major role in habitat and (particularly) nest-site choice of many species, and appears to be an underrated mechanism. In line with this, the main route for information transfer is from parents to offspring, so habitat imprinting would be a suitable mechanism for nest-site selection in birds (Glück 1984; Teuschl et al. 1998). Besides information transmission between parents and offspring, tradition may also be based on information gathered from unrelated conspecifics. When choosing their future breeding site, an individual may integrate social information about the present (Muller et al. 1997; Stamps 1988, 1994) or past reproductive success of conspecifics into their own dispersal and settlement decisions (Boulinier and Danchin 1997; Danchin and Wagner 1997; Doligez et al. 1999; Greig-Smith 1982; Haas 1998; Hoover 2003; Switzer 1997). Assuming that habitat quality is stable and predictable, as in landscapes with traditional farming, which are usually extensively managed, past reproductive success of conspecifics may be an even better predictor of the future reproductive success of the individual compared to only the presence of conspecifics (Boulinier and Danchin 1997; Danchin et al. 1998; Danchin and Wagner 1997). Under such environmental conditions, being conservative in terms of nest-site choice may be advantageous, so a strong nest-site tradition (repeated nest-site use) may evolve.

The lesser grey shrike (*Lanius minor*) is a highly endangered species; its numbers are decreasing all over Europe, and it is already extinct in several countries of Western Europe (Lefranc and Worfolk 1997). There are still isolated populations scattered across Europe, some of which are stable with a high breeding density (Krištín et al. 2000), but others already have very low numbers (Giralt and Valera 2003; Lefranc and Worfolk 1997). Specifically, regarding the size of the critical populations, it would be helpful to identify habitat-selection rules—whether and how social cues interact with habitat choice. These results could be very valuable to those involved in the conservation and management of small, isolated, but still healthy populations such as the lesser grey shrike population (Fahrig and Merriam 1994; Freemark et al. 1995).

In an earlier study (Wirtitsch et al. 2001), we found no obvious importance of habitat quality to nest-site selection in lesser grey shrikes, as male territory settlement was not directly related to habitat parameters, and territory selection varied over the years. However, conspecific attraction and the use of general social information are potential alternative strategies for habitat selection, since there are several ecological and biological aspects of this species that may favour them. These are: (1) lesser grey shrikes breed in open-cup nests and frequently form loose breeding aggregations (Krištín et al. 2000); (2) they show high nest-site tradition over successive years, which is almost exclusively due to different individuals using the same nest

sites (30% of all nest trees were occupied during successive years, and almost 60% of the nests were within 20 m of a nest from the previous year; Krištín et al. 2007); (3) the males more frequently return to the same breeding area than the females (Krištín et al. 2007); (4) breeding aggregations, together with an open habitat structure (Lovász et al. 2000; Wirtitsch et al. 2001, authors' unpublished observations), would enable individuals to perceive not only the presence and behaviour but also the reproductive success of neighbours without leaving their own territories.

In this study of lesser grey shrikes, we aimed to determine whether the use of social information is integrated into nest-site choice, and whether this explains nest-site tradition over successive years by different individuals. The specific points we addressed were whether successive use of the same nest site was related to (1) habitat characteristics and/or (2) reproductive success during the previous year. For this reason, we distinguished between traditional and non-traditional (new) nest sites. New nest sites were occupied by individuals that (1) settled in new instead of traditional sites over successive years or (2) bred at sites only once. Individuals at traditional sites were either those that reused the nest site of a conspecific in the following year or those whose nest-site choice was copied in the following year. Comparing these groups allowed us to carefully evaluate the role of the use of social information in habitat-selection strategies. Specifically, we tested the predictions that (1) reproducing individuals should have higher breeding success when following a traditional strategy rather than settling at a new breeding site, and (2) those individuals that reuse a nest site of conspecifics should have a lower breeding success than the conspecifics they copy in the year before they copy them.

Materials and methods

The study was conducted between May and July in the breeding seasons from 1989 to 2000 (most intensively between 1996 and 2000) in Central Slovakia (40°35–38'N, 19°18–22'E). The study area comprised 20 km² (450–850 m asl) of traditionally cultivated sites characterised by high habitat diversity (for detailed information and a description of the habitat, see Krištín et al. 2000; Wirtitsch et al. 2001).

A total of 146 adults and 790 nestlings were ringed during the years 1989–2000; most of them, however, were ringed between 1996 and 1999 (143 adults and 612 nestlings). The number of investigated breeding pairs per season varied from 63 to 75 (1996–2000). The breeding population has actually been found to be stable for a whole decade (Krištín et al. 2000). Adult birds were trapped and re-trapped by means of bowl traps, with a cricket inserted

as a lure, and the birds were fitted with one or two coloured aluminium rings combined with standard numbered aluminium rings (Ringing Centre of National Museum, Prague), which enabled individual identification by visual observation as well. In a few cases, recoveries were based on ring numbers and colour combinations of adult birds identified only with a telescope (Swarovski 20–60 × 70): six- to ten-day-old nestlings were ringed with standardised metal rings on the right leg.

Basic breeding data—such as time of breeding (i.e. start of nest-building or egg-laying), nest location, clutch size, number of fledglings, and breeding success—were recorded every year. We assumed that breeding success was equal to the number of chicks at the last check (chick age of at least ten days).

With regard to return rate to the breeding ground and reuse of territories and nest sites, we checked all individuals, territories and nests used over five successive years (1996–2000).

In our analyses of the use of social information, we distinguished between territory tradition, where a different pair settles within 100 m from the previous year's nest, and nest-site tradition, where the same nest tree (site) is used by a different individual the following year.

We then correlated fidelity to the breeding ground, territory-site tradition and nest-site tradition with past reproductive success.

To more closely investigate the importance of past reproductive success to future nesting decisions and reproductive success, we further separated breeding events as follows. (1) Breeding attempts of individuals that make a traditional decision (“traditional” breeding attempts at year t). These breeding attempts happened at nest sites that were occupied by conspecifics in the previous year (year $t - 1$). We assume that, in this case, information about the past reproductive success of the conspecific nesting attempt was integrated. (2) Breeding attempts of individuals from whom social information was used. These attempts happened at year $t - 1$ and are termed “original” breeding attempts here. (3) Breeding attempts at “non-traditional” sites. These nest sites are in a new area, at least 200 m from a known nest site, and have not been used before.

We decided that the unit for analysis was a breeding attempt, because individuals may be flexible and decision rules may change over the years.

We then compared (1) the reproductive success of “traditional” breeding attempts in the year when individuals followed a traditional strategy (year t) and the reproductive success of their breeding attempts the year before (year $t - 1$), controlling for year differences in reproductive success (Fig. 1), and (2) the reproductive success of “original” breeding attempts (year $t - 1$ relative to “traditional” breeding attempts), from which social information was

assumed to be used, and the reproductive success of breeding attempts of traditional individuals in the year before they used the traditional site (year $t - 1$) (see Fig. 1). (iii) Finally, we compared the reproductive successes of “traditional” and “non-traditional” (new) nest sites in year t (Fig. 1).

Determining habitat characteristics

A line intercept method (see Smith 1984) following eight 100 m transects in different directions starting from the nest site was used to determine the proportions (%) of the different habitat parameters (1–11) within each territory. The area recorded using this method approximately covers the territory of lesser grey shrikes (see Wirtitsch et al. 2001). To estimate habitat quality, we used the following habitat types in descending order: the amount of (1) meadows (most dominant habitat type), grassland with a vegetation height of about 20–35 cm during the settlement period (see Wirtitsch et al. 2001); (2) bare ground, soil land without plant cover (usually the most preferred hunting habitat, see Wirtitsch et al. 2001); (3) orchards, consisting mainly of pear, plum, apple, cherry and walnut trees; (4) gardens, usually near houses with different vegetables and flowers; (5) houses, area covered by houses and yards; (6) cornfields, with 10–20 cm high cereal during settlement; (7) streets, comprising asphalt and gravel roads; (8) forest, consisting mainly of coniferous trees; (9) bank vegetation along streams; (10) rural vegetation and shrubs. Furthermore, we used (11) the number of habitat types; (12) the number of ecotones: number of habitat switches; (13) tree density: all trees taller than 3 m and within a radius of 100 m of the nest, and; (14) maximum difference in height within a circle of 100 m around the nest.

For the analyses, we compared habitat characteristics between traditional, non-traditional and newly colonised nest sites.

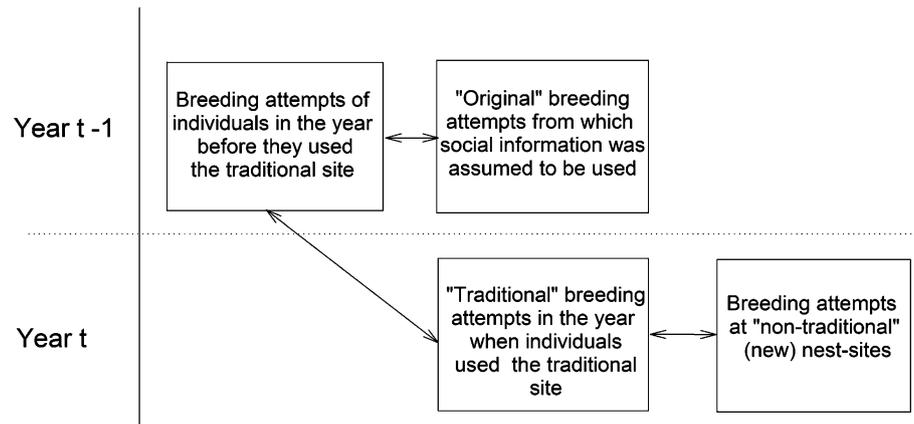
Statistical analysis

A stepwise multiple discriminant function analysis was used to determine whether nest site selection was influenced by habitat characteristics. We therefore compared habitat parameters (see above) between traditional sites (used in two successive years), non-traditional sites (only used in the first year), and sites that were newly colonized (sites that were known to be settled for the first time in the following year).

A logistic regression was used to measure the relative odds of nest-site reuse (dependent variable) in relation to the breeding success (clutch size and fledgling success as independent variables) of that site in the previous year.

Parametric tests were used when assumptions for normality were met. Data were checked for normality, and, if

Fig. 1 Different categories of breeding attempts in relation to “traditional” and “non-traditional” nest-site choices of individuals compared in the study. Arrows indicate the categories for which breeding success was compared



normality was required, either $\arcsin(x + 1)$ or $\log_{10}(x + 1)$ transformed.

To compare breeding successes in different years, we adjusted for differences in breeding success between different years (mean adjustment) using the average breeding success for year $t - 1$ (the year prior to) and year t (the year when “traditional” breeding attempts occurred).

A two-sample proportion test was used to compare two binomial proportions of, for example, returning birds in relation to breeding success and breeding success in relation to nest-site tradition.

Results

Do habitat characteristics influence nest-site selection and nest-site tradition?

Our results did not reveal any difference in the proportions of different habitat types around the nest when comparing “traditional” and “non-traditional” sites (occupied only in the first year) (no variable entered the discriminant function model, for all habitat parameters investigated, univariate F test, $p > 0.2$). Furthermore, there was no difference in habitat characteristics between traditional and newly established nest-sites (no variable entered the discriminant function model, for all habitat parameters, univariate F test, $p > 0.4$).

Comparing the values of the habitat parameters of a territory between successive years, we found no divergence for any of the parameters investigated (for all habitat parameters, paired t test, $p > 0.6$), implying highly stable territory conditions over the years.

Does past reproductive success influence nest-site tradition?

Examining the return rate to breeding grounds in relation to past reproductive success, we found no effect of previous

breeding success. There was no difference in the proportions of unsuccessful males or females that did or did not return. Two of 26 (7.73%) returning and one of nine (11.1%) non-returning ringed adult males were not successful in the previous breeding season (two-sample proportion test: $z = 0.3$, $p > 0.7$). One of ten (10%) returning and three of 52 (5.8%) non-returning females were not successful in the previous breeding season (two-sample proportion test: $z = -0.4$, $p > 0.6$).

However, regarding territory tradition in relation to past reproductive success, we found that out of 84 traditional territories, 68 (80.9%) were successful in the previous year and only 16 (19.1%) of the reused territories were previously unsuccessful (which significantly deviates from chance, two-sample proportion test: $z = 5.67$, $p < 0.0001$, $n = 84$).

With regard to nest-site tradition in relation to past reproductive success, we could in fact show that the relative odds of reusing a nest site significantly depended on the nesting success of the previous year (logistic regression model: $\chi^2 = 47.1$, $df = 20$, $p = 0.001$, $R^2 = 0.56$). The model revealed that it was not clutch size ($\chi^2 = 2.87$, $df = 3$, $p > 0.4$) but breeding success in terms of the number of nestlings fledged that was a significant predictor of future nesting attempts at that place ($\chi^2 = 47.1$, $df = 20$, $p = 0.001$) (Fig. 2).

To what degree is the use of social information an integrative part of nest-site selection, and is it an advantageous strategy?

Our results revealed that individuals following a traditional strategy had lower fledgling success than in the year before (controlled for year differences: paired t test: $t = -2.36$, $p = 0.031$, $n = 16$) (Fig. 3a).

Furthermore, we found no difference in fledgling success between original breeding attempts from which social information was assumed to be gathered and breeding

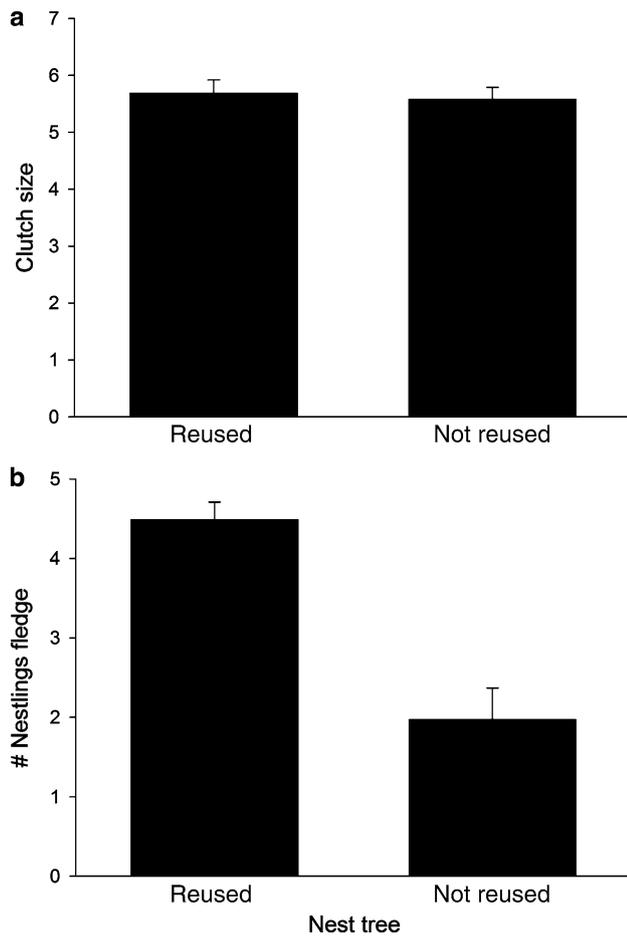


Fig. 2 Mean \pm SE clutch size, number of fledged nestlings of nest sites which were (“traditional”) or were not (“non-traditional”) reused in the next year. For this analysis, we used two pairs of successive years (1996–1997 and 1997–1998)

attempts of traditional individuals in the year before they used the traditional site (year $t - 1$). In effect, there almost seemed to be a reverse trend (paired t test: $t = 1.6, p > 0.1, n = 14$) (Fig. 3b).

Moreover, nest-site tradition did not seem beneficial, since the fledgling successes of traditional and non-traditional individuals did not significantly differ, considering all breeding attempts (including nests where no nestlings fledged) (t test: $t = 0.45, p > 0.6, n = 34, 31$) (Fig. 3c). Eleven out of 17 (64.7%) males were successful in the non-traditional group; similarly, 18 of 30 (60%) individuals were successful following a traditional decision (two-sample proportion test: $z = -0.31, p > 0.7$). Considering only those individuals who had at least one chick that fledged, differences were also not significant (t test: $t = 1.14, p > 0.2, n = 25, 22$) (Fig. 3c).

Finally, being conservative and using a “traditional” nest site did not seem to be advantageous, since individuals

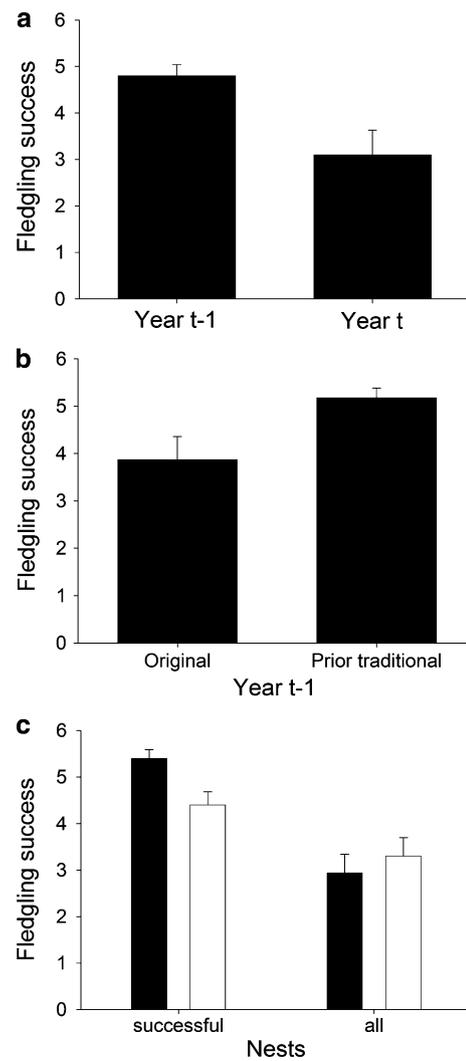


Fig. 3 Fledgling successes of breeding attempts of traditional individuals in the year before they used the traditional site (year $t - 1$) and when they use a traditional site—“traditional” breeding attempts in year t (upper graph), fledgling successes of “original” breeding attempts (those from which social information was assumed to be used) and breeding attempts of traditional individuals in the year before they used the traditional site (year $t - 1$) (middle graph), and fledgling successes in “non-traditional” (filled bars) versus traditional (open bars) breeding attempts for successful nests (at least one fledged chick) and for all nests (including those where no nestlings fledged). Mean \pm SE are given. Fledgling success for year t is adjusted for year differences

successfully settled into a new territory in 19 out of 31 (61.3%) cases, which was exactly the same as when a successful breeding site was reused [42 of 68 (61.7%), two-sample proportion test: $z = 0.04, p > 0.9$]. We obtained a similar result when examining males that returned to the same nest site [six males returned and all (100%) were successful] or to a different nest site [7 of 10 (70%) males were successful; $z = 1.4, p > 0.1$].

Discussion

Our results suggest that tradition is an important mechanism in nest-site choice of the lesser grey shrike population we studied, where information seems to be transferred between unrelated conspecifics by observing their previous breeding success. In contrast, habitat characteristics per se do not appear to be a decisive influence on nest-site selection, which supports our earlier findings (Wirtitsch et al. 2001), since we found no relationship between the value of any habitat parameter surrounding the nest and reproductive success. If habitat selection is adaptive, however, one would expect reproductive success to be directly related to important habitat variables (e.g. Hoi-Leitner et al. 1995; Ille and Hoi 1995; Orians and Wittenberger 1991). Furthermore, if nest-site tradition is based on habitat characteristics, we would predict that frequently used nest sites are of superior quality, which should consequently be reflected in habitat characteristics (e.g. Hoi-Leitner et al. 1995; Ille and Hoi 1995).

According to our results, the environmental situations in the studied territories appear to be very stable, since the habitat compositions of the territories were conservative and did not change over the years (see “Results”). This may be because there is almost no rotating harvesting regime in the breeding area, and fields are generally very small. Such environmental stability may favour nest-site tradition (Doligez et al. 2003; Switzer 1993), but other factors such as a high population density can hamper this (Tryjanowski et al. 2007).

Our results revealed that the return rate to breeding grounds was clearly not related to past reproductive success, which is an important finding in line with conservation actions. Regarding territory and nest-site tradition, however, past reproductive success does matter. Significantly fewer territories and nest sites were reused when previous reproductive success at those sites was low (see Fig. 2). This indicates that individuals return to the same breeding area but settle in different territories (if available) and try to avoid sites where they have previously been unsuccessful. Interestingly, these sites are avoided for future breeding attempts not only by unsuccessful pairs but by apparently all pairs. The fact that the previous reproductive success of a breeding pair influences the decisions of other pairs to occupy its nest site later on strongly suggests that social information is definitely used by lesser grey shrikes (see Boulinier and Danchin 1997; Doligez et al. 2003; Hoover 2003; Switzer 1997). Closer examination of our results, however, did not support a more detailed use of conspecific information. If individuals include, for example, the number of fledglings produced by conspecifics in their decision about whether to reuse a conspecific nest site for future breeding attempts, one

would predict that in the year they gather such information, their own breeding successes should be lower than of the conspecific copied, and they should produce more fledglings in the year they copy a conspecific than in the year before. However, when controlling for year-to-year variation in reproductive success (Hoi et al. 2004), we found that birds which made traditional decisions did not do any better than in the previous season, and there was in fact no reason to choose a traditional nest site, since the reproductive success at that site did not differ from that of the tutor pair in the year that the information was assumed to be gathered (see Fig. 3).

Furthermore, we found no indication that individuals that followed different strategies (traditional versus novel) had different breeding successes (see “Results”). This is surprising, because it suggests that earlier experience with a habitat is not very important in this species, and that there is no difference in reproductive success between individuals that reuse a known breeding habitat and those who do not. In fact, we were able to show that there was no difference in the risk of a failed breeding attempt between birds that reused and those that chose a new, unknown, breeding site. In conclusion, the use of social information by observing the breeding successes of conspecifics appears to be important, since individuals avoid breeding at sites where a previous breeding attempt was unsuccessful. On the other hand, there is no strong evidence of nest-site tradition being advantageous.

One possible explanation for this is that the strategy is chosen by individuals in accordance with their skills. For instance, younger birds or birds in worse condition may prefer to follow the habitat choices of older, more experienced birds or those in better condition (Lozano and Lemon 1999; Thompson et al. 1994). In contrast, older birds may be more likely to select their habitat based on the current suitability of the habitat or earlier experience (Ollason and Dunnet 1978). It may therefore be difficult to detect differences between traditional and non-traditional individuals because the choice of either strategy may be dependent on the situation or/and individuals that follow the two strategies may (because of that) perform equally well. Evidence against habitat copying, as proposed by Boulinier and Danchin (1997), is that pairs who were imitated had an almost significantly lower reproductive success rate than the imitating birds in the year before they copied their habitat choice. We would have predicted the opposite; namely, that lower-quality or less-experienced younger individuals make traditional decisions, and that they originally have lower reproductive success. Habitat copying in the sense described by Boulinier and Danchin (1997) and Danchin et al. (1998) only seemed to be partially fulfilled in our study population. These results, and the fact that birds do not disperse their territories equally

across the breeding area but instead breed in loose aggregations (Krištín et al. 2000), suggest that aside from habitat copying, conspecific attraction (Muller et al. 1997; Stamps 1988; Stamps 1994) may also play a role in nest-site selection by lesser grey shrikes.

The question of why birds who have bred successfully always change nest site rather than reusing the same one remains unsolved. One explanation could be that there is no obvious ecological constraint, so settlement decisions may follow other criteria, like optimal outbreeding (Bateson 1978; Greenwood 1980, 1989; LeBas 2002; Moore and Ali 1984). Individuals may prefer to settle at a site that is somewhat distant from their former place, which is actually the case with lesser grey shrikes, in order to avoid inbreeding. Krištín et al. (2007) showed that there are sex- and age-specific differences in dispersal distance, with males making the smallest and juveniles the largest movements. Inbreeding might be a problem in lesser grey shrikes, because the population is very isolated and philopatry in the investigated breeding area is relatively high (Krištín et al. 2007).

In conclusion, our study of the nest-site choices of lesser grey shrikes suggests that nest-site tradition, which seems to be largely unrecognised in our opinion, can be an important factor when choosing a nest site, independent of environmental factors. Furthermore, there is evidence that individuals integrate social information in terms of the presence of conspecifics (social attraction) and breeding success (whether at least one nestling fledged) when choosing their nest sites. Finally, given stable and favourable environmental conditions, mate-choice strategies (e.g. avoiding inbreeding) appear to play a role in the habitat selection of our study population as well.

Acknowledgments We would like to thank Renate Hengsberger for improving the manuscript. This study was funded by the Jubiläumsfondsproject (no. 7223), Grant of Slovak Grant Agency no. 2/01110/09.

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