

Patterns of breeding fidelity in the Red-backed Shrike (*Lanius collurio*)

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Received 21 March 2000, accepted 24 October 2000

Breeding fidelity was studied in Red-backed Shrike, *Lanius collurio*, in the Czech Republic from 1990 to 1999. The males tend to return more frequently than females, both to the whole research area and to the particular territory. The return rates for both sexes fluctuated from year to year. Male fluctuation was correlated with population density, whereas female fluctuation reflected the previous year's population nesting success of the first breedings. Older birds exhibited non-significantly higher philopatry. The territorial fidelity of males was found to be affected by breeding success and territory attractiveness. Breeding success was important also for female return rate. Most reproductive parameters (clutch size, eggs hatched, young fledged, asynchronous growth of young) were not correlated with the rate of philopatry of either of the sexes. Future philopatric females started their breeding earlier than others. Mate fidelity was recorded twice, apparently as a random result. Maximum age was 6 years (male). No more than 3–4% of young returned to breed in the natal area. Low return rates are believed to be the result of migration of both young and adult birds out of the research area.



1. Introduction

A common pattern in avian behaviour is the fidelity of adults to their breeding grounds while young mostly disperse from their natal sites. In most species, males tend to be more faithful to their previous year's territory than females (Greenwood 1980, Greenwood & Harvey 1982). Breeding site fidelity is exhibited by both migratory and sedentary species of birds. The strong ability of migratory birds to return precisely to the previously-used sites suggests that this particular behaviour provides some benefit. Knowledge of local food sources and predator habits is thought to enhance reproductive success and survival of

philopatric individuals (Hinde 1956). The hypothesis of prior local experience suggests that philopatric individuals return to known places because of prior breeding success (Haas 1998). Furthermore, familiarity with neighbouring potential breeding sites may also increase the probability of acquiring sites of a relatively better quality than the previous year's one (Greenwood 1980, Pärt & Gustafsson 1989, Bensch & Hasselquist 1991). However, despite such benefits of philopatry, many individuals frequently disperse from familiar areas.

The high risk of inbreeding and local competition for resources and/or mates are the determinant factors which may promote dispersal (Green-

wood 1980, Dobson & Jones 1985, Waser 1985, Pusey 1987). Dispersal patterns are believed to be the result of the balance of benefits and costs associated with philopatry (Greenwood 1980). It is probable that different degrees of philopatry between sex- and age-categories of different species are the result of this trade-off.

The low return rate of marked birds (both juvenile and adult) may result from mortality (Johnson & Marzluff 1990), dispersal (Högstedt 1981) or high time costs for searching and finding the way to home sites in migratory birds (Pärt 1991). Although there are marked and important differences between dispersal and mortality, they are very difficult to distinguish one from another (Haas 1998) and, similarly, precise data on immigration and emigration are difficult to obtain. Many empirical studies have confirmed links between reproductive success and site fidelity (e.g. Harvey *et al.* 1979, Gavin & Bollinger 1988, Payne & Payne 1993), reproductive success and survival (Pugesek & Diem 1990) and population density and dispersal (Weatherhead & Boak 1986, Arcese 1989).

The Red-backed Shrike, *Lanius collurio*, is a long-distance migratory passerine. Scattered bushes in open farmland most frequently form its breeding habitat. Breeding begins in early May and continues up to the end of July. Only one brood is reared per year in the Czech Republic. One to three compensatory clutches may follow a first unsuccessful breeding attempt (Hudec 1983).

In this study, the fidelity rate in one breeding population of Red-backed Shrike in the Czech Republic is described. Simultaneously, the components of reproductive success that could influence a shrike's decision to be philopatric or not are examined. Although the Red-backed Shrike

has exhibited population declines over large parts of its range (Tucker & Heath 1994), few long-term studies and fidelity analyses have been published in European countries (Fulín & Žolner 1985, Jakober & Stauber 1987, 1989, Massa *et al.* 1993, Diehl 1995) except for the Czech Republic.

2. Research area and methods

This study was conducted in South Bohemia near the town of Písek, in the Czech Republic (50°14' N, 14°15' E). The research area was about 15 km² and, geographically, distinctly separated from other similar suitable habitats for Red-backed Shrikes. Extensive forests, a deep river valley and large agriculture fields created boundaries for the research area. The main breeding habitat consists of dispersed wild rose (*Rosa sp.*) and blackthorn (*Prunus spinosus*) bushes and is also used most frequently as a nesting site. Arable land and mowed meadows comprised the main part of the study area (Table 1). The Red-backed Shrikes bred in three clusters in an east-west direction according to appropriate breeding habitats. Only a few pairs occupied large agriculture plots between these main breeding areas.

The Red-backed Shrikes' occurrence, breeding and fidelity were studied from 1990 to 1999. The study area was visited approximately three days a week from 1990 to 1996 and almost the whole breeding season in 1997, 1998 and 1999. Different numbers of shrikes bred and were ringed with aluminium rings during those years. Two colour plastic rings (six colours) were used in addition to an aluminium ring for all adults. The exclusive combination of three rings enabled identification of a particular individual by visual observation. Approximately 50% of the adult birds and more than 75% of the nestlings were ringed in every season. The adult birds were trapped by using bowl-traps with a mealworm inserted as a lure or by mist-nets located close to the nest during the late incubation or small hatchling period. Catching the birds in the nest vicinity did not influence subsequent breeding success (*pers. obs.*). Young between 7th and 10th day of age were fitted with numbered aluminium rings. More than 90% of breeding adults were annually checked

Table 1. Proportion of particular kinds of habitat presented in the study area.

Kind of habitat	%
Arable land	60
Mowed meadows	15
Small patches of mixed forest	9
Human built area	5
Orchards	< 1
Fishponds and water reservoirs	< 1

using binoculars for colour rings, some were recaptured and identified. In total 134 males, 144 females and 799 young were ringed during the years 1990–1998.

The mean number of breeding pairs per season was 53 (33 pairs as minimum in 1992 and 79 pairs as maximum in 1997). The population increased from 1992 to 1997 and slowly decreased during the last two years of the study. Data which were recorded every year included the date of the first egg laying, nest location, clutch-size, brood-size and breeding success.

The standardized measurements (Svensson 1992) of right wings (maximum length), within 0.5 mm, on a metric ruler, right tarsus, within 0.05 mm, on a vernier calliper and body mass, within 0.1 g, on a spring balance, were measured for each adult in the last three years. Based on the results of these measurements an attempt has been made to estimate body condition. Body condition index was calculated as body mass divided by tarsus length (Brown 1996). Because of a significant decrease in the female body mass during the breeding cycle (Šimek *unpubl.*), body mass of each female was recalculated for the mass expected at the day when she laid the first egg. This recalculation was used only for females that were still successful in their breeding effort at the time of catching.

Three categories of males were analyzed separately: territory-faithful males (those that precisely returned to the same territory next year), research-area faithful males (those that returned anywhere to the research area next year, but not to the same territory) and other ringed males (those that were ringed in the research area, but did not return next year). Only two categories (research-area faithful and other ringed, respectively) were used for females because of a lack of territory-faithful individuals. The method of capture was selective. Successful breeders exhibited a higher probability of being captured and ringed, because catching them in the vicinity of the occupied nest was more successful than catching the birds which were not breeding (for males $\chi^2_1 = 6.2$, $n = 561$, $P = 0.001$, for females $\chi^2_1 = 8.13$, $n = 559$, $P = 0.004$). Therefore, for breeding success versus philopatry investigation I did not test philopatric birds' breeding success against overall population breeding success, but against the

other ringed birds. The data obtained in the year 1996 was excluded from the analyses of influence of population success to the birds' return rate because insufficient breeding information was available that year. Breeding was considered successful when at least one young was reared.

Growth of nestlings is very often asynchronous and could be affected by food shortages (Schew & Ricklefs 1998) and parents' ability to sufficiently feed young under deteriorated feeding conditions (Gebhardt-Henrich & Richner 1998). An asynchronous growth index, which has been tested as a possible predictor for adult fidelity for every successful nest was defined as:

$$(\sum [b - b_{\max}] / b_{\max} \times 100) / n \quad (1)$$

where b is the body mass of the particular young, b_{\max} is the body mass of the heaviest young in the nest and n is the number of the young in the brood. This index was estimated for the seasons 1997–1999, when the body mass measurements of young were taken.

Timing of breeding was expressed as a ten-day period (TDP) of that month when the first breeding attempt started. TDP number one was fixed as the first TDP of May.

Territory attractiveness was quantified according to the nest quality evaluation by Montalvo and Potti (1992). They used an index that assumes that those nest-boxes for Collared Flycatchers (*Ficedula albicollis*), that are more often occupied, have higher attractiveness for flycatchers. Similarly, this index for the shrikes is defined as the proportion of the years during which the particular territory was occupied in relation to the overall number of occupied territories in a given year.

The index of between-year changes of population was defined as:

$$(p_{t+1} - p_t) \times 100 / p_t \quad (2)$$

where p_t and p_{t+1} are numbers of the breeding pairs in the year t and $t + 1$, respectively.

Between-year displacement distances in the movement of the birds were taken as the distances from nest to nest from a local map of a scale 1:10 000. The data from the two subsequent seasons only were taken into account.

Basic statistical evaluation was performed using the program Statistica Ver. 5. with signifi-

cance level set at 0.05, in standardized statistics tests (Zar 1984). All t-tests are for independent samples and two-tailed. Dispersion around mean values is given as $\bar{x} \pm$ a standard deviation ($\bar{x} \pm$ SD). In addition, between-year records of birds were considered as independent observations.

3. Results

3.1. Rate of fidelity

In the research area, 38 of 134 ringed males (28.4%) and 29 of 144 ringed females (20.1%) were recorded at least once during the subsequent years after the year of ringing, however the male-biased rate of fidelity is non-significant ($\chi^2_1 = 2.56$, $n = 278$, $P = 0.11$). Year-to-year fidelity rate fluctuated from 20.0 to 62.5% among males and from 10.0 to 28.6% among females. Thirty-six males and 25 females, respectively, were recorded in the first year after ringing. Return rate slightly increased with age. Nine (30.0%) of 30 males were located during their third year and 4 (66.6%) of 6 males returned also in their fourth year ($\chi^2_2 = 4.19$, $n = 173$, $P = 0.12$). Similarly, seven (30.4%) of 23 females were recorded in their third year and 3 (42.9%) of 7 females in their fourth year ($\chi^2_2 = 3.0$, $n = 179$, $P = 0.22$).

From a total of 799 ringed nestlings only 22 (2.8%) were caught in the research area during subsequent years. Thirteen of them were males and 9 females. Only 3 females and 8 males from these 22 philopatric young were recorded in the research area in their first year. Other young were located for the first time between their second and fifth year. Nine different males and one female were visually identified with aluminium rings only and any effort to catch and identify these birds was unsuccessful. There was not a difference be-

tween the return rate of young males and young females ($\chi^2_1 = 0.75$, $n = 22$, $P = 0.39$) assuming that the sex-ratio of the reared young was balanced. The return rate of adults (both males and females) is 24.1% and it is significantly higher than the 2.8% for young ($\chi^2_1 = 124$, $n = 1077$, $P < 0.001$).

Males returned to their own territory in 20 cases ($n = 53$) whereas females exhibited territory fidelity in only 6 cases ($n = 36$; $\chi^2_1 = 4.6$, $n = 89$, $P = 0.03$). Average distance of year-to-year movements was 272 ± 618 m (SD) and 488 ± 663 m (SD) for males and females, respectively (Kolmogorov-Smirnov two-sample test, $n_{1,2} = 53, 34$, $P = 0.025$, Table 2).

Males and females returned to the same breeding cluster in 49 and 31 cases, respectively. Year-to-year displacement from one cluster to another neighbouring cluster was registered four times for males and three times for females only. There was no difference between sexes in dispersal out of their previous breeding cluster in the extent and scale of the research area ($\chi^2_1 = 0.05$, $n = 87$, $P = 0.83$). I did not detect any case of movement from the easternmost to the westernmost cluster and *vice versa*.

3.2. Mate fidelity

During the years of field research 132 complete pairs were ringed. Both members of the pair returned to the research area only 8 times (6.1%) in the subsequent year. Mate fidelity was recorded only twice. In the first case, the second breeding effort occurred at the same locality as in the previous year. In addition, the male of this pair was also the oldest known shrike in the research area. His age was 6 years and he was still alive in the last season of the study. In the second case, both birds returned also to the same territory, but they moved to the neighbouring territory several days after pair-formation. One of these faithful pairs was successful and one unsuccessful during their first joint breeding. In the remaining six cases, when both members of the pair returned, three times males were faithful to their previous territory, and females started to breed on the other locality, and three times both birds built their nests on different localities, however males were always

Table 2. Year-to-year dispersal distances (m) of Red-backed Shrikes (incl. cases of territory fidelity).

Grouping	Mean	Median	SD	Range	n
Nestlings	1210	950	645	470–2150	11
Males	272	70	618	0–3250	53
Females	489	250	663	0–2750	34

on the neighbouring place to their previous year's territory.

3.3. Determinants of fidelity rate

Breeding success in a given year t seems to be the determining factor for males' territory-fidelity in the year $t + 1$ (Table 3). Territory-faithful males had higher breeding success in the previous year (95.0%) than other ringed males (68.2%, $n = 168$, Fisher exact test $P = 0.015$). The higher breeding success of subsequent year territory-faithful males was caused by higher success of their first breeding attempts of the season (85.0% for territory-faithful males, $n = 20$; 51.3% for other ringed males, $n = 152$; $\chi^2_1 = 8.11$, $n = 172$, $P = 0.004$). There was no difference in breeding success of the future research-area philopatric males and other ringed males ($\chi^2_1 = 0.05$, $n = 175$, $P = 0.83$) and also no difference in the breeding success of first breeding attempts of these two groups of males ($\chi^2_1 = 0.9$, $n = 183$, $P = 0.34$).

Of philopatric females, 88.2% ($n = 34$) bred successfully in the previous year, whereas breeding success for other ringed females was 69.5%

($n = 151$; $\chi^2_1 = 4.92$, $n = 185$, $P = 0.026$). Breeding success of first breeding attempts was similar for both categories of females (60.9% for philopatric females, $n = 41$; 51.9% for other ringed females, $n = 155$; $\chi^2_1 = 0.99$, $n = 196$, $P = 0.32$).

The mean numbers of eggs in the first clutch, eggs hatched and young fledged were not different between tested groups of both sexes (Table 4). The females that returned in the year $t + 1$ started their breeding in the year t significantly earlier in the season than females that did not return (Table 5, $U = 1020$, $n_{1,2} = 27, 26$, $P = 0.001$). This relationship was marginally significant for males (ANOVA, $F_{2,97} = 2.78$, $P = 0.067$). Territory faithful males started to breed earlier than other ringed males (Tukey test, $P = 0.055$).

Year-to-year fluctuation of males' return rate (see above) was correlated with between-year change of population size ($r = 0.8$, $n = 9$, $P = 0.01$, Fig. 1). This parameter was insignificant for females' fluctuation ($r = 0.10$, $n = 9$, $P = 0.80$). Females' year-to-year return rate fluctuation was marginally significantly correlated with overall population breeding success of the first breedings in the previous year ($r = 0.64$, $n = 8$, $P = 0.087$). Average breeding success did not influence males'

Table 3. Breeding success (n) of subsequent year philopatric shrikes in comparison to other ringed shrikes.

Breeding success	Territory faithful males	Breeding area faithful		Other ringed	
		Males	Females	Males	Females
Yes	19	19	30	101	105
No	1	8	4	47	46
Unknown	0	6	2	23	25
Ratio of "yes"	95.0	70.8	88.2	68.2	69.5

Table 4. Comparison of the means ($a =$ ANOVA, $u =$ Mann-Whitney U test) of reproductive variables in year t for males that returned in year $t + 1$ with other ringed males that did not return in year $t + 1$ (date of egg laying expressed as a ten-days' period, 1 = 1st. ten-days' period of May).

Variable	Territory faithful (n)	Breed. area faithful (n)	Other (n)	Test	P
Numb. of eggs in 1st. clutch	5.12 (17)	5.06 (16)	5.18 (38)	a	0.89
Hatched eggs	4.82 (17)	5.15 (13)	4.86 (50)	a	0.59
Fledged young	4.44 (18)	4.47 (15)	4.72 (39)	a	0.70
Date of egg laying	2.76 (17)	3.14 (22)	3.18 (61)	a	0.07
Asyn. growth	8.22 (8)*		9.93 (33)	u	0.40

* = pooled data for territory faithful and breeding area faithful categories.

return rate fluctuation at all ($r = 0.17$, $n = 8$, $P = 0.69$).

Territory attractiveness index was not in direct relationship with overall breeding success ($U = 15686$, $n_{1,2} = 113, 306$, $P = 0.15$), which is under the control of other factors. Males, which returned to the research area next year, more frequently occupied territories with higher or at least the same attractiveness index ($\chi^2_1 = 6.93$, $n = 104$, $P = 0.009$). Highly attractive territories had a higher probability to be occupied by the same male in the next year. Territories of the three tested groups of males significantly differed in attractiveness (ANOVA, $F_{2,188} = 4.77$, $P = 0.009$). Territories of territorially faithful males had higher attractiveness than territories of research-area faithful (Tukey test, $P = 0.013$) or other ringed males (Tukey test, $P = 0.01$). Finally, there was no difference between attractiveness of territories that were occupied by males that were faithful to the research area in the subsequent year and territories that were occupied by other ringed males (Tukey test, $P = 0.85$). Territory attractiveness was not an important factor for females, as there was not any relationship between territory attractiveness and females' fidelity rate ($U = 2352$, $n_{1,2} = 165, 34$, $P = 0.14$).

No relationship was found between body condition index and subsequent year fidelity rate ($t_{84} = 1.01$, $P = 0.31$ for males and $t_{41} = 1.16$, $P = 0.25$ for females). The rate of asynchronous growth of young was not different between examined groups of males and females, respectively (males: $U = 106$, $n_{1,2} = 8, 33$, $P = 0.39$; females: $U = 138$, $n_{1,2} = 9, 31$, $P = 0.96$).

4. Discussion

4.1. Rate of fidelity

The 28.4% return rates of adult males and 20.1% of adult females are not markedly different from the results published in other philopatry studies of shrikes (Jakober & Stauber 1980, Fulín & Žolner 1985, Jakober & Stauber 1987, Massa *et al.* 1993, Diehl 1995). Only Ash (1970) found very low fidelity rate in a decreasing population in England (5.8%). Very surprising and exceptional is the almost zero fidelity found in one Polish population (Tryjanowski & Kuźniak *unpubl.*). Older birds of both sexes tend to return more frequently as showed also on the ground of long-term ringing study of Jakober and Stauber (1989). Male biased return rate was not significant in this study, but there was only one particular year when females' return rate was higher than that for males. Male-biased return rate was found for other shrike species such as Loggerhead Shrike, *Lanius ludovicianus* (Collister & de Smet 1997), Great Gray Shrike, *Lanius excubitor* (Yosef 1992) and Lesser Grey Shrike, *Lanius minor* (Krištín *pers. comm.*) and it is a general phenomena for birds (Greenwood 1980, Greenwood & Harvey 1982, Clarke *et al.* 1997).

The nestling return rate of 2.8% is slightly lower than in other studies (4.8–10.5%; Jakober & Stauber 1980, 1987, Massa *et al.* 1993, Diehl 1995), but this number might be somewhat underestimated because young shrikes with aluminium rings were less conspicuous than colour-ringed adults. I did not identify several birds which

Table 5. Comparison of the means (Mann-Whitney U-test) of reproductive variables in year t for females that returned in year $t + 1$ with other ringed females that did not return in year $t + 1$. (date of egg laying expressed as a ten-days' period, 1 = 1st. ten-days' period of May).

Variables	Breeding area faithful (n)	Other ringed (n)	P
Numb. of eggs in 1st. clutch	5.32 (22)	5.11 (99)	0.22
Hatched eggs	4.89 (27)	4.90 (98)	0.74
Fledged young	4.58 (24)	4.55 (89)	0.63
Date of egg laying	2.44 (27)	3.02 (126)	< 0.01
Asyn. growth	9.07 (10)	9.40 (30)	0.68

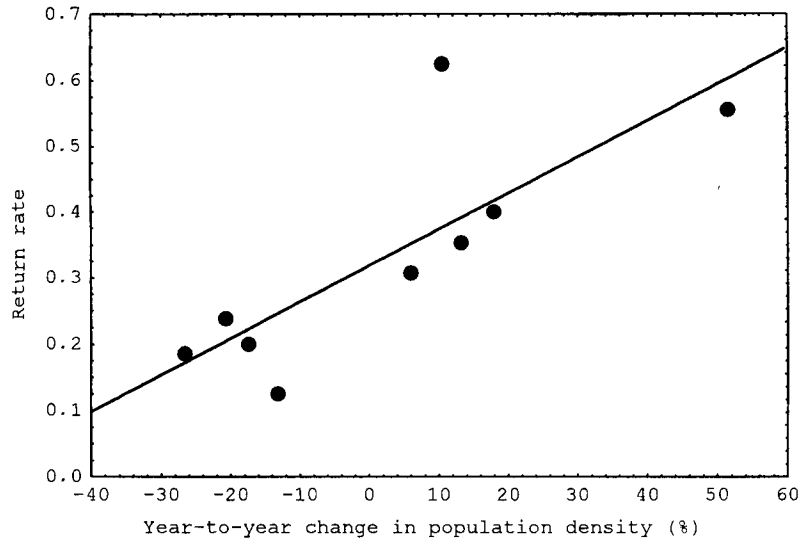


Fig. 1. Correlation between year-to-year change in population density and the males' return rate in the subsequent season ($r = 0.8$, $n = 9$, $P = 0.01$).

had an aluminium ring only. There was a high probability that these birds were ringed as nestlings in the study area. If such birds would be counted as philopatric young (all adults should have colour rings), then nestlings' return rate would be 4.0%.

The Red-backed Shrike is a tropical migrant and like many other bird species (Ketterson & Nolan 1983), males return earlier to their breeding grounds than females to establish breeding territories (Cramp & Perrins 1993). It is very advantageous for males to return to the well-known places because as expected, prior local experience facilitates nest site selection (Haas 1998). In my study, almost 40% of philopatric males returned to their previous year territory. Jakober and Stauber (1987) found 72.4% shrikes' males to be faithful to their territories, but they included returns within 200 m which overestimated territory fidelity *sensu stricto*. The corresponding number from my study is 75.5%.

Females showed a lower degree of both types of philopatry, to the research area and to the territory, and dispersed at longer distances. However, difference between sexes in the research area philopatry was not significant and dispersal pattern of both sexes was the same in the scope of breeding clusters. If we do not suppose female-

biased mortality and average age, which is more often higher for males (Payevsky *et al.* 1997), than the only plausible explanation is a small fraction of females, which perform long-distance dispersal out of the research area. Nevertheless, I did not confirm such long-distance dispersal.

4.2. Mate fidelity

I observed two instances of mate fidelity in the Red-backed Shrike. I did not find any other records about mate fidelity in this species. The probability that both members of the previous-year's pair return to the research area is 5.4% according to determined fidelity rate of adults. If 132 pairs were ringed, we would expect 7 pairs to return. In fact, 8 pairs were recorded returning to the area. The probability that both birds returned to their previous year's territory (it means mate fidelity) is 0.7%. In fact, two recorded events of mate fidelity occurred in 1.3% of the cases suggesting that mate fidelity was random. Cramp and Perrins (1993) found mate infidelity of the Red-backed Shrikes as the result of sex-biased philopatry. Neither was observed in the Woodchat Shrike (*Lanius sennator*, Cramp & Perrins 1993) and in the Lesser Grey Shrike (*Lanius minor*, Krištín *et*

al. 1999) whereas observations of wild and captive birds suggest pair-bond renewed in successive seasons in the Great Grey Shrikes (*Lanius excubitor*, Cramp & Perrins 1993).

4.3. Determinants of fidelity rate

Next-year philopatric shrikes had higher breeding success in the previous year than the other ringed birds. This positive correlation was found for both sexes but with small differences. Breeding success was found as the important predictor of next-year return rate for the territory-faithful males only. For females, breeding success was the important factor regardless of which part of the research area they returned to next-year. The importance of previous breeding success for the future rate of fidelity of the Red-backed Shrikes was reported also by Jakober and Stauber (1987). In general, a positive relationship between previous breeding success and return rate was reported for different species of passerines (e.g. Harvey *et al.* 1979, Gavin & Bollinger 1988, Bensch & Hasselquist 1991, Gowaty & Plissner 1997, Haas 1998), however some authors did not observe this relationship (Drilling & Thompson 1988).

Future territory-faithful male shrikes exhibited a higher ability to rear young already from their first breeding attempts, so they did not suffer from elevated energetic costs of compensatory breeding attempts. Renesting stress hypothesis as presented by Haas (1998) suggests that breeding failure increases reproductive effort by causing birds to reneest and this energetic stress increases the probability of mortality and, consequently, decreases the return rate. This hypothesis seems to be relevant on the basis of territory-faithful males' results. However, research area faithful males and all philopatric females did not differ from other ringed males and females, respectively, in their success of first breedings. Higher breeding success of future philopatric females was caused by their higher ability to rear young from compensatory breedings. This finding is in contradiction to the renesting stress hypothesis. I suggest that both the renesting stress hypothesis and a good prior local experience with the territory, where it was possible to rear successfully young already from the first breedings,

can reliably explain the high degree of males' territory faithfulness.

Of the examined reproductive parameters, only the timing of egg-laying was found to be related to the subsequent season's return rate. Females that started breeding earlier in the season, returned significantly more often to the research area in the next season. However, this relationship was only marginally significant for males. There is a trend that earlier breedings of shrikes are more successful than later ones (Šimek *unpubl.*), thus this finding is in accordance with breeding success importance for the rate of philopatry as described above. Slightly different conclusions were established by Jakober and Stauber (1989) who found that only breeding timing of young males was significantly correlated with their next year fidelity. Neither clutch size nor number of fledged young were in correlation with subsequent year return rate in contradiction to the results obtained for some other species (e.g. Blue Tits, *Parus caeruleus*, Julliard *et al.* 1996).

With increasing population density there might be an increasing risk that an individual searching for a better site will lose its territory to a floater (Weatherhead & Boak 1986, Arcese 1989), thus it is leading to suggestion of positive correlation between the level of philopatry and population density as found, for example, by Doligez *et al.* (1999) for male Collared Flycatchers. Population density was established as the predictor of next-year return rate of adult males of the Red-backed Shrikes whereas females' return rate fluctuation was not correlated with population density at all. No more than 4.0% of young that were born in the study area returned to breed there, so the majority of first-time breeders had their origin out of the area and almost no risk of inbreeding is suggested. Under this natal dispersal situation, breeding females are not forced to disperse because of the low threat of inbreeding and the only reason for dispersal is the effort to choose and find as good a male as possible.

Females' year-to-year return rate fluctuation was almost significantly correlated to the population breeding success of the first breedings, but not to the overall population success of both, the first and compensatory breedings together. A possible explanation is more or less speculative. I suggest, that individuals that finish breeding ear-

lier can leave their territory earlier and can disperse across a landscape before autumn migration. Although post-breeding dispersal was not rigorously studied, few such pre-migratory movements were registered in the study area. During these movements birds might gather information about overall breeding success at neighbouring sites and, subsequently, they may use this information for their decision where to return next year (Bollinger & Gawin 1989, Haas 1997, Danchin *et al.* 1998, Doligez *et al.* 1999). Females that finish their breeding early in the season might be out of the area during the latter part of the season, so they cannot take the results of the compensatory breedings (which change overall population success) into account and hence reported relationship between the return rate fluctuation and the population success of the first breedings.

Territory-faithful males of shrikes occupied more attractive territories than the other males. Arriving males choose their territory according to some special features that they suppose should be advantageous for a successful breeding season despite only a weak correlation between this attractiveness and real breeding success. Territory attractiveness is next among breeding success and population density as one of the main determining factors of males' territory fidelity. Movements out of the previous territories as a means of acquiring better territories have been published also in other studies (Brooke 1979, Newton & Marquiss 1982).

Acknowledgements: I am very grateful to my supervisor Prof. Z. Veselovský, Dr. A. Krištín, Dr. J. Jokimäki and Dr. P. Tryjanowski for comments on the manuscript and Dr. R. Wagner and Prof. A. Clarke for correcting the English. Part of this work was performed with financial support from the Dept. of Zoology at University of South Bohemia, Faculty of Biological Sciences.

Selostus: Pikkulepinkäisen pesimäpaikkauskollisuus Tšekissä

Tyypillinen piirre lintujen käyttäytymisessä on aikuisten yksilöiden taipumus palata takaisin edellisen vuoden pesimäalueilleen. Nuoret yksilöt yleensä levittäytyvät laajemmalle alueelle synnyinalueidensa ulkopuolelle. Useilla lintulajeilla on

koiraiden todettu olevan naaraita uskollisempia edellisen vuoden pesimäalueilleen. Voidaan olettaa, että vanhat linnut hyötyisivät jollain tavalla paluustaan aikaisemille pesimäalueilleen. Kirjoittaja seurasi pikkulepinkäisten tutkimusalueelle paluuta ja pesimäreviiriuskollisuutta Tšekissä vuosina 1990–1999. Samanaikaisesti seurattiin lintujen pesimämenestystä. Pesimämenestys voi vaikuttaa siihen, palaavatko yksilöt takaisin samalle alueelle tai yksittäiselle pesimäreviirille. Tutkimuksen aikana rengastettiin 134 aikuista koirasta, 144 aikuista naarasta ja 799 poikasta. Tutkimusalueen (15 km²) aikuisista pikkulepinkäisistä saatiin rengastettua vuosittain noin 50 % ja vastaavasti poikasista 75 %. Keskimäärin tutkimusalueella pesi vuosittain 53 pikkulepinkäisparia. Koiraiden paluuprosentti tutkimusalueelle oli 28.4 % ja naaraiden vastaavasti 20.1 %. Sukupuolten välinen ero tutkimusalueelle paluussa ei ollut merkitsevä. Sen sijaan pikkulepinkäiskoiraat palasivat naaraita useammin vanhalle pesimäreviirilleen. Sekä koiraiden että naaraiden paluussa esiintyi vuosien välistä vaihtelua. Rengastetuista poikasista palasi synnyinalueilleen myöhempinä vuosina vain 3–4 %. Tutkimuksen aikana saatiin rengastettua yhteensä 132 pesältä sekä koiras että naaras. Näiden pariin molemmat sukupuolet palasivat tutkimusalueelle kahdeksassa tapauksessa (6.1 %). Puolisouskollisuus voitiin todeta näissä tapauksissa vain kahdesti. Edellisen kesän pesimämenestys vaikutti sekä koiras- että naaraslintujen paluuseen samalle reviirille. Reviireilleen palanneiden yksilöiden pesintä onnistui edellisenä pesimäkautena useammin kuin yksilöiden, jotka eivät palanneet edellisen kesän reviirilleen. Useimmat pesimäparametrit, kuten munamäärä ja lentopoikasten määrä, eivät kuitenkaan korreloineet kummankaan sukupuolen pesimäpaikkauskollisuuden kanssa.

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