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Possible causes and consequences of philopatry and breeding dispersal in red-backed shrikes *Lanius collurio*

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Abstract Studies of animal breeding dispersal have often focused on possible causes, whereas its adaptive significance has received less attention. Using an information-theoretic approach, we assessed predictions of four hypotheses relating to causes and consequences of breeding dispersal in a migratory passerine, the red-backed shrike *Lanius collurio*. As predicted by the reproductive performance hypothesis, probability of breeding dispersal in females (though not in males) decreased with increasing annual average number of fledglings produced in the past year, but there was no association with conspecific reproductive performance in either sex. The site choice hypothesis, stating that individuals disperse to improve breeding site quality, received support in males only, as dispersal probability was positively associated to a measure indicating low territory quality. The social constraints hypothesis, referring to dispersal in relation to intraspecific interactions, received little support in either sex. The predation risk hypothesis was hardly supported either. Consequences of dispersal were marginal in both sexes because neither fledgling production in females, nor territory quality in males improved after dispersal. In addition, males settled on

territories closer to the forest edge than those occupied predispersal, which is opposite to the prediction of the predation risk hypothesis. We conclude that own reproductive success was the major factor determining dispersal behavior in females, whereas territory quality and possibly predation risk were most important in males. Overall, breeding dispersal appeared not to be adaptive in this dense population inhabiting an optimal habitat.

Keywords AIC · Reproductive performance · Site choice · Social constraints · Predation risk

Introduction

Dispersal in animals is supposed to be a response to ecological and social conditions on natal or breeding sites, ultimately resulting in an improvement of individual fitness, which may be mediated for example through higher habitat quality or reduced intraspecific competition on new territories compared to the former ones. Dispersal behavior can thus be studied from two perspectives, one that focuses on potential causes of dispersal, and a second one that examines the consequences of dispersal. With respect to breeding dispersal, the movement of individuals between subsequent breeding territories, surprisingly few studies have so far investigated both potential causes and consequences (Forero et al. 1999). In addition, whether breeding dispersal is adaptive remains unclear. Some studies have reported increased fitness for dispersing individuals (Pärt and Gustafsson 1989; Stenseth and Lidicker 1992; Payne and Payne 1993; Waser 1996; Forero et al. 1999; Newton 2001), whereas others have found no such effects (Newton and Marquiss 1982; Pusey and Packer 1987; Sedgwick 2004). Despite these contradictory find-

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ings, individuals are expected to benefit from dispersal, given that breeding dispersal can entail substantial costs, e.g., expressed as reduced survival compared to philopatric individuals (Daniels and Walters 2000; also see Yoder et al. 2004).

Here we examine philopatry and breeding dispersal of a migratory passerine, the red-backed shrike (*Lanius collurio*), using 5 years of data from a color-marked population living in a subalpine environment. Several hypotheses have been suggested to explain under which circumstances breeding dispersal should occur. Using an information-theoretic approach (Burnham and Anderson 2002), we first assessed which predictions of four of these hypotheses relating to ecological and social factors best explained breeding dispersal patterns in the red-backed shrike. We restricted our analyses to the four hypotheses outlined below because of lacking data to evaluate other hypotheses potentially influencing breeding dispersal, such as inbreeding avoidance or individual quality. According to the reproductive performance hypothesis, individuals may use their own reproductive performance to assess whether they should disperse from a site or remain philopatric (e.g., Switzer 1993, 1997; Haas 1998; Doligez et al. 1999; Forero et al. 1999; Daniels and Walters 2000; Hoover 2003; Sedgwick 2004), with dispersal being a response to low breeding success. This hypothesis predicts that probability of dispersal is negatively related to own breeding performance (prediction 1a, Table 1). Individuals may not only use their own reproductive performance (hereafter referred to as 'personal information'), but also that of conspecifics as a cue for local habitat quality and, therefore, for 'choosing' future breeding sites. The use of such 'public information' (i.e., performance of conspecifics, Valone and Giraldeau 1993) has been shown to influence breeding habitat selection in a variety of species (Danchin et al. 2001, 2004; Doligez et al. 2002). A second prediction of the reproductive performance hypothesis is therefore that individuals should disperse if reproductive performance on neighboring territories has been better relative to the own performance in the year before dispersal (prediction 1b, Table 1).

The site choice hypothesis states that individuals disperse to improve the quality of their breeding site (Montalvo and Potti 1992; Korpimaki 1993; Stanback and Rockwell 2003). In our study population, territory quality has been shown to influence local recruitment, with probability of recruitment increasing with territory quality (Müller et al. 2005). If site choice is important for dispersal, we therefore expect probability of breeding dispersal to be negatively related to quality of the territories held in the year before dispersal (prediction 2a, Table 1).

The social constraints hypothesis refers to situations in which individuals disperse as a consequence of intraspecific interactions (Payne and Payne 1993; Otter and Ratcliffe 1996), which may arise, for example, through high local density of conspecifics. In our study population, nesting success was found to decrease with increasing conspecific density in the neighborhood of a territory (Müller et al. 2005). We therefore predicted that probability of breeding dispersal is positively related to conspecific density around a territory (prediction 3a, Table 1).

Experimental and observational evidences suggest that nest predation can cause breeding dispersal (Dow and Fredga 1983; Haas 1998; Forero et al. 1999; Hakkarainen et al. 2001). Breeding sites should therefore be selected to minimize predation risk, which has been shown in red-backed shrikes (Roos 2002; Roos and Pärt 2004). In our study population, more than 66% of all nest losses ($n=241$ clutches) were due to predation. Accordingly, the predation risk hypothesis predicts that probability of dispersal is negatively related to the distance of territories to the edge of forests and/or settlements in the year before dispersal (prediction 4a, Table 1) because territories located close to forests and/or settlements are more likely included in home ranges of predators emanating from those areas (see Predation risk in the Materials and methods for more

Table 1 Overview of hypotheses and predictions examined in relation to philopatry and breeding dispersal

Hypothesis	Predictions
(1) Reproductive performance	Probability of dispersal is...
'Personal information'	(a) Negatively related to own previous reproductive performance
'Public information'	(b) More likely if reproductive performance on neighboring territories is higher than on own territory
(2) Site choice	(a) Negatively related to territory quality[1]
(3) Social constraints	(a) Positively related to conspecific density around the territory
(4) Predation risk	(a) Negatively related to distance of a territory to the forest edge and/or settlements
	(b) Negatively related to distance of a territory to the nearest corvid nest

[1] Territory quality measured through variables referring to foraging (percent low intensity meadows, percent unmanaged area), nest site quality (hedge length (m) and number of freestanding bushes and trees) and long-term performance (total number of fledglings produced over the five years and territory occupancy)

details on nest predators). A second prediction of the predation risk hypothesis (4b, Table 1) is that probability of dispersal should be negatively related to the distance of a territory to the nearest corvid nest (cf. Roos 2002; Roos and Pärt 2004).

In a second step, we examined the consequences of breeding dispersal for those factors, which had been shown to influence dispersal probability in the above-mentioned analyses. We expected to find positive effects of breeding dispersal, such that it led to an improvement of the factors potentially causing dispersal.

Materials and methods

Study area

The study was conducted in the Engadin, an alpine valley in eastern Switzerland (46°50′N/10°23′E). Here, red-backed shrikes reach densities up to 5.4 breeding pairs per 10 ha, making the Engadin one of the most important and densely populated breeding areas for the species in Switzerland (Müller and Leugger 1998). A study site of 192.5 ha was selected, which extended from 1,090 to 1,680 m a.s.l. The study site and the areas surrounding it were inhabited more or less continuously by red-backed shrikes. Hay meadows and pastures covered much of the study site. Agricultural practices during the study period were of low intensity. Hedges, orchards, single bushes, and trees resulted in high structural diversity of the study site, particularly close to the two villages Ramosch and Vnà. The study site was surrounded by spruce (*Picea abies*) and pine (*Pinus* sp.) forests, and, to a lesser extent, by gray alder (*Alnus incana*) forests, the river Inn, and a ravine. Further details on the study area can be found in Müller et al. (2005).

Field methods

Data were collected from 1988 to 1992, usually from arrival of the birds (end of April) until the young of the last nest had fledged (mid August). Although most nests were found during egg laying, nest checks were, with a few exceptions, delayed until the nestling period to minimize disturbances. As soon as adults were observed feeding, the age of the nestlings was estimated based on comparisons with reference nests that had been visited daily. On day 8 (day 1 = hatch date), nestlings were marked with a numbered aluminum band. Adults were caught during the nestling period with a mist net placed close to the nest and individually banded with two colored aluminum bands, each band bearing two colors to increase individual combinations.

Philopatry, breeding dispersal and sample sizes

Individuals were considered to be philopatric if they bred in the same territory as in the previous year. Conversely, individuals that changed breeding territories between two successive years were classified as breeding dispersers (Clobert et al. 2001). Red-backed shrikes defend all-purpose territories, in which all breeding and foraging activities take place (Glutz von Blotzheim and Bauer 1993). Each year, the boundaries of territories were determined by connecting the outermost observations of territorial disputes and foraging (10–20 per male). Overall, locations of territories among years were fairly stable (unpublished data).

We obtained data on 51 males and 34 females. Thirty-two males and 30 females were observed in two consecutive years and thus contributed one observation each (i.e., either dispersing or philopatric individual). An additional 19 males were observed for more than 2 years (15 in 3 years, four in 4 years), as were four females (three females in 3 years, one female in 4 years).

Variables used to test hypotheses

Reproductive performance

The red-backed shrike usually breeds once per season, unless the first breeding attempt is not successful, in which case a replacement clutch may be produced (Glutz von Blotzheim and Bauer 1993; Müller et al. 2005). Out of 475 breeding attempts of known status, 23.6% were replacement clutches. Each year, territories were classified as either successful if at least one fledgling was produced in any of the nesting attempts in that year, or as unsuccessful if otherwise (hereafter referred to as variable 'nest success'). As a second measure of reproductive performance, we used the annual average number of fledglings produced per breeding attempt on a territory (hereafter 'average number of fledglings'), which was obtained by dividing the total number of fledglings produced on that territory and year by the number of breeding attempts (defined as a nest with at least one egg) in that year. These two measures of reproductive performance were used to test the predictions referring to the use of 'personal information'.

In the case of 'public information', we determined the three territories located closest to each territory of philopatric and dispersing individuals using ArcView GIS 3.3 (ESRI Inc 1992–2002). Distances between territories were calculated on the basis of nest locations within territories. In case of more than one nesting attempt per territory and year, the average distance of the nests to the nest(s) in the nearest neighboring territory was calculated. We averaged the average number of fledglings produced on the three nearest

territories and subtracted this value from the average number of fledglings produced on the territory in question. We then created a binary variable by assigning all observations with a difference >0 into one category and all others into a second category ('performance 3 nearest territories'). Thus, the first category (difference >0) indicates that, on average, more fledglings had been produced on the next three territories relative to the territory in question, whereas the second category indicates no difference or higher fledgling production on the focal territory.

We focused on the three nearest territories to capture variation in fledgling production in the immediate neighborhood of a focal territory. We consider the immediate neighborhood relevant with respect to public information, because red-backed shrikes are highly territorial, likely making excursions to territories beyond the immediate neighborhood too costly for prospectors. Further, the use of a categorical variable was necessary because the continuous variable created by subtracting the average number of fledglings produced on the three nearest territories from the average number of fledglings produced on the territory of interest was, obviously, highly correlated with the average number of fledglings produced on that territory (Spearman rank correlation, females: $r_s = -0.89$, $p < 0.001$, $n = 38$; males: $r_s = -0.77$, $p < 0.001$, $n = 67$), which would have made it impossible to differentiate between effects of either variable.

Site choice

We measured territory quality through habitat variables known to be important for the ecology of the red-backed shrike (Glutz von Blotzheim and Bauer 1993; Leugger-Eggimann 1997; Müller et al. 2005), referring to foraging habitat and nest site quality. For foraging habitat quality, these variables were the percentage area of a territory covered by (1) meadows managed at low intensity and by dry meadows ('percent low intensity meadows') and (2) unmanaged area ('percent unmanaged area'). High values for variables (1) reflected high territory quality, whereas high values for variable (2) indicated low quality territories (Müller et al. 2005). For nest site quality, the variables considered were (3) the length of hedges (m) and (4) number of freestanding bushes and trees. Because high values for both variables indicated high quality territories, these two variables were entered into or removed from all analyses always jointly, and we refer to them as 'nest site quality'. In addition to these structural variables, we used two measures relating to the birds' long-term performance as further estimates of territory quality, these being (5) the total number of fledglings produced over the 5 years per territory and (6) territory occupancy (number of years a

territory was occupied by a breeding pair; 13 territories occupied in only 1 year, 18 in 2 years, 32 in 3 years, 31 in 4 years, 24 in 5 years). Territory occupancy has repeatedly been found to be a reliable surrogate of territory quality in various bird species (Sergio and Newton 2003). These two variables were entered into or removed from all analyses always jointly, and we refer to them as 'long-term performance'.

Social constraints

We used two variables to assess the influence of conspecific density on breeding dispersal probability: 1) the number of red-backed shrike territories within 150 m of a given territory ('nb. territories <150 m'), and 2) the distance (m) to the nearest conspecific territory ('nearest neighbor'). The latter corresponded to the shortest distance between the nest location of a philopatric or dispersing individual, respectively, and the nearest nest in an adjacent territory. In case of more than one nesting attempt per territory and year, the average distance of the nests to the nearest neighboring nest(s) was calculated.

Predation risk

Risk of predation for a given territory was estimated through the distances to the nearest forest edge, human settlement and active corvid nest, respectively. The first variable ('distance to forest') relates to predators coming mainly from forested areas (red fox, jay *Garrulus glandarius*, carrion crow *Corvus corone corone*), the second one ('distance to settlement') takes into account house cats and magpies (*Pica pica*), and the third ('distance to corvid nest') directly relates to predation risk by corvids (cf. Roos and Pärt 2004). All species just mentioned have been shown to be predators of red-backed shrike nests (Glutz von Blotzheim and Bauer 1993; Tryjanowski et al. 2000; Jakober and Stauber 2002). For each variable, the distance corresponds to the straight line between the nest location and the forest and settlement edge or the nearest corvid nest, respectively; in case of more than one nesting attempt per territory and year, an average distance was calculated.

Statistical analyses

Because dispersal in birds is generally sex-biased (Clarke et al. 1997), we conducted all analyses separately for each sex. We accounted for the repeated use of individuals across years by performing all generalized linear mixed models (GLMM) with individual as a random factor (Verbeke and Molenberghs 2000). All other variables were treated as fixed effects. Model fit was assessed with residual analysis (McCullagh and Nelder 1989).

Breeding dispersal (binary response variable) was related to the predictor variables using GLMMs with logit link and binomial error structure (PROC GLIMMIX in SAS 9.1.3, SAS Institute Inc 2002–2003). 'Nest success' and 'performance 3 nearest territories' were categorical variables, all others continuous variables. We did not include year as a factor, because its inclusion did not improve model fit based on both Akaike's information criterion (AIC) values (see below) and residual analyses relative to intercept-only models.

We used an information-theoretic approach to examine which variables and models of a set of candidate models representing the four competing hypotheses best described the data (Burnham and Anderson 2002). In a first step, variables referring to each of the four hypotheses were analyzed separately. For each hypothesis, we evaluated which of the models consisting of all possible combinations of the hypothesis-specific variables best explained breeding dispersal patterns (intercept term always included). In each such hypothesis-specific comparison of models, we included a model consisting of the intercept only to check whether models with variables deemed relevant for a given hypothesis better explained the data than a model without these variables (i.e., the intercept-only model). Akaike model weights, which are based on AIC (Akaike 1973) corrected for small sample sizes (AICc, Burnham and Anderson 2002), were then calculated for each model within the set of candidate models of each hypothesis. Akaike weights sum to one by definition and are considered a measure of the probability that a specific model best explains the data, given all the candidate models (Burnham and Anderson 2002; Johnson and Omland 2004). Because we were interested in jointly examining the effects of variables referring to different hypotheses on breeding dispersal behavior (see step 2 below), we needed to assess the relative importance of each variable per hypothesis. This was done by summing the Akaike weights over all the models, which contained the variable in question (Burnham and Anderson 2002; Johnson and Omland 2004). According to Burnham and Anderson (2002), this is superior to selecting variables based on AICc of the best model(s) because summing the Akaike weights over all the models in the candidate set accounts for model selection uncertainty. The approach requires that each variable appears a balanced number of times in the candidate models (Burnham and Anderson 2002), which was given here because we examined all possible models (i.e., all possible combinations of the variables in question but without any interactions) per hypothesis. We considered variables with a summed weight of >0.5 to be important for explaining dispersal behavior and retained these variables for further analyses. We consider this arbitrary weight threshold of 0.5 to be an acceptable compromise between being too liberal

(including too many variables as being important, when using a threshold lower than 0.5) or too conservative (excluding potentially important variables when using a threshold higher than 0.5).

In a second step, we examined how variables relating to different hypotheses jointly explained breeding dispersal behavior. The models evaluated were (1) the intercept-only model, (2) the models containing, in addition to the intercept, important variables as identified in step 1 (i.e., summed Akaike weights >0.5), and (3) all their possible combinations. These combinations thus consisted of variables from different hypotheses and allowed an assessment of the relevance of each hypothesis relative to others. Using this procedure, we evaluated 24 models in females and 44 models in males. This two-step process was applied to reduce the number of models to be calculated, which is consistent with model selection philosophy, and because examining combinations of variables from all hypotheses at once would have resulted in overfitted models (Burnham and Anderson 2002). For the same reasons, no interactions between variables were included. Akaike weights were again calculated, and the relative importance of variables assessed by summing these weights over the models containing the variables in question. As in step 1, variables with a summed weight of >0.5 were considered to be important for explaining dispersal behavior. Model averaging was used to obtain direction and magnitude of estimates and SEs for each variable over all models examined in step 2 (Burnham and Anderson 2002).

All but six correlation coefficients among predictor variables (out of 264 coefficients) were below 0.5 (Spearman rank correlations, $n=38$ and 67 in females and males, respectively), the exceptions being the correlations between 'percent unmanaged area' and one variable of 'nest site quality' (number of freestanding bushes and trees; $r_s=0.52$ in females), between 'nb. territories <150 m' and 'nearest neighbor' ($r_s=0.74$ in females, $r_s=0.71$ in males), between 'distance to settlement' and 'distance to forest' ($r_s=0.54$ in males), and between the two variables measuring long-term performance ($r_s=0.71$ in females and $r_s=0.54$ in males).

We also used an informatic–theoretic approach (Burnham and Anderson 2002) to examine the consequences of breeding dispersal in the red-backed shrike, i.e., whether breeding dispersal led to an improvement of the factors potentially causing dispersal. We focused on those factors shown to be important in the context of breeding dispersal in the preceding analyses because it was not our goal to examine changes in other factors not related to breeding dispersal. We investigated whether a model including a binary variable type (before vs after dispersal) as a factor in addition to the intercept term better explained variation in the dependent variable than a model with an intercept term only. Dependent variables were those variables found to be

relevant for breeding dispersal in step 2 (i.e., summed Akaike weights >0.5). Differences in AICc values between the models per dependent variable in question (i.e., one model with intercept only, the other with intercept and the variable type) were compared. Support for each model was assessed based on Akaike weights. Model averaging was used to obtain direction and magnitude of estimates and SEs for the variable type over the two models per dependent variable. Dependent (continuous) variables were related to the binary predictor variable type using linear mixed models with identity link and normal error structure (modeled with PROC GLIMMIX in SAS 9.1.3, SAS Institute Inc 2002–2003).

Results

General findings

Of the birds banded as breeders, 32.4% of the females (36 of 111 banded individuals) and 40.6% of the males (54 of 133) returned to breed in the study site from 1 year to a subsequent one. These numbers include two females and three males that were first resighted 2 years after banding; these individuals are no longer considered in all following analyses. In total, we recorded 30 and 43 between-year territory changes in females and males, respectively. Breeding dispersal distance, i.e., the median distance between subsequent breeding territories of dispersers (i.e., their nests), was 374 m (interquartile range 185–619 m) in females and 186 m (100–345 m) in males. Eight females and 24 males did not change territories between years, respectively.

Hypothesis-specific model selection

Reproductive performance In females, the model selection procedure yielded one best model including the average number of fledglings, a measure of personal information, as the only variable (Table 2). All other models had ΔAICc values >2 compared to this model. The relative importance of the variable average number of fledglings was very high

Table 2 Results of model selection per hypothesis and sex

Hypothesis	Sex	Selected models	LogL	K	AICc	ΔAICc	A_weight
Reproductive performance	F	Average number of fledglings	−13.50	2	28.48	0	0.52
	M	Average number of fledglings, performance 3 nearest territories	−41.10	3	88.58	0	0.27
		Average number of fledglings	−42.59	2	89.37	0.79	0.18
		Intercept	−43.71	1	89.48	0.90	0.17
Site choice	F	Long-term performance	−16.32	3	39.34	0	0.25
		Long-term performance, % low intensity meadows	−15.80	4	40.82	1.48	0.12
		Intercept	−19.56	1	41.22	1.89	0.10
	M	Percent unmanaged area	−42.15	2	88.49	0	0.30
		Intercept	−43.71	1	89.48	0.99	0.18
		Percent unmanaged area, percent low intensity meadows	−41.75	3	89.88	1.40	0.15
		Percent low intensity meadows	−43.11	2	90.40	1.91	0.11
Social constraints	F	Intercept	−19.56	1	41.22	0	0.51
		Nearest neighbor	−19.27	2	42.87	1.65	0.22
		Nb. territories <150 m	−19.38	2	43.10	1.87	0.20
	M	Nb. territories <150 m	−42.37	2	88.94	0	0.39
		Intercept	−43.71	1	89.48	0.54	0.29
		Nearest neighbor	−43.07	2	90.33	1.40	0.19
Predation	F	Distance to forest, distance to settlement	−15.12	3	36.95	0	0.30
		Distance to forest	−16.42	2	37.19	0.23	0.27
		Distance to forest, distance to corvid nest	−15.45	3	37.61	0.65	0.22
		Distance to forest, distance to settlement, distance to corvid nest	−14.58	4	38.37	1.42	0.15
	M	Distance to forest	−41.47	2	87.14	0	0.40
		Distance to forest, distance to settlement	−41.19	3	88.76	1.62	0.18

Shown are models with ΔAICc <2 to the best model within the set of candidate models examined per hypothesis. All models contain an intercept term. Models are ranked according to their Akaike weights calculated over candidate models within each hypothesis and sex (*F* = females, *M* = males). *n*=38 dispersal events in females and 67 in males

LogL maximum likelihood estimate from SAS, *K* number of parameters, *AICc* AIC value corrected for small sample size, *ΔAICc* difference in AICc to the best model, *A_weight* Akaike weight (indicates support of a model relative to all other models considered per hypothesis and sex)

(Table 3), whereas the variables nest success and performance 3 nearest territories appeared to be of little importance. In males, all models received weak support because the Akaike weight of the best model, which included the two variables average number of fledglings and performance 3 nearest territories, was only 0.27, and the difference in AICc values of this 'best' model to the intercept-only model was just 0.90 (Table 2). Average number of fledglings was the variable present in the two highest-ranked models, resulting in a relative importance of >0.5 for this variable (Table 3). Despite being in the 'best' model, the variable performance 3 nearest territories achieved a relative importance value below 0.5, indicating that the high ranking of the 'best' model was primarily due to the presence of average number of fledglings. Performance 3 nearest territories was therefore no longer considered in subsequent analyses.

Site choice In females, dispersal behavior was best explained by a model with the variables referring to long-term performance as a measure of territory quality (Table 2). The relative importance of long-term performance was fairly high (Table 3), whereas the importance of the variable percent low intensity meadows was well below the 0.5-threshold, despite belonging to the second best model. In addition, the small difference in the maximized log-likelihood between the two top models further showed that the inclusion of % low intensity meadows did not substantially improve model performance (cf. p. 131 in Burnham and Anderson 2002). Male dispersal behavior was best explained by four models, three of which referred

to foraging habitat quality and included percent unmanaged area and percent low intensity meadows, respectively. However, all models had only low Akaike weights (Table 2), and the second-best model was the intercept-only model. Not surprisingly, only the variable percent unmanaged area appeared to be of relatively high importance and was retained for further analyses (Table 3).

Social constraints The model selection process in females yielded three best models, with the intercept-only model being ranked highest (Table 2). The other two models contained the variables nearest neighbor and nb. territories <150 m, respectively. Both these variables did not substantially contribute to explaining female dispersal behavior (Table 2), which is further reflected by low values regarding their relative importance (Table 3). Thus, no variable referring to social constraints was retained for further analyses in females. In males, a model with the variable nb. territories <150 m best explained dispersal patterns. The second-best model only contained the intercept, and the third-best model included the variable nearest neighbor. However, only the variable from the best model received sufficient support after calculation of relative importance values (Table 3) to be retained for subsequent analyses.

Predation In both sexes, the variable distance to forest was included in the top-ranked model as well as in all models with ΔAICc <2 compared to this best model (Table 2). Accordingly, the relative importance values for distance to forest were high in both sexes (Table 3).

Across-hypothesis model selection

Females Model selection yielded two best models, with the top model being almost twice as well supported by the data than the second-best model (Table 4). The models included variables referring to the reproductive performance hypothesis and the predation hypothesis. More specifically, the average number of fledglings appeared to be the most important predictor variable of female dispersal behavior because the relative importance of this variable was very high (0.94) and the model-averaged estimate was considerably larger than the associated SE (-0.942 ± 0.484). Female red-backed shrikes were more likely to disperse to another territory if their reproductive success had been low in the preceding year (Fig. 1). In contrast, the variable distance to forest, included in the second-best model, had relatively low relative importance (0.38), and the model-averaged estimate was smaller than its SE (0.006 ± 0.010). If anything, female breeding dispersal probability appeared to increase with distance of a territory to the forest edge

Table 3 Relative importance of predictor variables

Hypothesis	Variable	Females	Males
Reproductive performance	Average number of fledglings	**0.93**	**0.62**
	Nest success	0.25	0.30
	Performance 3 nearest territories	0.29	0.48
Site choice	Percent low intensity meadows	0.37	0.35
	Percent unmanaged area	0.30	**0.59**
	Long-term performance	**0.71**	0.14
	Nest site quality	0.26	0.14
Social constraints	Nearest neighbor	0.29	0.32
	Nb. territories <150 m	0.27	**0.52**
Predation	Distance to corvid nest	0.38	0.26
	Distance to forest	**0.93**	**0.77**
	Distance to settlement	0.47	0.30

Numbers are Akaike weights (see text for calculation details) summed, for each hypothesis and sex separately, over all candidate models containing the variable in question. Variables alphabetically sorted within hypotheses. Bold numbers indicate variables >0.50 selected for further analysis.

Table 4 Results of across-hypothesis model selection analyses for females (F) and males (M)

Model	Sex	Variables included	LogL	K	AICc	ΔAICc	A_weight
1	F	Average number of fledglings	−13.50	2	31.35	0	0.48
2	F	Average number of fledglings Distance to forest	−12.93	3	32.56	1.21	0.26
1	M	Distance to forest Percent unmanaged area	−39.13	3	84.64	0	0.24
2	M	Distance to forest Percent unmanaged area Average number of fledglings	−38.44	4	85.53	0.88	0.16
3	M	Distance to forest Percent unmanaged area Nb. territories <150 m	−38.62	4	85.88	1.24	0.13

Shown are models with ΔAICc <2 to the best model within the set of candidate models examined per sex. All models include an intercept term. Models are ranked according to their Akaike weights (A_weight) calculated over candidate models within each sex. LogL, K, AICc and ΔAICc as in Table 2. $n=38$ dispersal events in females and 67 in males

(Fig. 1). Long-term performance, referring to the site choice hypothesis, was not included in the two best models; accordingly, the relative weight of this variable was low (0.23) and the model-averaged estimate was smaller than its SE (0.159±0.363).

Males Three best models were identified based on ΔAICc values, and all three had relatively low Akaike weights (Table 4). Nevertheless, ΔAICc of the best model to the intercept-only model was 4.84, and the best model was more than 11 times better supported by the data than the intercept-only model (Akaike weight of the latter 0.02). Thus, the best model (as well as the other two models) explained a substantial amount of the variation in dispersal patterns of males.

The variables distance to forest (predation hypothesis) and percent unmanaged area (site choice hypothesis) were included in all three top models and had relative importance values of 0.79 and 0.72, respectively. Male breeding dispersal probability increased with distance of a territory to the forest edge (model-averaged estimate ± SE: 0.010± 0.008) and with the amount of unmanaged area in a territory (1.813±1.631, Fig. 1). The variable average number of fledglings (reproductive performance hypothesis), included in the second-best model, was less important in males than in females (see above) because both relative importance of this variable was low (0.38), and the model-averaged estimate was smaller than the SE (−0.059±0.097). Still, the direction of the effect concurred with the situation in females because breeding dispersal in males appeared to be negatively related to reproductive success (Fig. 1). Finally, only a weak effect on breeding dispersal appeared to stem from the variable nb. territories <150 m (social constraints hypothesis), included only in the third-best model and considering the low relative importance value

of 0.36 and the small model-averaged estimate compared to its SE (0.066±0.115, Fig. 1).

Consequences of breeding dispersal

Females Because average number of fledglings appeared to be the only important variable substantially influencing breeding dispersal probability (see above), we investigated whether females improved reproductive success after, as compared to before, dispersal. The model with average number of fledglings as the dependent variable and type (i.e., before vs after breeding dispersal) as the independent categorical variable was less than half as well supported by the data than the intercept-only model (Table 5). Maximized log-likelihood values of these two models were very similar, and the model-averaged estimate of the variable type was considerably smaller than its SE (−0.035±0.203). Thus, there is little evidence that females improved reproductive success by dispersing between years (Fig. 2a).

Males Here, we focused on between-year changes in the variables distance to forest (predation hypothesis) and percent unmanaged area (site choice hypothesis) because only these variables appeared to be substantially associated to breeding dispersal (see above). The model with distance to forest as the dependent variable and type (i.e., before vs after breeding dispersal) as the independent categorical variable explained variation in the data much better than the intercept-only model, as indicated by a ΔAICc of 9.79 between these models (Table 5). The model-averaged estimate (±SE) of the variable type was −28.854±12.747. Males settled closer to the forest edge after dispersal compared to before dispersal (Fig. 2b). On the other hand, the intercept-only model with percent unmanaged area as

Fig. 1 Factors affecting the probability of breeding dispersal in females (*top two panels*) and in males (*other panels*). Model results of multiple logistic regressions including the variables **a** 'average number of fledglings' and **b** 'distance to forest' in females and **c** 'average number of fledglings', **d** 'distance to forest', **e** 'percent unmanaged area' and **f** 'nb. territories <150 m' in males. *Circles* are predicted values for dispersal probability from the logistic regression models. Number of observations per symbol indicated by circle size with larger circles reflecting higher sample size. *n*=38 dispersal events in females and 67 in males
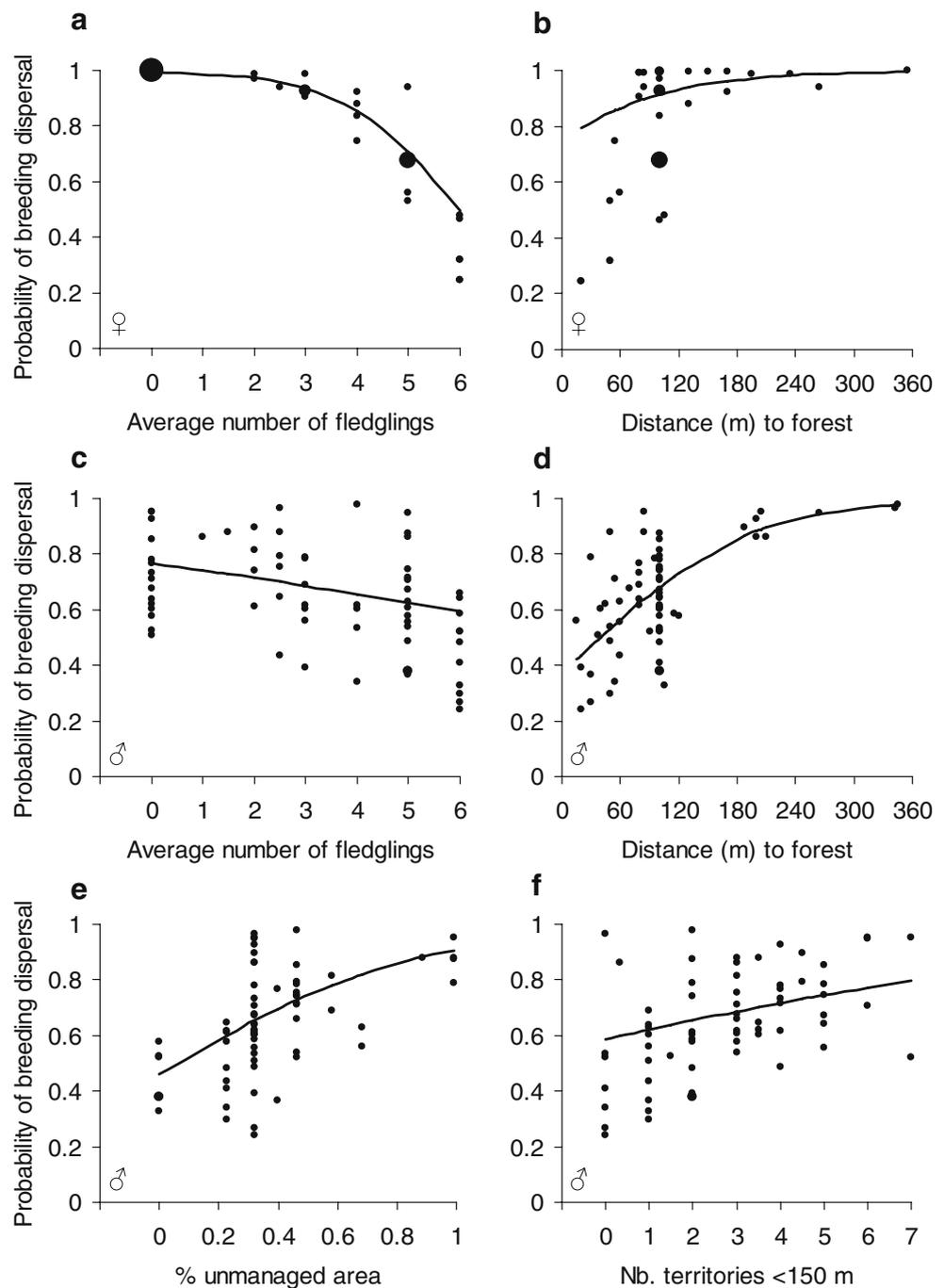
the dependent variable was better supported by the data than the model including the variable type (Table 5). This indicates that percent unmanaged area did not differ in territories before vs after dispersal. (Fig. 2c). Model-averaged estimates of the variable type were smaller than the associated SEs (−0.000±0.002).

To summarize, although breeding dispersal probabilities increased with decreasing reproductive success in females and with distance of a territory to the forest edge as well as with increasing percentage cover of unmanaged area in a territory in males (Table 4), breeding dispersal only resulted in a shift of territory location relative to the forest edge in males, but neither female reproductive success, nor male territory quality (with respect to percent unmanaged area) were improved.

Discussion

Dispersal 'decisions' in animals are generally thought to be affected by multiple factors (Dobson and Jones 1985; Forero et al. 1999; Pasinelli and Walters 2002). In this

Table 5 Model selection in relation to consequences of breeding dispersal

Dependent variable	Sex	Models	LogL	K	AICc	ΔAICc	A_weight
Average number of fledglings	F	Intercept	−133.57	2	271.58	0	0.70
		Type	−133.17	3	273.26	1.68	0.30
Distance to forest	M	Type	−464.81	3	936.23	0	0.99
		Intercept	−470.86	2	946.02	9.79	0.01
Percent unmanaged area	M	Intercept	0.182	2	3.936	0	0.96
		Type	−1.875	3	10.364	6.43	0.04

Examined were models with variables shown to influence breeding dispersal probability as dependent variables (see Table 4). All models include an intercept term. Type is a categorical variable (before vs after dispersal). Models are ranked according to their Akaike weights (A_weight) calculated over the two models per dependent variable and sex class. LogL, K, AICc and ΔAICc as in Table 2. $n=30$ dispersal events in females (F) and 43 in males (M)

study, however, only a few of the examined ecological and social factors appeared to be related to dispersal behavior, the most important one being own reproductive success in females as well as the distance to forest edge (referring to predation risk) and the percentage cover of unmanaged area in a territory (territory quality), respectively, in males. Whether these factors are causally related to breeding dispersal in the shrikes cannot be answered by our correlational study; disentangling the contributions of the factors examined here as well as others not considered, for example phenotypic quality, requires experiments, which however are not easy to conduct in dispersal studies.

Our results indicate that breeding dispersal of female red-backed shrikes was not adaptive, given that reproductive performance after dispersal was not enhanced. We found consequences of breeding dispersal in males because males settled closer to the forest edge after than before dispersal.

Possible causes of breeding dispersal

Reproductive performance

Many studies have found breeding dispersal in birds to be associated with low own reproductive success in the year before dispersal (e.g., Newton and Marquiss 1982; Pärt and Gustafsson 1989; Bensch and Hasselquist 1991; Payne and Payne 1993; Doligez et al. 1999; Forero et al. 1999; Daniels and Walters 2000; Newton 2001; Sedgwick 2004), and this is confirmed by experimental investigations (Bollinger and Gavin 1989; Gowaty and Plissner 1997; Haas 1998; Hoover 2003). In the red-backed shrike, the reproductive performance hypothesis referring to own breeding performance (personal information) was supported in females, as the probability to disperse increased with decreasing number of fledglings. Contrary to the findings of Jakober and Stauber (1989) and Simek (2001), nest success, i.e., whether a nest produced at least one fledgling,
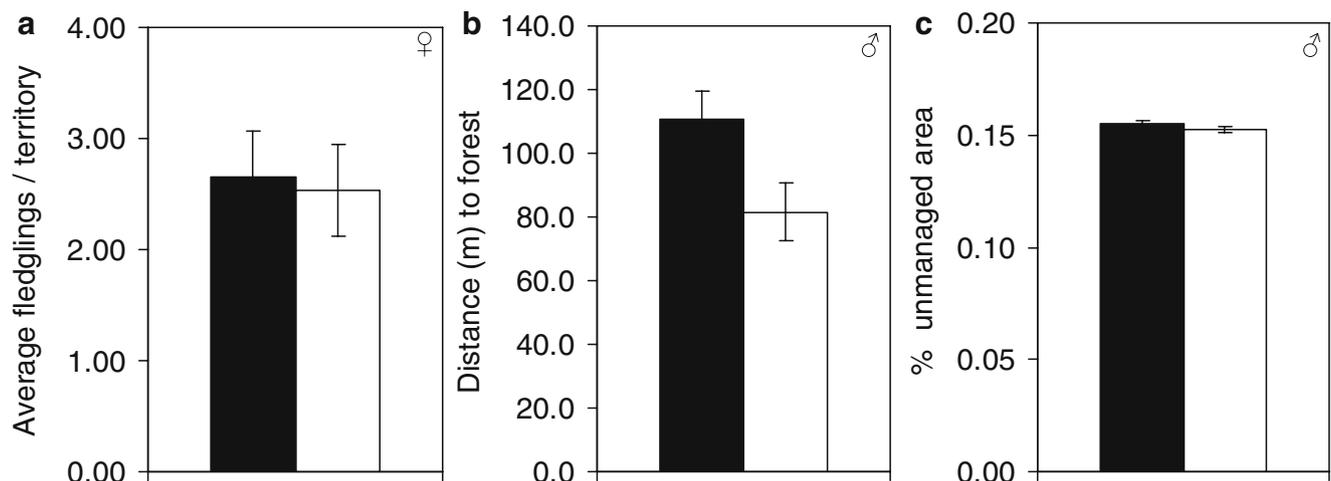
Fig. 2 Consequences of breeding dispersal in red-backed shrikes. Shown are least square means (±SE) from mixed model analyses for **a** average number of fledglings in females, **b** distance to forest and **c** percent unmanaged area in males before dispersal (*filled bars*) and after dispersal (*open bars*). $n=30$ dispersal events in females and 43 in males

alone did not appear to influence the probability of dispersal in this study, which agrees with the results of Roos and Pärt (2004). Clearly, the use of personal information for decision-making is straightforward, because it is readily available and can be considered a direct measure of the expected future payoff of a given territory by incorporating individual experience and any component of habitat quality relating to that territory.

In males, own reproductive performance appeared to be of some importance for dispersal behavior in the single-hypothesis comparison only (Tables 2 and 3), but this importance vanished in the across-hypotheses comparison (Table 4). This suggests that factors other than own reproductive performance are more relevant for breeding dispersal decisions in males, as for example territory quality (see below).

'Public information', i.e., the performance of conspecifics, has been suggested to be a more efficient and reliable way of obtaining information on the quality of habitats and the associated fitness payoffs than personal information (see reviews in Danchin et al. 2001, 2004), but there was no such evidence in our study. One assumption of the public information hypothesis is that the indicators of habitat quality are sufficiently predictable over time (Danchin et al. 2001). One explanation for the lack of importance of public information in our study may thus be that the assumption of temporal predictability or autocorrelation was violated. In fact, reproductive success on individual territories was not correlated between two consecutive years (first-order Durbin Watson statistic dw=1.96, p=0.338, n=207 between-year comparisons of 114 territories, autocorrelation coefficient = 0.021, PROC AUTOREG in SAS 9.1.3). Given the lack of temporal autocorrelation, it may not be surprising that we failed to find support for public information as being important for breeding dispersal decisions, although we acknowledge our study may have been too short to reliably estimate temporal autocorrelation of reproductive success. It is possible that other cues not evaluated here, but suggested conveying public information on habitat quality, such as conspecific density (Stamps 2001; Doligez et al. 2004; Serrano et al. 2004) or feeding rate (Pärt and Doligez 2003), may influence dispersal behavior of the red-backed shrike.

Site choice

Empirical and experimental evidences suggest that individuals switch breeding sites in response to the quality of resources (e.g., nest sites, food, habitat structures) on the territory (Montalvo and Potti 1992; Korpimaki 1993; Gowaty and Plissner 1997; Stanback and Rockwell 2003; Roos and Pärt 2004). In our study, the site choice hypothesis was supported to some extent in males, but not in females, as the probability of males to disperse increased with percentage cover of unmanaged area. Neither of the other variables referring to habitat structure substantially explained variation in breeding dispersal patterns of males or females. Earlier, the percentage cover of unmanaged area had been found to negatively affect recruitment probability in red-backed shrikes (Müller et al. 2005). Our findings and those of Müller et al. (2005) thus suggest that increased amounts of unmanaged area in a territory indicate low territory quality to shrikes.

Territory occupancy (number of years a territory was occupied by a breeding pair) has been found to reliably indicate territory quality in other bird species (Sergio and Newton 2003 and references therein). We did not detect any clear effect of long-term performance (combined effects of territory occupancy and long-term reproductive success) on breeding dispersal behavior of the red-backed shrike because long-term performance appeared to be of some importance in the hypothesis-specific analysis in females, but no longer so in the across-hypothesis comparison.

Social constraints

The social constraints hypothesis hardly received support in this study. The probability of dispersal of males, but not of females, was positively associated with the density of conspecifics in the hypothesis-specific analysis, but this effect did not persist when simultaneously considering other possible causes of breeding dispersal in the across-hypothesis analysis. Other factors potentially related to the social constraints hypothesis, such as individual quality and age, were not assessed. The importance of individual quality (other than age) for breeding dispersal has generally received little attention, whereas age-related effects on breeding dispersal were found in some studies (Pärt and Gustafsson 1989; Payne and Payne 1993; Daniels and Walters 2000; Newton 2001; Blakesley et al. 2006), but not in others (Forero et al. 1999; Serrano et al. 2001; Hoover 2003; Sedgwick 2004).

Predation risk

Nest predation is a major cause of reproductive failure in birds (e.g., Martin 1995), and observational and experimental studies have found nest losses due to predators to result in increased breeding dispersal rates (Forero et al. 1999; Hakkarainen et al. 2001; also see Hoover 2003). Roos and Pärt (2004) recently suggested predation risk to influence habitat selection in the red-backed shrike because changes in the spatial distribution of magpie and hooded crow *Corvus corone cornix* nests affected the spatial patterns and dynamics of territory occupancy in their red-backed shrike population.

In our study site, we found support for the predation risk hypothesis in relation to breeding dispersal probability, although in ways other than expected. In both sexes, probability of dispersal increased with distance, and not as predicted with proximity, of a territory to the nearest forest edge. Currently, we do not have an explanation for this pattern, although it is possible that forest edges may be attractive as foraging sites. On the other hand, territories located farther from the forest edge were not substantially different than those located closer in any of the variables measured (own unpublished data), and distance to forest had not had any influence on reproduction or local recruitment in an earlier study (Müller et al. 2005). Alternatively, the dispersal patterns observed may reflect that individuals are not free in the choice of their future territory.

It is possible that our measures did not sufficiently capture predation risk. Yet, Roos and Pärt (2004) demonstrated associations between almost the same variables as used here and patterns of nest losses in red-backed shrikes. On the other hand, predation pressure may have been so high throughout our study site (see Introduction), the latter being small relative to that of Roos and Pärt (2004) that our measures perhaps underestimated actual predation risk. In our study population, nest concealment is a central factor for nest success and the number of fledglings produced per nest (Müller et al. 2005), which underlines the pressure exerted by predators at least on nest site selection of red-backed shrikes here as well.

Consequences of breeding dispersal

While many studies have focused on the potential causes of breeding dispersal and philopatry, examinations of the fitness consequences of breeding dispersal decisions are far less numerous and have shown ambiguous results (see Introduction). Our study reflects this ambiguity in terms of benefits of breeding dispersal. On the one hand, females did not produce more fledglings after, compared to before, dispersal, although the annual average fledgling production was the most important factor influencing female breeding dispersal. On the other hand, only one of the two variables most strongly associated with male breeding dispersal changed substantially after compared to before dispersal: males settled on territories closer to the forest edge than the ones held in the previous year. Although this change is in accordance with the results of the analysis concerning potential causes of breeding dispersal, it is opposite to what we had expected in the first place. The benefits male red-backed shrikes might gain by settling closer to the forest edge are not known.

One reason for the lack of fitness benefits in females may be that the study area offered high quality habitat overall (in terms of habitat structure and composition, see above). Under less optimal conditions, i.e., if variation in habitat quality among territories is higher than in our study site, breeding dispersal may well be adaptive.

Alternatively, red-backed shrikes may have been unable to reliably estimate the quality of a territory in our study site upon arrival on the breeding grounds, as it has been suggested by Bollmann et al. (1997) for water pipits (Anthus spinoletta), which were unable to predict nest predation, the major factor influencing reproductive success. Likewise, nest predation plays a key role for reproductive performance of the red-backed shrike (Müller et al. 2005), and it may thus be that, if these birds are also unable to correctly assess predation risk when they settle after migration (but see Roos and Pärt 2004), territory 'choice' may be largely random with respect to future nest predation. In addition, the territory 'choice' may depend on factors other than reducing nest predation risk, as for example the 'choices' made by other individuals.

Red-backed shrikes may be under severe time constraints, when searching for a new territory. After returning to the breeding grounds, males occupy territories within a few days (unpublished data). Individuals searching too long for another territory may risk losing an already inspected territory of possibly acceptable quality to other males. In addition, reproductive success declines seasonally (Müller et al. 2005), implying that males should settle and attract a female as early as possible to avoid delays in clutch initiation. An early onset of breeding also permits a replacement clutch, given that the breeding period in our subalpine study site only lasts fewer than 9 weeks.

Because breeding dispersal can be costly (Daniels and Walters 2000; Yoder et al. 2004), individuals are expected to benefit from dispersal. Costs of breeding dispersal are generally thought to include, for example, increased energy expenditure or likelihood of predation compared to philopatry. However, both factors may be considered negligible for a long-distance migrant such as the red-backed shrike because both philopatric and dispersing individuals migrate. Other costs of breeding dispersal, such as those of moving through and inhabiting unfamiliar space (Yoder et al. 2004), may be more relevant, but given the high rates of breeding dispersal as opposed to philopatry observed in the red-backed shrike, such costs may be of only modest importance. Thus, breeding dispersal in the red-backed shrike may be relatively cheap, which may explain its prevalence in this study.

Conclusions

Own reproductive success appears to be used by female red-backed shrikes as a cue to determine whether to return to the same territory or to disperse to another one the

following breeding season. At the same time, temporal autocorrelation in terms of breeding success was low in our study, indicating low predictability of breeding success over time. These findings are counterintuitive and are also in contrast to the modeling results of Switzer (1993), who suggested that individuals living in unpredictable habitats should not base their settlement decisions on previous reproductive outcome. On the other hand, temporal variability in the environment has been suggested to select for dispersal (Johnson and Gaines 1990; Travis and Dytham 1999). The high dispersal rates observed in both sexes of the red-backed shrike and the low temporal autocorrelation in terms of breeding success are in accordance with this suggestion. Our study might thus be an example for how temporal variability in the environment affects dispersal behavior.

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