

Sex-biased survival and breeding dispersal probability in a patchy population of the Rock Sparrow *Petronia petronia*

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Demographic parameters of the polygynous Rock Sparrow *Petronia petronia* were investigated in a small patchy population in the Italian Alps. The population included two distinct breeding patches that differed in altitude and breeding success. Survival parameters were estimated by capture–recapture analysis of 170 individually marked animals. At the whole population level (Cormack–Jolly Seber model), no sex difference in local survival probability was detected. We then used a multisite capture–recapture approach (Arnason–Schwarz model) to investigate patch-specific survival probability and between-patch dispersal rate conditional on survival. Female local survival in the higher-altitude patch (mean \pm se: 0.54 ± 0.04) was significantly greater than in the other patch (0.37 ± 0.04), probably because permanent emigration from the study area was greater. In the higher-altitude patch, breeding dispersal was constrained by the altitude limit and breeding movements were directed toward the patch at lower altitude. The probability of changing patch in the next breeding season was significantly higher for females (range 0.16–0.21) than for males (0.01–0.03). Breeding success varied between years and patches, being lower in the patch where frequency of polygamy and female local mortality were higher.

Dispersal probability is increasingly being taken into account in theoretical and empirical studies (Watkinson & Sutherland 1995, Pulliam 1996, Smith *et al.* 1996, Amarasekare 1998, Hanski 1998). This is not only because of its effects on the genetic structure of populations, but also because of its influence on population dynamics (Matthysen *et al.* 1995, Doebeli & Ruxton 1997, Bohonak 1999, Dieckmann *et al.* 1999, Lande *et al.* 1999, Paradis *et al.* 1999). The pattern of sex-biased breeding dispersal is thought to have evolved in response to sex-specific benefits in site fidelity (Greenwood 1980, Greenwood & Harvey 1982, Switzer 1993). According to Greenwood's 'resource-defence' hypothesis (Greenwood 1980), site fidelity should benefit the sex for which competition for resources is higher, because familiarity with habitat (Harvey *et al.*

1984, Jackson 1994) or neighbours (Lambrechts & Dhondt 1995) might give advantages in competition (Greenwood & Harvey 1982). Consequently, for bird species in which males compete for high-quality territories, females are less faithful to breeding sites (Greenwood 1980). However, Clarke *et al.* (1997) have recently reviewed several exceptions to Greenwood's hypothesis and concluded that great variation in sex-biased breeding dispersal exists within populations as well as among species. This interrelation between species' life-history traits (Bensch & Hasselquist 1991, Paradis *et al.* 1998), individual strategies (Harvey *et al.* 1984, Pärt & Gustafsson 1989) and habitat quality may complicate interpretations of observed patterns of breeding dispersal (Clarke *et al.* 1997). In addition, any attempt to investigate sex differences in breeding dispersal (distance moved from previous site or probability of leaving the previous site), must take into account sex-related recapture and survival probability that could otherwise lead to seriously biased results (Koenig *et al.* 1996, Boulinier *et al.* 1997).

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The Rock Sparrow *Petronia petronia* is a small passerine that shows very little sexual dimorphism. Individuals present two morphological characteristics, which distinguish them from other similar passerine species: a pale yellow badge under the throat and white spots on tail feather tips (Cramp & Perrins 1994). It breeds in cavities from North Africa to Manchuria, in open and sunny areas (Lebreton 1975, Hagemeyer & Blair 1997). In Europe its distribution is confined mainly to the Mediterranean area: Spain, southern France, southern Italy and Greece. In these areas, it is usually found breeding at low density in small groups near human settlements (Muntaner *et al.* 1983, Cramp & Perrins 1994, Hagemeyer & Blair 1997). The result is a naturally patchy structure of small populations (Debru 1958).

Probably as a consequence of this scattered distribution and of the nesting habit, very little is known about the general ecology of the species. The few available data refer mainly to breeding biology (Debru 1961, Muntaner *et al.* 1983, Ivanitzkii 1986), but an important role in population maintenance in this species is probably also played by movements of individuals, the extent and pattern of which are still unknown. Recent models for the analysis of capture–recapture or capture–resighting data collected on more than one site (Arnason 1973, Brownie *et al.* 1993, Schwarz *et al.* 1993) simultaneously estimate site-specific survival and between-site movement probability.

The aim of this study was to estimate adult local survival and sex-specific breeding dispersal probability in two neighbouring breeding patches (or sites) using data collected in the course of a long-term study on the ecology and breeding biology of an alpine population (Mingozzi *et al.* 1994). Because breeding success is a proximate factor that might influence breeding dispersion probability, we first estimated the breeding parameters for both patches (average clutch size, laying date and breeding success). We then used a single-site capture–recapture model (Cormack 1964, Jolly 1965, Seber 1965) to test whether sexes differ in mortality probability at the whole population level. We subsequently investigated within-patch processes using recent multisite capture–recapture models (Arnason 1973, Brownie *et al.* 1993, Schwarz *et al.* 1993) to estimate the sex-specific probability of between-patches breeding dispersal, conditional on survival and whether these movements were influenced by breeding patch reproductive output.

MATERIALS AND METHODS

Study area

The study population is at the northern limits of the Rock Sparrow's alpine range in the Italian Cottian Alps (6°53'E; 44°57'N, Fig. 1). Considering the western alpine range of the species, the population studied seems to be an extension of the larger population breeding on the French side of the Alps (Mingozzi *et al.* 1994). The exact degree of isolation of the population is unknown, although birds marked in Italy have occasionally been observed wintering in France, and unmarked breeding birds were regularly recorded in the study population. Despite its marginal conditions, this evidence suggests that the population is not closed (more details can be found in Mingozzi *et al.* 1997). Birds bred in nestboxes specially designed for Rock Sparrows, and since 1989 adults and fledglings have been individually marked with standard metal and colour ring combinations (Mingozzi *et al.* 1994). The data for this study come from nestboxes set up in two small villages (Fig. 1), San Sicario (1570 m) and Champlas Janvier (1780 m), hereafter called patch SS and patch CJ, respectively. The two patches are separated by 210 m of altitude and 3.1 km of distance, with patch CJ at higher altitude and more marginal in respect to the local distribution of Rock Sparrows (Fig. 1). A total of 270 encounters collected from 1990 to 1998 on 170 sexed breeding birds were examined, 54% (147) at patch SS. Breeding birds were sexed by a cross validation of measurements (e.g. wing-length) and behavioural observations (e.g. courtship). (Recent results on sex determination by genetic methods are consistent with field determination of sex in breeding birds.)

BREEDING PARAMETERS

We compared means of laying date (days from 1 January), clutch size and breeding success among years and patch using generalized linear models (Crawley 1993) in the program SAS (SAS Institute Inc., procedure GENMOD). Breeding success was calculated as the proportion of chicks fledging per egg laid using nests in which at least one egg was laid. Breeding attempts (i.e. pairs which built a nest but did not lay any eggs) were excluded. Poisson and binomial error structures were used in the analyses of counts and proportions, respectively. Model selection procedure followed the parsimony principle

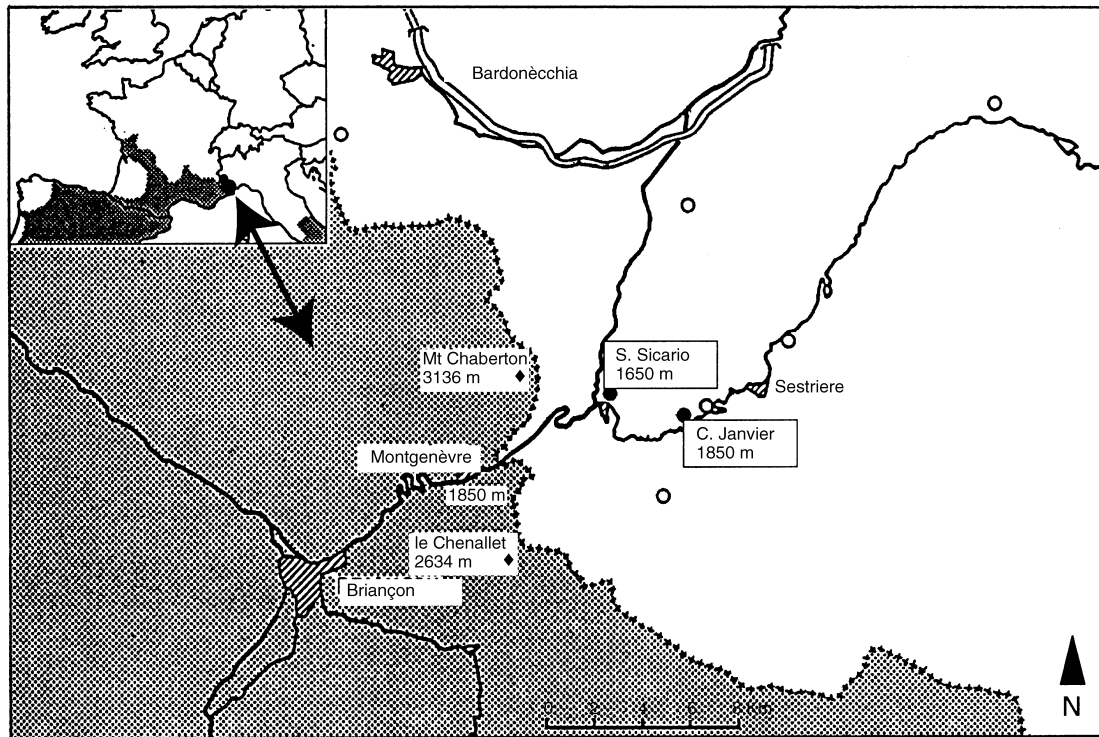


Figure 1. Location of the study area. The breeding distribution of the Rock Sparrow *Petronia petronia* in west-southern Europe is shown in grey in the smaller square (redrawn from Hagemeyer & Blair 1997). In the larger square, the grey area indicates the French side of the Alps where Rock Sparrows have not been counted (though known to be present). On the Italian side, most of the sites (or patches) occupied in 1989 were abandoned (empty dots), and the two studied patches (black dots) are the only known breeding populations left in the Cozie Alps (T. Mingozi in prep.).

using a modified Akaike's Information Criterion (AIC or QAIC when a scale parameter is needed to correct for over-dispersion; Akaike 1973, Burnham & Anderson 1998). The significance of each factor was tested using an approximate *F*-test to account for over-dispersion (significance level $\alpha = 0.05$). Although the Rock Sparrow is considered to be a polygynous species (Cramp & Perrins 1994) the mating system in our population has been shown to include sequential polyandry (Pilastro *et al.* 2001). In estimating patch-specific breeding parameters, we considered all breeding systems together and the proportion of polygamous males was considered to be a patch-specific characteristic. A two-tailed Fisher exact test (Zar 1984, p. 393) was used to test whether the two patches differed in the frequency of polygynous males.

SURVIVAL AND BREEDING DISPERSAL ESTIMATIONS

An insight into population dynamics can be obtained by the estimation of survival and breeding dispersal

probability using appropriate statistical methods for the analysis of capture–recapture data. These methods are necessary to take into account a resighting or recapture probability different from 1.00 (e.g. a marked individual known to be present in the population might not be captured or resighted on a particular occasion). Survival and breeding dispersal probability for adult birds were estimated using maximum likelihood from capture histories (Lebreton *et al.* 1992) of birds marked and resighted from 1990 to 1998. Analyses were made using the program MARK1.9 (White & Burnham 1999). To estimate survival of marked birds at the population level, we built a first data set by pooling all encounters made on any of the two breeding patches (SS and CJ) as if they had come from a single site. A preliminary analysis of this data set was done using the program RELEASE (Burnham *et al.* 1987) to test for the general assumptions of capture–recapture models by a goodness of fit test (Test2 and Test3 in Burnham *et al.* 1987). As for the analysis of breeding parameters, the model selection procedure followed the AIC. In addition to the use of the AIC value, the

level of significance of specific effects was investigated using a log-likelihood ratio test (LRT) between nested models. Spatial heterogeneity of survival and recapture rates and the estimation of between-patch dispersal rate were investigated by a second analysis in which encounters were coded (stratified) in relation to patch. Parameters were modelled using multisite models for stratified data, a multiple strata extension of the classical Cormack–Jolly Seber model (Arnason 1973, Hestbeck *et al.* 1991, Brownie *et al.* 1993, Schwarz *et al.* 1993). To reduce the number of parameters in the model, we first modelled sex and patch effects on recapture and survival probabilities (Lebreton *et al.* 1992, Pradel *et al.* 1990, Lindberg *et al.* 1998). To account for the model selection uncertainty, we estimate model parameters by the model averaging procedure, which considers the relative importance of each fitted model (Burnham & Anderson 1998). (Note that the lack of specific goodness of fit tests in multisite models made it impossible to detect problems caused by an over-dispersion of the data; Wintrebert 1998.) Differences between specific estimates can then be done by a Z statistic (Zar 1984, p. 86) with variance and covariance matrix for model averaging estimates.

RESULTS

Patch-specific breeding parameters

The number of breeding birds increased slightly over the study period (Fig. 2). Breeding parameters were investigated using 80 nests in SS and 66 in CJ for which laying date, number of eggs and breeding success were known. The proportion of second clutches (0.16) and clutches after failure (0.10) did not differ between patches ($\chi^2_1 = 1.292$, $P = 0.256$ and $\chi^2_1 = 0.063$, $P = 0.802$, for second and second after failure clutches, respectively), and thus for subsequent analyses all clutches have been pooled. In both mean laying date and clutch size analyses, the interaction between year and patch was not significant ($F_{7,130} = 1.29$, $P = 0.258$, and $F_{7,128} = 1.15$, $P = 0.334$, respectively). On average, laying took place around 25 June, generally 5 days earlier in SS ($F_{1,135} = 3.77$, $P = 0.054$), but did not show a marked variation over years ($F_{1,135} = 1.23$, $P = 0.288$). In contrast, the clutch size was changed over the study period ($F_{1,137} = 2.70$, $P = 0.012$) being lowest in 1993 and highest in 1991 (5.1 and 6.3 eggs, respectively). The mean clutch size was similar in both patches ($F_{1,137} = 1.22$, $P = 0.271$).

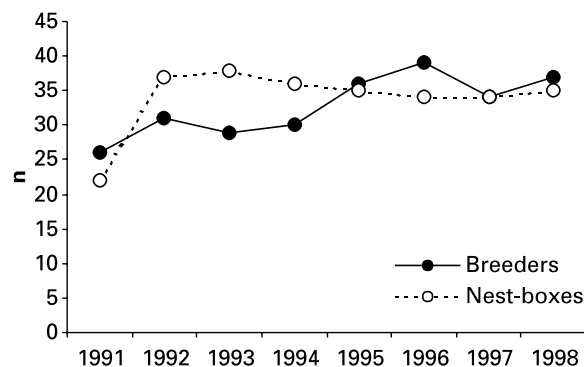


Figure 2. Number of breeding birds in relation to year and nest-box availability. Birds whose nest was not found are excluded, whereas unmarked birds known to have bred in nest-boxes are included.

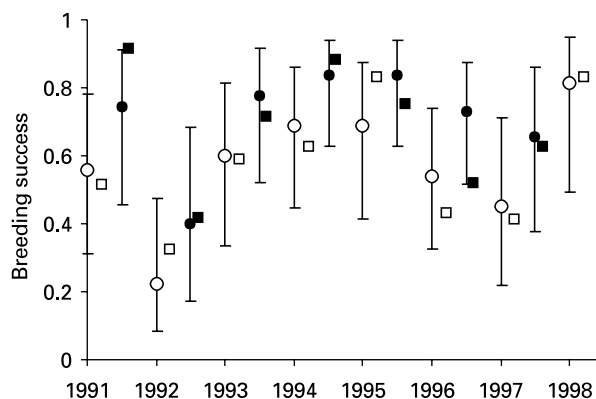


Figure 3. Breeding success and 95% confidence interval according to the logit linear model assuming additive effect of year and patch (no interaction effect). Filled dots = patch CJ. Empty dots = patch SS. The corresponding squares are the bare proportions obtained from the general model including the interaction term (filled squares = CJ; empty squares = SS).

For breeding success, there was no evidence of an interaction between patch and year ($F_{7,130} = 4.92$, $P = 0.669$). Both year and patch effects significantly influenced breeding success ($F_{7,130} = 18.57$, $P = 0.010$, and $F_{1,130} = 3.90$, $P = 0.04$, respectively). Breeding success was higher in patch CJ (Fig. 3). These results did not change even when first clutches were considered exclusively (data not shown). The mean breeding success was 0.54 (0.45–0.63) in patch SS and 0.70 (0.60–0.79) in patch CJ (values estimated from the model without the year effect, $F_{1,144} = 5.74$, $P = 0.018$). The frequency of polygyny was higher in patch SS (37% compared with 14% in site CJ), although the difference was not significant (Fisher exact test: $P = 0.07$).

Table 1. Single-site analysis results (pooled data). Eliminating non-significant effects from the general year-dependent model, ϕ_t, ρ_t . Model notation: s = sex effect, t = year effect, . = no effect, ϕ = survival rate; P = recapture probability.

Model	Np	Deviance	AICc	AICc-weight	LRT
ϕ_t, ρ_t	15	98.93	425.45	0.000	
$\phi., \rho_t$	9	105.44	416.31	0.005	
ϕ_t, P	9	102.48	413.55	0.023	
$\phi., \rho_s$	3	112.05	410.24	0.107	
ϕ_s, ρ_s	4	108.16	408.42	0.266	$P = 0.128$ (ϕ_s, ρ_s v $\phi., P$)
$\phi., P$	2	112.27	408.41	0.268	$P = 0.639$ ($\phi., \rho_s$ v $\phi., P$)
ϕ_s, P	3	109.79	407.98	0.332	$P = 0.115$ (ϕ_s, P v $\phi., P$)

Table 2. Estimates of survival and recapture probabilities at the population level (obtained by model averaging of the last four models in Table 1). 95% confidence limits are given in parentheses. P = significance level of the difference between the estimates (two-tailed Z-test).

	Males	Females	P
ϕ	0.54 (0.44–0.63)	0.47 (0.37–0.56)	0.37
P	0.76 (0.59–0.88)	0.72 (0.59–0.81)	0.68

POPULATION LEVEL: SINGLE-SITE ANALYSIS

We analysed 170 recapture histories from 92 females and 72 males marked and resighted from 1990 to 1998.

The data fitted the general assumptions of the Cormack–Jolly Seber model (GOF = 9.219, $df = 18$, $P = 0.954$). There was no evidence for annual variation in either recapture or survival probabilities (model $\phi.P$ with constant probabilities had a lower AIC value than any of the time-varying models; Table 1). Survival and recapture probability estimates from model $\phi.P$ were 0.51 (0.43–0.59) and 0.73 (0.67–0.79), respectively. In this parsimonious context, we tested for a sex effect on survival and recapture probability. The model $\phi_s P$ had a lower AIC value than $\phi.P$, suggesting that females had a lower, but not significant ($Z = 0.904$, $P = 0.37$), apparent survival (Tables 1 and 2).

PATCHY LEVEL: MULTISITE ANALYSES

This second analysis considered the patch in which birds were resighted. We focused on patch- and sex-specific estimates of survival, recapture and dispersal probability, ignoring year effects because they were negligible in the single-site analysis (Table 1) and because the high number of parameters would have

led to over-fitted models (Burnham & Anderson 1998). We found no evidence for sex and patch effects on recapture probability (unduly high AIC for models 3, 9 and 10 in Table 3). No sex effect on survival probability was apparent in patch CJ, but it was retained for SS (model 12 in Table 3), where males survived better than females ($\chi_1^2 = 10.6$, $P = 0.001$). Further testing for differences among the four sex-by-patch categories singled out females on patch SS as having the lowest annual survival probability (model 13 in Table 3); this was confirmed by the model averaging method (Table 4). Female survival probability differed significantly between patches ($Z = 2.35$, $P = 0.02$), unlike that for males ($Z = 0.28$, $P = 0.78$). Recapture and survival estimates for males, whether from single- or multisite models, were similar (Tables 2–5). However, the analysis at the patch level showed that the slight difference between male and female survival found at the whole population level (pooling data from the two patches) was mainly due to a difference in SS (Table 5). Breeding dispersal probability was not found to vary between patches ($\chi_2^2 = 2.653$, $P = 0.265$), but to vary between sexes ($\chi_1^2 = 10.6$, $P = 0.001$). Females were almost 10 times more likely to disperse (average dispersal probability 0.19) than males (0.02). A summary of patch-specific results is shown in Table 5.

DISCUSSION

Breeding output

When considering the few data available in the literature on Rock Sparrow breeding ecology (Debru 1958, 1961, Muntaner *et al.* 1983, Cramp & Perrins 1994), the most striking difference from our results is the frequency of second clutches. Most studies have documented two broods (Debru 1958, Cramp & Perrins 1994), whilst in our population the

Table 3. Multisite analysis. Eliminating non-significant effect from the general model $S_{s+l} P_{s+l} \psi_{s+l}$, which includes effects of patch (l) and sex (s), on survival (S), recapture (P) and emigration probabilities (ψ). See text for more details. Model notation: l = patch (SS = S. Sicario, CJ = C. Janvier), s = sex (f, females; m, males), . = no effect.

	Model	np	Deviance	AICc	AICc-weight
1	$S_{(SS)} S_{(CJ)}, P., \psi_{s+l}$	8	456.96	472.96	0.004
2	$S_{fSS} S_{mSS=CJ}, P., \psi$	4	464.87	472.87	0.005
3	$S_{s+l}, P_{s+l}, \psi_{s+l}$	12	448.45	472.45	0.006
4	$S_{fSS} S_{mSS=CJ}, P., \psi_l$	5	462.35	472.35	0.007
5	$S_l, P., \psi_{s+l}$	7	457.19	471.19	0.012
6	S_{s+l}, P_s, ψ_{s+l}	10	450.18	470.18	0.015
7	$S_l, P., \psi_s$	5	459.71	469.71	0.027
8	$S_s, P., \psi_{s+l}$	7	454.88	468.88	0.034
9	S_{s+l}, P_l, ψ_{s+l}	10	448.56	468.56	0.037
10	$S_{s+l}, P., \psi_{s+l}$	9	450.19	468.19	0.045
11	$S., P., \psi_s$	4	459.83	467.83	0.073
12	$S_{(SS)} S_{(CJ)}, P., \psi_{s+l}$	8	450.5	466.50	0.114
13	$S_{fSS} S_{mSS=CJ}, P., \psi_{s+l}$	7	451.57	465.57	0.193
14	$S_{fSS} S_{mSS=CJ}, P., \psi_s$	5	454.22	464.23	0.427

Table 4. Estimates of survival (S), recapture (P) and emigration probability (ψ) according to the sex and the patch. Estimates are obtained by model averaging of models in Table 3. Standard errors are in parentheses.

Patch	Survival (S)		Recapture probability (P)		Dispersal probability (ψ)	
	Males	Females	Males	Females	Males	Females
SS	0.56 (0.04)	0.39 (0.05)	0.73 (0.05)	0.74 (0.05)	0.01 (0.01)	0.16 (0.06)
CJ	0.54 (0.04)	0.54 (0.04)	0.74 (0.05)	0.73 (0.05)	0.03 (0.02)	0.21 (0.06)

Table 5. Ecological and demographic characteristics of patches. *P* = significant level of the patch effect (see text for details of the tests used).

	San Sicario	<i>n</i>	Champlat Janvier	<i>n</i>	<i>P</i>
Altitude	1570 m		1780 m		
Distance from the nearest population	6.8 km		9.5 km		
Proportion of second clutches	0.13	10	0.20	13	0.26
Proportion of clutches after failure	0.11	9	0.09	6	0.80
Clutch size	5.76 (5.55–6.03)	80	5.49 (5.20–5.79)	66	0.27
Laying date	22 June	79	27 June	65	0.05
Breeding success	0.54 (0.45–0.63)	80	0.70 (0.60–0.79)	66	0.02
Proportion of polygynous males	0.37	67	0.14	57	0.07
Female survival	0.39 (0.29–0.49)	54	0.54 (0.46–0.62)	38	0.02
Male survival	0.56 (0.49–0.63)	37	0.54 (0.46–0.62)	41	0.77
Female breeding dispersal	0.16 (0.04–0.27)	54	0.21 (0.09–0.33)	38	0.64
Male breeding dispersal	0.01 (0.00–0.03)	37	0.03 (0.00–0.07)	41	0.55

frequency of second clutches was low (varying from 0.13 to 0.20 in patches SS and CJ, respectively). This difference is probably due to the shorter alpine breeding season. Note that information on breeding biology in Glutz von Blotzheim and Bauer (1997) and Hagemeijer and Blair (1997) is derived from the same population that we studied.

Despite the fact that food availability (i.e. Orthoptera species) during the breeding season is similar (G.

Venuto pers. comm.), we found that the average breeding success differed significantly between the two patches (0.54 and 0.70 in SS and CJ, respectively). This might reflect the proportion of polygamous males in the population, which was higher in SS. In nests from a polygamous system, the average number of fledglings is lower than in ‘monogamous’ nests (see Davies 1991, 1992). Because we considered all breeding systems together, a difference in the

frequency of polygamy between patches could cause a difference in the average breeding output, but sample size was too small to test this hypothesis controlling for year and site effects. A second possible explanation is that breeding success at the lower patch is affected by human disturbance. Rock Sparrow nests are located near houses, which are mainly holiday homes inhabited when birds are rearing young. Village SS is larger and consequently has a greater human presence during summer. However, we did not quantify human presence specifically, and are unable to test this hypothesis (also see below for more discussion on patch-specific quality).

Sex-specific breeding dispersal probability

It has been suggested that sex-biased breeding dispersal evolved in relation to selective forces promoting a sex-biased site-fidelity (Greenwood 1980, Arcese 1989). According to this hypothesis, male Rock Sparrows should benefit from being site faithful because habitat familiarity may give advantages in competition (Greenwood & Harvey 1982). However, in the polygynous Great Reed Warbler *Acrocephalus arundinaceus*, Bensch and Hasselquist (1991) found that males were more prone than females to leave a breeding site. They suggested that, in a variable environment, the polygynous mating system allows males to overcome the fitness cost of dispersal by a greater benefit if they succeed in occupying a territory. Polygamy may thus contribute to relaxation of the selective pressures acting on male site fidelity, especially when territories are highly heterogeneous in quality. Although the Rock Sparrow is considered to be a polygynous species (Cramp & Perrins 1994, but see also Pilastro *et al.* 2000), we found that between-patch breeding dispersal of Rock Sparrows, conditional on survival, was strongly female-biased. This suggests that for male Rock Sparrows, the benefits of polygyny do not overcome the cost of changing a territory. Similarly, Pärt and Gustafsson (1989) found that the mating system did not influence the breeding dispersal of male Collared flycatchers *Ficedula albicollis*.

Within-patch processes

Recent work on metapopulations of birds demonstrated the importance of a multisite approach to the simultaneous study of survival and movement parameters in the different patches of the population

(Hestbeck *et al.* 1991, Spindel *et al.* 1995, Lindberg *et al.* 1998). In our case, the multisite analysis clearly improved information derived from a larger-scale approach by showing an influence of the breeding patch on local survival of females. Those breeding at lower altitude (patch SS) have a higher apparent mortality. The power of the tests between models in the multisite analysis must be low because of the small sample size. Despite this, the difference between local survival of females was large enough to be detected. This difference may be caused by a patch-specific mortality (e.g. difference in habitat quality or predator abundance) or by a site-dependent permanent emigration from the study area. Neither multisite nor single-site capture–recapture models can distinguish between these two effects. At present we have no evidence for a difference in patch quality. Clutch size, which might reflect female condition at laying, did not differ between patches. Thus, habitat quality should impair female survival in SS only through chick-rearing costs (see for example Monaghan *et al.* 1998). Because individuals are expected to invest energy in relation to environment quality or the amount of energy available (e.g. individual quality, Stearns 1992) such a trade-off is not expected without clutch size manipulation (Monaghan *et al.* 1998).

It seems more likely that the apparent lower survival of females in patch SS is due to sex-biased permanent dispersal. Because breeding success was low at patch SS, this would agree with the general finding that breeding dispersal probability is influenced by previous breeding experience (Harvey *et al.* 1984, Pärt & Gustafsson 1989, Montalvo & Potti 1992, Payne & Payne 1993, Jackson 1994, Paton & Edwards 1996, Clark *et al.* 1997, Flynn *et al.* 1999). Pilastro *et al.* (2000) showed that female Rock Sparrow breeding strategy depended on the number of available mates. Similarly, male mating strategy might be influenced by the number of females (Ivanitzkii 1986), suggesting that it is the pattern of sex-specific dispersal that influences the mating system (Davies 1991) rather than the opposite (Greenwood 1980, Bensch & Hasselquist 1991). In this scenario, ecological factors that constrain dispersal, such as the altitude or the patch isolation, might result in a change in the frequency of polygyny and have an indirect influence on population dynamics.

Despite an asymmetric demography, and in contrast to other studies on subdivided populations of passerines (Smith *et al.* 1996, Seather *et al.* 1999), breeding success fluctuated synchronously in both patches. This suggests that some factors capable of

influencing breeding output are acting at a regional scale rather than at a patch level. Synchronous changes in breeding success between patches may increase population extinction probability (Hanski 1998), especially in a short-lived species where demography is more sensitive to a change in breeding output than in adult survival (Lebreton & Clobert 1991). Future studies on juvenile survival, patch-specific recruitment probability and patch quality (e.g. interspecific competition) will help to investigate population viability. A critical point for further discussion of the influence of these characteristics on population dynamics will be to compare our results with those from populations in a more 'typical' area of the species' distribution. Unfortunately, at present, such studies are lacking.

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