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Patchy population structure in a short-distance migrant: evidence from genetic and demographic data

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Abstract

Species often occur in subdivided populations as a consequence of spatial heterogeneity of the habitat. To describe the spatial organization of subpopulations, existing theory proposes three main population models, which predict different levels of connectivity among and extinction risks of subpopulations: patchy population, metapopulation and isolated populations. However, spatially discrete subpopulations are commonly considered to be organized as metapopulations, although explicit tests of metapopulation assumptions are rare. Here, we test predictions of the three models on the basis of demographic and genetic data, a combined approach so far surprisingly little used in mobile organisms. From 2002-2005, we studied nine subpopulations of the wetland-restricted reed bunting (*Emberiza schoeniclus*) in the southeastern part of the Canton Zurich (Switzerland), from where local declines of the species have been reported. Here, wetlands are as small as 2.7 ha and separated through intensively used agricultural landscapes. Demographic data referred to dispersal of colour-banded individuals among subpopulations, immigration rates and extinction-/recolonization dynamics. Genetic data were based on the distribution of genetic variability and gene flow among subpopulations derived from the analysis of nine microsatellite loci. Both demographic and genetic data revealed that the patchy population model best described the spatial organization of reed bunting subpopulations. High levels of dispersal among subpopulations, high immigration into the patchy population, and genetic admixture suggested little risk of extinction of both subpopulations and the entire patchy population. This study exemplifies that spatially discrete subpopulations may be organized in ways other than a metapopulation, which has implications for the conservation of subpopulations and species.

Introduction

Species often occur in subdivided local populations as a consequence of spatial heterogeneity of the habitat. Heterogeneity of the habitat may have two reasons (Fischer & Lindenmayer 2007). First, the habitat has a naturally fragmented distribution or second, formerly continuous habitats have been destroyed and subdivided into fragments due to anthropogenic landscape modifications. Because the ongoing destruction and fragmentation of habitats due to human land use generally reduces the size and the connectivity of the remaining local populations, species having evolved both in continuous habitats and in naturally fragmented habitats may be affected (Frankham *et al.* 2002). However, the consequences of continued habitat loss and fragmentation for species occurring in naturally fragmented habitats are little studied.

Small local population size and restricted gene flow lead to genetic differentiation between populations. Population subdivision intensifies the effects of genetic stochasticity in local populations leading to loss of genetic variation through random genetic drift (Frankham *et al.* 2002) and loss of fitness due to inbreeding (Frankham 1995; Keller *et al.* 2002). Loss of genetic variation and fitness are predicted to enhance the risk of local extinction, especially in populations that have recently declined in size. Theoretical studies have shown that viability of populations critically depends on the connectivity among local populations (Gilpin & Hanski 1991; Harrison 1991).

To describe the spatial organization of subpopulations, three main population models can be identified. These models of spatial population structure represent steps of a continuum, here presented in the order of decreasing connectivity: (1) patchy population, (2) metapopulation and (3) isolated populations. Other forms of spatial organizations of subpopulations (mainland-island, source-sink) were not considered because these forms are

very similar to each other and to the patchy population or metapopulation scenario. For example, source-sink systems may occur in either metapopulations or patchy populations, making specific predictions for distinguishing source-sink population structure from metapopulation or patchy population structure difficult if not impossible. According to the first model, subpopulations are considered to be part of a patchy population (Harrison 1991). The subpopulations are well connected by dispersal, that is, they represent one single population with little potential for local extinction of single subpopulations. The second model proposes that subpopulations are organized as a metapopulation, here defined as a collection of partially isolated habitat patches, which may support local breeding subpopulations, with extinction and recolonization of subpopulations occurring. Due to recolonizations of extinct subpopulations the entire metapopulation usually persists much longer than each of the local subpopulations (Levins 1970). In the third model, subpopulations are isolated from each other, that is, the subpopulations are separate small populations. "Subpopulations" may represent fragments of a formerly continuous population. Once extinct, fragments will not be recolonized (Frankham *et al.* 2002).

Distinguishing between these models of spatial population structure by empirical estimates of dispersal among subpopulations is difficult, for example due to the great logistic challenges associated with banding and re-observing individuals in multiple subpopulations. In addition, direct observations of dispersal only partially reveal the patterns of individual movements (Koenig *et al.* 1996) and may represent an inadequate estimation of gene flow, because gene flow requires successful reproduction of the immigrant (Boughton 1998; Hedrick 2005). Furthermore, the significance of direct dispersal estimates is limited to the study of contemporary population dynamics. In turn, indirect estimates of gene flow based on the distribution of allele frequencies among populations depend on levels of gene flow

averaged over long times and may therefore be the result of past rather than current dispersal (Slatkin 1987). However, identification of real-time migrants using genetic assignment methods (see Manel *et al.* 2005 for review) is also possible but restricted to cases where populations are genetically sufficiently structured (Cornuet *et al.* 1999; Paetkau *et al.* 2004). The most promising approach is therefore to combine direct and indirect estimates of dispersal and gene flow because they yield information on current and past gene flow (Slatkin 1987). Surprisingly, however, relatively few studies on mobile organisms have adopted such a combined approach so far.

The three models of spatial population structure make contrasting predictions with respect to dispersal and gene flow patterns and the distribution of genetic variation within and among local subpopulations (Table 1). (1) The patchy population model predicts high dispersal among all subpopulations and, due to generally high levels of dispersal, also substantial immigration into the patchy population. Since local extinction risk is low, we expect no extinctions or recolonizations of subpopulations. The patchy population model further predicts no significant genetic differentiation among subpopulations due to the high amount of gene flow homogenizing any genetic structure (Harrison 1991). The entire patchy population is therefore in Hardy-Weinberg equilibrium and isolation-by-distance is not expected to occur on local scales (Slatkin 1993). Linkage disequilibrium among unlinked nuclear loci may be caused by the effects of genetic drift in small populations (Hedrick 2005). However, due to the high amount of gene flow among subpopulations, genetic drift acts at the level of the entire patchy population, and the magnitude of linkage disequilibrium within single subpopulations should therefore not be related to subpopulation size. Population structure can also be assessed without imposing any preconceived assumptions on the number and distribution of subpopulations. In this case, individuals of the patchy population are

expected to form a single genetic cluster. (2) The metapopulation model predicts dispersal to be restricted and thus mostly occurring among neighbouring populations. Accordingly, immigration into the metapopulation is low. Metapopulation structure predicts the occurrence of extinctions and recolonizations of subpopulations (Hanski 1999). All local subpopulations have a substantial probability of extinction but patches that are unsettled due to local extinction events are recolonized by founder individuals from other subpopulations. The metapopulation model further predicts that gene flow among subpopulations is low and that subpopulations are hence genetically significantly differentiated (Hastings & Harrison 1994). Analysis at total population level, i.e. when considering all subpopulations collectively, should reveal significant deviation from Hardy-Weinberg equilibrium with a deficit of heterozygotes, since the whole metapopulation is composed of genetically differing subpopulations (Wahlund 1928, as cited in Hedrick 2005). Since genetic exchange occurs mainly between neighbouring subpopulations, genetic differentiation is explained by isolation-by-distance (Slatkin 1993). Depending on subpopulation size, stochastic fluctuations result in nonrandom associations between alleles at different loci (Hedrick 2005). The strength of linkage disequilibrium in subpopulations of the metapopulation should therefore be negatively related to subpopulation size. The metapopulation is expected to consist of more than one genetic cluster. (3) The isolated population model predicts no dispersal among and no immigration into “subpopulations” (Table 1). Isolated populations may go extinct but will not be recolonized. Due to isolation, subpopulations are highly differentiated from each other. Differences in allele frequencies among subpopulations cause deviation from Hardy-Weinberg equilibrium at total population level, resulting in heterozygote deficiency (Wahlund 1928, as cited in Hedrick 2005). Since subpopulations evolve independently due to complete isolation, genetic differences between subpopulations are not related to geographic distance

(Hutchison & Templeton 1999). Within subpopulations, the strong effects of genetic drift and inbreeding generate a relatively high level of linkage disequilibrium, which should be negatively related to subpopulation size (Hedrick 2005). Due to complete isolation, the number of genetic clusters is expected to correspond to the number of subpopulations.

In this study we investigate the spatial population structure of subpopulations of the reed bunting (*Emberiza schoeniclus*). The reed bunting is a small Palaearctic short-distance migratory songbird restricted to wetlands. Due to its specific habitat requirements, the spatial distribution and size of reed bunting subpopulations depend on the distribution and size of wetlands (Glutz von Blotzheim & Bauer 1997). Wetlands have been destroyed worldwide due to anthropogenic land use (Keddy 1999). As a consequence, the reed bunting has strongly suffered from the destruction and perhaps also the deterioration of its habitat (Blümel 1995). Between the 1970s and early 1990s, reed bunting declines have been reported for several European countries, for example in Italy, Germany, Belgium, Finland and England (Heath *et al.* 2000).

In Switzerland, wetland protection programmes were developed in the 1970s to stop further destruction of wetland habitat. Since 1975 the size of wetlands in the Swiss lowlands has remained constant (Weggler *et al.* 2004). Accordingly, the overall distribution of reed buntings in Switzerland has not changed in the recent years, except that the species has disappeared at the edges of its distribution range (Antoniazza 1998). In the southeastern part of the Canton Zurich, where this study took place, wetlands are as small as 2.7 ha and separated by intensively managed agricultural landscapes. Between 1993 and 2006, a decline of breeding reed buntings has been reported for the three largest wetlands in the Canton Zurich for reasons yet unknown (Weggler & Widmer 2001; M. Weggler, personal communication). Reed buntings regularly breed in these wetlands, but it is unknown, whether

and how the wetlands are connected by dispersal, given the apparently short dispersal distances reported for this species (Paradis *et al.* 1998).

To summarise, the specific objectives of this paper are to assess the spatial organisation of reed bunting subpopulations by testing theoretical predictions of the three population models with demographic and genetic data. According to the best-supported model, we discuss implications for the conservation management of this locally declining species.

Materials and Methods

Sampling

The study took place in a 200 km² area of the Zürcher Oberland in the south eastern part of the Canton Zurich, Switzerland. Here, 19 wetland fragments were examined from 2002 to 2005 in the context of a study on the population ecology of the reed bunting (see Pasinelli *et al.* (2008a) for further details). All these fragments are nature reserves offering, to variable extent, old reed habitats, which represent the only suitable breeding habitat for reed buntings in the whole study area. The presence of old reed *Phragmites* sp. is the most important cue for territory establishment when males return from the wintering grounds (Surmacki 2004). To prevent the overgrowth with reed all fragments are partially mown in autumn. Only small bands of reed along water bodies as well as a few distinct patches are spared from the annual cut. All fragments border at intensively used agricultural areas. Because some of these fragments clearly hosted too few birds to for reliable estimates of genetic parameters we aggregated fragments to nine subpopulations according to their spatial location. Within subpopulations, distances between pooled fragments were below 900 m, which has been reported to be the average juvenile dispersal distance in the reed bunting (Paradis *et al.* 1998). Because pooling of fragments may have an impact on the distribution of genetic variation of

subpopulations, we first tested for genetic differentiation among fragments, which were to be pooled using the same methods as described later in the 'Genetic data' section. No genetic differences and also no deviation from Hardy-Weinberg equilibrium could be detected. We found a deviation from Hardy-Weinberg equilibrium in the subpopulation Lützelsee (Table 3). However, this deviation was not due to the pooling of three fragments, because deviation from Hardy-Weinberg equilibrium was also detected, when the fragment Lützelsee was separately analysed. Subpopulations hosted 1 to 50 breeding pairs per year. All breeding pairs were completely monitored in each subpopulation except in the three largest subpopulations Greifensee, Lützelsee, and Pfäffikersee, where we focused on a sub-sample of at least 10 breeding pairs annually (Table 2).

Reed buntings were annually monitored from early March, when males return from their wintering grounds, to the end of the breeding period in early August. Nests were located by observing females building their nest, leaving their nest and returning to it during incubation, or when the parents were feeding the young. The young were banded between nestling day 6 and 9, with each nestling obtaining a numbered aluminium ring as well as a unique combination of three coloured plastic rings allowing individual identification by telescope observation. To catch and band males, a mist net was set up at the border of a territory, and a loudspeaker was placed in front of the net. Females were caught with a net placed at a distance of at least 2 m from the nest, when flying to the nest to feed their young. Adults were individually marked (see above) and a blood sample (max. 100 µl) from each individual was taken by puncturing the brachial vein (permission number from the Cantonal Veterinary Office Zurich: 169/2001). Blood was absorbed with heparinized microcapillaries. Samples were either stored in microcapillaries directly or blown into APS-buffer (Arctander

1988) and stored at -20° C. A total of 253 breeding individuals (132 males and 121 females) were used for data analysis.

Demographic data

To get data on dispersal and immigration we annually monitored all reed buntings of all subpopulations at least twice a week from early March to early August and documented their movements within and among all subpopulations. From May to July 2003 – 2007 we also systematically searched for banded birds outside the intensively monitored old reed areas of the three largest wetland fragments and opportunistically in wetlands of the Canton Zurich outside the 200 km² – study area. We focused our search for banded reed buntings on wetlands, because the species does not use habitats other than wetlands during breeding time in the Canton Zurich. The period between May and July corresponds to the breeding season of the reed bunting in our study area; individuals observed during that time are considered territorial breeding birds. Non-breeding territorial individuals were extremely rare (unpublished data, G. Pasinelli). We considered as natal dispersal event the movement of a bird born in a subpopulation and breeding in a different subpopulation or outside the study area in the subsequent year, respectively. Breeding dispersal was defined as the movement of an adult individual to another subpopulation or to outside the study area between two breeding attempts, either within the same or between subsequent years.

Obtaining estimates of immigration rates was complicated because not all individuals in each subpopulation could be banded every year (proportion of banded individuals across years: mean \pm SD, 83.73 % \pm 4.77). We calculated annual immigration rate over all subpopulations by dividing the number of individuals that were unbanded and territorial at the beginning of the breeding season by the entire number of individuals (banded and unbanded).

Unbanded individuals may cause problems in estimating immigration rate because, for a specific year, it is not possible to distinguish between new unbanded individuals (i.e. true immigrants) and unbanded philopatric individuals that already have bred in the study area in the previous year. To account for the potential bias, we treated unbanded individuals in the calculation of immigration rate in three different ways, in the following exemplified for 2003: (1) we assumed that all individuals who remained unbanded at the end of the breeding season in 2002 did not return to the study area in 2003. All unbanded individuals in 2003 are therefore treated as true immigrants, which will give the maximum immigration rate; (2) we assumed that all these individuals were philopatric, which will give the minimum immigration rate. The true immigration rate will lie between the minimum and maximum estimates, and we further approximated it by treating unbanded individuals of the previous year as immigrants, but correcting for the number of assumed unbanded philopatric individuals. This was done in the following way: (3) assuming that the probability of being philopatric is the same for both unbanded and banded breeding individuals (philopatry rates of banded adult females across years: 0.436 (95% CI 0.428-0.445), Pasinelli *et al.* 2008b, submitted) we determined the number of unbanded but presumably philopatric individuals for 2002. This number was then subtracted from the number of unbanded individuals observed in 2003.

A subpopulation was defined as extinct, when no territorial bird settled despite the presence of suitable habitat. Recolonizations were considered to have occurred, when unoccupied suitable habitat was subsequently held by breeding individuals.

Genetic data

Laboratory analysis

For DNA preparation two extraction kits were used: the Roche "High Pure PCR Template Preparation Kit" following exactly the protocol (Vogelstein & Gillespie 1979) and the Qiagen "Biosprint 96 DNA Blood Kit". We used a set of 11 autosomal microsatellite loci (Emb 03, Emb 07, Emb 12, Emb 17, Emb 19, Emb 27, Emb 79, Emb 81, Emb 89, Emb 90, Emb 112, and Emb 116) for population genetic analysis as described previously (Mayer *et al.* 2007). Polymerase chain reaction amplification and genotyping were conducted as described in (Mayer *et al.* 2007).

Genetic variation

Genetic variation within each subpopulation was measured by using allele frequency data, from which the number of alleles per locus (A), the allelic richness (R) averaged over loci (Petit *et al.* 1998) and F_{IS} were calculated with FSTAT 2.93 (Goudet 2001). Observed (H_o) and expected (H_e) heterozygosities (Nei 1987) were calculated with ARLEQUIN 3.1 (Excoffier *et al.* 2005). Departure from Hardy-Weinberg expectations was tested with GENEPOP on the web (<http://genepop.curtin.edu.au/>) (Raymond & Rousset 1995), both within each subpopulation and at total population level, i.e. when subpopulations were pooled. These tests were conducted using a Markov chain with 5'000 batches each iterated 1'000 times and a dememorization number of 10000 (Guo & Thompson 1992; Raymond & Rousset 1995).

Null alleles

The software MICRO-CHECKER 2.2.3 (van Oosterhout *et al.* 2004) was used to check for appearance of long allele dropout or scoring errors due to stutter rate and to test for the occurrence of null alleles. We found evidence for the existence of null alleles at loci Emb 81

and Emb 116. Conducting statistical analysis on data sets containing null alleles may lead to misinterpretation of the data and wrong biological conclusions (Dewoody *et al.* 2006). Since these two loci caused significant deviation from Hardy-Weinberg equilibrium, we excluded them from all analyses.

Linkage disequilibrium

The strength of linkage disequilibrium within each subpopulation was assessed using r_d (Agapow & Burt 2001) as a measure of multilocus linkage disequilibrium. This measure is equal to the index of association (I_A) but corrected for the number of loci used for analysis. We also used a randomization procedure (1000 iterations) to test the hypothesis of complete panmixia between alleles at different loci. Calculations were done in MULTILOCUS 1.3 (Agapow & Burt 2001), and r_d – values were then regressed on subpopulation size using SPSS 12.0.2 for Windows.

Genetic differentiation

We tested for allele frequency differences between subpopulations with an exact probability test using GENEPOP on the web (<http://genepop.curtin.edu.au/>) (Raymond & Rousset 1995). Differentiation among subpopulations was described with F_{ST} (Wright 1951). We did not use R_{ST} (Chakraborty & Nei 1982; Slatkin 1995), because the allelic distributions of five microsatellite loci revealed large gaps and one locus showed single base pair shifts, suggesting that these loci did not follow a strict stepwise mutation model. In addition, F_{ST} has been shown to be the best estimator in cases, when genetic differentiation among populations is expected to be low (Balloux & Goudet 2002). F_{ST} estimates were calculated over all subpopulations and for all subpopulation pairs according to Weir & Cockerham (1984) and

tested for significance by permuting genotypes among samples (5000 permutations) with FSTAT 2.9.3.2 (Goudet 2001). To assess whether geographical distance between subpopulations may explain genetic differentiation, isolation by distance was examined using a Mantel test (90'000 permutations) in ARLEQUIN 3.1 (Excoffier *et al.* 2005). Pairwise genetic distance defined as $F_{ST}/(1-F_{ST})$ was regressed on the logarithms of geographical distance. This regression is considered linear in a two-dimensional model (Rousset 1997).

Differentiation among subpopulations was also evaluated with the model-based clustering method of Pritchard *et al.* (2000) implemented in STRUCTURE 2.1. This method uses a Bayesian approach to detect potentially existing genetic structure without imposing any preconceived ideas of population substructure. The method assigns individuals, based on Hardy-Weinberg expectations, to a user-defined number of genetic clusters (K). A Markov chain Monte Carlo (MCMC) procedure is conducted to estimate the log probability of data $\Pr(X | K)$ (equation 12 in Pritchard *et al.* (2000)) for each value of K . STRUCTURE also calculates a proportional membership Q to each cluster (K) for each individual. STRUCTURE was applied without any prior information about the geographic origin of individuals using the following parameter settings: admixture model, correlated allele frequencies among populations, a burn-in period of 50'000 steps, and a chain length of 5×10^5 . The calculation for each K between 1 and 9 was performed 20 times.

Results

Demographic data

Of 813 banded nestlings, 44 (5.41 %) recruited within the study area. Of these, 55 % dispersed to a subpopulation other than their natal one. All subpopulations except the two smallest ones (Brüschweid and Feldbach) received recruits from a different subpopulation,

and every subpopulation except Aathal contributed at least one recruit to another subpopulation. Of the 105 adults that bred in two subsequent years seven (6.67 %) bred in a different subpopulation in the second year. Across years, immigration rates were (1) maximally $61.37 \% \pm 0.06$ (mean \pm SD), (2) minimally $43.78 \% \pm 0.1$, and (3) corrected for unbanded philopatric individuals $53.70 \% \pm 0.08$. We did not observe any extinction of subpopulations.

Genetic data

All loci were highly polymorphic within each of the nine subpopulations (Table 3). Overall, a total of 144 alleles was found at 9 microsatellite loci, with an average of 16 ± 3.3 (mean \pm SD) alleles per locus ranging from 11 alleles at Emb 17 to 22 alleles at Emb 112. Per subpopulation, the number of alleles averaged over loci was 10.3 ± 2.7 and varied from 6.2 in Brüscheid to 13.4 in Lütelsee. Mean allelic richness and observed heterozygosity ranged from 5.64 in Brüscheid to 6.05 in Feldbach und Uerzikon (mean \pm SD, 5.91 ± 0.13) and from 0.796 in Brüscheid to 0.862 in Greifensee (0.842 ± 0.025), respectively. All subpopulations were in Hardy-Weinberg equilibrium (HWE) after Bonferroni correction except subpopulation Lütelsee (Table 3). We found no significant departure from HWE at total population level (locus combination Fisher's method: $\chi^2 = 24.9$, $df = 18$, $p > 0.124$). The magnitude of linkage disequilibrium measured as r_d ranged from -0.0041 in Brüscheid to 0.0329 in Aathal (mean \pm SD, 0.0125 ± 0.013 , Table 3), but only values for Bubikon and Lütelsee were significant after the randomization procedure ($p < 0.009$). Linkage disequilibrium was not explained by subpopulation size ($R^2 = 0.01$, $F = 0.07$, $p = 0.798$).

The exact probability test showed a significant difference in allele frequencies among subpopulations (test combination Fisher's method: $\chi^2 = 72.1$, $df = 22$, $p < 0.001$). However,

considering the overall F_{ST} -value of 0.005 (CI 95% 0.003 – 0.008) across subpopulations the degree of differentiation was very low. Calculation of pairwise F_{ST} -values generated almost only positive values, but all of them were smaller than 0.028 and not significant, except for the F_{ST} -value between Pfäffikersee and Uerzikon, which was significant after the permutation process followed by a Bonferroni correction (Table 4). No relation between geographic and genetic distances was found (Mantel test, $p = 0.209$). The cluster analysis performed with STRUCTURE indicated that most likely all subpopulations form one genetic cluster (that is $K = 1$, see Fig. 2). When regarding the proportional membership Q for the different values of K , each individual was assigned to each genetic cluster to nearly the same extent ($Q \approx 1/K$), also suggesting that all individuals belong to only one single cluster. This assignment was independent of an individuals' subpopulation of origin.

Discussion

Demographic data and the analyses of genetic variation within and among subpopulations of the reed bunting suggest that the spatial population structure of this species is consistent with the patchy population model. This model predicts regular exchange of individuals between all subpopulations, which we primarily found for juveniles. Accordingly, as predicted from the model, immigration into the study area was also high. The estimated immigration rate for the reed bunting fits within the range of values reported for other migratory (e.g. Great reed warbler, *Acrocephalus arundinaceus*: 54.6%, Hansson *et al.* 2004) and sedentary bird species (e.g. Willow tit, *Parus montanus*: 69.4%, Kvist *et al.* 2001; Orell 1999), for which high levels of gene flow among populations had also been shown (Bensch & Hasselquist 1999; Kvist *et al.* 2001). Unfortunately, we cannot distinguish whether immigrants came from the less-intensively monitored areas along Greifensee, Lützelsee, and

Pfäffikersee or from populations farther away. However, in the former case, immigration from less-intensively to intensively monitored parts of the study area (see Methods) should have roughly equalled emigration from intensively to less-intensively monitored areas, but we did not find evidence for that. Only nine individuals moved from intensively to less-intensively monitored areas, indicating that almost all immigrants originated from outside the study area. The absence of extinctions or recolonizations further agrees with predictions from the patchy population model. However, even if extinction risk of local subpopulations was high, five years of study may not have been sufficient to observe any extinctions or recolonizations, despite an average life expectancy of only two years (based on non-migratory British adults, Glutz von Blotzheim & Bauer 1997) and a generation time of 1.8 year (calculated following Lande *et al.* 2003). On the other hand, extinctions of subpopulations may be prevented by the high movement rates observed.

In line with the demographic data, our genetic data also support the patchy population model. According to this model, genetic diversity was high in all subpopulations, which suggests that all subpopulations were exposed to gene flow. The majority of the subpopulations was in Hardy-Weinberg equilibrium, as was the total population. We did not find any significant relationship between genetic and geographic distance, which also suggest that gene flow was high among subpopulations. However, lack of isolation-by-distance may also be explained by, for example, recent colonization processes, or a rapidly expanding population (Hutchison & Templeton 1999; Slatkin 1993). No correlation between the magnitude of linkage disequilibrium and subpopulation size was found, indicating that genetic drift is not a relevant factor at the level of subpopulations. Besides drift gene flow also could produce nonrandom associations of alleles resulting in a substantial magnitude of linkage disequilibrium, if immigrants were genetically different to local birds (Hedrick 2005).

However, due to the small sizes of most subpopulations and the unknown immigration status of unbanded breeding individuals (see Methods), we were not able to calculate reliable estimates of subpopulation-specific immigration rates to test the influence of gene flow on the strength of linkage disequilibrium within subpopulations. When assigning individuals to one or more genetic clusters without a priori information on an individual's subpopulation of origin, we got clear evidence for only one genetic cluster in our study area.

One prediction of the patchy population model was only partly supported. In contrast to the prediction, we detected a significant difference in the allelic composition among subpopulations overall. In line with the prediction, on the other hand, pairwise comparisons indicated no significant differentiation between subpopulations in all but one case. However, both overall and pairwise F_{st} -values were always small, indicating very low magnitude of genetic differentiation. Slight differences among subpopulations could have been caused by small sample sizes, or by only a few immigrating individuals, if their population of origin had been genetically differentiated from the study population.

The genetic consequences of the three population models proposed would only be observed if the subpopulations have behaved as predicted by the models for some period of time. For example, if connectivity among subpopulations had decreased very recently, no genetic differentiation between subpopulations would be observed, since our genetic estimates resemble past rather than current gene flow. However, our direct estimates of contemporary dispersal among subpopulations are in agreement with our genetic data on past gene flow, and combined they provide strong support for the patchy population model.

Both demographic and genetic results clearly rule out the isolated population model. This is in line with the general finding of weak genetic isolation between local bird populations (Walters 1998), and that occurrence of isolated populations may be restricted to

species living on remote islands or to situations, in which distances between populations greatly exceed dispersal abilities (Pettersson 1985). Our data do not support the metapopulation hypothesis either. On the one hand, a patchy distribution of a species' habitat has often led to the a priori assumption that the species exhibits some form of metapopulation structure, not only when dispersal ability is restricted like, for example, in amphibians (Smith & Green 2005), but also in highly mobile species like migrating birds (Esler 2000; Hansson *et al.* 2002; Opdam 1991). Most studies rely on patch occupancy patterns to infer spatial population structure and end up suggesting evidence for metapopulation structure while genetic data are missing. However, studies having tested predictions for the distribution of neutral genetic diversity derived from metapopulation theory are rare. Evidence for metapopulation structure derived from genetic data has been found in plants (Tero *et al.* 2003), insects (Brookes *et al.* 1997), fishes (Garant *et al.* 2000), amphibians (Rowe *et al.* 2000) and mammals (Stewart *et al.* 1999). In birds, however, metapopulation structure derived from genetic data has only been shown for the capercaillie (*Tetrao urogallus*) in the Alps (Segelbacher & Storch 2002) and the Florida scrub-jay (*Aphelocoma coerulescens*, Coulon *et al.* 2008). There, genetic differentiation among subpopulations had been attributed to declines in subpopulation sizes caused by habitat deterioration owing to human land use. On the other hand and in contrast to metapopulation theory, Barrowclough (1983) has assumed that the high dispersal capacity of highly mobile taxa like birds will lead to admixture of populations despite the fragmentation of their habitat. Moreover, a spatially aggregated distribution of individuals does not necessarily demonstrate metapopulation structure, because restricted dispersal is not the only cause for localized groups of individuals of a taxon (Sutcliffe *et al.* 1997). Aggregated distributions can also occur in systems where individuals are highly mobile, but show some sort of aggregative behaviour in favoured

patches (Koopman *et al.* 2007; Sutcliffe *et al.* 1997). This seems to be the case in our study system. The patchy distribution of breeding habitat in combination with the reed buntings' narrow habitat preferences has not led to restricted dispersal or gene flow among subpopulations, low immigration or genetic structuring of subpopulations. Similarly, in many other migratory bird species lack of genetic structure has been found (Ball & Avise 1992; Kimura *et al.* 2002; Lovette *et al.* 2004; Mila *et al.* 2000; Ruegg & Smith 2002), even in species sensitive to habitat fragmentation (Veit *et al.* 2005).

The apparent lack of genetic structure in our study population may be explained by several hypotheses. First, birds are moving in response to habitat loss and/or fragmentation. It has been debated whether or not species change their dispersal behaviour following habitat loss and/or fragmentation (Ferraz *et al.* 2007; Opdam 1991). However, many examples exist where bird species did not disperse over increasing distances in response to habitat fragmentation (Cooper & Walters 2002; Matthysen 1999; Stouffer & Bierregaard 1995), whereas others did (Pasinelli *et al.* 2004; Van Houtan *et al.* 2007). Median natal dispersal distance in our study area was 4 km (interquartile range: 0.98 – 5.22 km, $n = 30$) and therefore more than four times larger than average dispersal distances reported for the reed bunting so far (Paradis *et al.* 1998). Increasing dispersal distances in response to habitat loss and/or fragmentation counteract population differentiation, which seems plausible for our study species when taking into account that the reed bunting is adapted to a naturally fragmented habitat, although levels of wetland fragmentation nowadays are undoubtedly far from natural. Second, migratory bird species have been shown to disperse longer distances than resident ones (Paradis *et al.* 1998), potentially leading to admixture of populations. The study reporting short dispersal distances for reed buntings (Paradis *et al.* 1998) has been conducted in the UK, where reed buntings do not migrate (Prys-Jones 1984), while reed buntings in

Switzerland do. However, it has not only been shown that migratory bird species disperse further than resident ones (Paradis *et al.* 1998), but also that migrating populations disperse further and show weaker genetic differentiation than sedentary populations of the same species (Arguedas & Parker 2000). The greater dispersal distance of migratory populations has been attributed to pre-migratory dispersal behaviour, which may familiarize the birds with several sites, from which they might be able to choose, when returning from their wintering grounds the next breeding season. Thus, migratory behaviour may explain why reed buntings in our study area disperse irrespective of distance between subpopulations (no IBD), ultimately resulting in genetic admixture of subpopulations. Finally, the whole study population may be a sink sustained by one or more neighbouring populations acting as sources. If immigration rate is high, the study population would closely resemble the genetic constitution of its source population(s) resulting in genetic admixture (Gaggiotti & Smouse 1996). A source-sink situation on a regional scale (i.e. beyond the scale of our study) could therefore explain high immigration into and the apparent lack of genetic structure in our study population. In fact, demographic data indicate that the entire patchy population in our study area is a sink (Pasinelli *et al.* 2008b, submitted). Lack of genetic differentiation among subpopulations therefore indicates either unidirectional immigration from one source population, which could be genetically discrete, or immigration from several source-populations, which are connected by gene flow. However, if our study population is a sink population, it could weaken potential source populations by drawing individuals away from better sites (Gaona *et al.* 1998; Howe *et al.* 1991). On the other hand, wetland fragments in our study area may serve as a site of temporary residence for individuals that await an opportunity to disperse back to a source, in which case the presence of the sink may be beneficial for the species. Evaluation of these hypotheses will require more data on long

distance dispersal and analysis of dispersal rates among our study population in the southeastern part of the Canton Zurich and neighbouring reed bunting populations at the border to Germany and in the middle and western part of the Swiss lowlands at least 50 km apart (Mayer *et al.* in prep.). Further studies are needed to confirm the general validity of our findings in terms of the patchy population model for other reed bunting populations and for other species with similar patterns of distribution and dispersal abilities.

Conservation implications

Knowing the spatial structure of local populations is not only of theoretical interest, but is also a crucial step in conservation planning for species living in a fragmented habitat (Lande & Barrowclough 1987). Our results give strong evidence for a genetically uniform patchy population consisting of several small breeding localities distributed according to available habitat. Despite high levels of habitat fragmentation, substantial contemporary dispersal and gene flow ensures connectivity among disjunct breeding localities. Consequently, there is only little risk for both local subpopulations and therefore also for the entire patchy population to go extinct. Conservation management should focus on the maintenance of this network of suitable breeding localities to promote the persistence of the patchy population. However, in the recent years, management of wetland reserves, particularly in the Canton Zurich, has focused on promoting species living outside reed beds such as orchids (*Orchidaceae*) or dragonflies (*Odonata*), preventing natural succession and eradicating exotic plant species (e.g. *Solidago* sp.). The intensive management leaves only narrow bands of old reed along water bodies and in some of the small wetland fragments, no reed was left in some years. Consequently, those wetland fragments were not occupied by reed buntings in those years. Due to their high dispersal ability, reed buntings are capable of

recolonizing wetland fragments immediately when habitat conditions have again become favourable. Ironically, in Canton Zurich management of wetlands for conservation seems to be the most important threat for the reed bunting. Since reproduction and demographic contributions of small and large wetland fragments did not differ (Pasinelli *et al.* 2008a) small fragments are of importance for the whole patchy population. Conservation management in favour of the reed bunting should therefore focus on the protection of all local breeding localities independently of size, to promote the persistence of the patchy reed bunting population in Canton Zurich and in other similarly fragmented landscapes.

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Table 1 Predictions about direct and indirect estimates of dispersal, the distribution of genetic variation and gene flow among local populations proposed from the three models of population structure '-': not observed/absent, '+': moderate level, '++': high level. Note that the patchy population model and the isolated population model represent extremes of a continuum of possible spatial population structure models, with the metapopulation model laying in-between the other two models.

	patchy population	metapopulation	isolated populations
<i>Direct estimates</i>			
Dispersal	++	+	-
Immigration	++	+	-
Extinctions / Recolonizations	- / -	+ / +	+ / -
<i>Indirect estimates</i>			
Genetic differentiation	-	+	+
Isolation by distance	-	+	-
Hardy-Weinberg equilibrium at total population level	+	-	-
Linkage disequilibrium	-	+*	+*
Gene flow	++	+	-
Number of genetic clusters	1	>1	>1 ^{\$}

* negatively related to subpopulation size, ^{\$} equivalent to the number of subpopulations

Table 2 Location, size, number of fragments per subpopulations, coordinates, mean number of breeding pairs (BP) monitored per year, and samples collected from the nine subpopulations between 2002 – 2005.

Subpopulation	Size [ha]	Number of fragments	Coordinates	Mean BP / year	Sample size
Aathal	8.6	2	47°18'/08°45'	2.8 ± 1	10
Brüschweid	57.1	3	47°18'/08°48'	1.3 ± 0.5	6
Bubikon	46.4	4	47°16'/08°49'	7.5 ± 1.7	35
Feldbach	2.7	1	47°14'/08°48'	2.0 ± 0.8	7
Greifensee	44.1	1	47°19'/08°42'	12.0 ± 1.8	61
Lützelsee	58.9	3	47°16'/08°47'	12.3 ± 1.5	56
Nänikon	21.7	2	47°22'/08°42'	3.5 ± 0.6	13
Pfäffikersee	247.2	1	47°21'/08°47'	10.3 ± 1	44
Uerzikon	16.1	2	47°16'/08°46'	5.3 ± 1.7	21

Table 3 Estimates of average genetic diversity in the nine subpopulations. n = number of adults sampled, A = mean number of alleles per locus, R = mean allelic richness, observed (H_o) and expected (H_e) heterozygosity, HW = departure from Hardy-Weinberg expectations (n.s. = not significant, * = $p < 0.05$), mean F_{IS} per subpopulation and r_d (significant values are in bold).

Subpopulation	n	A	R	H_o	H_e	HW	F_{IS}	r_d
Aathal	10	8.56	5.95	0.849	0.842	n.s.	-0.009	0.0329
Brüschweid	6	6.22	5.64	0.796	0.825	n.s.	0.038	-0.0041
Bubikon	35	11.98	5.98	0.823	0.858	n.s.	0.042	0.0313
Feldbach	7	7.00	6.05	0.855	0.865	n.s.	0.013	0.0048
Greifensee	61	13.22	5.85	0.862	0.853	n.s.	-0.011	0.0065
Lützelsee	56	13.44	5.87	0.821	0.851	*	0.036	0.0179
Nänikon	13	9.22	5.96	0.880	0.861	n.s.	-0.022	0.0154
Pfäffikersee	44	12.65	5.82	0.837	0.850	n.s.	0.016	0.0065
Uerzikon	21	10.89	6.05	0.856	0.865	n.s.	0.011	0.0009

Table 4 Genotypic differentiation between pairs of subpopulations based on pairwise F_{ST} – values (below diagonal) and p-values from a G-based likelihood ratio test (above diagonal; after Bonferroni-correction p-values < 0.0014 are considered to be significant) for the nine reed bunting subpopulations (significant values are presented in bold).

	AA	BR	BU	FE	GR	LU	NA	PF	UE
Aathal (AA)		- 0.09583	0.04444	0.75556	0.00833	0.15833	0.64167	0.13333	0.00694
Brüscheid (BR)	0.0234		- 0.66944	0.73611	0.29167	0.08194	0.00972	0.03333	0.51806
Bubikon (BU)	0.0114	0.0025		- 0.91806	0.25556	0.19861	0.08194	0.00556	0.18333
Feldbach (FE)	-0.0033	-0.0079	-0.0091		- 0.31944	0.72917	0.28333	0.23333	0.3625
Greifensee (GR)	0.0078	0.0098	0.0055	0.0010		- 0.13889	0.16528	0.04167	0.07222
Lützelsee (LU)	0.0087	0.0213	0.0056	-0.0062	0.0022		- 0.31806	0.00278	0.09167
Nänikon (NA)	0.0090	0.0277	0.0057	0.0040	0.0035	0.0040		- 0.25278	0.08333
Pfäffikersee (PF)	0.0111	0.0152	0.0057	0.0054	0.0033	0.0075	0.0009		- 0.00139
Uerzikon (UE)	0.0145	-0.0033	0.0028	-0.0036	0.0052	0.0065	0.0100	0.0126	

Figure legends

Fig. 1 Location of the nine subpopulations with number of adults sampled per subpopulation. For details see Table 2.

Fig. 2 Mean (\pm SD) likelihood values ($\text{Pr}(X | K)$) for each hypothesized genetic cluster (K).

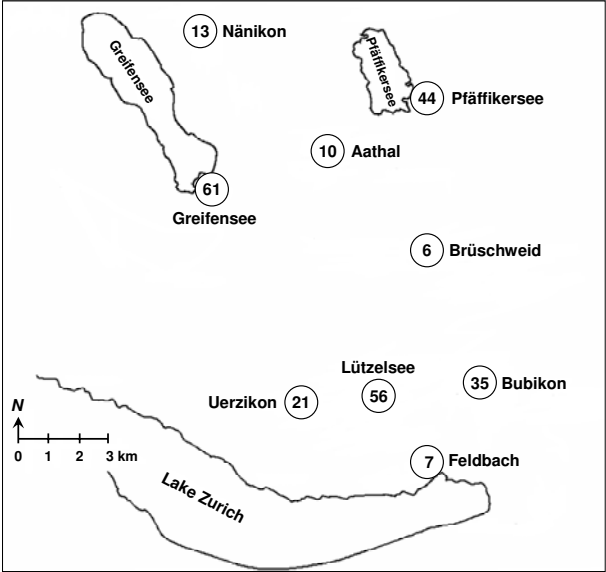


Fig. 1

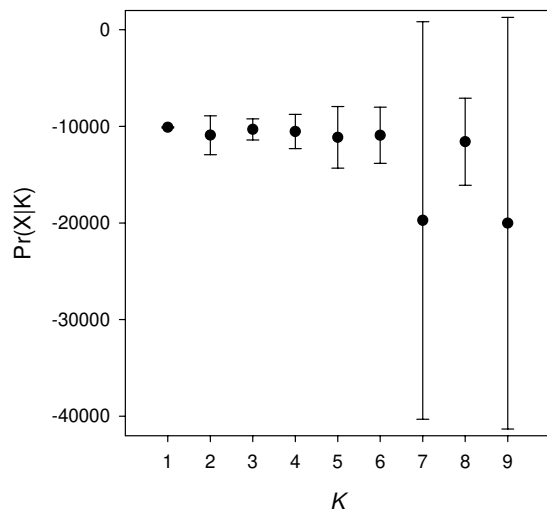


Fig. 2

This is a pre-peer reviewed version of the following article: Mayer C, Schiegg K, Pasinelli G (2009) Patchy population structure in a short-distance migrant: evidence from genetic and demographic data. *Molecular Ecology*, **18**, 2353-2364, which has been published in the final form at [<http://www3.interscience.wiley.com/journal/117989598/issue>].