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A new approach to study dispersal: immigration of novel alleles reveals female-biased dispersal in great reed warblers

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Abstract

We use the assignment technique and a new approach, the 'novel allele technique', to detect sex-biased dispersal in great reed warblers *Acrocephalus arundinaceus*. The data set consisted of immigrants and philopatric birds in a semi-isolated population in Sweden scored at 21 microsatellite loci. Fourteen cohorts were represented of which the four earliest were used to define a reference population. Female immigrants had lower assignment probability than males (i.e. were less likely to have been sampled in the reference population), and carried the majority of 'novel alleles' (i.e. alleles observed in the population for the first time). The difference in number of novel alleles between sexes was caused by a strong overrepresentation of females among the few individuals that carried several novel alleles, and there was a tendency for a corresponding female bias among individuals with low assignment probabilities. Immigrant males had similar or lower reproductive success than females. These results lead us to conclude that important interregional gene flow in great reed warblers depends on relatively few dispersing females, and that the novel allele technique may be a useful complement to the assignment technique when evaluating dispersal patterns from temporally structured data.

Keywords: assignment analysis, gene flow, great reed warbler, microsatellite, sex-biased dispersal

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Introduction

Dispersal is an important parameter in evolutionary ecology and conservation biology as it is crucial for colonization and gene flow (Rockwell & Barrowclough 1987; Slatkin 1987; Hanski & Gilpin 1997; Ronce *et al.* 2001). The propensity to disperse varies between species and also between phenotypes within species. In several species, the pattern of dispersal differs between males and females. Interestingly, and for reasons that are not yet fully resolved (Goudet *et al.* 2002), male-biased dispersal is the norm in mammals, whereas female-biased dispersal is most common in birds (Greenwood 1980; Weatherhead & Forbes 1994). These conclusions are based mainly on direct field observations of the level of philopatry and pattern of short-distance dispersal within a limited geographical area. Complementary data of the sex bias in dispersal over longer dispersal distances, as well as dispersal data of species that are difficult to observe directly, may be

obtained by molecular methods (Crochet 1996; Bohonak 1999; Goudet *et al.* 2002). However, there are some disagreements about the general ability of molecular methods to reveal sex-biased dispersal. Often-expressed doubts are that offspring of both sexes will inherit alleles introduced to the population even if immigrants are of one sex only, that the statistical power will be low when immigrants are rare, and that alleles will be undifferentiated between populations when immigrants are common (Goudet *et al.* 2002). Nevertheless, empirical studies have detected sex-specific dispersal patterns from genetic data successfully, for example, by contrasting the population differentiation of maternally and biparentally inherited markers (Melnick & Hoelzer 1992; Lyrholm *et al.* 1999; Piertney *et al.* 2000) or by applying assignment analyses (Favre *et al.* 1997; Mossman & Waser 1999; Dallimer *et al.* 2002).

The great reed warbler *Acrocephalus arundinaceus* is a migratory songbird breeding in reed lakes over large parts of the Palaearctic (Cramp 1992). Previous analyses of capture–recapture data collected in a 15-km wide study area suggested that great reed warblers do not exhibit any sex

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bias in level of philopatry or short-distance dispersal (Hansson *et al.* 2002). This is in contrast to the general pattern of female-biased dispersal in birds (Greenwood 1980; Weatherhead & Forbes 1994). Here, we use genetic analyses to evaluate whether male and female great reed warblers differ in propensity to disperse at distances outside the restricted area used in the previous study. For this purpose immigrants and philopatric individuals at our Swedish study site, Lake Kvismaren (Bensch 1996; Hasselquist 1998), were scored at 21 microsatellite loci (Hansson *et al.* 2000b). The data set includes 14 cohorts of birds of which the four earliest are used in the analyses to define a reference population of individuals and their alleles. We analyse the data in two ways. First, we use the assignment technique to determine the probability that the genotypes of males and females were originally from the reference population (Favre *et al.* 1997; Cornuet *et al.* 1999). As in other studies using this technique, we assume that the most genetically aberrant individuals (i.e. those with lowest assignment probabilities) have been dispersing the furthest (Favre *et al.* 1997; Mossman & Waser 1999; Dallimer *et al.* 2002). Second, we propose and use a new and simple approach to study dispersal from temporally structured data sets, the 'novel allele technique'. This technique focuses on alleles that are observed in the population for the first time, i.e. 'novel alleles', and the male and female immigrants that carry them into the population. In line with the reasoning for the assignment technique, we assume that immigrants with several novel alleles are more likely to originate from genetically different populations than individuals with no or few novel alleles. Novel alleles will appear in all types of populations of finite size that exchange individuals with other populations, but the number of them are likely to depend on population size and degree of isolation. We expected novel alleles to be relatively common in our study population, because this population is relatively recently founded and has experienced an increase in genetic variation over time (Bensch & Hasselquist 1999; Bensch *et al.* 2000; Hansson *et al.* 2000b).

Materials and methods

Study species and population

The great reed warbler is a long-distance migrant wintering in tropical Africa. From late April, birds return to their north European breeding lakes where males defend territories at the reed-water interface (Cramp 1992). The species is facultatively socially polygynous (Catchpole *et al.* 1985; Dyrce 1986). In our main study area, about 40% of the males form pairbonds with 2–5 females in a season, whereas about 20% of the territorial males remain unpaired (Hasselquist 1998). The great reed warbler

colonized Sweden in the 1960s, and after a gradual population increase during the 1970s and 1980s the current population estimate in Sweden is about 450 singing males (Hansson *et al.* 2000b, 2002). Less than 15 larger breeding localities hold approximately 85% of the total Swedish population (Hansson *et al.* 2002). The nearest populations outside Sweden are in the Baltic countries about 400 km to the east (Estonia and Latvia; Cramp 1992).

We have studied the breeding ecology of great reed warblers at Lake Kvismaren in southern Central Sweden (59°10' N, 15°25' E) between 1983 and 2002 (e.g. Bensch & Hasselquist 1991; Bensch 1996; Hasselquist *et al.* 1996; Hasselquist 1998; Hansson *et al.* 2000a, 2002). More than 95% (100% in most years) of all adult males and females and their chicks have been ringed annually since 1985. Breeding birds and unpaired territorial males were captured in mist nets and marked with individual-specific combinations of aluminium and colour plastic rings. We use the number of nestlings in the brood nine days after the first egg had hatched as a measure of reproductive success (see Bensch 1996; Bensch *et al.* 1998; Hasselquist 1998 for details regarding the field work at Lake Kvismaren).

Microsatellite genotyping

We have collected blood samples from all great reed warblers examined at Lake Kvismaren since 1987 and isolated DNA with phenol/chloroform-isoamylalcohol extraction. We scored the birds for allelic variation at 21 microsatellite loci. The loci were: Aar1–Aar5, Aar8 (Hansson *et al.* 2000b), G61 (Nishiumi *et al.* 1996), Ppi2 (Martinez *et al.* 1999), HrU5 (Primmer *et al.* 1996), Sjr 4 (D. B. McDonalds & W. K. Potts unpublished, see Hansson *et al.* 2000b), Ase7, Ase9, Ase11, Ase18, Ase34, Ase42, Ase44, Ase58, Ase50, Ase60 (Richardson *et al.* 2000) and Ase15 (D. S. Richardson *et al.* unpublished). Primer sequences and amplification conditions are given in Hansson *et al.* (2000b), and Richardson *et al.* (2000; unpublished). The Aar1, G61 and Ase50 loci are located on the sex-specific Z-chromosome, which means that females have one copy only. Observed heterozygosity in the data set varied between 11% at the Ase50 locus and 92% at Ppi2 (B. Hansson unpublished).

Data set and analyses

The present analyses are based on breeding great reed warblers at Lake Kvismaren belonging to the cohorts hatched between 1983 and 1996 ($n = 347$). Because we started to sample DNA in 1987, only a subsample of the breeding birds of the cohorts 1983–85 ($n = 1, 6$ and 18, respectively) are included in the data set, whereas almost all breeders and unpaired males from cohort 1986–96

Cohort	No. of immigrants		No. of novel alleles		No. of immigrants with novel alleles	
	Males	Females	Males	Females	Males	Females
1987	7	7	3† (5.8)	8 (5.2)	3 (3.8)	4 (3.2)
1988	8	8	8 (10.5)	13 (10.5)	6 (6.5)	7 (6.5)
1989	8	4	0 (0)	0 (0)	0 (0)	0 (0)
1990	7	9	3 (3.6)	4 (3.4)	2 (2.1)	2 (1.9)
1991	7	7	2‡ (2.7)	3 (2.3)	2 (2.2)	2 (1.8)
1992	7	11	3 (3.4)	4 (3.6)	3 (2.9)	3 (3.1)
1993	3	10	0 (1.8)	4 (2.2)	0 (1.4)	3 (1.6)
1994	15	10	4‡ (2.1)	0 (1.9)	4 (2.1)	0 (1.9)
1995	5	15	0 (2.4)	5‡ (2.6)	0 (2.4)	5 (2.6)
1996	10	12	1 (2.3)	4 (2.7)	1 (1.8)	3 (2.2)
Total	77	93	24 (34.7)	45 (34.3)	21 (25.2)	29 (24.8)

Table 1 Number of immigrants and novel alleles in different cohorts of great reed warblers at Lake Kvismaren. Expected numbers are given in parenthesis (see Material and methods)

†Two Z-linked alleles. ‡One Z-linked allele.

are included. Each cohort consists of locally hatched previously ringed birds as well as previously unringed immigrants whose age (and thus cohort) was determined using eye and tarsus colouration, and tongue spot distinctiveness (Bensch *et al.* 1998). Unringed birds were identified as immigrants because almost all locally produced nestlings have been marked (95–100%) each year since 1985 (Bensch *et al.* 1998; Hansson *et al.* 2002). In the years 1989 and 1990, 13 female great reed warblers were experimentally introduced to the study site from Lake Tåkern, about 100 km south of Lake Kvismaren (Bensch & Hasselquist 1992). As we intended to examine naturally occurring gene flow in the species, these individuals were not included in the data set.

In the analyses, we used the individuals from the cohorts 1983–86 as a reference population ($n = 48$ individuals). We chose these cohorts because this sample of individuals should be large enough to (i) include alleles that were regularly occurring at Lake Kvismaren and at neighbouring breeding sites (data used when applying the novel allele technique), and (ii) produce robust estimates of allele frequencies (data used when applying the assignment technique).

Assignment probabilities of immigrants of the cohorts 1987–96 ($n = 168$ individuals; see Table 1) were calculated using the software GENECLASS (version 1.0.02; Cornuet *et al.* 1999). We use the Bayesian method because this is believed to be the best choice when there are many rare alleles in the data set (Rannala & Mountain 1997; Cornuet *et al.* 1999). GENECLASS calculates the probability with which the genotype of each immigrant occurs in the reference population, and the output, the 'assignment probability', is given as 'minus the log likelihood'. In this study we will present the assignment probability in terms of the 'log likelihood', which means that a very low value (e.g. -27.8) equals a

very low probability of belonging to the reference population ($10^{-27.8}$). In the assignment analyses we excluded the sex-specific Z-linked loci and based the calculations of assignment probabilities on the 18 autosomal loci.

The novel allele technique proceeded in the following steps. First, alleles occurring among individuals of cohorts 1987–96 but not in the reference population were detected, and the individual and the cohort in which these alleles were observed for the first time were registered (Table 1). Second, the observed number of novel alleles that were carried by male and female immigrants were examined against what was randomly expected from the number of males and females that had entered the population up to and including the allele-specific cohort (e.g. the seven alleles entering the population with individuals of cohort 1990 yielded an expectation of 3.6 alleles for males (seven novel alleles \times 30 immigrant males/58 immigrants) and 3.4 alleles for females ($7 \times 28/58$); see Table 1). In the calculations of the expected number of Z-linked novel alleles in males and females, we also accounted for the unequal number of Z-chromosomes in males and females. Because some individuals carried between two and four novel alleles, we did a similar analysis on an individual basis.

In order to evaluate whether a potential sex bias in dispersal is likely to result in sex-biased gene flow, data of the reproductive success of male and female immigrants are needed. In a previous study of the great reed warbler population at Lake Kvismaren, Bensch *et al.* (1998) have evaluated the reproductive success of immigrants (and philopatric individuals) of both sexes. Therefore, we perform only complementary analyses of the reproductive success (lifetime number of fledglings) of males and females with novel alleles in the present study.

Statistical tests are two-tailed and were carried out in SYSTAT 8.0 (SPSS Inc. 1998).

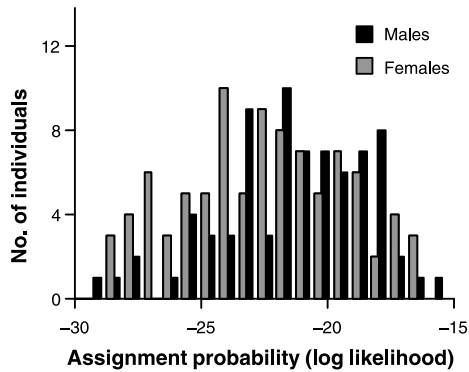


Fig. 1 Frequency distribution of the assignment probability of male (black) and female (grey) immigrant great reed warblers at Lake Kvismaren. Data are for cohorts 1987–96. The assignment probability is given in log likelihood, which means that a very low value (e.g. -27.8) equals a very low probability of belonging to the reference population ($10^{-27.8}$).

Results

Assignment probabilities

In total, 77 males and 93 females of cohorts 1987–96 immigrated to Lake Kvismaren (Table 1). Male immigrants had higher assignment probability (log likelihood \pm SE: -21.2 ± 0.35) than females (-22.1 ± 0.32 ; $F_{1,168} = 4.36$, $P = 0.038$; Fig. 1). This shows that female immigrants on average were less likely to belong to the reference population than males. A visual inspection of the distributions of assignment probabilities might suggest that this difference mainly was an effect of a difference in number of males and females among individuals with very low assignment probabilities (Fig. 1). However, in analyses of the number of males and females in different categories of low and high assignment probabilities this was not supported (test of the number of males and females in (i) two groups of individuals with low and high assignment probabilities, respectively: $\chi^2 = 2.87$, d.f. = 1, $P = 0.090$; (ii) three groups of individuals with low, intermediate and high assignment probabilities, respectively: $\chi^2 = 4.30$, d.f. = 2, $P = 0.117$; and (iii) four groups of individuals with low, intermediate–low, intermediate–high and high assignment probabilities, respectively: $\chi^2 = 3.72$, d.f. = 3, $P = 0.293$).

Novel alleles

There were 159 alleles present at the 21 loci in the cohorts 1983–86. In total, 69 novel alleles were brought into the population by the immigrants of cohorts 1987–96 (Table 1). Each of these novel alleles was found in a single individual of the specific cohort in which they were first observed. Only 24 novel alleles (of which four were Z-linked) were carried by immigrant males, whereas 45 novel alleles (one

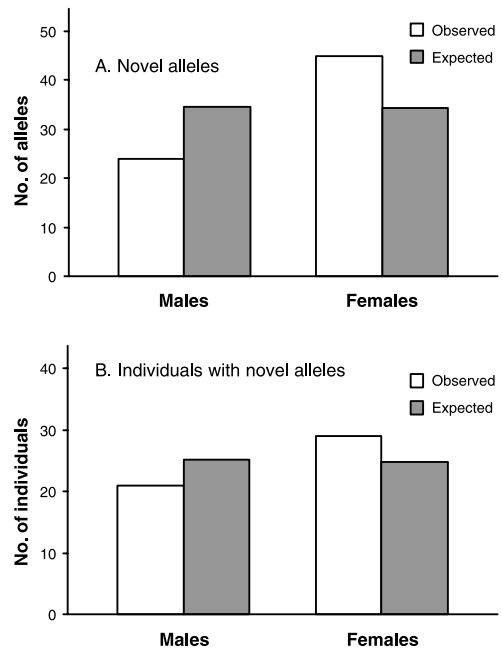


Fig. 2 (a) Observed (white) and expected (grey) number of novel alleles brought into our study population by immigrant males and females. (b) Observed (white) and expected (grey) number of immigrant males and females carrying novel alleles.

Z-linked) were carried by females (Table 1). This distribution differed significantly from a random expectation (34.7 in males and 34.3 in females, respectively; $\chi^2 = 6.64$, d.f. = 1, $P < 0.01$; Fig. 2a). The number of males ($n = 21$) and females ($n = 29$) carrying novel alleles were not, however, significantly different from what was expected by chance (25.2 males and 24.8 females, respectively; $\chi^2 = 1.38$, d.f. = 1, $P > 0.2$; Fig. 2b). These relationships suggest that more females than males carried more than one novel allele. This was indeed the case: 45% of the females and 14% of the males with novel alleles carried more than one novel allele ($\chi^2 = 5.22$, d.f. = 1, $P = 0.022$; Fig. 3). With the exception of two females with three and four novel alleles, respectively, all these individuals carried two novel alleles. In all individuals carrying several novel alleles, the alleles were located on different loci. Mutations could give rise to novel alleles also in locally hatched individuals. However, none of the 69 novel alleles detected in the present study was found in locally hatched individuals ($n = 129$ individuals of cohorts 1987–96).

Immigrant males with novel alleles produced fewer nestlings throughout their lives (mean \pm SE: 2.8 ± 1.08 nestlings per individual; $n = 21$ males) than immigrant females with novel alleles (7.3 ± 1.52 ; $n = 29$ females; $U_{21,29} = 161.5$, $P = 0.004$). This difference between sexes was partly an effect of low mating success among males: nine of the 21 males (43%) failed to attract any breeding partner at our study site, whereas all females were breeding.

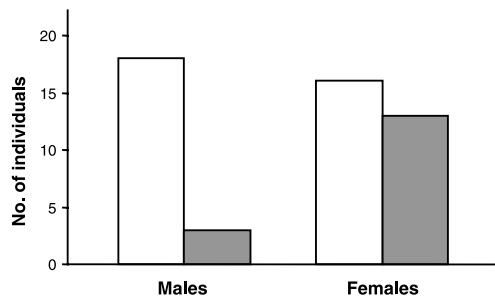


Fig. 3 Number of immigrant males and females carrying one novel allele (white), or more than one novel allele (grey), respectively. With the exception of two females with three and four novel alleles, respectively, all individuals with more than one novel allele carried two novel alleles.

Discussion

The results from the present study on great reed warblers show that female immigrants had lower assignment probability (were less likely to have been sampled in the reference population) than males, and that females carried the majority of novel alleles into the population. The difference in number of novel alleles between the sexes was caused by a strong over-representation of females among the few individuals that carried several novel alleles, and there was a tendency for a corresponding female bias among individuals with low assignment probabilities. It is plausible to assume that immigrants with low assignment probability and several novel alleles are more likely to originate from genetically different populations than individuals with high assignment probability and no or few novel alleles, and similarly that genetically different populations are located farther from the study population than genetically similar populations (cf. Favre *et al.* 1997; Rannala & Mountain 1997; Cornuet *et al.* 1999; Mossman & Waser 1999; Dallimer *et al.* 2002; Goudet *et al.* 2002). Therefore, both the assignment technique and the novel allele technique suggest that female great reed warblers disperse more than males, and especially so at longer distances. The view that the female bias concerns longer dispersal distances is supported by field observations showing that male and female great reed warblers have very similar patterns of short-distance dispersal (distances up to 15 km) (Hansson *et al.* 2002; see also Bensch & Hasselquist 1991; Bensch *et al.* 1998). Male and female immigrants to our study site on average experience similar lifetime reproductive success (Bensch *et al.* 1998), and in the individuals carrying novel alleles males had lower reproductive output than females. Therefore, the gene flow should be, if anything, even more female-biased than the genetic analyses of dispersal suggest. These relationships lead us to conclude that relatively few females give an

important contribution to gene flow between distantly located great reed warbler populations.

In a capture–recapture study of male great reed warblers over the species' whole Swedish breeding range, we found that 16% of the birds dispersed between 70 and 100 km and 2% over 100 km (Hansson *et al.* 2002). These data suggest that males occasionally disperse between most of the breeding sites in Sweden. Consequently, to have a higher rate of long-distance dispersal than males, females have to disperse more frequently within Sweden, as well as occasionally also between more distant localities. There are large populations of great reed warblers in eastern and central Europe (Cramp 1992). Analyses of mitochondrial DNA data have shown that European great reed warbler populations are genetically differentiated, and indicate that the gene flow between these populations is restricted to a degree that permits a structuring of nuclear genes, such as microsatellites (Bensch & Hasselquist 1999). This suggests that the most genetically different immigrants in our study population originated from European populations outside Sweden.

Sex-biased dispersal has been revealed by molecular analyses also in other species of birds and mammals (Melnick & Hoelzer 1992; Favre *et al.* 1997; Lyrholm *et al.* 1999; Mossman & Waser 1999; Pieltney *et al.* 2000; Dallimer *et al.* 2002). Commonly, these analyses concern multipopulation data, and in recent years the assignment technique has gained increased accessibility (Cornuet *et al.* 1999) and popularity (Favre *et al.* 1997; Mossman & Waser 1999; Dallimer *et al.* 2002). The idea of using information of rare alleles in the study of gene flow as we have done in the present study is far from new and is, for example, explored in Slatkin's (1985) rare allele method. However, that method relies on temporally unstructured multipopulation data (Slatkin 1985). To our knowledge, our study is the first where dispersal patterns have been investigated by using data of novel alleles entering a population over time. We suggest that this simple approach may be useful in revealing dispersal patterns among species in general, provided the detected number of novel alleles are sufficient for powerful analyses. Therefore, the usefulness of the novel allele technique will depend on the ability to include a very large proportion of the population in the data set, the number of scored markers, and their variability, and on the population structure and dynamics of the studied species.

A qualitative difference between the assignment technique and the novel allele technique is that an allele is considered to be novel only in the individual that first carries it to the population, whereas a rare allele will cause low assignment probabilities in all its bearers, e.g. within a pedigree. This distinction may be important in studies of populations that are continuously changing their genetic content over time (as the studied great reed warbler population; Hansson *et al.* 2000b). In such situations, the novel

allele technique should be as likely as the assignment technique to detect individuals actually dispersing between genetically differentiated populations (i.e. individuals that are genetically different because of dispersal *per se*), but will be less likely to include their descendants dispersing (between subpopulations) within the population. This scenario helps to explain why we found that the novel allele technique gave stronger statistical support for a sex bias among the presumed long-distance dispersers than did the assignment technique. Studies of other populations and species are needed to evaluate the general usefulness of the novel allele technique in detecting immigrants originating from genetically different populations. Methods quantifying infrequently occurring long-distance gene flow are highly requested, since this type of gene flow is especially important for the long-term persistence of populations (Ingvarsson 2001; Keller *et al.* 2001).

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