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Hansson, Bengt; Bensch, Staffan; Hasselquist, Dennis

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PO Box 117
221 00 Lund
+46 46-222 00 00

LETTER

Heritability of dispersal in the great reed warbler

B. Hansson*, S. Bensch

and D. Hasselquist

Department of Animal Ecology,
Lund University, Ecology
Building, SE-22362 Lund,
Sweden

*Correspondence: E-mail:
bengt.hansson@zooekol.lu.se

Abstract

Dispersal is commonly considered to be a condition-dependent behaviour with no or low heritability. Here, we show that dispersal in the great reed warbler (*Acrocephalus arundinaceus*) has a high heritability. Analyses of capture–recapture data of male great reed warblers gathered from the species' whole Swedish breeding range revealed a remarkable offspring–parent resemblance in dispersal behaviour (philopatry vs. inter-population dispersal). Also, the degree of dispersal differed between cohorts, which shows that dispersal was partly conditionally dependent. The offspring to mid-parent estimate of heritability was 0.50. In a previous study of the same data set of male offspring, we did not detect associations between dispersal and several relevant environmental, parental and offspring condition factors. Thus, our results indicate that variation in dispersal partly has a genetic basis in great reed warblers.

Keywords

Bird, dispersal, heritability.

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INTRODUCTION

Dispersal plays a central role in evolutionary biology, ecology and conservation biology (Ronce *et al.* 2001). In several species the decision to disperse is triggered by some external factors, such as high population density or habitat change (Harrison 1980; O'Riain *et al.* 1996; Verhulst *et al.* 1997). This has led to a common generalization that dispersal is a condition-induced trait with no or low heritability (Ims & Hjermann 2001). In contrast, high heritabilities of dispersal traits have been documented in laboratory studies of wing-dimorphic insects (Roff & Fairbairn 2001), and field studies have shown that dispersal strategies frequently evolve in response to natural selection in such species (Thomas *et al.* 2001).

Among vertebrates there is so far no well-documented case of heritability of dispersal (Greenwood *et al.* 1979; van Noordwijk 1984; Roff & Fairbairn 2001). This may in part reflect that dispersal heritabilities will be biased if evaluated from data gathered within study plots that are small relative to the dispersal distance of the species (van Noordwijk 1984). The reason for this is that parents and offspring at nest sites located peripherally in a study area will on average be associated with longer dispersal distances than will individuals at nest sites in the core of that area. Such spurious correlations between parent–offspring dispersal distances will result in erroneous conclusions about dispersal heritabilities (van Noordwijk 1984). Hence, unbiased

estimates of the heritability of realized dispersal can only be obtained from data of long-distance dispersal between populations, but such data are intrinsically difficult to collect (Koenig *et al.* 1996).

The great reed warbler (*Acrocephalus arundinaceus*) is a songbird breeding in the reed–water interface of productive lakes in Europe and Asia. In a research programme covering three adjacent breeding lakes in Sweden initiated in 1983, we have routinely marked almost all of the locally produced nestling great reed warblers (Bensch *et al.* 1998; Hansson *et al.* 2002a). As a consequence, parents entering these breeding lakes could be assigned as either philopatric (ringed as nestling in the specific lake) or dispersing (unringed or ringed elsewhere; Bensch *et al.* 1998; Hansson *et al.* 2002a).

To study variation in inter-population dispersal of great reed warblers, we recaptured surviving male progeny of these philopatric and dispersing parents over the species' whole Swedish breeding range. We examined *c.* 50% of the territorial male great reed warblers in Sweden each of three study years (1998–2000), which resulted in the recapture of a high proportion of the surviving male progeny hatched and marked in the years 1996–1998 (Hansson *et al.* 2002a, b). Most of these offspring either became philopatric or dispersed to closely situated breeding lakes (Hansson *et al.* 2002a). The proportion of dispersing offspring differed significantly between different cohorts (hatch-years), but did not associate with other relevant environmental, parental

and offspring condition factors (Hansson *et al.* 2002b). In the present paper, we provide data showing that dispersal in the great reed warbler has a high heritability.

MATERIAL AND METHODS

The great reed warbler is a migrant bird wintering in tropical Africa. During the breeding season, the species inhabits reed beds of wetlands in large parts of the Palearctic (Cramp 1992). Great reed warblers are facultatively socially polygynous (Cramp 1992; Hasselquist 1998). Currently, the population in Sweden consists of about 450 singing males of which 85% are found at less than 15 localities (Hansson *et al.* 2002a).

We have studied the ecology of the great reed warbler at three nearby, similarly sized breeding lakes in southern Central Sweden (59°10' N, 15°25' E), two (Fågelsjön and Rysjön in the Kvismare area) between 1983 and 2001, and one (Segersjö) between 1987 and 2001 (see map in Hansson *et al.* 2002b). We trapped birds in mist nets and ringed them with individual-specific combinations of aluminium and colour plastic rings. At examination, size and body mass were measured. The positions of the nests within territories were marked during nest building (and in a few cases during incubation or feeding). We visited the nests approximately every third day to get data of clutch size, hatching success and number of fledglings. Nestlings were ringed 9 days after the hatching of the first chick in the nest. In the three populations, almost all locally produced nestlings have been marked (90–100%) each year during the last decade (Bensch *et al.* 1998; Hasselquist 1998; Hansson *et al.* 2002a).

To study variation in inter-population dispersal of great reed warblers, we visited almost all larger breeding populations (≥ 5 males) in Sweden in 1998–2000 (Hansson *et al.* 2002a, b). We opportunistically searched for territorial males and trapped individuals by using mist nets and song playback. Females, that are difficult to capture, were not included in the study. In the analyses, we included males ringed as nestlings in our main study area (Fågelsjön, Rysjön and Segersjö) between 1996 and 1998, and that were encountered (within Sweden) as adults at an age of 1 or 2 years (i.e. the ages at which most individuals breed for the first time; Bensch *et al.* 1998). We confirmed that the social parents also were the genetic parents of 39 of the 48 offspring included in the present study. This was achieved by using either DNA-fingerprinting (Hasselquist *et al.* 1996) or microsatellite genotyping (data from five loci; D. Arlt *et al.*, unpublished manuscript). Moreover, extra-pair paternity is very unlikely to have occurred in any of the nine remaining nestlings, because the overall frequency of extra-pair young is low (3% of all young) in our study area (Hasselquist *et al.* 1996).

The association in dispersal strategies between offspring and parents was evaluated with generalized linear models (SAS genmod module with binomial error distribution, logit link function, and type 3 option; SAS Institute 1990) by treating dispersal as a two-state variable (philopatry scored 0; inter-population dispersal scored 1). We included cohort in the models because it was known from a previous analysis that this variable significantly explained variation in dispersal (Hansson *et al.* 2002b). We could not include the interaction term, cohort \times parental dispersal behaviour, in the models because data were lacking for one of the nine cohort–dispersal combinations (SAS Institute 1990): no offspring raised in 1997 by pairs of philopatric parents were encountered (Fig. 1). Therefore, we also analysed the

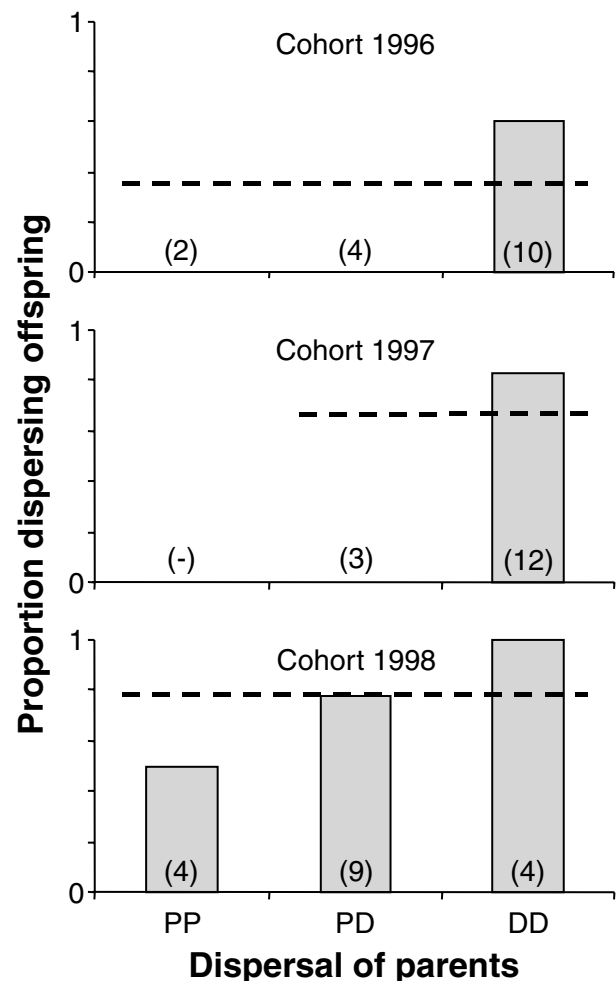


Figure 1 Proportion of dispersing male offspring of pairs of philopatric (P) and dispersing (D) great reed warblers. Panels are for different cohorts. Mean proportion of dispersers (dotted line), and number of offspring (in parenthesis), are shown. The proportion of dispersing individuals differed significantly between cohorts ($P < 0.001$) and parental dispersal categories ($P < 0.001$).

offspring–parent association in dispersal for each cohort separately. Some offspring were full-siblings. To avoid problems with non-independence, we analysed a partial data set that included only the first offspring from each family that was encountered in the census. Models were not or very little over-dispersed (range of scale parameter: 0.83–1.08), and thus two-tailed significance was assigned with a chi-square-test (Crawley 1993).

We tested the directional hypothesis that the proportion (f) of dispersing offspring varied between categories of dispersing (D) and philopatric (P) parents as $f_{DD} > f_{DP} > f_{PP}$. This was performed by using a two-tailed (thus we did not *a priori* exclude the possibility that $f_{DD} < f_{DP} < f_{PP}$) ordered heterogeneity test (Rice & Gaines 1994), with non-parametric correlation and generalized linear model as underlying test statistics.

Heritability of dispersal was estimated by regressing progeny phenotype on mid-parent, paternal and maternal phenotype, respectively (mid-parent: $b = b^2$; paternal/maternal: $b = b^2/2$; Falconer & Mackay 1996).

RESULTS

We ringed 509 nestlings in the three lakes in our main study area in 1996–1998. Assuming equal sex-ratio among nestlings (Westerdahl *et al.* 1997), and a survival rate to adulthood of 30% (Hansson *et al.* 2002a), we could calculate that in total 76 male offspring were expected to survive to breeding age. We encountered 48 previously ringed male progeny from these cohorts during our census of the adult population in Sweden, i.e. 63.2% of the expected number of survivors. Of the 48 encountered males, 39.6% returned to breed in the natal lake, i.e. they were philopatric, whereas 60.4% dispersed to breed elsewhere. The 48 male offspring came from 36 different broods.

The proportion of dispersing male offspring differed significantly between categories of parents with different dispersal behaviours (generalized linear model, $\chi^2 = 19.5$, d.f. = 2, $P < 0.001$; $n = 48$) and between cohorts ($\chi^2 = 18.3$, d.f. = 2, $P < 0.001$; Fig. 1). Overall, the lowest proportion of dispersers was produced by pairs of philopatric parents, and the highest proportion of dispersers was produced by pairs of two dispersing parents, respectively (ordered heterogeneity test, $r_s P_c > 0.999$, $k = 3$, $P < 0.001$; Fig. 1). When cohorts were analysed separately, the parent–offspring association in dispersal was statistically significant in 1996 and 1997 (generalized linear model, cohort 1996: $\chi^2 = 7.71$, d.f. = 2, $P = 0.021$; 1997: $\chi^2 = 8.28$, d.f. = 1, $P = 0.004$; 1998: $\chi^2 = 3.47$, d.f. = 2, $P = 0.176$). Also, the proportion of dispersing offspring differed significantly between parental dispersal categories when only the first-encountered offspring in each family was included in the

data set (parental dispersal category: $\chi^2 = 13.2$, d.f. = 2, $P = 0.001$; cohort: $\chi^2 = 16.9$, d.f. = 2, $P < 0.001$; $n = 36$).

The dispersal strategy of the offspring associated both with that of their fathers (father's dispersal strategy: $\chi^2 = 13.7$, d.f. = 1, $P < 0.001$; cohort: $\chi^2 = 15.3$, d.f. = 2, $P < 0.001$; $n = 48$) and their mothers (mother's dispersal strategy: $\chi^2 = 4.9$, d.f. = 1, $P = 0.027$; cohort: $\chi^2 = 7.1$, d.f. = 2, $P = 0.029$; $n = 48$).

The estimated heritability of dispersal ($b^2 \pm \text{SE}$) was 0.50 (± 0.19 , mid-parent regression; $n = 48$). In this data set, there was no evidence of assortative mating of pair-mates in respect to dispersal ($\chi^2 = 1.92$, d.f. = 1, $P = 0.17$; $n = 36$). Thus, this factor should not confound the estimated heritability (Falconer & Mackay 1996). The dispersal heritability between offspring and fathers was similar to that between offspring and mothers (father: 0.60 ± 0.29 ; mother: 0.62 ± 0.33 ; $n = 48$).

There was statistical consistency in dispersal categories within groups of full-siblings (shared dispersal behaviour in four of six sibling dyads, and in two of three triads; exact probability test, $P = 0.006$; calculated by using the average frequency of dispersing and philopatric offspring). The dispersing and philopatric offspring did not differ in body mass and size measures when examined as adults (mass, $t = 0.81$, $P = 0.42$; amount of body fat, $t = 0.47$, $P = 0.64$; length of wing, $t = 0.58$, $P = 0.57$; bill, $t = 0.47$, $P = 0.64$; tarsus, $t = 0.66$, $P = 0.52$; $n = 46$).

DISCUSSION

Our analyses revealed a remarkable offspring–parent resemblance, and a high heritability, in the dispersal behaviour of male great reed warblers. Because we analysed dispersal as a two-state character, i.e. philopatry vs. inter-population dispersal, our results do not suffer from the methodological problems characteristic for studies of heritability of dispersal distances within small study sites (van Noordwijk 1984). Therefore, our study provides a novel example of heritable dispersal in vertebrates studied in the wild.

This dispersal heritability can arise both from genetic and environmental components. In a previous analysis of the same data set of male offspring, we have shown that there is no association between dispersal and several relevant environmental, parental and offspring condition factors, i.e. hatching date, body size and mass at fledging, brood size, age of the parents, quality of the territory of the parents, social status of the mother, and breeding lake ($P > 0.19$ in generalized linear models including cohort; Hansson *et al.* 2002b). Also, the dispersing and philopatric offspring had similar body mass and size when examined as full-grown adults (this study). Moreover, maternal effects seem not to be decisive for dispersal, as both the father's and the mother's dispersal strategy predicted dispersal of the male

offspring (and the father's strategy actually showing the strongest statistical relationship). Consequently, despite considerable effort, we were unable to associate dispersal with spatial and parental effects such as hatching site and maternal quality (Hansson *et al.* 2002b; this study). Together, these results suggest that dispersal has a genetic component in great reed warblers. However, dispersal was also partly affected by environmental factors in the species, as indicated by the significant difference in degree of dispersal between cohorts.

So why then might dispersal be partly genetically determined in great reed warblers? One explanation could be that dispersal polymorphisms are evolutionarily stable, and therefore should persist, in species inhabiting heterogeneous environments (Cohen & Levin 1991; McPeck & Holt 1992; Mathias *et al.* 2001). According to this theory, spatial variation in patch quality favours philopatry, whereas temporal quality fluctuations favour inter-population dispersal. The breeding conditions in the lakes preferred by great reed warblers fluctuate both in time and space. This is likely to be an effect of site-specific fluctuations in nest predation and inter-specific competition for food (Hansson *et al.* 2000a; Bensch *et al.* 2001), habitat alterations caused by, e.g. winter damage of reed, variation in water depth and occasional restoration efforts of wetlands (Hertzman *et al.* 1999), and density-dependent fecundity (Hansson *et al.* 1997; Bensch *et al.* 1998). An alternative explanation may apply to species that – like the great reed warbler (Hansson *et al.* 2000b) – have experienced recent range expansions (Thomas *et al.* 2001). In such species, dispersal could be selected for at the edge of the expanding range, where unsaturated and unoccupied breeding localities are available for dispersers (e.g. in Sweden in the case of the great reed warbler; Hansson *et al.* 2000b), whereas philopatry is selected for in the saturated core area (Thomas *et al.* 2001). According to this scenario, where dispersal evolves in different directions in different parts of the breeding range, genes expressing philopatry and dispersal, respectively, will coexist within a population because of gene flow.

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