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Predictors of natal dispersal in great reed warblers: results from small and large census areas

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For most species, it is currently not known whether individual characteristics and population parameters affecting dispersal distances within the local population are also affecting dispersal of individuals emigrating longer distances. We evaluated this in the great reed warbler *Acrocephalus arundinaceus* by analysing data of natal dispersal distances within (1) the local hatching area in southern Central Sweden and (2) the species' whole breeding range in Sweden. The different scales gave conflicting results. Site of birth was the main predictor of natal dispersal distance in the local census area, whereas in the larger census area the dispersal distance differed significantly between hatching years. Previous studies have shown that the recruitment rate of great reed warblers within the local study area differs between hatching years and also that it declines during the course of the breeding season. It was not known, however, whether these relationships reflected variation in survival or dispersal. The results from the present study suggest that the differences in local recruitment rate between hatching years is partly caused by annual variation in emigration rate, whereas the decline in local recruitment rate with season mainly reflects mortality of late-hatched nestlings. Our study shows a twofold advantage of a large census area when studying dispersal. First, predictors of longer-distance dispersal will be revealed and, second, the variation in local recruitment rate can be separated into the two components, survival and dispersal.

Dispersal may result in gene flow between populations and is therefore a key parameter in evolutionary biology, population genetics and conservation (Hanski and Gilpin 1997, Clobert et al. 2001). It is well established that size of the census area is crucial when evaluating dispersal distances in a population or a species and that studies based on data from too small census areas will underestimate actual distances (Moore and Dolbeer 1989, Koenig et al. 1996). In contrast, for most species it is not known whether the predictors of dispersal, i.e. individual characteristics and population parameters associated with dispersal, are scale sensitive (Reed and Oring 1993). This uncertainty probably stems from the intrinsic difficulties in keeping track of individuals over large potential breeding areas and that detailed and long-term field studies are needed to produce useful breeding data.

We have previously reported on the distribution of natal and breeding dispersal distances in the migratory great reed warbler *Acrocephalus arundinaceus* from an extensive capture-recapture study within the species' whole breeding range in Sweden (Hansson et al. 2002). Analyses of these data show that Swedish great reed warblers exhibit among the highest levels of philopatry observed in non-tropical passerines (Weatherhead and Forbes 1994, Bensch et al. 1998, Hansson et al. 2002) and that the majority of individuals that do disperse settle at nearby breeding sites (Hansson et al. 2002).

In the present study, we examine whether the predictors of natal dispersal in great reed warblers differ when the analyses are based on data gathered from (1) our local study area, at Kvismaren and Segersjö (maximum dispersal distance 15 km; Bensch 1996, Hasselquist 1998), and (2) the species' Swedish breeding range

(maximum dispersal distance 180 km; Hansson et al. 2002), respectively. This is important to evaluate both for the general understanding of inter-population processes (Hanski and Gilpin 1997, Clobert et al. 2001) and to understand results from life-history analyses based on recruitment rates within small local populations (Barba et al. 1995, Verhulst et al. 1997, Lambrechts et al. 1999).

Materials and methods

Study species and field methods

The great reed warbler breeds in lakes and marshes in the Palaearctic and winters in tropical Africa (Cramp 1992). In Sweden, the majority (85%) of about 450 males breeds in less than 15 populations with 10 or more males (Fig. 1A; Hansson et al. 2002).

At Kvismaren, southern Central Sweden (59°10'N, 15°25'E), we have studied the species' breeding ecology between 1983 and 2000. Since 1985 almost all breeding individuals and fledged young have been ringed with individual-specific combinations of one aluminium and several colour rings (Bensch 1996, Hasselquist 1998). In this area, the birds breed at two adjacent marshes (Fig. 1B). Between 1987 and 2000, we also studied the species at Segersjö, located approximately 11 km east of Kvismaren (Fig. 1B; Hansson et al. 2002). At this locality, the census effort was somewhat lower than at Kvismaren and some breeding birds, especially females,

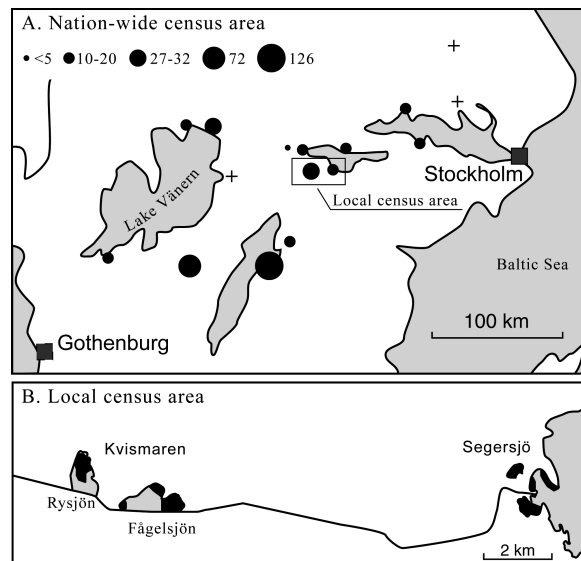


Fig. 1. (A) Map of the nation-wide census area showing the number of great reed warbler males in 1999 at localities included in the census. Localities with small but stable populations not included in the census are indicated (+). (B) Map of the local census area showing reed beds preferred by breeding great reed warblers (black).

might have escaped our attention in the first study years (Hansson et al. 2002).

To evaluate the species' dispersal pattern over a larger census area, we visited most of the species' breeding localities in Sweden in 1998 and 1999 and captured and examined as many territorial great reed warbler males as possible. We examined approximately 56% of the Swedish great reed warbler males breeding in these two years (Hansson et al. 2002). In 2000, the census was restricted to the four largest and three smaller populations, and about 30% of the Swedish male population was examined. We captured few females outside Kvismaren and Segersjö (Hansson et al. 2002).

Analyses

In the analyses, we include great reed warblers ringed as nestlings at Kvismaren or Segersjö that were encountered at an age of one or two years, i.e. the ages at which most individuals breed for the first time (Bensch et al. 1998). For birds examined in more than one year, we only considered the first breeding occasion. In the analyses of natal dispersal within Kvismaren and Segersjö, from here on referred to as the "local census area", we included males and females hatched between 1990 and 1998. In the analyses of natal dispersal within Sweden, from here on referred to as the "nation-wide census area", we included males that hatched in 1996–1998.

Possible predictors of natal dispersal were evaluated by general linear models with dispersal distance (\log_{10} -transformed) as the dependent variable (Sokal and Rohlf 1995). Of the independent variables used to test for association with dispersal distance, hatching year (1990–1998 in the local census area; 1996–1998 in the nation-wide census area), brood size (3–6 chicks; one brood with one chick only was excluded from the analyses), the mother's harem status during nestling feeding (primary or secondary female), site of birth (the two breeding lakes at Kvismaren were treated separately), age of the parents (one year old or older), and sex (only for the local census area analyses) were treated as categorical variables. Nestling body mass and size (length of the innermost primary flight feather) were standardized for age (days after hatching) and time of day when examined (Westerdahl et al. 2000). Territory attractiveness rank was calculated according to Bensch (1996) and Hasselquist (1998). Statistically significant relationships and trends from the general linear models (see Results) were very similar (results not shown) when tested with non-parametric statistics (Spearman's rank or Kruskal-Wallis tests; Siegel and Castellan 1989) and with logistic regression (treating dispersal as a two-state categorical variable: breeding in

the lake of birth or breeding outside the lake of birth; SAS 1990). All tests are two-tailed.

Results

Dispersal within the local study area

There was no statistical difference in dispersal distance between nestlings hatched in different years ($F_{8,136} = 0.86$, $P = 0.55$; Fig. 2A). Neither was variation in dispersal distance explained by hatching date ($F_{1,137} = 0.71$, $P = 0.40$), brood size ($F_{3,141} = 1.39$, $P = 0.25$), age of the parents (father: $F_{1,138} = 0.01$, $P = 0.93$; mother: $F_{1,131} = 2.03$, $P = 0.16$), harem status of the mother ($F_{1,126} = 0.23$, $P = 0.63$), territory attractiveness rank ($F_{1,126} = 1.10$, $P = 0.30$) nor size of nestling (standardized mass: $F_{1,135} = 1.15$, $P = 0.29$; standardized feather length: $F_{1,133} = 1.91$, $P = 0.17$). Furthermore, males and females showed similar dispersal distances ($F_{1,142} < 0.001$, $P = 1.00$). There was, however, a pronounced difference in dispersal distance between birds born at different sites ($F_{2,142} = 9.95$, $P < 0.001$), with birds hatched at Segersjö dispersing longer distances (Fig. 2B). Adding the previously tested parameters (one by one) to a multiple regression model including site of

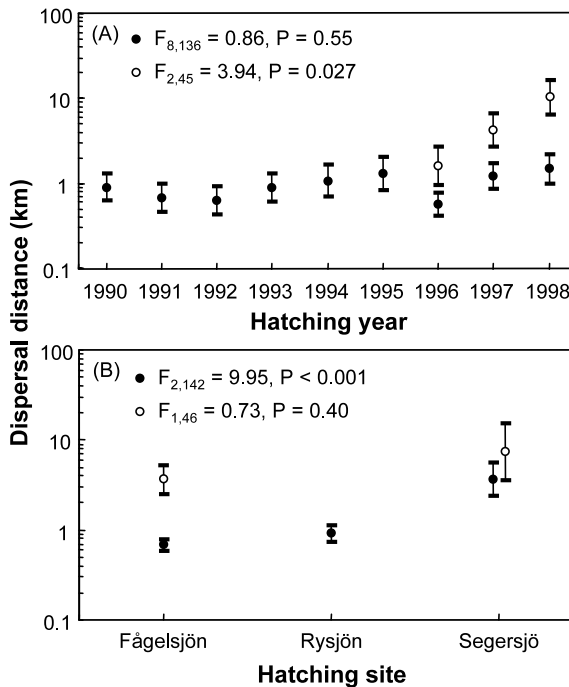


Fig. 2. Natal dispersal distances (mean \pm s.e.) of great reed warblers hatched in different years (A), and at different localities (B): males and females within the local census area (filled circles), and males within the nation-wide census area (open circles). Note that dispersal distances are presented on a logarithmic scale.

birth revealed no further significant relationships ($P > 0.1$ in all cases).

The relationship between dispersal distance and site of birth was also statistically significant when we restricted the data set to the 1995–1998 cohorts, i.e. including birds entering the population as adults in years when the vast majority of breeding males ($> 95\%$) and females ($> 80\%$) were examined also at Segersjö (males and females included: $F_{2,67} = 6.88$, $P = 0.002$; only males included: $F_{2,39} = 4.17$, $P = 0.023$). Hence, the relationship between dispersal distance and site of birth was not an effect of a lower proportion of the breeders being identified at Segersjö than at Kvismaren early in our study.

Dispersal of males within the nation-wide census area

In the data set of male great reed warblers dispersing within the nation-wide census area, there was a significant difference in dispersal distance between birds hatched in different years ($F_{2,45} = 3.94$, $P = 0.027$; Fig. 2A). The resighting rate was similar between hatching years (16.1–18.6%; $\chi^2 = 0.22$, d.f. = 2, $P > 0.5$). Hatching date and territory attractiveness rank tended to be negatively correlated with dispersal distance ($F_{1,46} = 3.54$, $P = 0.07$, and $F_{1,36} = 3.48$, $P = 0.07$, respectively). Brood size ($F_{3,44} = 0.24$, $P = 0.87$), age of the parents (father: $F_{1,46} = 0.02$, $P = 0.89$; mother: $F_{1,46} = 0.29$, $P = 0.60$), harem status of the mother ($F_{1,46} = 0.20$, $P = 0.66$), nestling size (standardized mass: $F_{1,44} = 0.001$, $P = 0.98$; standardized feather length: $F_{1,44} = 0.02$, $P = 0.90$) and site of birth ($F_{1,46} = 0.73$, $P = 0.40$) were not associated with dispersal distance.

When included in the same multiple regression model as hatching year, both hatching date and territory attractiveness rank lost their tendency to explain dispersal distance ($F_{1,44} = 1.94$, $P = 0.21$, and $F_{1,34} = 0.98$, $P = 0.33$, respectively). There was no statistically significant difference in mean hatching date between years ($F_{2,45} = 1.61$, $P = 0.21$).

Discussion

To date, most evaluations of possible predictors of natal dispersal come from data gathered within relatively small areas (Greenwood et al. 1979, Arcese 1989, Verhulst et al. 1997), whereas studies including long-distance dispersal between well separated breeding localities are rare (Wiggett and Boag 1987, Hanski and Gilpin 1997, Negro et al. 1997). Here we present evidence that the variation in dispersal distance in the great reed warbler is associated with different parameters in small and large census areas.

Analyses of data from the local census area (maximum dispersal distance 15 km) identified site of birth as the sole predictor of natal dispersal distance: great reed warblers hatched at Segersjö more frequently changed site between hatching and breeding, and dispersed longer distances, than birds hatched at Kvismaren. In contrast, there was a significant difference in dispersal distance between cohorts in the nation-wide census. In one of the few studies comparing dispersal data at two geographical scales, male and female spotted sandpipers *Actitis macularia* were as likely to settle within the small local census area (maximum dispersal distance < 1 km) but on a somewhat larger scale (maximum dispersal distance 4 km) more males than females returned (Reed and Oring 1993). Thus, our study and Reed and Oring (1993) emphasise that predictors of dispersal between populations should be evaluated from data including longer-distance dispersal and that small scale data may be misleading in revealing inter-population processes.

Previous life-history analyses of within-population data in great reed warblers and other species (Barba et al. 1995, Verboven and Visser 1998) have shown that the recruitment success declines during the course of the breeding season (Bensch 1996, Hansson et al. 2000). This pattern may either result from high levels of mortality, or high levels of dispersal, among late-hatched offspring (Barba et al. 1995, Verhulst et al. 1997, Lambrechts et al. 1999). In our data set, there was no indication that late-hatched birds dispersed longer than early-hatched ones. If anything, the relationship was the opposite, with a negative trend between dispersal distance and hatching date when annual variation in dispersal distance was not controlled for. Hence, the decline in local recruitment rate over the breeding season (Bensch 1996, Hansson et al. 2000) is likely to be caused by high mortality among late-hatched offspring (rather than by dispersal). Following the same line of argument, the different dispersal distances, and similar resighting rates, within the nation-wide census area of young hatched in different years suggest that the previously observed difference between cohorts in recruitment rate within the local census area (Bensch 1996) mainly was an effect of variation in dispersal, as opposed to survival.

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Badge size, paternity assurance behaviours and paternity losses in male house sparrows

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Male quality may influence both the outcome of sperm competition and female faithfulness. In male house sparrows *Passer domesticus*, the size of the black throat patch (badge) signals dominance and perhaps attractiveness. So far, however, no study has reported any significant relationships between badge size, paternity and paternity assurance behaviours in this species. We found that the time mates spent together at the nest was positively correlated with badge size. Furthermore, although paternity losses were influenced by both the time spent at the nest and within-pair copulation frequency, we found no relationship between copulation rate and badge size. It seems therefore

that copulation frequency served as a paternity assurance behaviour, whereas the time mates stayed together at the nest may have reflected male attractiveness. Alternatively, females may have decided to stay with large-badged males because they were better able to protect them from harassment by strange males. We also found that paternity losses were related to male badge size; average-badged males cuckolded were more often than males with smaller or larger badges. We suggest that average-badged males suffered higher paternity losses because they had different time allocation strategies than other males.