Juvenile Reed Warblers Acrocephalus scirpaceus see the world but settle close to home

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In this paper we analyse distances of juvenile movements of Reed Warblers and their natal dispersal distances. This analysis showed that, in spite of high mobility in the postfledging period (mean distance 10.4 ± 2.39 [SE] km, range 0.01–26.8 km, median 9.35 n = 16), the birds breed in the subsequent year rather close to the natal site: range 0.01 – 3.66 km (males, n = 32), and 0.09–19.90 km (females, n = 20). They breed significantly closer to the natal site than predicted by the model of their random settling within our study area (Wilcoxon matched pairs test: z = -2.798, P < 0.005 for males and z = -2.346, P < 0.019 for females). We hypothesise that during postfledging flights juvenile Reed Warblers not only perform exploration aimed at selecting the site of breeding in the subsequent year, but also create the navigational target for return migration in spring. This target is significantly larger than the patch of reeds where the birds breed in the subsequent year. Broad movements in the postfledging period and a much smaller distance of natal dispersal suggest that postfledging movements are a more complex event than just the search for future breeding sites.

Key words: natal dispersal, postfledging movements, migration, exploration, Reed Warbler.

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1. Introduction

During the short period between fledging and the onset of autumn migration hatching-year birds have to undergo several stages of their development. An important event in this period is juvenile dispersal, i.e. active movements of young birds

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in the broad vicinity of the natal site in the pre-migratory period. The main reason behind juvenile dispersal is believed to be the search and selection of future breeding sites, given that the individual survives and returns to breed in this area (Berndt & Sternberg 1968). Thus, if breeding site selection takes place during postfledging movements before autumn migratory departure, one may assume that juvenile dispersal is responsible for the spatial distribution of individuals observed during the first breeding of yearlings (Greenwood & Harvey 1982).

Another reason that might force juveniles to perform active movements in the pre-migratory period may be the necessity to create the navigational goal for return migration in spring. Some current hypotheses assume that juveniles need to create a mosaic map of their natal area to be able to navigate back to it when returning to the breeding area from winter quarters (Mouritsen 2003, Wallraff 2005). Irrespective of the physical nature of the parameters used, these concepts emphasize the necessity to perform broad exploratory flights for creating a navigation target. Creation of such a familiar area should happen before autumn migratory departure during postfledging movements when the birds study the vicinity of their future breeding site by exploratory flights (Baker 1993).

In this study, we analysed captures and recaptures of breeding Reed Warblers *Acrocephalus scirpaceus* in order to test for the possible role of postfledging movements of juveniles for selecting the future breeding site and creating a familiar area that could be the target of spring migration in the future.

We hypothesise that if the main aim of postfledging movements is the breeding site selection, the range of movements of juveniles in the pre-migratory period should be roughly comparable to the natal dispersal distances. However, if the main function of these movements is to study the vicinity of the natal area to form the target of spring migration, and search for suitable breeding habitats is of secondary importance, the range of postfledging movements and natal dispersal distances may differ considerably.

2. Material and methods

The study was done on the Courish Spit on the Baltic Sea (55°00′–55°09′ N, 20°34′–20°51′ E) in 2002–2007. The Courish Spit is a long and narrow peninsula running along the north-east – south-west axis, ca. 98 km long that separates the Courish Lagoon from the Baltic Sea. Several reedbed plots where the study was conducted are shown in Fig. 1 and denoted by letters A, B, C, D, E. The pattern of reedbeds varies from relatively small patches around small lakes (B, D, E [0.4, 0.3, 0.5 ha, respectively]) to the reed belt along the shore of the Courish Lagoon (A, C [60, 6.5 ha, respectively]), with small gaps (up to 700 m).

In 2002–2006 we ringed chicks in all nests found in the study plots. In 2003–2007 we captured breeding adults during feeding their chicks by semi-automatic traps (Zimin & Artemyev 1981). Nest coordinates were recorded by GPS (Garmin "Map-60") to the nearest 4–6 m.

The data on the range of postfledging movements were obtained from recaptures of previously ringed birds by two methods:
1) in mist-nets (2004–2005) situated in Rybachy (plot C) in the standardised trapping project (Bairlein 1995). Birds previously ringed as nestlings in all plots were captured in the daytime, the overall net length was 150 m;

2) by tape-luring. This method was used at night in a habitat atypical of Reed Warblers (sand dunes) and made it possible to attract and capture the birds during postfledging movements between the reedbed patches on the Courish Spit (Bulyuk et al. 2001, Mukhin 2004). The song was played back by a car audio system with two 30 W loudspeakers located near mist-nets. The playback site was located in the middle between the two largest reedbeds. The next reed plots were located 6 km to the NE (site A, Fig. 1) and 10 km to the SW (site B, Fig. 1) of the capture site (Mukhin et al. 2008).

To decide whether males and females select their breeding sites non-randomly in respect to their natal site, we compared the frequency distribution of natal dispersal distances with a null model, which assumed that distribution of breeding birds was random (Chernetsov et al. 2006). To construct this model, we calculated the distances between all possible pairs of nests from which Reed Warbler chicks suc-
cessfully fledged in year $i$ and where a male or a female was captured in the year $i + 1$. This yielded a frequency distribution of predicted natal dispersal distances if Reed Warblers returned randomly to any site in our study area. The predicted distribution was already corrected for recapture effort, as only nests where at least one parent was captured were included in the analyses. It showed the pattern that should emerge if the birds settle randomly at any site within our study area.

Simulations were run separately for males and females, because: (i) recapture probability was sex-related, and (ii) natal dispersal distances may differ between the sexes (Greenwood 1980, Sokolov 1997, Morton 1997). To increase the sample size of the observed natal dispersal distances, we included the birds captured in the year $i + 2$, if they were recorded as breeding in two subsequent years. We believe that as adults show a high degree of breeding site fidelity, it is safe to assume that the nest in the year $i + 2$ was built within a hundred metres from the nest in the year $i + 1$. The distance between the breeding sites in subsequent years should be much less than the natal dispersal distance, as breeding site fidelity in passerines is generally known to be much greater than natal site fidelity (Greenwood & Harvey, 1982, Morton 1997, Paradis et al. 1998, Hansson et al. 2002).

3. Results

During postfledging movements a total of 16 juvenile Reed Warblers previously ringed as chicks at the age of 4–7 days were recaptured at song playback (site S) and in stationary mist-nets (site B). The mean distance between the natal and the recapture site was $10.4 \pm 2.39$ (SE) km (range $0.01 - 26.8$ km, median $9.35$).

In 2002–2006, 1976 Reed Warblers were ringed as pulli in 448 nests. In 2003–2007, 502 breeding adults were captured when feeding their chicks. Recaptures of birds previously ringed as nestlings in our study plot were 32 (12.9%) males и 20 (7.8%) females. Natal dispersal distances were: males ($n = 32$): range $0.01 - 3.66$ km, mean $0.91 \pm 0.17$, median $0.55$ km; females ($n = 20$): range $0.09 - 19.90$ km, mean $1.66 \pm 0.97$, median $0.60$ km. Sex-related difference in the natal dispersal distance was not significant (Mann-Whitney $U$-test, $z = -0.12$, $P > 0.90$). The number of birds that moved towards the north-east and the south-west along the Courish Spit in both sex groups was nearly equal: 13 males towards the SW and 19 towards the NE, 11 females towards the SW and 9 towards the NE. Thus, natal dispersal of Reed Warblers on the Courish Spit was not directed.

Frequency distribution of natal dispersal distances of males was significantly different from the null hypothesis (Fig. 2, Wilcoxon matched pairs test: $z = -2.798$, $P < 0.005$). The same was true for females (Fig. 3, Wilcoxon matched pairs test: $z = -2.346$, $P < 0.019$). Moreover, two-tailed sign test showed that both males and females built nests significantly closer to their natal sites than assumed by the null hypothesis: most real nests were built closer to the natal site than the median distance of the predicted nest distribution: females $z = -2.459$, $P = 0.012$; males $z = -3.359$; $P = 0.007$. 


Figure 2. Frequency distributions of natal dispersal distances of Reed Warbler females on the Courish Spit. The distributions of observed dispersal distances are compared with predicted frequencies generated by a null model.

Figure 3. Frequency distributions of natal dispersal distances of Reed Warbler males on the Courish Spit. The distributions of observed dispersal distances are compared with predicted frequencies generated by a null model.
4. Discussion

Our data on the range of postfledging movements of Reed Warblers show that juveniles at the age of 38–50 days perform flights for >10 km from their natal nests. The maximum distance between the natal and the capture site was 26.8 km, which is in agreement with the previous data that juvenile Reed Warblers can cover more than 20 km during their postfledging movements (Bulyuk et al. 2000, Mukhin 2004). The question arises, why do hatching-year birds fly for more than 10 km (10.4 ± 2.39 [SE]) during the pre-migratory period, if the nest in the subsequent year will be built within 4 km (median distance of natal dispersal 0.55 km for males and 0.60 km for females) from the natal site?

It is difficult to assume that the main reason why 38–50-day-old juveniles cover >10 km across suboptimal habitats (in our case ca. 16 km, which is the distance between A and C) is to select the breeding site. Only one female was found breeding 19.9 km from her natal site, the remaining 95% of females and 100% of males bred within 4 km from the nest where they hatched.

One may suggest that vulnerability of reedbeds during the movements of ice in winter and spring shaped the necessity to remember several potential breeding sites scattered across a significant distance, so that reed in at least one of them survives winter and spring and is available for breeding. If so, Reed Warblers make their preliminary choice during the pre-migratory period and the final choice after spring arrival. However, this is mere speculation, we have no data supporting it.

The analysis of frequency distribution of natal dispersal distances shows that both sexes settle significantly closer to their natal sites than predicted by the model based on random settlement within the whole study area (Fig. 2, 3). The median distance was 0.55 km for males and 0.60 km for females, suggesting that for both sexes their natal area is the most attractive site. Lack of sex-related difference known for many passerine species (Greenwood 1980, Sokolov 1997, Morton 1997) might be due to the insufficient sample size, but it should be kept in mind that confidence level is very low (P > 0.90), so similar dispersal distance of both sexes might be the actual phenomenon in this species.

However, before a migrant nests it should be able to return to the area. This means that the bird should remember the area and form the migratory target for spring migration. It is assumed that during return migration in spring the birds show true navigation, i.e. they know where they are going to (Berthold 2001, Wallraff 2005). Therefore, some information must be obtained before the onset of autumn migration: some gradients (olfactory, magnetic) should be sampled, landmarks or sun information memorised etc.

Some navigation hypotheses (Wallraff 1974, 2005; Mouritsen 2003) imply that to create the navigation target, the birds need to sample the vicinity of the future breeding site during exploratory flights. The existence of such flights was shown by recapture analysis of juveniles (Baker 1993), and by tracking radio-tagged hatching-year birds (Mukhin et al. 2005). The navigation target is much greater than the immediate natal reed patch. During the exploratory flights juvenile Reed Warblers study a relatively large area around the natal site (with a diameter of tens of kilo-
metres). When making broad exploratory flights between the reed patches, a bird might remember its position, form a mental map of the area and navigation target, so that the vicinity of the natal sites becomes a familiar area (Baker 1978). We may hypothesise that the enlarged familiar area increases the chances of successful return during spring migration. The relatively large scale of exploratory flights, and, thus, large familiar area might facilitate pinpoint navigation recorded in several species of long-distance migrants, the Reed Warbler including (Bulyuk 2006).

The bird may remember several potentially suitable breeding sites but select only one, normally the closest one to the natal site. More distant areas are only used as “plan B” if the habitat at the natal site is destroyed during the non-breeding period (that is not uncommon for the reeds) or if the first breeding attempt fails. Thus, the difference in scale of natal dispersal and postfledging exploration might be due to their different function.

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