Breeding site fidelity of reed-nesting *Acrocephalus* warblers was investigated at Lake Kolon in Central Hungary. Sampling was carried out during the breeding seasons of 2001 to 2005 by mist-netting. We analyzed data of more than 20,000 capture and recapture records belonging to four species (*Moustached Warbler Acrocephalus melanopogon*, *Sedge Warbler Acrocephalus schoenobaenus*, *Reed Warbler Acrocephalus scirpaceus*, and *Great Reed Warbler Acrocephalus arundinaceus*), differentiated between age and sex groups. The landscape-scale site fidelity varied significantly between both the four species and the age groups. Of the four species, the Moustached Warbler showed the highest returning rate, which could be explained by the strong habitat preference of this species that may have resulted in lower dispersal rate. Also, in the case of all species, adults showed 4.03 to 6.10 times higher returning rate than juveniles. Adult males were more faithful to their breeding area than females, which is likely to be explained by the higher breeding dispersion rate of females. The natal site fidelity of males was higher than that of females in the case of all species but the Moustached Warbler, which could probably be caused by the higher mortality of males between fledging and their first breeding season. In general, adults showed preference for occupying the same territory or its close neighbourhood in consecutive years.

Key words: Lake Kolon, natal site fidelity, reedbeds

INTRODUCTION

In the case of migratory bird species site fidelity is a characteristic phenomenon, which is observable in both breeding and wintering grounds (Weatherhead & Forbes 1994) and, to a certain extent, at stop-over sites during the migration as well (Catry et al. 2004). Breeding site fidelity of almost all avian taxa has been investigated so far (as examples: Sordahl 1984, Ganter & Cooke 1998, Pyle et al. 2001), culminating in some general principles (and in some contradictions) as a result. High degree of site fidelity in breeding ground can be interpreted in a way that the particular breeding area provides optimal conditions for nesting and breeding for the investigated bird species (McNicholl 1975, Greenwood 1980, Bollinger & Gavin 1989). In a stable and high quality breeding area, site fidelity can lead to higher reproductive success through the avoidance of predation and nest predation, improved feeding skills, and better adaptation to local circumstances in
general. Overall, due to the lack of any reliable method to investigate the mortality and dispersal of individuals, our knowledge is still limited regarding breeding site fidelity (Greenwood & Harvey 1982, Brawn & Robinson 1996, Haas 1998). It is not always easy to study a bird population ‘in situ’. Reed-nesting passerine species, for example, are usually relatively hard to investigate since in homogenous reedbeds it is considerably harder to continuously trace the individuals. Long-term ringing projects can provide suitable data on the site fidelity of these species (Prochážka & Reif 2002). Very little research has been carried out aiming at the investigation of the territorial fidelity of Acrocephalus warblers in huge, contiguous reedbeds. In this study, not only the large (landscape) scale site fidelity but also its fine spatial structure were investigated, which may add new information to our knowledge on both breeding site and territorial fidelity of Acrocephalus warblers. Even the European population size estimates of reed-nesting Acrocephalus warblers show the populations to be stable (as in the case of the Moustached Warbler, the Reed Warbler and the Sedge Warbler) or declining moderately (as in the case of the Great Reed Warbler) (BirdLife International 2004), in fact these bird species are threatened by the deterioration and destruction of suitable breeding habitats, the wetlands (Halls 1997). With this study, we would like to contribute to our knowledge on breeding area and territory fidelity of reed-nesting Acrocephalus warblers, and to support their conservation.

MATERIALS AND METHODS

The study was carried out at Lake Kolon (46°48′N 19°20′E) in the Kiskunság National Park in Central Hungary. This lake is one of the few remaining large wetlands that covered the major part of the Danube–Tisza Interflow region beforehand. Considering the OECD boundary system, the lake can be characterized by eutrophic water body state. With its 1000-hectare size, Lake Kolon is one of the biggest contiguous reedbeds in Hungary.

Sampling was carried out during the breeding seasons by mist-netting from 2001 to 2005. Mist-nets were placed along a 1.6 km long dike crossing the reedbed in 50 m long blocks, with 1–1.5 meter gaps between two consecutive blocks. In total, 31 blocks of mist-nets were placed with standard distribution (i.e. the beginning and the end of the blocks were at exactly the same place in each year). Accordingly, the place of capture and recapture was recorded with a precision of 50 m. Only recaptures within successive breeding seasons (i.e. returning birds) were analyzed. Recaptured birds in their second calendar year are referred to as returning juveniles. Recaptured birds that had been captured for the first time as older than their first calendar year are referred to as returning adults. Sex groups (male or female birds) were differentiated by the morphology of the cloacal protuberance and breeding patch. With this method, it is impossible to identify the sex of juvenile birds but for adults it provides reliable data for 85–90% of individuals. Thus, the sex of juvenile birds could be determined only if they were recaptured.

In this study, the phenomenon of ‘site fidelity’ regarding the breeding ground is divided into two subcategories, such as ‘breeding site fidelity’ and ‘natal site fidelity’. ‘Breeding site fidelity’ re-
fers to those adult birds that return to the same area for breeding in subsequent breeding seasons. The term ‘natal site fidelity’ refers to those second calendar year old birds that return to their natal area for the first breeding season. Similarly, between-year dispersion of individuals is divided into two equivalent categories, such as ‘natal dispersion’ and ‘breeding dispersion’.

Site fidelity was analyzed from more than 20,000 capture and recapture records of four Acrocephalus species (Moustached Warbler – *A. melanopogon*, Sedge Warbler – *A. schoenobaenus*, Reed Warbler – *A. scirpaceus* and Great Reed Warbler – *A. arundinaceus*), differentiated according to age and sex groups. The term ‘recapture rate’ refers to the percentage ratio between the number of recaptured birds and the total number of ringed individuals of the particular species, age, and sex group. The recapture rate of different species, age, and sex groups were compared using the Chi-square ($\chi^2$) test.

For the description of the distance distribution between two territories in consecutive years, the data of returning adults were analyzed. This method involved a kind of transformation of the distribution function. We investigated whether and how the result distribution function differs from the random distribution function. For that, the likelihood of each distance group in result function was divided by the adequate likelihood of the random distribution function.

There are three basic assumptions in our site fidelity analysis. These hypotheses are thought to be evident but could not or could be only partially tested in field conditions. (1) There is a positive linear correlation between the recapture rate and the returning rate. (2) The place of capture/recapture indicates the place of the territory (in the case of adult birds). This presumption is based on two facts: (a) the adult birds spend most of their time in the proximity of their nest (in their territory) and (b) in 80% of all cases the same-year recaptures were recaptured within 100m proximity of the place of the first capture. (3) In the case of captured juveniles, a certain part of individuals originates from other breeding areas since on average the post-fledging movements (dispersion/migration) are started earlier than the time when adult birds finish the breeding. This could influence the calculated returning rate of juveniles, but due to the lack of any suitable method of distinguishing the local fledged and ‘incomer’ juvenile birds, it could not be transformed to exact numerical value.

RESULTS

At first, the recapture rate of individuals of the four species was analyzed, differentiated according to age and sex groups (Table 1). The Moustached Warbler

<table>
<thead>
<tr>
<th>Species</th>
<th>Proportion of recaptured males, ringed as juvenile</th>
<th>Proportion of recaptured females, ringed as juvenile</th>
<th>Proportion of recaptured males, ringed as adult</th>
<th>Proportion of recaptured females, ringed as adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moustached warbler</td>
<td>3.64% (n=1213)</td>
<td>4.89% (n=1213)</td>
<td>24.88% (n=725)</td>
<td>19.04% (n=649)</td>
</tr>
<tr>
<td>Reed warbler</td>
<td>1.71% (n=3405.5)</td>
<td>1.24% (n=3405.5)</td>
<td>13.95% (n=1102)</td>
<td>4.04% (n=831)</td>
</tr>
<tr>
<td>Sedge warbler</td>
<td>0.54% (n=2860.5)</td>
<td>0.30% (n=2860.5)</td>
<td>2.79% (n=667)</td>
<td>1.95% (n=778)</td>
</tr>
<tr>
<td>Great reed warbler</td>
<td>1.97% (n=592.5)</td>
<td>1.41% (n=592.5)</td>
<td>7.59% (n=445)</td>
<td>5.98% (n=354)</td>
</tr>
</tbody>
</table>
Table 2. The ratio between the recapture rates of different age and sex groups in four reedbed passerine species at Lake Kolon, Central Hungary

<table>
<thead>
<tr>
<th>Species</th>
<th>Ratio between the recapture rate of adults and the recapture rate of juveniles</th>
<th>Ratio between the recapture rate of adult males and the recapture rate of adult females</th>
<th>Ratio between the recapture rate of juvenile males and the recapture rate of juvenile females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moustached Warbler</td>
<td>5.19</td>
<td>1.31</td>
<td>0.75</td>
</tr>
<tr>
<td>Reed Warbler</td>
<td>6.57</td>
<td>3.46</td>
<td>1.38</td>
</tr>
<tr>
<td>Sedge Warbler</td>
<td>5.56</td>
<td>1.43</td>
<td>1.80</td>
</tr>
<tr>
<td>Great reed Warbler</td>
<td>4.07</td>
<td>1.27</td>
<td>1.40</td>
</tr>
</tbody>
</table>

Fig. 1. The distance between the place of capture and the place of recapture of adult birds in consecutive years in four Acrocephalus warblers at Lake Kolon, Central Hungary
showed a higher recapture rate than the other three species in each age and sex group. The Sedge Warbler showed the least recapture rate in each age and sex group. The Reed Warbler and the Great Reed Warbler presented intermediate values between Moustached and Sedge Warbler in each age and sex group.

In the case of each species the recapture rate of adults was always significantly higher than that of juveniles. Also, in the case of each species the recapture rate of adult males was always significantly higher than that of adult females. In the case of the Reed Warbler this value was extremely high, almost 3.5. The recapture rate of juvenile males was higher than that of juvenile females in the case of the Reed Warbler, the Sedge Warbler, and the Great Reed Warbler but showed reversed ratio in the case of the Moustached Warbler (Table 2).

Secondly, we analyzed the distances between the place of capture and the place of recapture of adult birds in successive breeding seasons in the case of the four species, distinguishing the two sex groups. The result was a distribution function for each sex group of the four species. By comparing it with the random distribution pattern (e.g. when returning individuals would not show any preference within the whole area; for details see Materials and Methods), we established a preference function (Fig. 1). In general, birds having returned to the same area in the following year after their previous capture showed a marked preference to return to the same territory. This phenomenon is represented by the section of values 0m to 250 m (or even to 500m, in the case of the Moustached Warbler) on the x (distance) axis. If an individual did not return to the same territory or to its 250 (~500) m wide surrounding area, it made no preference regarding the distance from the previous year’s territory when occupying the new territory. This is represented by the linear part of the figures from the middle to larger distance part.

DISCUSSION

In our study, breeding site fidelity was investigated by calculating the recapture rate of individuals and by calculating distances between the places of captures and recaptures. Recapture rate, as a measurable manifestation of site fidelity, was supposed to be in positive correlation with the quality of the breeding area (MCNICHOLL 1975, GREENWOOD 1980, BOLLINGER & GAVIN 1989). Supposing that the overall population size is stable (i.e. the investigated populations are not representative of sink populations) (BRAWN & ROBINSON 1996), recapture rates can indicate the relative quality of the particular breeding area regarding each investigated species. Relative quality of a breeding area is referred to as the rank of
the particular area among all the areas reachable with individual dispersion (i.e. the metapopulation area).

We found a marked difference in the recapture rates of the four investigated species. The Moustached Warbler showed the highest level of breeding site fidelity in each age and sex group, which indicates that the relative quality of the breeding site is the highest in the case of this species. This is in accordance with our presumed hypothesis, since the other three species are more generalists regarding their choice of a breeding area, while the Moustached Warbler seems to have more specific demands regarding the breeding habitat (Catchpole 1982, Leisler 1989, Csörgő 1995a,b, Prokeskova & Kocian 2004, Báldi 2005, GrubaroVA et al. 2005). The higher returning rate of the Moustached Warbler can be interpreted as the manifestation of a smaller breeding dispersion, which correlates with the smaller absolute size of suitable breeding areas of this species compared to the three other reed-nesting Acrocephalus species. Based on the total ringing data (unpublished data of the Hungarian Bird Ringing Centre) representing 460 different geographical areas, out of five areas where any of these Acrocephalus species have been caught in May and June (i.e. in the breeding season), the Moustached Warbler was caught in only one area. It can be interpreted that the other three species can find much more suitable nesting areas in Central Hungary, so dispersion rates within those metapopulations are presumably higher.

The difference between the level of breeding site fidelity and the level of natal site fidelity is markedly present in the case of each species. The ratio between the recapture rate of adult and juvenile birds varied between 4.03 and 6.10, with the recapture rate of adult birds always being much higher. This phenomenon supports expectations, since both the mortality and the dispersion (between the natal area and the first breeding area) of juvenile birds are usually much higher than that of adults (Weatherhead & Forbes 1994, Divoky & Horton 1995).

In each species, adult males presented higher breeding site fidelity than adult females. In most studies, if any difference could be found in breeding site fidelity between the two sexes at all, males tended to be more faithful to their breeding area (Greenwood & Harvey 1982, Clarke et al. 1997, Ward & Weatherhead 2005). Supposedly, this difference in breeding site fidelity can be attributed to the difference in breeding dispersion of the sexes. Acrocephalus warblers are susceptible to polygyny to a varying extent. The highest level of polygyny is associated with the Great Reed Warbler, followed by the Sedge Warbler, while the Reed Warbler and the Moustached Warbler are reported to be typically monogynous species (Leisler & Catchpole 1992). In the case of the polygynic mating system, population size can be stable even if there is a certain level of difference in mortality of the sexes but only with males showing higher mortality rate between two consecu-
tive breeding seasons. Since the presence and the level of polygyny can be interpreted as breeding area quality indicator (i.e. the particular breeding place is a high quality area) (Hoří et al. 1995), it would be reasonable to carry out our studies including those kinds of investigations.

The same sexual difference can be observed regarding the natal site fidelity in the case of the Sedge Warbler, the Reed Warbler, and the Great Reed Warblers, which can be explained by the different dispersion rate of juvenile males and females as well. Interestingly, the Moustached Warbler shows a reversed ratio regarding the recapture rate of juvenile males and females. When searching for reasons for this phenomenon, we can only rely on premises. Here, the difference in mortality between juvenile (to be more precise: first winter) males and females can lead to this phenomenon. While all the other three species are long-distance migrants, the Moustached Warbler is a short-distance migrant, and there can be different migration strategies in the case of the two sexes, as there is in the case of other short distance migrants (OtaHAL 1995, Miklay & Csörgő 1998). In spring migration, males are usually present earlier at nesting areas since the order of occupation of territories is a main factor contributing to their reproductive success (Bensch & Hasselquist 1991). That is why male Moustached Warblers can risk wintering in more northern areas than females. Of course, this hypothesis, whether the proportion of sexes is different from 1:1 or not, should be tested by investigating the wintering populations of the Moustached Warbler in different latitudes.

Also, it would be very interesting to compare our results with other studies. Unfortunately, numerical rates in our results could not be compared with returning rates calculated in other site fidelity studies. Especially as we only sampled the population of Lake Kolon, and therefore only a small proportion of individuals could be captured every year. The exact rate between captured individuals and the total of all the individuals present cannot be precisely estimated. In the case of sampling when only a certain proportion of the population can be investigated (due to huge area size), the correlation between recapture rate and total suitable breeding area size is likely to be negative. It can heavily influence the recapture rate, because individuals returning to the same area (on landscape scale) often occupy another territory – even though they usually try to occupy the same one, in optimal breeding sites, at least.

Acknowledgements – We would like to thank Dr. A. Báldi and Dr. J. Gyurácz for their comments on the manuscript. We are grateful to the Directorate of Kiskunság National Park, for financial and operative support. We would like to thank every volunteer for their help with sample collection.
REFERENCES


Acta zool. hung. 54, 2008


Revised version received September 6, 2007, accepted October 3, 2007, published December 30, 2008