Modelling Small-Scale Dispersal of the Great Reed Warbler Acrocephalus arundinaceus in a Fragmented Landscape

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Modelling small-scale dispersal of the Great Reed Warbler *Acrocephalus arundinaceus* in a fragmented landscape

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We studied dispersal of Great Reed Warblers *Acrocephalus arundinaceus*, using a mark–resight model for dispersal. We assessed the relevance of ecological distance, defined as movement along reed edges, as opposed to straight line distance for predicting the distribution of dispersal. In a mark–resight study in the northern Netherlands, 1158 birds were ringed. 178 birds were resighted at least once, with 254 movements between known nesting locations in successive years. Dispersal was defined as movement between successive nesting sites, and modelled as an exponential function of ecological and geographical distances. To correctly model dispersal probabilities in the fragmented study area, the model discriminates between suitable habitat sections and intermediate gaps. Several nested models for dispersal were compared by means of the likelihood ratio test. Models incorporating ecological distance gave a better fit than models using geographical distance, although the difference was not large. To describe dispersal probabilities, combined models were necessary at both local and long distance scales, and separate models were needed for juveniles and adults. For a landscape without gaps, the parameter estimates of the best model can be interpreted as follows. An estimated 65% of the adult dispersal distances were within a close range of the previous nesting location with a mean ecological dispersal distance of 0.58 km. The remaining 35% had an estimated mean distance of 10.3 km. An estimated 39% of the juvenile movements were random over the study area. The remaining 61% had a mean dispersal distance of 3.1 km. These results suggest that there might be two dispersal strategies in the Great Reed Warbler. There is also an indication that adults disperse further when connectivity decreases. These findings indicate that dispersal of Great Reed Warblers is not random, but smaller dispersal distances are more likely than larger distances. This might result in a limited dispersal ability of the species over the fragmented landscape.

Key words: ecological distance, fragmentation, mark-resight, reed warbler, *acrocephalus*

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Habitat fragmentation affects species persistence in a variety of ecosystems (Diamond 1984, Soulé 1987, Opdam *et al.* 1994). Metapopulation theory holds that insufficient spatial cohesion of the habitat can lead to local extinctions that are not counterbalanced by recolonisation processes (Levins 1970, Opdam 1991, Hanski 1994, Opdam *et al.* 2003). The key process for recolonisation of habitat fragments within a metapopulation, and the exchange between them, is dispersal (Opdam 1990, Hanski 2001). For the conservation of species in fragmented habitat it is therefore essential to understand and quantify the dispersal mechanisms of the species, and the effect of the landscape configuration on its dispersal behaviour (Pither & Taylor 1998, Opdam *et al.* 2001, Vos *et al.* 2002).

There has been scepticism about landscape influences on the dispersal of birds, because birds can cover large distances by flying and would therefore not be influenced by barriers in the landscape (Bélisle *et al.* 2001). However, the distributions of many bird populations depend on spatial cohesion of habitat patches in the landscape (Brown & Dinsmore 1986, Opdam *et al.* 1994, Foppen *et al.* 1999, Foppen *et al.* 2000), and it has been suggested that dispersal of several bird species is influenced by landscape features (van Dorp & Opdam 1987, Desrochers & Hannon 1997). A recent review on the importance of hedgerows as corridors (Davies & Pullin 2007) showed that bird species presence, abundance and species richness were positively related to the number of hedgerows connected into the study wood, greater hedgerow structural complexity and hedgerow density within the surrounding landscape. Although a review by Bowne & Bowers (2004) based on various taxa did report that interpatch movement rates have in majority positive population effects, (64% positive, 31% neutral and 5% negative), no population effects were reported for bird species in this particular review.

It has been argued that even small gaps in forest cover can limit the movement of forest birds (Desrochers & Hannon 1997, St.Clair *et al.* 1998), and this creates a significant cumulative barrier effect at the landscape scale (Bélisle & St. Clair 2001, Gobeil & Villard 2002). These results suggest that the behavioural component of dispersal might be an important component of bird movements through the landscape.

For the Reed Warbler *Acrocephalus scirpaceus*, a marshland passerine, a relation was found between spatial parameters of reed patches and local extinctions and recolonizations of the metapopulation (Foppen *et al.* 2000). In field experiments it was also found that displaced Reed Warblers choose to cross smaller reed gaps more frequently than larger gaps (Bosschieter & Goedhart 2005). When these local decisions would also hold during dispersal, this would imply that habitat patches connected by reed edges would have higher exchange probabilities. Real dispersal events are necessary to test this hypothesis. The Great Reed Warbler is a marshland species that has become rare in The Netherlands because suitable habitat for this species is degrading by eutrophication and unnatural water table management (Graveland 1998). The fragmentation of its habitat may be an additional contributing factor in explaining the decrease of the species in The Netherlands. It has been suggested that the dispersal capacity of the species in relation to the fragmented nature of its habitat is a limiting factor for metapopulation viability (Foppen 2001). Natal and breeding dispersal is quite limited; breeding birds for instance on average settled within one kilometre from former sites (Foppen 2001). Also, Hansson *et al.* (2002b) reported a limited gene flow in Swedish populations, resulting in low genetic variation. Rather than physical constraints that limit dispersal distances it might be the dispersal behaviour of the species that restricts natal and breeding dispersal distances.

The aim of our study was to model dispersal distances of the Great Reed Warbler in a fragmented habitat, while taking the spatial configuration of its habitat into account. Insight can be obtained by using a dispersal–distance function that is characteristic of a particular species, sex, environment, and time (Wiens 2001). The data necessary for estimating such a function can be gathered in mark–resight experiments. We integrated capture–resight methods with a spatial analysis of the fragmented landscape that distinguished between suitable habitat and non suitable habitat, so-called 'gaps' (Matthysen *et al.* 1995, Bélisle & St. Clair 2001). To describe dispersal often negative exponential functions are used (Skellam 1951, Hanski & Thomas 1994, Conrad *et al.* 1999), i.e. there is a high probability of staying close to the previous nest site and a low probability of dispersing further away. This distribution has indeed been shown for Great Reed Warblers, as for many other songbirds (Greenwood and Harvey 1982; Foppen 2001; Hansson *et al.* 2002a,b). In dispersal–distance functions, distances usually are straight lines between successive locations of bird presence. Often this will not be the real dispersal distance travelled, particularly when the actual route is influenced by decisions based on the local landscape configuration (Wiens 2001). For forest birds, for instance, it was shown that the actual dispersal trajectory was not in a straight line crossing forest gaps but a detour was taken along the forest edge (Bélisle & St. Clair 2001). The Great Reed Warbler is mainly found in reed beds *Phragmites australis* during the breeding season (Graveland 1998, Foppen 2001). Preliminary results of two radio-tagged juvenile Great Reed Warblers showed that their dispersal movements were mainly restricted to reed patches (Bosschieter, unpubl. results). Thus the actual dispersal distance could be defined as the distance travelled along the reed edge trajectory. This 'ecological distance' will generally be much longer than the geographical distance, and the dispersal–distance curve will change considerably. We therefore assessed the relevance of ecological distance, i.e. the distance along reed edges, as opposed to straight line distance for predicting the distribution of dispersal movements.

METHODS

Study area

A mark–resight study was conducted on the shores of a chain of lakes in the northeastern Netherlands (52°38'N, 5°55'E, Fig. 1). Yearly, about 175 pairs breed in this region; this represents more than 50% of the Dutch population (Foppen 2001). A small population of about 20 breeding pairs, located at least 10 km away, was not included in the analyses. The next-largest population had about 60 breeding pairs, at 70 km of our study area. The nearest populations outside The Netherlands, in France and Germany, are at least 200 km away (Hagemeijer & Blair 1997).

Mark–resight data

Every spring from 1994–2000, adults and juveniles were individually marked by means of unique colour ring combinations (Foppen 2001). A recording of the bird's song was used to lure adult birds into a mist net. Juveniles were ringed in the nest just before fledging. The sex of each marked adult was established, and the sex of a juvenile was determined when resighted as an adult. Although mistnetting effort differed for parts of the study area, it was assumed that 80% of the adult males and 90% of the juveniles were colour-marked. Throughout the study period birds were resighted in their territories and checked for coloured rings. Individuals in others marshlands in The Netherlands were checked for colour-rings as well. We estimate that more than 75% of the Dutch male breeding population has been checked for colour-rings in the study period. Observations were plotted on digitised maps of the study area.

Definition of ecological distance and of habitat sections

For our mark–resight model, dispersal distance was defined as the distance travelled between successive years. For juveniles, this is natal dispersal (Greenwood & Harvey 1982): the distance between the nest where they were born and their first nest as adult. For adults, this is breeding dispersal: the distance between consecutive nests. To measure the ecological distance, it was assumed that Great Reed Warblers disperse along reed edges, and, when there are none, along the lake shore. This produced trajectories called 'ecological dispersal routes' (Fig. 1). The line demarcating the lake edge was divided into 86 'sections' each no longer than 500 m. *Geographical distance* was defined as the Euclidian distance between the centres of the sections, *ecological distance* as the distance between the centres when dispersing along the ecological dispersal route.

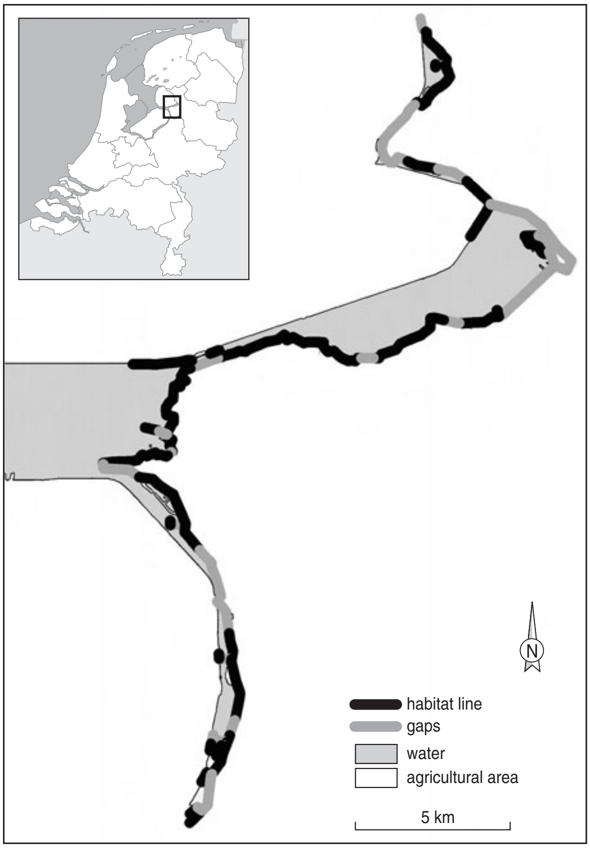

Figure 1. Map of the main study area in north-west Overijssel, and its position in The Netherlands (inset). The ecological dispersal route is drawn as a linear representation of the landscape, with suitable habitat sections and intermediate gaps. The surrounding landscape is farmed and therefore unsuitable habitat.

Habitat in the study area is fragmented with many parts where breeding is impossible. To discriminate between suitable habitat and intermediate gaps, we evaluated habitat quality on the basis of field visits. Great Reed Warblers mostly breed in 'water reed': pure reed vegetation standing in water, close to the water edge of the lake (Graveland 1998). Suitable habitat was defined as a reed-fringed edge at least 80 m wide and a width of at least 1 m of water reed, or a smaller continuous reed edge where the width of water reed exceeded 6 m (Graveland, unpubl. data). Quality and area of the reed were monitored during the study period. Small parts of the reed were mowed, but the fringe of water reed was mostly left intact. It is therefore assumed that the suitable breeding habitat was constant throughout the study period. Gaps were defined as interruptions in the reed vegetation that were at least 300 m long. Every mark and resight location was assigned to one section, which permits defining a corresponding probability of dispersal from one section to another. For each habitat section also a connectivity measure was calculated (Hanski 1994). The connectivity of a habitat section was defined as the total length of reed edges within a circle of 3700 m around the centre of the section. This is further denoted as C_{3700}.

Preliminary statistical analysis

Observed ecological dispersal distances between consecutive years were separately analysed by means of a log-linear model with random bird effects (Breslow & Clayton 1993). The effect of sex and age (juvenile vs. adult) of the bird, connectivity C_{3700} of the departure section, and year was assessed by means of Chi-squared tests.

Mark–resight model for dispersal distance

A mark–resight model was developed, in which the probability of dispersal between sections is a function of the geographical or ecological distance between the sections. The Cormack–Jolly–Seber (CJS) model provides a general framework for estimating survival and resight rates (Lebreton *et al.* 1992), and the MARK program can analyse such data (Cooch & White 2010). Multi-state models of movement, developed by Arnason (1972, 1973), have been incorporated into the CJS model (Schwarz *et al.* 1993) and subsequently in MARK. Dispersal rates can be estimated separately from survival probabilities at the condition that survival depends on the departure site only (see Hestbeck *et al.* 1991). The Arnason–Schwarz multi-state movement model employs a separate probability of moving between sections from one year to the next. These movement probabilities are collected in a Markov transition matrix. For a part of our study area, Foppen (2001) used the Arnason–Schwarz movement model to estimate emigration rates. However, in our study with 86 sections, the Markov transition matrix consisted of 86 × 85 = 7310 probabilities and these cannot be estimated from our data. Transition probabilities between sections were therefore modelled as a function of a small number of parameters and the distance between the sections (Spendelow *et al.* 1995).

The simplest assumption is that Great Reed Warblers disperse randomly over the study area. This can be modelled by employing a uniform distribution for dispersal distances. It follows that under random dispersal the probability of moving to a section is proportional to the length of that section (Table 1). However, dispersal distances of birds often follow exponential distributions (Greenwood & Harvey 1982, Bensch & Hasselquist 1991, Hanski 1994). Therefore, in our model, it is assumed that the distance d between subsequent nests follows a double exponential distribution with probability density (1), in which σ is a parameter for dispersal.

$$(1)\quad f(d;\sigma) = 0.5\sigma e^{-\sigma|d|} \qquad -\infty < d < \infty$$

This is a decreasing symmetrical function of distance, and thus assumes that moving a long distance is less likely than moving a short distance. The mean dispersal distance moved under this model is $1/\sigma$ and the variance is $1/\sigma^2$. This model requires only one parameter (σ) to be estimated instead of the 7310 required in the full Arnason–Schwarz approach. We further define υ_{rs} as the probability of dispersing from a habitat section r of length a_r to a habitat section s of length a_s with a distance d_{rs} between the centres of the sections. Equation (2) assumes that the location x of a bird in the departure section follows a uniform distribution, and likewise for the location y in the arrival section. Figure 2A displays an example of resulting dispersal probabilities for continuous habitat.

$$(2)\quad \upsilon_{rs}(\sigma) = \frac{1}{a_r}\int_{-a_r/2}^{a_r/2}\int_{d_{rs}-a_s/2}^{d_{rs}+a_s/2} f(y-x;\sigma)\,\partial y\,\partial x$$

For an infinite landscape without gaps, the sum of all probabilities from any departure section r equals 1. In a fragmented landscape, with a finite nature, there is no dispersal to or from gaps, as was the case in our study area. Then the transition probabilities as defined by (2) do not add up to 1, and they are therefore rescaled, according to (3). The resulting probabilities, ϖ_{rs}, are larger, and now sum to 1 by definition (Fig. 2B).

$$(3)\quad \varpi_{rs}(\sigma) = \frac{\upsilon_{rs}(\sigma)}{\sum_s \upsilon_{rs}(\sigma)}$$

With exponential distributions, long distance dispersal events are often underestimated (Bullock & Clarke 2000). This can be remedied by using distributions with heavier tails. In order to stay close to the double exponential distribution, models combining two func-

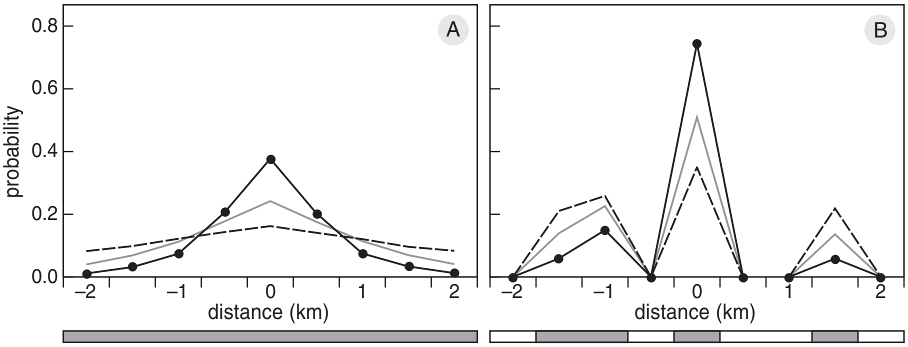

Figure 2. Transition probabilities according to a double exponential distribution (see eq. 2). A continuous landscape is displayed in (A) with suitable habitat sections throughout (grey bar) and no gaps. In (B) gaps (white bars) are added. The resulting probabilities are larger than in A, while in the gaps, the probabilities are 0, and all should sum to 1. The probabilities are modelled from the centre of a certain section at 0 km to the centres of the other sections for two imaginary landscapes of length 4.5 km. The sections are 0.5 km long. The exact values are indicated for $\sigma = 2.0$ with a black line for visual interpretation. For $\sigma = 1.0$ (grey line) and $\sigma = 0.4$ (dashed line) only the lines are given.

tions for dispersal distance distribution were tested (Table 1). The first model was a combination of two double exponential distributions with mixing parameter π and dispersal parameters σ_1 and σ_2. The mixing parameter π is the proportion of movements with short mean dispersal distance $1/\sigma_1$, and $(1–\pi)$ is the proportion with long mean dispersal distance $1/\sigma_2$. The second model employs a combination of a random model and a double exponential distribution. In this model a proportion π moves randomly, irrespective of the previous nesting position, while a proportion of $(1–\pi)$ of all movements follows an exponential distribution from the previous nesting section.

Given that juvenile and adult Great Reed Warblers show different dispersal distances (Foppen 2001, Hannson *et al.* 2002b), the dispersal parameters were allowed to differ between juveniles and adults. $\Omega_{juv}^{(1)}$ and $\Omega_{ad}^{(1)}$ are defined as the Markov matrices with transition probabilities for juvenile and adult dispersal in one year, given that the bird is alive. The elements of the transition matrix of equation (4) are defined by equations 1, 2 and 3, or for combined models are defined in Table 1. The conditional dispersal probabilities that a juvenile is alive after k years are then given by (4A). For adults equation (4B) holds. An example of different dispersal parameters can be seen in Fig. 2.

Table 1. Equations for the different models for Great Reed Warbler movement. υ_{rs} is the probability of dispersing from habitat section r to section s, with a distance d_{rs} between the centres of the sections, see equation (2). The scaled probability ω_{rs} is defined in equation (3). σ, σ_1 and σ_2 are dispersal parameters, while π indicates the mixing proportion in the combined model. The total length of the sections (a) summed over all sections is denoted by $A = \sum_s a_s$. For a full explanation, see text.

Model description	Model equation
Random	$f(d;\sigma) =$ Constant or $\omega_{rs}^{(0)} = a_s/A$
Exponential	$\upsilon_{rs}(\sigma) = \dfrac{1}{a_r}\displaystyle\int_{-a_r/2}^{a_r/2}\int_{d_{rs}-a_r/2}^{d_{rs}+a_r/2} f(y-x;\sigma)\,\partial y\,\partial x$ $\omega_{rs}^{(1)}(\sigma) = \dfrac{\upsilon_{rs}(\sigma)}{\sum_s \upsilon_{rs}(\sigma)}$
Combination of two exponentials	$\omega_{rs}^{(2)}(\sigma_1,\sigma_2,\pi) = \pi\,\omega_{rs}^{(1)}(\sigma_1) + (1-\pi)\,\omega_{rs}^{(1)}(\sigma_2)$
Combination of random and exponential	$\omega_{rs}^{(3)}(\sigma,\pi) = \pi\,a_s/A + (1-\pi)\,\omega_{rs}^{(1)}(\sigma)$

$$(4)\quad (A)\ \ \Omega_{juv}^{(k)} = \Omega_{juv}^{(1)}\,\Omega_{ad}^{(k-1)}$$

$$(B)\ \ \Omega_{ad}^{(k)} = \Omega_{ad}^{(1)}\,\Omega_{ad}^{(k-1)}$$

Different models were fitted for both ecological and geographical distance (Table 3). First, two models were tested with equal parameters for juveniles and adults: a random model and an exponential model. Next, juveniles and adults were modelled separately, giving four models with different combinations of models.

Estimation of dispersal parameters

Dispersal parameters were estimated by means of maximum likelihood using the multinomial likelihood. It is assumed that survival and resight do not depend on the location of a bird. The likelihood can then be split into a part containing survival and resight parameters and a second part containing only dispersal parameters. Consequently, movement can be estimated independent of survival and resight (Cooch & White 2010). Only observed movements contribute to the movement part of the likelihood, and therefore the dataset was reduced to observed movements only. The log-likelihood contribution of an observed movement is given by the logarithm of the corresponding element of one of the transition matrices from equation (4). The log-likelihood is the sum over all observed movements and this can be maximised to obtain maximum likelihood estimates of the movement parameters. The dispersal parameter σ must be positive, and for that reason the log-likelihood was optimised over $\sigma^* = \log(\sigma)$ rather than σ. Likewise the mixing parameter π must be in the interval (0,1) and so $\pi^* = \mathrm{logit}(\pi)$ was used instead of π. Smaller negative log-likelihoods indicate a better fit to the data. Significance testing of nested models can be done by comparing twice the difference of two log-likelihoods with a Chi-squared distribution with degrees of freedom equal to the difference in number of parameters. Such tests are known as likelihood ratio tests. Other methods for model selection, such as AIC, will give similar results for the limited set of models used.

After the best model was selected, it was tested whether the dispersal or mixing parameters are related to the connectivity measure C_{3700} of the departure section. Birds nesting in sections which are well connected might travel less far for their subsequent nest, and vice versa. This was incorporated by letting $\log(\sigma) = \alpha + \beta\, C_{3700}$ or by specifying $\mathrm{logit}(\pi) = \alpha + \beta\, C_{3700}$. The log-likelihood is then optimised over (α, β) rather than over σ or π. This type of modelling is similar to generalised linear models (McCullagh & Nelder 1989) and to the modelling in MARK (Cooch & White 2010).

The log-likelihood was optimised using a double precision FORTRAN program which employs the general purpose optimisation routine DUMINF from the IMSL FORTRAN 90 MP Library version 4.01 for Microsoft Windows (IMSL 1997). The variance–covariance-matrix of the parameters was approximated by the Hessian of the log-likelihood, using IMSL subroutine DFDHES.

RESULTS

In total 1157 Great Reed Warblers were colour-ringed: 989 juveniles of unknown sex, 127 males and 41 females. 178 birds (15%) were resighted at least once in the study area: 127 males, 27 females and 5 unsexed juveniles. There were 254 movements between known nesting locations; 199 of these were between consecutive years. We recorded more adult than juvenile dispersal events (Table 2). As distance increased, we found a decrease in the number of Great Reed Warblers resightings; juveniles moved further than adults (Fig. 3). The ecological distance between sections was longer than the geographical distances, with bigger differences at larger distances (Fig. 3C). This is in accordance with the spatial configuration of the study area (Fig. 1).

The preliminary statistical analysis of dispersal distances between consecutive years indicated different dispersal distances between years ($P = 0.070$), a significant effect of the connectivity measure C_{3700} of the departure section ($P = 0.011$) and a strong difference between juveniles and adults ($P < 0.001$). There was no significant sex effect ($P = 0.264$), nor interactions between the effects. The dispersal distance of juveniles was estimated to be a factor 2.4 larger than for adults. Each increase of 1 km of the connectivity measure C_{3700} reduced the mean dispersal distance with an estimated factor of 0.88.

Models using ecological distance were generally better than models using geographical distance, although the difference is not large (Table 3). Model 1, with exponential dispersal equal for juveniles and adults, is a great improvement over model 0, with

Table 2. Observed number of movements of juvenile and adult Great Reed Warblers, where birds are seen 'nyears' after the previous sighting.

Age / nyears	1	2	3	4	5
Juvenile	57	27	6	2	1
Adult	142	16	3	0	0

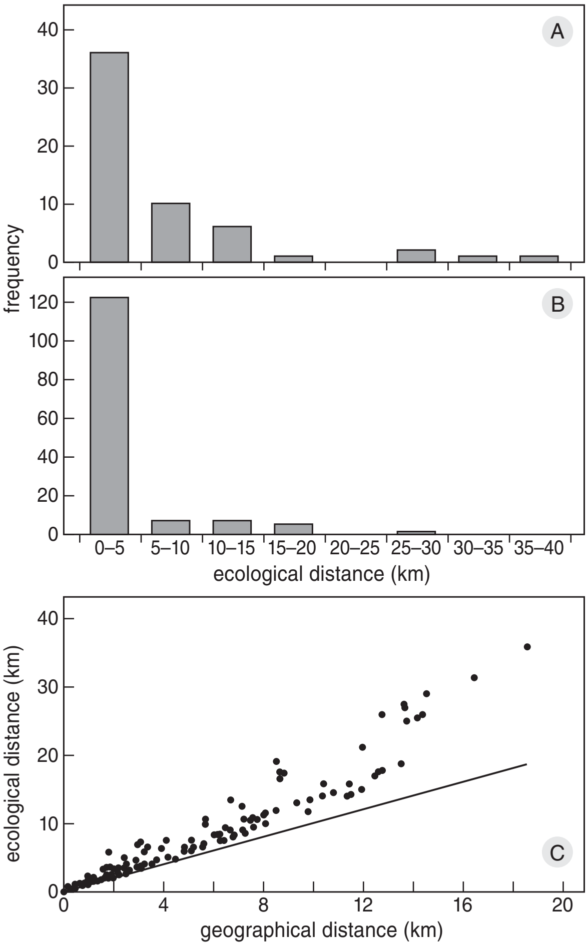

Figure 3. Ecological distances moved in one year for juvenile Great Reed Warblers (A) and adults (B), obtained from a mark–resight study. Only movements between successive years are included. (C) The relationship between the ecological distances and geographical distances. The drawn line is the function $y = x$.

random dispersal. Model 2 is significantly better than 1, from which we conclude that it is better to model juveniles and adults separately. Models 4 and 5 have the lowest log-likelihood and are significantly better than all other models ($P < 0.002$). Since model 5 has less parameters for juvenile dispersal, we conclude that model 5, with ecological distance, is the best description of the observed data.

Parameter estimates

The confidence intervals for juvenile parameters are larger than for adult parameters (Table 4); this reflects the fact that more adult dispersal events were observed. For a landscape without gaps, the parameter estimates can be interpreted as follows. About 39% of juvenile dispersal movements are homogeneously over the study area; the remaining 61% dispersed according to an exponential distribution with a mean ecological distance of 3.14 km (= 1/0.318) from the previous nest. For adults, 65% of the movements are according to an exponential distribution with mean ecological distance

Table 4. Parameter estimates and confidence intervals in parentheses for Model 5 with ecological distance. This is a mixture of a random and an exponential distribution for juvenile movement, and a mixture of two exponential distributions for adult movement.

Parameter	Estimate	
Juvenile dispersal σ_{ju}	0.318	(0.159 , 0.635)
Juvenile random dispersal π_{ju}	0.391	(0.186 , 0.644)
Adult dispersal (1) $\sigma_{ad,1}$	1.725	(1.227 , 2.425)
Adult dispersal (2) $\sigma_{ad,2}$	0.097	(0.059 , 0.160)
Adult mixing parameter π_{ad}	0.653	(0.537 , 0.753)

Table 3. Negative log-likelihoods of six dispersal models for juvenile and adult Great Reed Warblers for both the ecological distance and the geographical distance. NP: the number of parameters. The differences between the models were all significant ($P < 0.001$), except for models 3 and 6 vs. model 4 (with ecological distance $P < 0.01$; with geographical distance $P < 0.05$) and vs. model 5 (with geographical distance $P < 0.01$).

Model	Juvenile Model	Adult Model	NP	Ecological distance	Geographical distance
0	Random		0	1101.51	1101.51
1	Exponential		1	936.39	938.48
2	Exponential	Exponential	2	918.97	920.98
3	Random + Exponential	Random + Exponential	4	862.15	872.45
4	2 Exponentials	2 Exponentials	6	853.55	865.98
5	Random + Exponential	2 Exponentials	5	853.55	865.98
6	Exponential	2 Exponentials	4	860.15	870.85

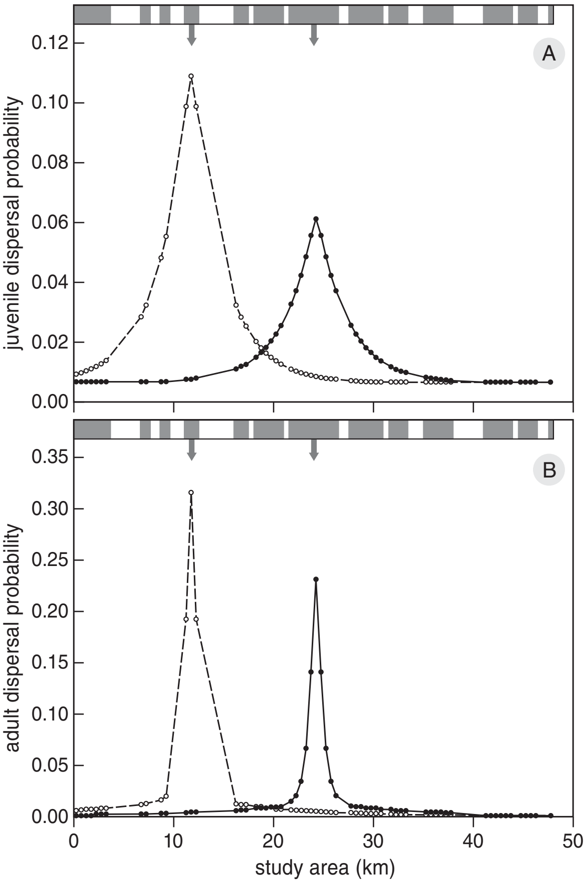

Figure 4. Estimated probabilities for dispersal of juvenile Great Reed Warblers (A) and adults (B) in the study area, according to model 5 using ecological distance. From the study area, the ecological distance from the upper north section (0 km) to the southernmost section is given as the x-axis. A linear representation of the study area has been drawn, including the habitat sections (black), gaps (white) and previous nesting sections (arrows). The first arrow indicates a section with many gaps around it (open symbols), the second arrow a section with mostly habitat in the surroundings (black symbols). The lines are added for visual interpretation.

0.58 km, while 35% spread according to an exponential distribution with a mean of 10.3 km.

It is clear that juveniles spread more homogeneously over the study area and, compared to adults, and have higher probabilities for longer ecological distances (Fig. 4). The adults show high probabilities for staying close to the previous nesting position, and thus have low probabilities for moving far. The two different starting positions show how the probabilities are affected by the rescaling equation (3). In the situation with many gaps, the probabilities for staying close to the previous nesting position are higher, both for juveniles and adults.

Dependence of model parameters on the connectivity measure

For model 5 it was tested whether any of the parameters was related to C_{3700}. The juvenile parameters σ_{ju} and π_{ju} , and the adult parameter $\sigma_{ad,2}$ were not significantly ($P > 0.28$) related to C_{3700}. However there was a significant relationship for the (short) dispersal adult parameter $\sigma_{ad,1}$ ($P = 0.010$) and for the adult mixing parameter π_{ad} ($P = 0.004$). A larger value of C_{3700} results in a larger $\sigma_{ad,1}$ and thus shorter mean distances, and in an increase in π_{ad}, resulting in a larger proportion of movements which follow the exponential distribution with the smallest mean dispersal distance. For both parameters this indicates that more adults stay closer to their previous nests when connectivity increases, and that more adults disperse further when connectivity decreases.

DISCUSSION

The preliminary statistical analysis shows that adult dispersal is more restricted than juvenile dispersal, with adult mean dispersal distances a factor 2.4 smaller than those for juveniles. This was also found by Hansson *et al.* (2002b) who reported a factor of 2.8 (17.3 km for juveniles as opposed to 6.2 km for adults). The indication of differences between years and the lack of significant sex effects are also in accordance with Hansson *et al.* (2002a, 2000b). The lack of sex effects supports the inclusion of both males and females in the analysis. The choice of a radius of 3700 meter in the definition of the connectivity measure C_{3700} was rather arbitrary. We tested also other radii that gave comparable results; however, C_{3700} was the most significant connectivity measure. The significant effect of C_{3700} on dispersal distance motivated us to define the more detailed mark–resight models.

The mark–resight models also show that there are large differences in dispersal behaviour between juveniles and adults. During the post-fledging period, juveniles disperse from the nest site in search of a future breeding site (Catchpole 1972). They clearly disperse further than adults, and this was also found in other studies (Morton *et al.* 1991, Noordwijk 1995, Machtans *et al.* 1996, Paradis *et al.* 1998, Hansson *et al.* 2002b). Juvenile movements are for 39% random over the study area. This suggests that the study area is, at least to some extent, permeable and well connected for dispersing juveniles. Adults tend to breed close to their former breeding site and many do not show dispersal more than 100 m (Bensch & Hasselquist 1991, Foppen

2001), but our results indicate that some adult dispersal movements are further away. About two-third of the adult dispersals are rather close (mean 0.58 km) to the previous nesting position. The other third are more adventurous with a mean distance of 10 km, indicating that also for adults large gaps between patches of suitable habitat are not insurmountable.

We have demonstrated that ecological distance is a better predictor for dispersal probability than the geographical distance. There are many examples for different taxa that have shown that 'ecological distance' measures, in which corrections for the preference and avoidance of habitat types during dispersal are incorporated, give better explanations of distribution patterns, compared with geographical distances (e.g. birds: Matthysen *et al.* 1995, Brooker *et al.* 1999, mammals: Bright 1998; Verbeylen *et al.* 2003, amphibians: Ray *et al.* 2002; butterflies: Sutcliffe *et al.* 2003; Baguette *et al.* 2000; Chardon *et al.* 2003). However, in our study the difference between the models using ecological distance or geographical distance was not large. This could be due to the configuration of the study area. The difference between ecological distances and geographical distances increased for longer distances, but in our study area most dispersal events concerned small distances. Other measures for ecological distance might result in an even better explanation of the observed distribution pattern. In line with other researchers (Saunders & Rebeira 1991; St.Clair *et al.* 1998), we would argue that more behavioural field studies are needed to elucidate the behaviour near gaps. This might lead to alternative ecological distance measures that account for gaps (e.g. Brooker *et al.* 1999; Baguette *et al.* 2000).

Our results suggest that there are two dispersal strategies in the Great Reed Warbler both for juveniles and adults. Part of the dispersal movements is represented by an exponential model with small mean dispersal distance. The remaining part represents much larger dispersal distances. For adults this might indicate that a proportion of the birds are philopatric and that a smaller proportion is dispersing away from the former breeding site. For many species it has been shown that breeding success influences dispersal behaviour: after loss of nests individuals are more inclined to look for a new breeding area the year after (Foppen & Reijnen 1994). It could be that this proportion of individuals exhibiting longer dispersal distances consists of breeders that experienced nest failure. An alternative explanation comes from Hansson *et al.* (2003). They found for Swedish Great Reed Warblers that dispersal strategy (philopatry vs. inter-population dispersal) had a high heritability.

Note that all birds were ringed in the centre of the study area. Since this section is generally well connected with few gaps, the observed movements might not be representative of all movements in the study area. This might have biased our results towards shorter movements.

The differences in dispersal probabilities between sections with and without gaps (Fig. 4) are a direct consequence of the necessity to rescale the dispersal probabilities, see equation (3). This is therefore no proof of any relationship with the landscape configuration. However, the relationship with the connectivity measure C_{3700} found in the preliminary statistical analysis indicates that individuals need to disperse further when there is limited suitable habitat in the neighbourhood of a previous nest. Moreover, the mark–resight analysis indicates that the adult dispersal parameters were related to connectivity. This suggests that when there is lack of suitable habitat in the direct neighbourhood, adults disperse further than when there is sufficient habitat. This effect was not found for juveniles. Their partly random dispersal and the mean dispersal distance of 3 km suggest that juvenile dispersal is less affected by local landscape characteristics.

What are the consequences of these dispersal mechanisms for the resulting distribution of birds over the area? Because of the limited dispersal ability of adults, it may take some time before relatively isolated unoccupied patches are recolonised. As a consequence, patches of good habitat quality might remain unoccupied, as has been found for Nuthatch *Sitta europaea* (Opdam *et al.* 1994, Matthysen *et al.* 1995). The partly random dispersal distances of juveniles could balance the limited spread of the other juveniles and adults. However, juveniles of the Great Reed Warbler in their first breeding season probably are attracted by singing older males and preferably settle in the immediate vicinity as has been shown for many passerine species (Ahlering & Faaborg 2006). This 'social attraction' leads to clustering of territories and lowers the probability of recolonizing suitable empty patches. Thus, in a fragmented area the species does not necessarily occupy the best quality nesting sites, resulting in lower reproductive success. The non-optimal distribution of individuals might become fatal in extreme situations, and lead to extinction of metapopulations (Stephens & Sutherland 1999).

Dispersal model

Many researchers have suggested adding landscape features to dispersal models (Noordwijk 1995, Pither & Taylor 1998; Baguette *et al.* 2000). Our study contributes to the research using mark–resight techniques

(Lebreton & North 1993). In our model, landscape configuration was integrated in two ways. Firstly, we included ecological distance and geographical distance in a concise way, to assess our hypothesis about dispersal of Great Reed Warblers along linear reed edges. Secondly, we defined gaps where dispersal probabilities were zero, and we modelled rescaled dispersal probabilities for suitable habitats. The introduction of gaps in the mark–resight analyses is new.

We have already noted that combined models, other than single exponential distance models, were necessary to describe a proportion of individuals with large dispersal distances. Hill *et al.* (1996) used inverse power models, whereas Bullock & Clarke (2000) and Nathan & Muller-Landau (2000) used other combined models. The dispersal model used here resembles the Arnason–Schwarz movement model for discrete strata (Arnason 1973). However, our model is more suitable for a large number of locations, because only a small number of parameters need to be estimated. We greatly reduced the number of parameters by linking the movement probabilities between sections to the distance between the sections. Though similar models have been developed (Spendelow *et al.* 1995, Hanski *et al.* 2000, Ricketts 2001), an important feature in our model is the distinction between habitat and gaps.

There are limitations in our study. The first is the assumption that survival and resight do not depend on the location of a bird. This assumption is reasonable for survival, but less certain for the probability of resight, as more effort was spend (more visits) to territories in the central region of the study area. We do think, however, that more than 90% of all territories in the study area have been found and, at least for the males, have been checked for colour-rings. The effect of this can be determined by formulating a model in which the probability of resight is in some way related to the location of the bird. Survival, resight and movement must then be estimated simultaneously (Schwarz *et al.* 1993). Our approach is a useful starting point for such a more complex way of modelling.

The second limitation is that our model only employs dispersal within the study area. For the conservation success of a metapopulation not only local dispersal is important, but also immigration and emigration. The positive effect of immigration is reduced by the reported lower lifetime fitness for male immigrants as opposed to philopatric males (Bensch *et al.* 1988). The definition of habitat sections and gaps is necessarily somewhat arbitrary. Since we used the centre of the habitat sections for calculating distances, it is unlikely that another partitioning will give different results.

How applicable are the results of this study to other landscapes? The parameter estimates are, in principle, linked to the specific linear spatial configuration of the habitat sections in this study. It is unlikely that these estimates can also be used for a landscape with much more scattered habitat sections, where more ecological routes could be defined. But for landscapes similar to the one in our study area our models will provide crude estimates of movement probabilities.

In conclusion, dispersal distances were transformed to rates of exchange between suitable habitat sections that are situated at various distances from each other. In this way a continuous space, which is very complex to model, was converted into discrete space with movements between sections, while losing very little information. Dispersal of the Great Reed Warbler seems to follow two strategies, one for small dispersal distance and one for much larger distances. Adult dispersal was much more restricted than juvenile dispersal and there is an indication that adults disperse further when connectivity decreases. Models using ecological distance gave a better fit than models employing geographical distance.

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SAMENVATTING

De Grote Karekiet *Acrocephalus arundinaceus* is in Nederland als broedvogel sterk afgenomen. Het laatste bolwerk bevindt zich langs de randmeren van Noordwest-Overijssel, waar in de jaren negentig van de 20ste eeuw nog 175 paren werden geteld (toentertijd de helft van de Nederlandse populatie, de dichtstbijzijnde populatie zat op 70 km afstand en telde 60 paren). In Noordwest-Overijssel werden 1.157 Grote Karekieten van kleurringen voorzien. De meeste van deze karekieten (85%) waren juveniele vogels waarvan het geslacht onbekend was. In het studiegebied werden vervolgens 178 vogels minstens één keer afgelezen. Tussen bekende nestlocaties werden 254 bewegingen genoteerd, waarvan er 199 betrekking hadden op verplaatsingen tussen opeenvolgende jaren. Het aantal aflezingen nam af met een toenemende afstand tot de ringplaats. Desondanks kon worden aangetoond dat juveniele vogels zich over grotere afstanden verplaatsten dan adulte vogels (in het laatste geval: geen verschil tussen beide geslachten). De volwassen vogels tendeerden naar broeden in de buurt van de eerdere broedplaats. Bijna tweederde deel werd teruggezien op gemiddeld 580 m van de vorige nestplaats. De resterende vogels werden op een gemiddelde afstand van 10 km teruggezien. Net als bij juveniele vogels, die voor bijna 40% willekeurige dispersierichtingen te zien gaven, lijken gaten met ongeschikt habitat te midden van rietstroken en rietvelden geen belemmering te zijn voor dispersie onder adulte vogels. Of adulte vogels inderdaad grotere dispersieafstanden gingen vertonen naarmate het geschikte leefgebied meer verbrokkeld was, moet nader onderzoek uitwijzen. Dat geldt ook voor het al of niet bestaan van twee dispersiestrategieën: in de buurt van de nest- of geboorteplek blijven versus grotere dispersieafstanden afleggen (al dan niet in willekeurige richtingen). In het eerste geval zou habitatfragmentatie dramatischer kunnen uitpakken dan in het tweede geval.