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*Research Article*

# Gap crossing decisions by reed warblers (*Acrocephalus scirpaceus*) in agricultural landscapes

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**Abstract**

To meet the need for research on the requirements for corridors for marshland birds, this study set out to quantify gap crossing decisions made by reed warblers moving through the landscape. In three experiments, reed warblers were released into landscape situations with different gap sizes and their movement towards reed patches fringing a watercourse were monitored. In all experiments, most birds flew over the smallest gap towards the nearest reed patch. In the experiment with two gap sizes, the probability of crossing a gap was a function of the ratio between distances to the reed patches. In the experiment with increasing gap sizes, most birds crossed the smaller gaps frequently. Near the bigger gaps, birds did not cross the gaps; instead, they only crossed the watercourse repeatedly. In the third experiment with more realistic landscape configurations, the birds preferred nearby non-reed landscape elements to more distant reed patches. It is concluded that reed warblers were reluctant to cross gaps wider than 50 m. The results suggest that the presence and size of gaps in reed patches affect reed warblers' local gap-crossing decisions: when given a choice, the birds prefer to cross the smallest gap. Furthermore, reed warblers may be directed towards suitable marshlands by creating corridors of reed vegetation with gaps no wider than 50 m. The surrounding agricultural landscape and the presence of trees and ditches could decrease the reluctance to cross gaps in corridors.

## Introduction

Marshlands are very important ecosystems in the Netherlands, harbouring many species of high conservation value (DenBoer 2000). However, human activity has led to the disappearance of many marshland areas; those that remain are smaller and more isolated (Leerdam and Vermeer 1992). The habitat quality of the remaining marshlands has decreased, because of the effects of water drawdown, water pollution, and unfavourable water level management (Graveland 1998). These processes are probably responsible for the decline in many marshland bird species and their appearance on Red Lists (Osieck and Hustings 1994). Dutch policymakers responded to this situation, acknowledging the international importance of the Dutch marshlands. A plan was proposed to create a nationwide ecological infrastructure linking the large marshland areas in a network (NPP 1990, 2000). This plan foresaw marshland restoration sites linked by corridors, i.e. landscape structures that facilitate the dispersal of organisms between suitable habitat patches in fragmented landscapes (Vos et al. 2002). Corridors need not be linear habitat strips; they may consist of a heterogeneous zone of landscape elements that enhance dispersal and that differ from the surrounding matrix (Bennett 1999; Vos et al. 2002). Presently, hundreds of kilometres of corridors are being planned, many of which are wet.

The plan rests on scientific research that has stressed the importance of corridors for different species. However, there is still a need for research on the quantitative requirements for corridors for different species groups, and for the effectiveness of corridors in ecological networks to be tested. Behavioural studies on individuals can quantify how a species moves through landscape mosaics (Wiens 2001). It has been found that corridors of certain habitat types are preferred above the surrounding landscape by a variety of species (Merriam and Lanuoue 1990; Bowne et al. 1999; Vos 1999). Moreover, corridors can facilitate movement, as has been shown for several butterfly species (Sutcliffe and Thomas 1996; Bennett 1999; Haddad 1999).

If corridors are interrupted by gaps of unsuitable habitat, species dispersal may be hampered. The use of corridors usually means a species is avoiding surrounding landscape types (Wauters et al. 1994; Beier 1995; Bennett 1999), and is reluctant to cross gaps of unsuitable habitat (Mansergh and Scotts 1989). It has been suggested that interpatch distances determine the relative effectiveness of corridors for butterflies (Haddad 2000). And movements of root voles (*Microtus oeconomus*) decreased when gap sizes between patches increased (Andreassen et al. 1996).

Most movement studies done on birds have focused on woodland species. They have produced some empirical evidence that linear landscape elements enhance or direct the dispersal of these birds. Hedgerows are important landscape features for the presence of birds in small and isolated forest patches (Wegner and Merriam 1979; Saunders and Rebeira 1991; Haas 1995). Furthermore, woodland birds took longer to return via a route with several unforested gaps than via a forested route (Bélisle and St. Clair 2001; Bélisle et al. 2001). Although these studies imply the potential effectiveness of corridors, more research is needed to refine the methods for obtaining quantitative guidelines (Inglis and Underwood 1992), and to elucidate bird movements in unforested landscapes. Studies in marshland ecosystems are particularly scarce.

In the agricultural landscapes in the Netherlands, marshlands alternate with small reed patches and reed edges along watercourses and ditches. This landscape constitutes a potential network of natural dispersal corridors for marshland birds, though with many gaps. For marshland birds, the most important habitats for breeding and probably also for dispersal are patches of reed vegetation (*Phragmites australis*). In fragmented landscapes, marshland bird populations might be hampered in moving between habitats and populations and this could affect their population viability (Opdam et al. 2002). The abundance of reed warblers (*Acrocephalus scirpaceus*) has indeed been found to be lower in fragmented Dutchlandscapes compared to regions in the Netherlands with a high spatial cohesion (Foppen et al. 2000). The underlying processes are described by metapopulation theory, which holds that insufficient spatial cohesion of the landscape can lead to local extinctions that are not counterbalanced by recolonisation processes (Levins 1970; Opdam 1991; Hanski 1994). The key process for the recolonisation of fragmented populations and the exchange between them is dispersal (Opdam 1990). From this it follows that it is important to study the dispersal and, on a local scale, the movement behaviour of individual birds (Pither and Taylor 1998; Opdam 2002).

Individual great reed warblers (*Acrocephalus arundinaceus*) preferentially dispersed along reed edges (Bosschieter, unpublished data). This raises the question of what specific quantitative requirements corridors should meet to be effective for marshland birds.

The purpose of the study reported here was to quantify gap crossing decisions by reed warblers moving through the landscape. We set out to answer two questions. The first was whether the presence of reed patches at certain distances affects the decisions reed warblers make about local movements. The second was to ascertain the effect of gap size: what sizes can the birds cross and what sizes do they not cross or cross less frequently. The experiment was set up with the aim of subsequently using the information on the gap crossing decisions in a model of the movement of individuals, so that local effects could be scaled up to the population level (Harrison and Taylor 1997; Ruckelshaus et al. 1997; Vos et al. 2001). The hypotheses were that birds would always opt for the smallest gap size present, and that smaller gaps would be crossed more frequently than larger gaps. We hoped that the results would be useful for drawing up quantitative guidelines, and would improve understanding of whether and how reed warbler movements can be directed by the landscape structure and of which landscape elements are important for corridors in ecological networks.

## Materials and methods

### *Species, capture techniques, and study areas*

Gap crossing decisions of reed warblers were studied in three different experiments in which reed warblers were released in different spatial situations, and their movements monitored. The reed warbler was chosen because it is an abundant marshland songbird, which is easy to study. To mimic the behaviour of dispersers in unfamiliar landscapes (Rüfenacht and Knight 1995; Mauritzen et al. 1999; Vos 1999), individuals were translocated into various landscape configurations. After being captured in mist nets in reed patches the birds were transported in a box, and released within 3 h in different locations 0.5–10 km away. The study areas were located in north-western Overijssel in the Netherlands. In this region there are many reed patches and reed edges in several spatial configurations in agricultural landscapes. From visual inspection, we concluded that the habitat quality was similar.

### *Overview of experiments*

In experiment 1, translocated reed warblers had to choose between two gap sizes between two reed patches. In experiment 2, the design of gap sizes was more complex: a pattern of different increasing gap sizes was designed, where a bird could choose between three gap sizes. Experiment 3 was a test in five complex locations with more realistic landscape configurations: birds were released in five locations at different distances from a single reed patch and other landscape elements.

Experiments 1 and 3 took place in spring with adults. Experiment 2 took place in summer with juveniles.

### *Choice between two gap sizes*

In May 2000, 52 adult reed warblers were released between two reed patches at three different release points A, B and C, at distances varying from 15 to 80 m (Figure 1). It was noted which gap the birds crossed and in which of the two patches they landed. To compare the three release points, the ratio between the gap sizes towards patch 1 and patch 2 was calculated (Table 1). The flight took a few seconds. A time interval of at least 10 min between releases prevented the birds from influencing each other, as by then the previous birds had flown away or were hidden in the reeds and not detectable.

The birds were released from a small box that could be opened with a string from a distance of 3 m to reduce the influence of the observer. The observer was positioned so as not to influence the choice between patch 1 or 2. At each of the release locations the birds were released in the middle of the road on the dyke; this minimised possible differences in the effect of the road. Note that the number of birds released varied per release point and was largest at point B, where the distances were equal. However, the numbers were large enough for statistical analysis.

The first hypothesis tested was that there was no preference for either gap; the alternative hypothesis was that there was a preference for the nearest patch. The probability of flying towards the nearest patch was taken as $p$, then the null hypothesis was $H_0$: $p = 0.5$; for the alternative hypothesis $H_1$: $p > 0.5$. The ratio of gap sizes for release point A was equal to the inverse of the ratio for release point C, and therefore the Fisher exact test was used to test whether the probability of flying to the nearest patch would be the same for A and C. Furthermore, in a combined analysis the probability of moving to the nearest patch $p(x)$ was modelled as a function of the ratio $x$ of the two distances. This function had to meet two

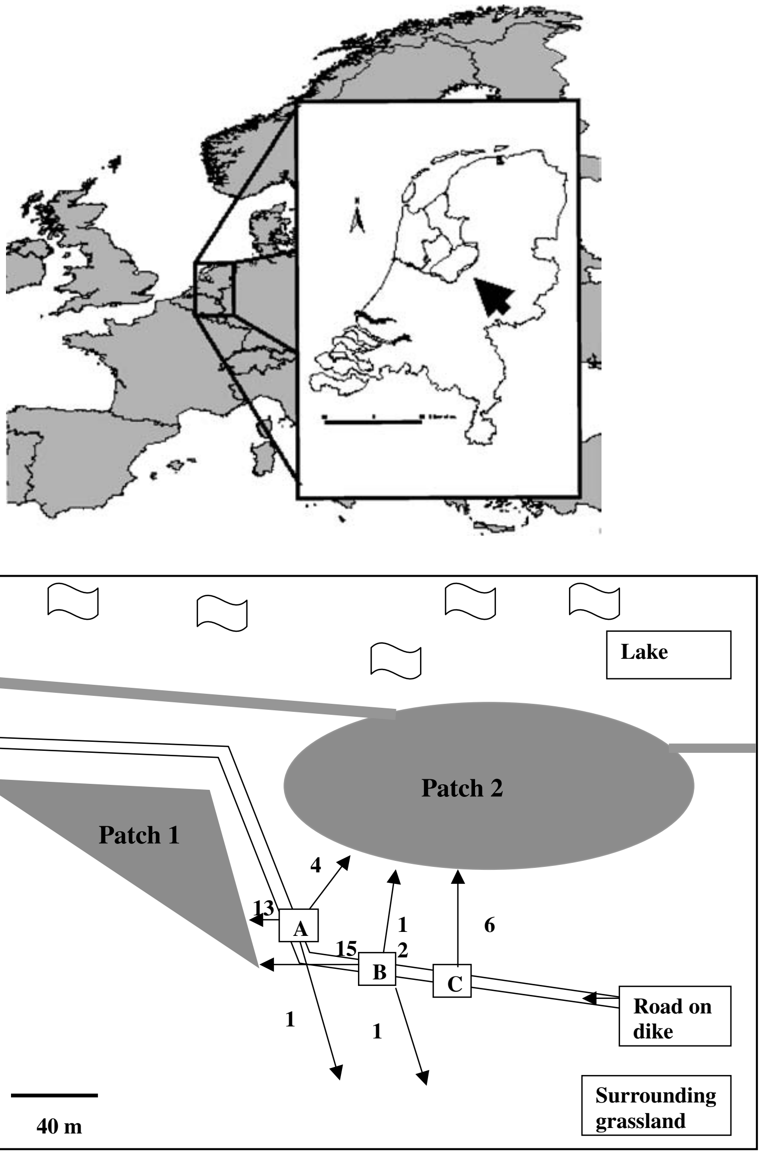



*Figure 1.* Location where 52 reed warblers were released at points A, B and C between two reed patches, and its position in Europe and the Netherlands (52°30′N, 5°52′E). The numbers of birds that chose a certain gap size are shown near the arrows.

*Table 1.* Gap crossing decisions of 52 reed warblers released between two reed patches.

| Release points | Distance to patch 1 (m) | Distance to patch 2 (m) | Ratio of gap sizes | No. birds to patch 1 | No. birds to patch 2 | No. birds other | Total no. birds |
|---|---|---|---|---|---|---|---|
| A | 15 | 30 | 0.5 | 13 | 4 | 1 | 18 |
| B | 50 | 50 | 1 | 15 | 12 | 1 | 28 |
| C | 80 | 40 | 2 | 0 | 6 | 0 | 6 |
| Total no. birds | | | | 28 | 22 | 2 | 52 |

requirements. With equal gap sizes the probability of crossing either gap must be equal: $p(1) = 0.5$. Furthermore the function must not depend on using $x$ or $1/x$ as the ratio of the two distances. This requires that the function is symmetrical $p(1/x) = 1 - p(x)$. The following special form of the logistic regression fulfils both requirements:

$$\text{logit } (p(x)) = \beta \log(x). \quad (1)$$

*Choice between three gap sizes*

In August 2000, an experiment was performed to study the gap-crossing behaviour of reed warblers near three gaps of different size. The study area was a straight watercourse in the middle of an arable area, with two small reed edges of 2 m wide on each bank. In both reed edges six gaps of incremental width were mown: 10, 25, 50, 100, 200, and 300 m (Figure 2). Radio transmitters (Holohil Systems Ltd: Type BD2A) weighing 0.65 g and with a life of 3 weeks were glued to the back of 12 juvenile birds, just between the wings. Then the 12 juveniles were released into the reed patches between the gaps. The releases of individuals were distributed over the different patches and spread over 3 weeks to avoid interaction between the birds (Table 2). More birds were released near the large gaps, to increase the probability of observing crossings over these gaps.

At every reed patch, birds were faced with three possible crossings: (i) the minimum gap size along the watercourse, (ii) the maximum gap size along the watercourse, and (iii) the crossing over the water to the opposite bank. The latter gap was 15 m over open water. We assumed marshland birds would make similar decisions for gaps over land or water on a scale of 15 m. At regular intervals of 1 h, birds were monitored for their presence in the different patches. A change of presence in the different patches was interpreted as the bird having crossed the gap; the actual gap crossing was not often observed.

For the analyses, movements of all birds were pooled, assuming that all movements were independent of each other and that there were no bird-specific effects. We tested this assumption by checking for bird-specific effects in the statistic analyses. If a bird crossed more than one gap in one time interval, this movement was split into separate movements over the different gap sizes. It

*Table 2.* Movements of individual reed warblers released alongside a watercourse with mown reed edges.

| Bird no. | Release point | No. days[a] | No. movements[b] | Patches visited |
|---|---|---|---|---|
| 1 | A2 | 2 | 4 | A, B |
| 2 | B2 | 15 | – | Mostly in fields |
| 3 | B2 | 5 | 21 | A, B, C, D |
| 4 | C2 | 7 | 34 | A, B, C, D |
| 5 | D1 | 4 | 16 | A, B, C and in fields |
| 6 | D2 | 3 | 6 | D1, D2 |
| 7 | E1 | 2 | 8 | E1, E2 |
| 8 | E1 | 2 | 2 | E1, E2 |
| 9 | E2 | 8 | 4 | Mostly D and in fields |
| 10 | E2 | 3 | 9 | A, B, C, D |
| 11 | F1 | 9 | 12 | F and in fields |
| 12 | F2 | 6 | 4 | F |
| Total no. | | 66 | 120 | |

Bird 2 was excluded from the analyses.
[a]No. of days each individual bird was monitored in the study area.
[b]No. of movements per individual bird during the total no. of days.

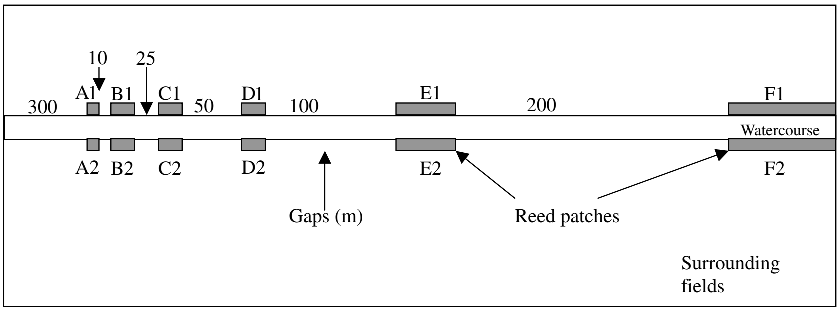



*Figure 2.* Schematic layout of reed patches and mown gap sizes along a watercourse where 12 reed warblers tagged with radio transmitters were released. The gaps varied in width from 10 to 300 m. The reed patches (shaded rectangles) were coded A1 to F1 along one bank of the watercourse, and A2 to F2 along the other bank.

was further assumed that the patches on both banks offered similar choices in similar landscape conditions. Therefore these patches were pooled. Some birds moved through the fields behind the reeds. In a first analysis, these movements were excluded from the analyses, because of the difficulty of interpreting them. In a second analysis these movements were interpreted as if the birds had crossed the gaps directly. Other birds moved diagonally over more than one gap size, to reach the opposite bank. These gap crossings were also excluded from the first analysis. In a second analysis they were split into two movements: one movement over the watercourse, and one movement over the specific gap. Patch F was excluded from the analysis, because the reed edge of this patch continued along the channel, and the minimum gap size could not be defined. Movements to the patch were included in the analysis.

Using multinomial logistic regression we modelled the probabilities of crossing the three possible gaps, with the minimum and maximum gap size as dependent variables. Multinomial logistic regression is an extension of ordinary logistic regression, and is capable of modelling multiple possible outcomes (McCullagh and Nelder 1989). In the multinomial logistic model, the probabilities of crossing the minimum gap size ($\pi_1$), the maximum gap size ($\pi_2$) and the gap across open water ($\pi_3$) were defined by

$$\begin{aligned} \pi_1 &= \exp(\eta_1)/[\exp(\eta_1) + \exp(\eta_2) + 1] \\ \pi_2 &= \exp(\eta_2)/[\exp(\eta_1) + \exp(\eta_2) + 1] \\ \pi_3 &= 1/[\exp(\eta_1) + \exp(\eta_2) + 1] \end{aligned} \tag{2}$$

in which the linear predictors $\eta_1$ and $\eta_2$ are related to the dependent variables as follows:

$$\begin{aligned} \eta_1 &= \alpha_1 + \beta_1 \text{min} + \gamma_1 \text{max}; \\ \eta_2 &= \alpha_2 + \beta_2 \text{min} + \gamma_2 \text{max}. \end{aligned} \tag{3}$$

This ensures that the resulting probabilities are functions of the minimum and maximum gap sizes, are in the interval (0,1), and the sum of the three probabilities equals one. In formula (3) $\alpha$, $\beta$ and $\gamma$ are regression parameters to be estimated from the data. One extra condition was made: when the minimal gap size equals the maximal gap size, then $\pi_1 = \pi_2$ has to be true for each minimal gap size. From this it follows that $\alpha_1 = \alpha_2$ and that $\beta_1 + \gamma_1 = \beta_2 + \gamma_2$.

Instead of six parameters, the model thus has the four parameters $\alpha$, $\beta_1$, $\gamma_1$ and $\beta_2$. To check for bird-specific effects, i.e. individual variation in crossing probabilities, we tested whether these parameters were equal for all individuals. This was done separately for each parameter, using the likelihood ratio test.

*Choice in different locations*

In May 1999, 87 adult reed warblers were released in five different locations with different landscape configurations at distances varying from 10 to 200 m between the release point and a single reed patch (Table 3). Each location contained 2–4 release points, one reed patch, and several other landscape elements at varying distances from the release points. These elements were ditches, trees, and surrounding fields or rank vegetation. We observed whether the bird flew into the reed patch or whether it flew to other landscape elements. This flight lasted a few seconds, and the observation then ceased. A time interval of at least 10 min between releases prevented the birds from influencing each other. In a logistic regression analysis we tested whether the probability ($p$) of flying into the reed patch depended on the gap size in the direction of the reed patch. In the analysis we corrected for differences between locations. The model was

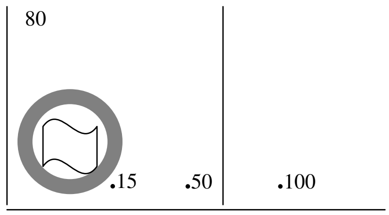
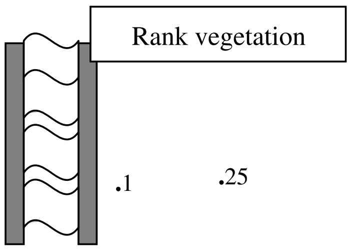
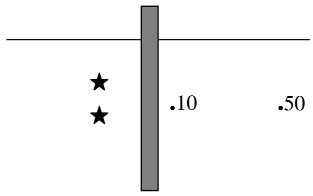
$$\text{logit}(p) = \text{landscape } j + \beta \text{ gap size} \tag{4}$$

## Results

*Choice between two gap sizes*

Most birds flew directly into one of the reed patches (Table 1). Only two of the 52 birds flew out of the study area, and had to be excluded from the analysis. Except for the 80-m gap, which was never crossed, all gap sizes were crossed in a few seconds. From release points A and C, most birds flew over the smallest gap size towards the nearest patch, in accordance with the alternative hypothesis (Table 4). For release point B, with equal gap sizes towards patches 1 and 2, we found that the hypothesis of equal probabilities for either gap size could not be rejected.

*Table 3.* Schematic layouts and descriptions of five locations where 87 reed warblers were released.

| Scheme | Location and characteristics |
| --- | --- |
|   | 1. Patch of reed; size: 50 m wide, perimeter 50 m; other elements: ditch (20 m away), trees (200 m away); adjacent grassland |
|   | 2. Pond with reed edge, bullrushes, and water; size: 1 m wide, 100 m long; other elements: ditches (20 m away); adjacent hayfields |
|   | 3. Strip of reed; size: 10 m wide, 200 m long; other elements: trees (20–70 m away); bare adjacent field |
|   | 4. Watercourse with reed edges and water; size: 1 m wide, 200 m long; other elements: strip (25 m wide) of rank vegetation; bare adjacent field |
|   | 5. Ditch with reed edge; size: 1 m wide, 150 m long; other elements: Ditch (50 m away), trees (50–100 m away); adjacent grassland |

Reed patches (shaded areas), release points at distances from reed patch (the reed is about 2 m high – points), ditches (the ditches were surrounded by rank vegetation ( $<$ 1 m in height) – black lines), trees (trees were taller than 3 m – stars), water (waves) are given in the surrounding fields (white areas).

With equivalent ratios between the gap sizes at release points A (15/30 m) and C (80/40 m), the number of birds flying towards the nearest patch from both release points was not significantly different (Fisher exact test, $p = 0.538$). So, although the distances from release point C were longer than the distances from A, the effect in A and C was similar. These results indicate that reed warblers fly towards the nearest patch, and that, within the limited range studied here, the probability of moving towards the nearest patch depends only on the ratio of the distances. Other landscape features, such as shape and size of the patch, seemed to be less important. The birds did

*Table 4.* Test of hypothesis that in a translocation experiment of 52 reed warblers there was no preference for either gap, with the alternative that there was a preference for the nearest patch ($H_0$: $p = 0.5$; $H_1$: $p > 0.5$).

| Release points | 95% confidence interval | $p$-value $H_0$ | Conclusion |
|---|---|---|---|
| A | 0.501–0.932 | 0.025 | $H_0$ rejected : $p > 0.5$ |
| B | 0.353–0.745 | 0.351 | $H_0$ not rejected: $p = 0.5$ |
| C | 0.541–1.000 | 0.016 | $H_0$ rejected: $p > 0.5$ |

The 95% confidence interval for the probability of moving to the nearest patch is shown.

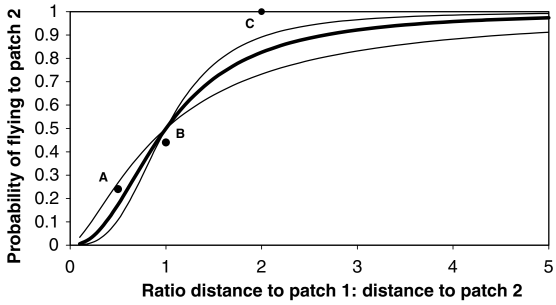



*Figure 3.* Logistic regression of the ratio of gap sizes and the probability that birds will cross the gap towards patch 2. This was based on an experiment in which 52 adult reed warblers were released between two reed patches, at distances varying from 15 to 80 m. The black line represents the significant relationship ($p = 0.005$), the thin lines are the 95% confidence limits. Release points A, B and C are also indicated.

not fly to other nearby non-reed landscape elements.

Model (1) was fitted to combined data of the three release points. The estimate for $\beta$ was 2.2 (S.E. = 0.8, $p = 0.005$). The resulting fitted curve as a function of the ratio is given in Figure 3. It is clear that the fitted curve meets the requirement $p(1) = 0.5$, and that with increasing ratios, the probability of moving to the nearest patch approaches 1. Note that the resulting curve is tentative, as it is based solely on three different release points, with ratios 0.5, 1, and 2, and distances between 15 and 80 m.

### *Choice between three gap sizes*

In total, 120 movements by 12 juveniles were observed (Table 2). Three birds moved more than 15 times: these were birds moving around the smaller gaps. Four birds visited the field of sugar beet (*Beta* spp.) bordering the watercourse. They fed in this field during the day, but always returned to the reeds before dark. One of these birds was excluded from the analyses, because it never visited the reed patches during the day. Most birds flew over water and not over land during gap crossing.

Small gaps were crossed more frequently than large gaps (Table 5). The gap of 100 m was crossed only once, but as this bird dispersed through the fields of sugar beet this crossing was only included in the second analysis. The gaps of 200 and 300 m were never crossed. In total, there were 11 movements over gaps via the adjacent fields. The second analysis included 50 additional movements, because movements diagonally over the water were split into one movement to the opposite bank and one movement over the gap.

The length of time we observed each individual bird varied from 2 to 15 days. Most movements occurred during daytime. We monitored the sites for several nights, but never observed any nocturnal flights. The transmission range in the field was about 100 m at ground level. Because of the intensive measurements, we assume that we did

*Table 5.* Number of reed warblers that crossed the three possible gap sizes along a watercourse with mown reed edges.

| Patch | Size of the patch | Min. gap (m) | Max. gap (m) | No. birds over min. gap | No. birds over max. gap | No. birds over watercourse | Total no. movements |
|---|---|---|---|---|---|---|---|
| A | 10 | 10 | 300 | 10 | 0 | 4 | 14 |
| B | 25 | 10 | 25 | 7 | 15 | 8 | 30 |
| C | 25 | 25 | 50 | 14 | 7 | 7 | 28 |
| D | 25 | 50 | 100 | 5 | 0 | 10 | 15 |
| E | 50 | 100 | 200 | 0 | 0 | 17 | 17 |
| F | – | – | 200 | – | 0 | 16 | 16 |
| Total no. movements | | | | 36 | 22 | 62 | 120 |

12 birds were released in the reed patches next to varying gap sizes: a minimum gap size (min. gap), a maximum gap size (max. gap), and the opposite bank of the watercourse. These data were used in the first analysis.

*Table 6*. Parameter estimates for the multinomial logistic regression model of the probabilities of reed warblers crossing three gap sizes along a watercourse with mown reed edges.

| Parameter | Estimate | S.E. | *t*-value | *p*-value | *p*-value bird-specific effects |
|---|---|---|---|---|---|
| $\alpha$ | 1.4127 | 0.4651 | 3.04 | 0.002 | 0.113 |
| $\beta_1$ | −0.0493 | 0.0124 | −3.99 | 0.000 | 0.085 |
| $\gamma_1$ | −0.0001 | 0.0025 | −0.03 | 0.979 | 0.061 |
| $\beta_2$ | −0.0285 | 0.0169 | −1.68 | 0.092 | 0.906 |

Also the *p*-values of the likelihood ratio tests for bird-specific effects are given.

not miss any movements within a radius of one kilometre. We excluded movements further away because we were solely interested in local gap crossing decisions.

We did not observe any direct effects of the transmitters on flight or moving behaviour, but transmitters often affect birds (White and Garrot 1990). In this experiment, seven birds (58%) pulled out the transmitters after a few days. Though this suggests that the birds were uncomfortable with the transmitters, it does not necessarily follow that their movements were influenced.

The parameter estimates of the multinomial model are given in Table 6, along with the *p*-values of the likelihood ratio tests for bird-specific effects. Although there is some indication that different birds have different parameters $\beta_1$ and $\gamma_1$, the assumption of no bird-specific effects seems reasonable.

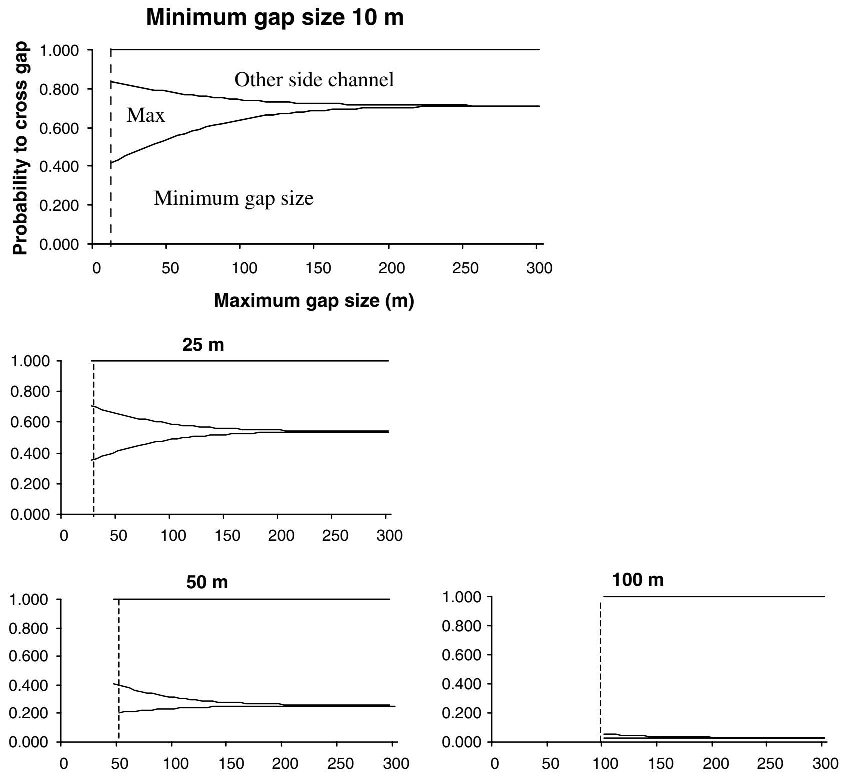



*Figure 4*. Multinomial logistic regression model of the probabilities of reed warblers crossing three gap sizes: minimum (min), maximum (max), and the other side of the watercourse, with the dependent variables being minimum and maximum gap size. The curves are the cumulative probabilities, which sum to 1. The graphs are given for four minimum gap sizes.

*Table 7.* Gap crossing decisions of 87 reed warblers released in five locations at different release points at 1–200 m distance from a certain reed patch.

| Location | Release points (m) | Total no. birds | No. birds to reed | No. birds to other landscape elements | | |
|---|---|---|---|---|---|---|
| | | | | Ditch | Trees | |
| 1 | 10 | 4 | 4 | 0 | 0 | |
| 1 | 100 | 3 | 1 | 1 | 1 | |
| 1 | 200 | 3 | 1 | 1 | 1 | |
| | | | | Ditch | Hayfields | |
| 2 | 15 | 4 | 3 | 1 | 0 | |
| 2 | 50 | 6 | 0 | 4 | 2 | |
| 2 | 80 | 8 | 6 | 1 | 1a | |
| 2 | 100 | 6 | 0 | 6 | 0 | |
| | | | | Trees | | |
| 3 | 5 | 4 | 2 | 2 | | |
| 3 | 10 | 6 | 5 | 1 | | |
| 3 | 25 | 12 | 7 | 5 | | |
| 3 | 50 | 6 | 4 | 2 | | |
| | | | | Rank vegetation | Bare field | |
| 4 | 1 | 7 | 4 | 3 | 0 | |
| 4 | 25 | 10 | 5 | 4 | 1 | |
| | | | | Ditch | Trees | Grassland |
| 5 | 10 | 5 | 3 | 0 | 1 | 1 |
| 5 | 50 | 3 | 0 | 1 | 1 | 1 |

The resulting probabilities as a function of the maximum gap size are shown in a series of graphs (Figure 4), where each individual graph is for a fixed minimum gap size. The combination of the different gap sizes defined the probabilities that birds would cross the gaps. For each fixed minimum gap size, as the maximum gap size increases, the probability of crossing the maximum gap size approaches 0 and there is an increased probability of crossing either the minimum gap size or the watercourse. When the minimum gap size increases, the probability of crossing that gap decreases and consequently so does the probability of crossing the watercourse. This was seen in the field near the large gaps, where most birds flew to and fro between both sides of the watercourse. At a minimum or maximum gap size of 100 m, the probability of crossing this gap was less than 0.1,

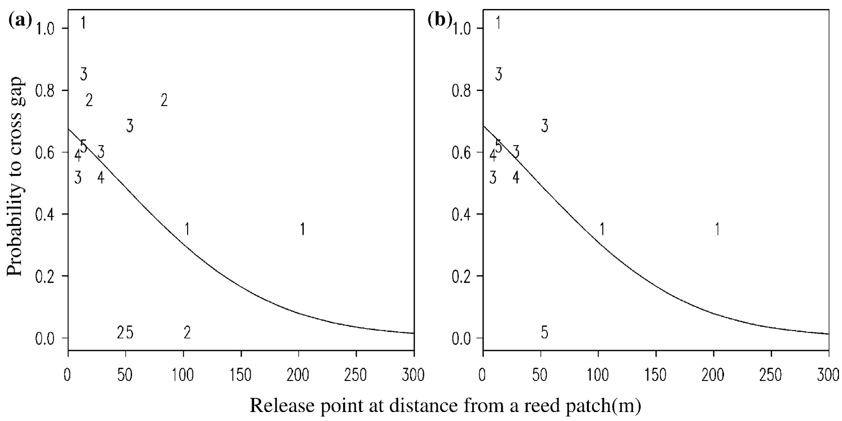



*Figure 5.* Logistic regression of gap crossing decisions by 87 reed warblers released (a) in five locations and (b) in the same locations but with landscape 2 excluded. The numbers of the locations 1–5 indicate the results per location (see also Tables 3 and 7).

and at 150 m the likelihood of crossing this gap was very small. A gap of 100 m was already sufficient to limit the movements of the reed warblers.

Because the estimate of $\gamma_1$ (see formula (3)) roughly equals 0, the ratio $\pi_1/\pi_3$ is almost independent of the maximum gap size, and is thus only a function of the minimum gap size. For example, at a minimum gap size of 25 m, this ratio is 1.2. Because the parameter estimates were negative, except for $\alpha$, for very large minimum gap sizes the crossing of the watercourse will equal 1. Furthermore, as $\gamma_1$ and $\beta_2$ were not significant, they could be omitted from the model. However, the fit of a model with $\gamma_1$ and $\beta_2$ set at 0 was only slightly different, so has not been presented here.

In the second analysis we tested a model that included gap crossings via the fields and diagonally over the watercourse. The estimates yielded by these models were not significantly different for $\alpha$ ($p = 0.4$) or for $\beta_1$ ($p = 0.3$), indicating that the model is a sound representation of the results.

### *Choice in different locations*

The results for the five more realistic locations with different landscape configurations are somewhat complex. Small gaps were crossed more frequently than large gaps, and most birds flew into the reed patch (Table 7). However, per location per release point, some birds opted to fly into reed, but some opted to fly to ditches, trees or even into fields. Overall, when confronted with larger gaps, birds chose to cross smaller gaps into nearby non-reed landscape elements. Sometimes, they even flew towards elements that were further away than the reed patches.

In the logistic regression analysis, only the distance towards the reed patch was analysed. After incorporating all the data into this model, we found overdispersion with respect to the binomial distribution. In the model, distance was not significant ($p = 0.170$), with $\beta$ estimated as $-0.0178$ (S.E. = 0.0119) (Figure 5a). The largest three residuals were for landscape 2. This might be because bullrush (*Scirpus acutus*) was also abundant in the reeds here, which could have made the decision to fly towards the reed patch more variable. Furthermore, there were three ditches nearby, which were also attractive destinations. When landscape 2 was excluded, the data did not show overdispersion, and distance was significant ($p = 0.030$). The estimate of $\beta$ was $-0.0187$ (S.E. 0.0099), meaning that the probability of flying to the reed patch decreased with increasing distance to the patch (Figure 5b). At 50 m from the reed patch, the probability of flying towards this reed patch was 0.5, at 100 m the probability was 0.25. And even very close to the reed patch, the probability never exceeded 0.7.

## Discussion

In all three experiments, the presence of reed structures affected reed warblers' decisions about local movement. In line with the hypotheses, the birds preferentially flew into reed vegetation. They mostly chose to fly to the nearest reed patch, and therefore chose the smallest gap present. Our finding that smaller gaps were crossed more frequently than larger gaps may be interpreted as evidence that reed warblers are reluctant to cross gap sizes larger than 50 m.

Our findings on local movements of marshland birds are in agreement with other studies. In a similar experimental set-up, Conradt et al. (2000) found that butterflies' movement decisions were oriented towards suitable habitat, but this occurred on a much smaller scale than in our study. Desrochers and Hannon (1997) found that when faced with gap sizes similar to those we used, forest birds were also limited in their movements: the forest birds were three times less likely to cross 70 m than 30 m gaps in forest cover. Different studies have also found that if gap sizes increased, the probabilities of birds crossing the gaps decreased (Andreassen et al. 1996; Desrochers and Hannon 1997). We obtained quantitative guidelines for a marshland species in unforested landscapes, providing innovative statistical methods.

Four limitations of our experiments should be discussed. The first is that the conclusion of experiment 1 is based on 52 birds, released at three release points. The resulting curve is therefore tentative. The second limitation is that in the set-up of experiment 2, birds always had a shorter option available than the maximum gap size, if they wanted to switch patches. Our experiments reflect the gap crossing decisions that birds make in simple situations. Birds are able to see over long distances (Lima and Zollner 1996), and reed warblers disperse over long distances (Paradis et al. 1998: geometric mean 3–5 km). It seems likely that in real life, when smaller gaps are not available, reed warblers will probably cross gaps larger than the ones we used. It has been found that woodland birds were able to cross large gaps, and that it took them longer to return via a route with several gaps than via a forested route (Bélisle et al. 2001). A third limitation is the absence of a control situation for movements in continuous habitats. This makes that we can conclude that gaps in habitat can affect local movements in reed warblers, but the degree of limitation and the influence on longer distance movements can only be speculated on. A fourth limitation: In the model of experiment 2, we elucidated the complex relationships arising from the case of three gap sizes. In real landscapes, there will be more than three gap sizes. Experiment 3 shows that more realistic situations might produce less clear-cut results. This underlines the value of combining several types of experiments, as we did. The more realistic results of experiment 3 could only be interpreted in conjunction with the results from the simpler experiments.

Unexpectedly, in some situations the reed warblers preferred nearby non-reed landscape elements to more distant reed patches. Supplementary feeding behaviour in surrounding landscapes has been reported (Borowiec 1992), but in our study the fields made it easier for the birds to cross larger gaps in the watercourse. Further study needs to be done in order to be able to make precise quantitative predictions about the effect of these landscape elements on the probability that birds will cross larger gaps more frequently.

The gap-crossing behaviour we measured could have been a short-term response to a local situation, but might it also resemble longer-term movement, i.e. dispersal? Dispersal is the one-way movement of individuals towards a future breeding territory (Greenwood and Harvey 1982). In most bird species, juveniles are the main dispersers, dispersing from the nest site (Morton et al. 1991; Noordwijk 1995; Machtans et al. 1996, Paradis et al. 1998). Adults tend to breed close to their former breeding site, so they disperse less far than juveniles (Greenwood and Harvey 1982; Bensch and Hasselquist 1991; Fisher and Haupt 1994). In our set-up we tried to mimic the dispersal situation by creating a dispersal motivation to force birds to make gap crossing decisions. In experiments 1 and 3 we used adults, who had a strong motivation to return to their territories. In experiment 2, we studied fledged juveniles, who probably had a natural predilection to disperse. In all three experiments we released the birds in unknown environments to create a situation similar to a dispersal situation (MacDonald and Johnson 2001). Furthermore, we assumed that other effects, such as stress and the influence of transmitters, did not influence the movements we measured.

To be able to draw further conclusions about dispersal we would have had to extrapolate the local gap crossing decisions of reed warblers in a movement model, and then compare the findings with the results of natural dispersal processes (Beier and Noss 1998; Vos et al. 2002).

Although the local movements we measured were not really dispersal movements, it is nevertheless possible that the observed gap crossing decisions of reed warblers also play a role during dispersal. Let us assume that this is the case, and extrapolate the results to a dispersal level. Although gaps are not insurmountable barriers, local gap crossing decisions may result in higher numbers of dispersers near large gaps, which will reduce the probability of certain habitat patches being reached. Several studies have pointed out that this can impact on the population level (e.g. a low abundance of reed warblers in fragmented landscapes: Foppen et al. 2000).

In my experiments the reed warblers always opted for the smallest gapsize. The findings presented here suggest that the presence and structure of reed patches may help reed warblers to move in a certain direction towards the nearest marshlands. Local gap crossing decisions can create significant cumulative barrier effects at the landscape scale (Bélisle and St. Clair 2001; Gobeil and Villard 2002). This being so, the practical implications of our study are that reed warblers may be directed towards suitable marshlands by creating corridors of reed vegetation with gaps no wider than 50 m. The surrounding agricultural landscape and the presence of trees and ditches could decrease the reluctance to cross gaps in corridors.

In the future we will apply an individual dispersal model to scale up our local results to the population level (Harrison and Taylor 1997; Ruckelshaus et al. 1997; Vos et al. 2001). This will enable us to answer questions about the most effective structure of the marshland landscape for reed warblers, and about the other specific quantitative requirements needed for corridors.

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## References

Andreassen H.P., Ims R.A. and Steinset O.K. 1996. Discontinuous habitat corridors: effect on male root vole movements. J. Appl. Ecol. 33: 555–560.

Beier P. 1995. Dispersal of juvenile cougars in fragmented habitat. J. Wildlife Manage. 59: 228–237.

Beier P. and Noss R.F. 1998. Do habitat corridors provide connectivity? Review. Conserv. Biol. 12: 1241–1252.

Bélisle M. and St. Clair C.C. 2001. Cumulative effects of barriers on the movements of forest birds. Conserv. Ecol. 5(2): 9.

Bélisle M., Desrochers A. and Fortin M.J. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. Ecol. Washington, DC 82: 1893–1904.

Bennett A.F. 1999. Linkages in the landscape: the role of corridors and connectivity in Wildlife conservation. The World Conservation Union (IUCN) Forest Conservation Programme, Gland, Switzerland and Cambridge, United Kingdom.

Bensch S. and Hasselquist D. 1991. Territory infidelity in the polygynous great reed warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. J. Anim. Ecol. 60: 857–871.

Borowiec M. 1992. Breeding ethology and ecology of Reed Warbler, *Acrocephalus scirpaceus* at Milicz, SW Poland. Acta Zool. Cracov 35(2): 315–350.

Bowne D.R., Peles J.D. and Barret G.W. 1999. Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). Landscape Ecol. 14: 53–65.

Conradt L., Bodsworth E.J., Roper T.J. and Thomas C.D. 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. Proc. R. Soc. Lond. B 267: 1505–1570.

DenBoer T. 2000. Beschermingsplan moerasvogels 2000–2004. Rapport directie natuurbeheer nr. 47, Wageningen, 183 p. (in Dutch).

Desrochers A. and Hannon S.J. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. Conserv. Biol. 11: 1204–1210.

Fischer S. and Haupt H. 1994. Settling patterns and movements of East-German Great Reed Warblers (*Acrocephalus arundinaceus*) – an analysis of ringing recoveries of the Hiddensee birdringing station. Vogelwarte 37: 183–189.

Foppen R.P.B., Chardon J.P. and Liefveld W. 2000. Understanding the role of sink patches in source-sink metapopulations: reed warblers in an agricultural landscape. Conserv. Biol. 14: 1881–1892.

Gobeil J.-F. and Villard M.-A. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. Oikos 98: 447–458.

Graveland J. 1998. Reed die-back, water level management and the decline of the Great Reed Warbler (*Acrocephalus arundinaceus*) in the Netherlands. Ardea 86: 187–201.

Greenwood P.J. and Harvey P.H. 1982. The natal and breeding dispersal of birds. Annu. Rev. Ecol. Systemat. 13: 1–21.

Haas C.A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. Conserv. Biol. 9: 845–854.

Haddad N.M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. Ecol. Appl. 9: 612–622.

Haddad N. 2000. Corridor length and patch colonization by a butterfly, *Junonia coenia*. Conserv. Biol. 14: 738–745.

Hanski I. 1994. A practical model of metapopulation dynamics. J. Anim. Ecol. 63: 151–162.

Harrison S. and Taylor A.D. 1997. Migration within metapopulations, the impact upon local population dynamics. In: Hansi and Gilpin (eds), Metapopulation Biology; Ecology, Genetics, and Evolution. Academic Press, San Diego.

Inglis G. and Underwood A.J. 1992. Comments on some designs proposed for experiments on the biological importance of corridors. Conserv. Biol. 6: 581–586.

Leerdam A. van and Vermeer J.G. 1992. Natuur uit het moeras! Naar een duurzame ecologische ontwikkeling in laagveenmoerassen. LNV.

Levins R. 1970. Extinctions. In: Gerstenhaber (ed.), Some Mathematical Questions in Biology. Lectures on Mathematics in the Life Sciences, vol. 2. The American Mathematical Society, Providence, RI, pp. 77–107.

Lima S.L. and Zollner P.A. 1996. Towards a behavioral ecology of ecological landscapes. Trends Ecol. Evol. 11: 131–134.

MacDonald D.W. and Johnson D.P. 2001. Dispersal in theory and practice consequences for conservation biology. In: Clobert J., Danchin E., Dhondt A.A. and Nichols J.D. (eds), Dispersal. Oxford University Press, pp. 358–372.

Machtans C.S., Villard M.-A. and Hannon S.J. 1996. Use of riparian buffer strips as movement corridors by forest birds. Conserv. Biol. 10: 1366–1379.

Mansergh I.M. and Scotts D.J. 1989. Habitat continuity and social organization of the mountain pygmy-possum restored by tunnel. J. Wild. Manage. 53: 701–707.

Mauritzen M., Bergers P.J.M., Andreassen H.P., Bussink H. and Barendse R. 1999. Root vole movement patterns: do ditches function as habitat corridors? J. Appl. Ecol. 36: 215–222.

McCullagh P. and Nelder J.A. 1989. Generalized Linear Models, 2nd Ed. Chapman and Hall, London.

Merriam G. and Lanuoue A. 1990. Corridor use by small mammals: field measurements for three experimental types of *Peromyscus leucopus*. Landscape Ecol. 4: 123–131.

Morton M.L., Wakamatsu M.W., Pereyra M.E. and Morton G.A. 1991. Postfledging dispersal, habitat inprinting and philopatry in a montane, migratory sparrow. Ornis Scand. 22: 98–106.

Noordwijk A.J.V. 1995. On bias due to observer distribution in the analysis of data on natal dispersal in birds. J. Appl. Stat. 22: 683–694.

NPP 1990. Nature Policy Plan. Ministry of Agriculture, Nature Conservation and Fisheries. SDU, The Hague (in Dutch).

NPP 2000. Nature Policy Plan: Nature for People, People for Nature. Ministry of Agriculture, Nature Conservation and Fisheries. SDU, The Hague (in Dutch).

Opdam P. 1990. Dispersal in fragmented populations: the key to survival. In: Bunce R.G.H. and Howards D.C. (eds), Species Dispersal in Agricultural Habitats. Belhaven Press, London.

Opdam P. 1991. Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. Landscape Ecol. 5: 93–106.

Opdam P., Foppen R. and Vos C.C. 2002. Bridging the gap between ecology and spatial planning in landscape ecology. Landscape Ecol. 16: 767–779.

Osieck E.R. and Hustings F. 1994. Rode lijst van bedreigde soorten en blauwe lijst van belangrijke soorten in Nederland. Technisch rapport Vogelbescherming Nederland 12. Vogebescherming Nederland, Zeist (in Dutch).

Paradis E., Baillie S.R., Sutherland W.J. and Gregory R.D. 1998. Patterns of natal and breeding dispersal in birds. J. Anim. Ecol. 67: 518–536.

Pither J. and Taylor P.D. 1998. An experimental assessment of landscape connectivity. Oikos 83: 166–174.

Ruckelshaus M., Hartway C. and Kareiva P. 1997. Assessing the data requirements of spatially explicit dispersal models. Conserv. Biol. 11: 1298–1306.

Rüfenacht B. and Knight R.L. 1995. Influences of corridor continuity and width on survival and movement of deermice *Peromyscus maniculatus*. Biol. Conserv. 71: 269–274.

Saunders D.A. and de Rebeira C.P. 1991. Values of corridors to avian populations in a fragmented landscape. In: Saunders D.A. and Hobbs R.J. (eds), Nature Conservation 2: the Role of Corridors.

Sutcliffe O.L. and Thomas C.D. 1996. Open corridors appear to facilitate dispersal by Ringlet Butterflies (*Aphantopus hyperantus*) between woodland clearings. Conserv. Biol. 10: 1359–1365.

Vos and C.C. 1999.A frog's-eye view of the landscape. Ph.D. Dissertation. Wageningen University and DLO Institute for Forestry and Nature Research, Wageningen, the Netherlands.

Vos C.C., Verboom J., Opdam P.F.M. and TerBraak C.J.F. 2001. Towards ecologically scaled landscape indices. Am. Nat. 157: 24–41.

Vos C.C., Baveco J.M. and Grashof-Bokdam C. 2002. Corridors and species dispersal. In: Gutzwiller K.J. (eds), In Applications in Landscape Ecology. Springer, pp. 84–104.

Wauters L., Casale P. and Dhondt A. 1994. Space use and dispersal of red squirrels in fragmented habitats. Oikos 69: 140–146.

Wegner J.F. and Merriam G. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. J. Appl. Ecol. 16: 349–357.

White G.C. and Garrot R.A. 1990. Analysis of Wildlife Radio-tracking Data. Academic Press Inc., San Diego, CA.

Wiens J.A. 2001. The landscape context of dispersal. In: Clobert J.E., Danchin A.A., Dhondt and Nichols J.D. (eds), Dispersal. Oxford University Press, USA, pp. 96–109.