

# The effects of car traffic on breeding bird populations in woodland. II. Breeding dispersal of male willow warblers (*Phylloscopus trochilus*) in relation to the proximity of a highway

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## Summary

1. In this study the dispersal activity of male willow warblers *Phylloscopus trochilus* breeding next to a highway carrying heavy traffic was investigated.
2. Breeding dispersal distances of yearling males along the road were larger than at further distances and were in the same order of magnitude as natal dispersal distances (medians being 303 and 515 m, respectively).
3. A simulation of dispersal directions, adjusted for actual landscape features, indicated that breeding dispersal was actively directed away from the road.
4. There appeared to be a relation between dispersal and breeding performance for yearling males, unsuccessful males moving more frequently and further (median 294 m) than successful males (median 120 m).
5. At the individual level, the increased dispersal activity of yearlings close to the highway constitutes an 'escape' mechanism from low quality areas. At the population level it possibly stabilizes source populations. Dispersal characteristics should be incorporated into spatial population models.

*Key-words:* breeding success, natal dispersal, source–sink.

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## Introduction

The proportion of yearling males in breeding bird populations is often higher in marginal habitats than in high quality habitats (e.g. Krebs 1971; Brooke 1979; Baeyens 1981; Ulfstrand *et al.* 1981; Gezelius *et al.* 1984; Labhardt 1988; Holmes & Sherry 1992). This larger proportion of yearlings might reflect an increased emigration of adult males. Alternatively it could be the result of an increased mortality rate in poor habitat. Movements from one territory to a better one, usually following an unsuccessful breeding season, have been reported in several studies (e.g. Brooke 1979; Greenwood & Harvey 1982; Weatherhead & Boak 1986; Gavin & Bollinger 1988). Since by definition breeding success is lower in marginal habitats, a larger proportion of the population in a given year is expected to disperse from such habitats. However, for many passerine birds it has been shown that breeding dispersal distances (distances between two succeeding breeding sites) usually are much shorter than natal dispersal distances (distance between site of birth and first site of breeding) (Villard 1991). So it is questionable

whether breeding dispersal distances are large enough to allow redistribution over habitats. Evidence for movements from low to high quality habitats is rare (see e.g. Krebs 1971).

Habitats next to our study highway showed many characteristics of a low quality habitat. Breeding success was significantly lower close to the road than in areas further away. High proportions of yearling males were found and there was evidence that the high proportion of yearling males was not caused by an increased mortality (Reijnen & Foppen 1994).

This paper examines the extent and direction of breeding dispersal for a population of willow warblers (*Phylloscopus trochilus* L.) breeding next to a highway, and the relationship between dispersal and breeding success.

## Study area and methods

The study area, total size about 165 ha, was located in the centre of the Netherlands along a highway carrying heavy traffic. For a detailed description see Reijnen & Foppen (1994).

During the years 1988–91, territorial males

were caught and given individual colour-ring combinations. Although ageing adult willow warblers based on plumage characteristics is almost impossible (Hogstad 1988), a yearling male group (against a group of older males) could be distinguished (Reijnen & Foppen 1994). All the observations of males were plotted on territory maps, and from this the centre of the territory was determined graphically.

To analyse the data the area was divided into zones, starting from the road verge: a 'road' zone up to 200 m from the road; an intermediate zone from 200 to 400 m; and a control zone farther than 400 m. Data from corresponding zones on both sides of the road were combined since no influence of road side was to be expected.

To collect data on breeding dispersal, we looked for banded individuals in the study area, but also in all suitable habitat in the neighbourhood up to a distance of 1 km from the boundary. The extent of the area surveyed was based on breeding dispersal data from the literature (Tiainen 1983; Lawn 1982). Breeding dispersal distance between subsequent years in the period 1989–91 was calculated as the difference between the centres of the breeding territories. In order to relate dispersal to breeding performance, data on breeding success published elsewhere were used (Reijnen & Foppen 1994). In 1990, 222 nestlings from 40 nests were colour-ringed. Since natal dispersal distances usually exceed breeding dispersal distances, a much larger area was surveyed in the spring of 1991. Suitable habitat in a 5-km circle around our main study area was checked for colour-ringed birds (Fig 1.).

To test whether dispersing males moved randomly or actively avoided the areas next to the road, a Monte Carlo test (Manly 1990) was carried out. As a

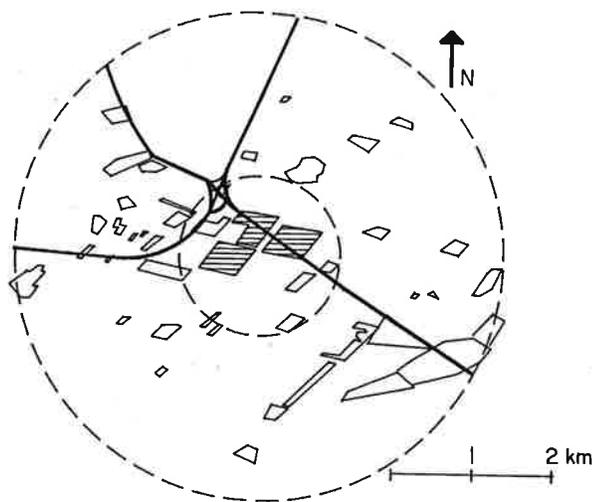


Fig. 1. Map of the study area and its surroundings. Hatched areas indicate the main study sites. Indicated are the two circles of 1 and 5 km radius where all available habitat patches (clear areas) were surveyed for colour-ringed individuals (for further information see text).

test statistic the mean displacement relative to the road was used, meaning the difference between the distance to the road in year  $x + 1$  minus the distance to the road in year  $x$ . Simulations of the null model of random dispersal directions were conditional on the former territory centres. Thus, for each male, a circle was drawn based on the former territory centres with the dispersal distance as the radius. Those parts of the circle lying in non-habitat areas (meadows, clearings) were omitted. Next, random points on the remainder of the circle were chosen and distance to the road was measured. To derive a frequency distribution of mean displacements under the null model this procedure was carried out 200 times. The Monte Carlo significance level  $P$  is then the rank number for the observed test statistic divided by the number of simulations + 1 (Manly 1990).

## Results

### DISPERSAL DISTANCE

Because territory size covers about 0.2–0.3 ha (radius about 30 m) males that moved less than 50 m were considered site-tenacious. Although many males tended to be very site-tenacious, low site-faithfulness was observed for yearling males in the road zone (Table 1). In this zone the proportion of dispersing yearling males was significantly larger than for older males ( $\chi^2$  test, 1 df,  $P < 0.01$ ). In the other zones older males tended to be also more site-tenacious than yearling males, but these differences were not significant, possibly due to small sample sizes.

The same picture arises from the analysis of dispersal distances. Usually, dispersing males stayed within 300 m of their former territory centre (Fig. 2), but yearling males in the road zone exhibited significantly longer dispersal distances. The median distance moved was about 3–4 times as high as in other zones (see Fig. 2) and differed significantly from that in the other combinations of age and zone (Kruskal-Wallis test, 5 df,  $P < 0.005$ ). Again, the difference between yearlings and older males was significant only in the road zone (Mann-Whitney  $U$ -test,  $P < 0.02$ ).

When comparing successive breeding dispersal distances for a set of individuals the breeding dispersal

Table 1. Percentage of site-tenacious males in the different zones for yearling and older males. The total number of males is shown in parentheses

Zone	Total (%)	Yearling (%)	Old (%)
Road	18 (45)	6 (33)	50 (12)
Intermediate	38 (34)	36 (25)	45 (9)
Control	36 (91)	35 (75)	44 (16)

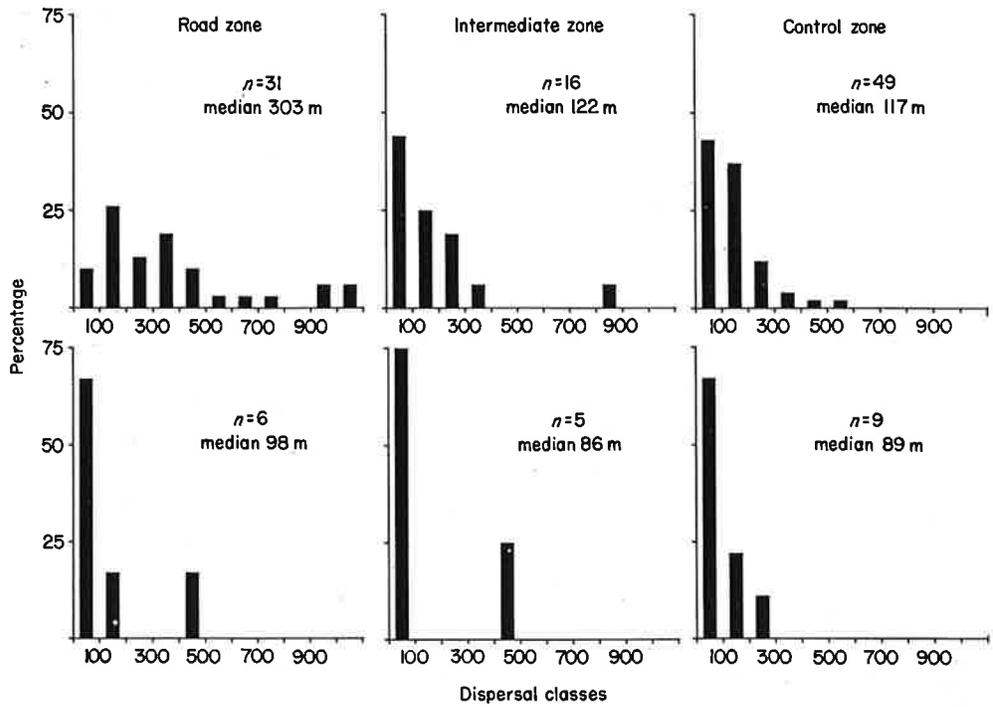


Fig. 2. Frequency distributions of dispersal distances for yearling (above) and older males (below) in the three zones. Dispersal distances are shown in classes of 100 m; distances above 1000 m are combined.

distance for the first year was significantly longer than in subsequent years (Fig. 3). The difference was greatest for males in the road zone (mean difference 310 m, Wilcoxon matched-pairs test,  $P < 0.01$ ), but also applied to the other zones (pooled data: mean difference 40 m, Wilcoxon matched-pairs test,  $P < 0.05$ ).

In conclusion, yearling males close to the road almost all disperse, and they move much farther than older males or yearlings in other zones.

To judge the extent of these increased breeding

dispersal distances, comparisons were made with natal dispersal data for the same population. A total of 905 territorial males was checked for colour-rings in the 5-km circle. In total, 16 yearling males were found which had been ringed as nestlings in our main study area the year before (7% return). Site-tenacious males included, median (515 m) and maximum (4125 m) natal dispersal distances were considerably longer than breeding dispersal distances of old males (median 55 m, maximum 446 m), but were not even twice as large as the breeding dispersal

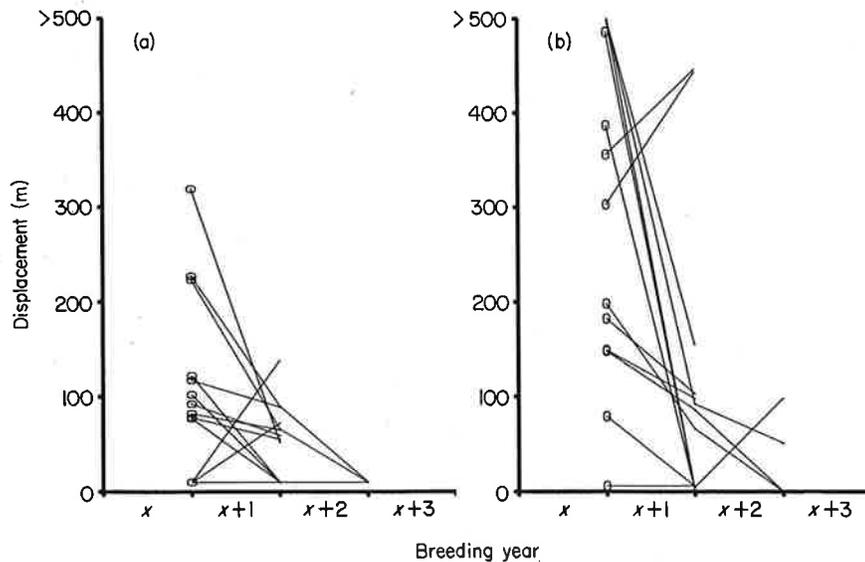


Fig. 3. Individual displacements of males which held territories in more than two years. Lines connect dispersal of individuals after first year of breeding ( $x$ ) and subsequent years ( $x + 1$  or  $x + 2$ ). (a) Individuals breeding for the first time in the intermediate and control zone; (b) Individuals breeding for the first time in the road zone.

distances of yearlings in the road zone (median 282 m, range 3000 m). Direction of natal dispersal seemed random. Nestlings from zones close to the road ended up in the control zone and vice versa. The small sample size did not permit statistical analysis of this pattern.

#### DIRECTION OF BREEDING DISPERSAL

During the 1988–91 period, 40 between-year movements of males breeding in the road zone were recorded. More than half of these males (63%) moved out from this zone and occupied territories mostly in the intermediate (50%) but also in the control zone (13%). In interpreting these data, it should be noted that a withdrawal from the road zone is to be expected by random movement: when a male close to the road moves, the probability of moving even closer to the road is very small. Furthermore, the landscape structure surrounding the territory probably influences random dispersal. However, the observed distances to the road also appeared to be larger than expected on the basis of our generated random model (Fig. 4, 40 males, Monte Carlo test, one-tailed,  $P=0.03$ ). On the other hand, in the control zone, observed directions did not differ from a randomly generated pattern (Fig. 4, 38 males, Monte Carlo test, one-tailed,  $P=0.51$ ).

#### EFFECT OF FORMER BREEDING PERFORMANCE ON BREEDING DISPERSAL

The relationship was examined between the dispersal data of individuals in 1991 and their breeding per-

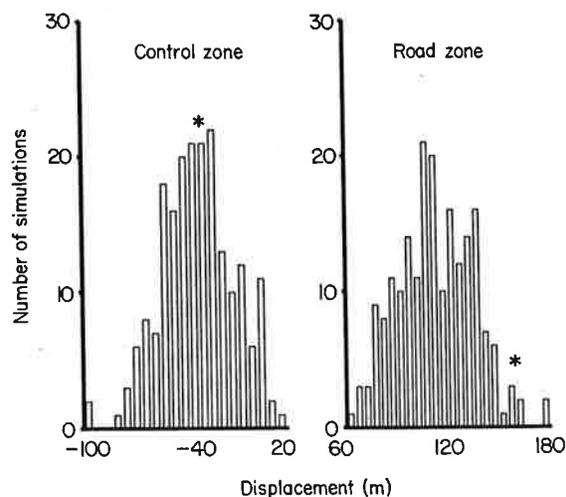


Fig. 4. Frequency distributions of simulated mean perpendicular displacements from the road for the group of males along the road and the group in the control zone (each 200 simulations). Asterisk (\*) indicates the actual recorded mean displacement to the road. A negative value means a displacement towards the road, a positive a displacement away from the road.

formance in 1990. For yearlings, dispersal probability was significantly correlated with their breeding performance in the previous year (Table 2). Among yearlings, successful males (having raised at least one young) dispersed less often than unsuccessful males. The breeding performance of old males did not correlate with their probability of dispersal (Table 2). Only for unsuccessful yearling males were there sufficient data to compare dispersal distances among the three zones. Distances moved in the road zone were clearly larger than in the other zones combined (median 294 and 120 m respectively, Mann-Whitney  $U$ -test,  $P < 0.05$ ).

## Discussion

### BREEDING DISPERSAL ACTIVITY

The results support the idea that the high proportion of yearlings in the road zone is a consequence of a higher breeding dispersal from this zone than from those further from the road. Dispersal distances were quite large in the road zone and areas a longer distance from the road were favoured. For most passerines, breeding dispersal distances reported do not exceed 2 or 3 times the territory size or 150 m (e.g. Darley, Scott & Taylor 1977; Harvey, Greenwood & Perrins 1979; Lanyon & Thompson 1986; Nyholm 1986; Drilling & Thompson 1988; Pärt & Gustafsson 1989; Winkel & Frantzen 1991). Short dispersal distances have also been reported in adult willow warblers (Lawn 1982; Tiainen 1983; Jakobsson 1988). Even in long-distance migrants, males are believed to disperse only short distances between years in order to occupy better quality territories in familiar areas around their own territory (Beletsky & Orians 1987). Indeed, it has been shown that males are able to increase their breeding success the year after dispersal (Baeyens 1981; Beletsky & Orians 1987; Pärt & Gustafsson 1989). In contrast, Lanyon & Thompson (1986) consider territory improvement for painted buntings *Passerines ciris* to be hampered by strong site-tenacity.

Although yearling males of passerines have been reported to have an increased probability of dispersing (e.g. Rheinwald & Gutscher 1969; Green-

Table 2. Relation between former breeding performance and amount of site tenacity of male willow warbler. The numbers of individuals are compared and tested by a  $\chi^2$  test (1 df)

	Age			
	Yearling		Older	
	Moved	Not moved	Moved	Not moved
Successful	9	10	5	9
Unsuccessful	15	3	2	3
	$P < 0.05$			NS

wood & Harvey 1976; Mikkonen 1983; Labhardt 1988), only in a few cases have breeding dispersal movements over long distances (several hundred metres or even a few kilometres) been observed. Krebs (1971) observed young males of the great tit *Parus major* moving from hedgerows (marginal) to woodland (optimal) after removing territory holders in the latter habitat. However, these movements took place during the breeding season and the short replacement time indicated that the moving males also 'knew' their future territories. Few other studies have shown males switching from low quality areas to higher quality areas after their first breeding season. To our knowledge, in passerines this has been reported only in the whinchat (Labhardt 1988) and magpie (Baeyens 1981). In the nuthatch *Sitta europea*, Matthyssen (1990) also found changes to higher quality territories; however, this concerned birds moving before their first breeding season.

The reason why long-distance breeding dispersal is very rarely observed might be due to the fact that the study areas are often too small to allow detection of such movements. This might result in low return rates due to males settling far from their former breeding site. Indeed, lower return rates have often been reported for yearling males or for males in marginal habitats (Solonen 1979; Gauthreaux 1982; Nyholm & Myhrberg 1983; Labhardt 1988; Holmes & Sherry 1992). The possibility that part of these low return rates is caused by an increased mortality rate must not be ruled out (Pärt & Gustafsson 1989), but this was certainly not the case in our study area (Reijnen & Foppen 1994).

#### EFFECT OF FORMER BREEDING PERFORMANCE ON BREEDING DISPERSAL

Breeding success seems to act as a proximate cue for dispersal. Yearling males that experience poor breeding success are more likely to move away from their previous territories. Males probably react according to their total former breeding experience rather than to their most recent breeding performance and this causes the observed differences in influence of former breeding success between yearling and older males (see also Beletsky & Orians 1987). There appears to be a trade-off between the risk of moving to a new area and the risk of another failure in the same area. Facing a poor breeding performance, old males, with a better knowledge of their present area, probably benefit most from staying, while yearling males benefit more from leaving. An identical relation between age, breeding experience and dispersal has been reported in the pied flycatcher *Ficedula hypoleuca* (von Haartman 1949; Harvey *et al.* 1984), collared flycatcher *Ficedula albicollis* (Pärt & Gustafsson 1989), whinchat *Saxicola rubetra* (Labhardt 1988), red-backed shrike *Lanius collurio* (Jakober & Stauber 1989) and magpie *Pica pica*

(Baeyens 1981). The comparatively long dispersal distances shown by yearling males close to the road require a different explanation in terms of decision-making. Males probably evaluate also the total quality of the breeding area by monitoring other males (Beletsky & Orians 1987). Based on both former breeding experience and the judgement on total quality of the area, they can make a decision about whether or not and how far to disperse. In the case of unsuccessful yearling males in low quality areas, this leads to long-distance dispersal. In contrast, as expected, unsuccessful yearling males in the high quality areas did not disperse far.

The proximate cause for the high numbers of yearling males starting to defend a territory in the road zone is yet unknown. Old males are dominant over yearlings (Jakobsson 1988) and we can confirm this by anecdotal observations. So probably a yearling male only has the option to fill vacant territories (about 50% of the total regarding the annual mortality). It is unknown whether yearling males immediately 'recognize' habitats further from the road as more suitable, whether individuals are forced out of these more preferred zones by other individuals, or whether the process follows a random distribution: filling open places in what appear to be suitable habitats in spite of the possible proximity of the road. Comparisons of clutch size and raised number of offspring do not support the idea that the potential of yearlings in the road zone is lower than in zones further from the road (Reijnen & Foppen 1994).

#### CONCLUSIONS

At the individual level, dispersal constitutes a mechanism for yearling males to 'escape' from the highway-induced low quality habitat. Low reproductive success may occur in only one year. However, in small passerines most individuals will not survive until their second breeding season, so a large proportion of males in the road zone will never reproduce. For a short-lived species such as the willow warbler (mean life expectancy less than 2 years) this also means that the lifetime reproduction figure for those males will be much lower (Smith 1988).

Long-distance breeding dispersal of yearling passerine males in poor quality habitats seems to be a common phenomenon based on the high proportion of young males that disperse, and the return rates recorded for yearlings. It constitutes an effective mechanism to 'escape' from low quality habitats and it optimizes habitat distribution without losing all the advantages of being site-tenacious.

The willow warbler dispersal flow from areas next to the road to areas far from the road is quite large since not only are the distances large, the number of individuals involved is also quite considerable. In the opposite direction, there will be a net natal

dispersal flow directed towards the road, since it was shown that offspring production close to the road is much smaller than in control areas and is probably also insufficient to compensate for yearly losses (Reijnen & Foppen 1994).

It has been suggested that low quality habitats are not only spill-overs for high quality habitats, but that they contribute to the stability of the latter populations and act as a buffer (Kluyver & Tinbergen 1953; Brown 1969; Bernstein, Krebs & Kacelnik 1991). Howe, Davis & Mosca (1991), using simulation modelling, showed that the natal dispersal flow out of relatively large sink areas can stabilize a source population. The extra breeding dispersal flow towards 'source areas' also contributes to the stabilization of these populations and, on the other hand, it strengthens the 'sink' character of low quality habitats. Age-dependent dispersal characteristics therefore cannot be neglected when modelling source-sink situations, though usually modelling is primarily based upon natal dispersal features (e.g. Pulliam, Dunning & Jiango 1992).

Little is known about how dispersal is influenced by the configuration of the landscape. Field data are scarce and development of theoretical tools (e.g. modelling techniques) has only recently started (Johnson *et al.* 1992). Our data contribute to a better understanding of how animals respond to habitat patchiness and what kind of mechanisms are involved. However, at least for passerines, the conclusions probably only are applicable to situations where low and high quality areas are not greatly separated spatially (possibly not more than a few kilometres). A patchy environment probably alters the habitat selection and redistribution of birds over habitat (Verboom *et al.* 1991) and the challenge of clarifying this influence remains.

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### References

- Baeyens, G. (1981) Functional aspects of serial monogamy; the magpie pair bond in relation to its territorial system. *Ardea*, **69**, 145–166.

- Beletsky, L.D. & Orians, G.H. (1987) Territoriality among male red-winged blackbirds. I. Site fidelity and movement patterns. *Behavioral Ecology and Sociobiology*, **20**, 21–34.
- Bernstein, C., Krebs, J.R. & Kacelnik, A. (1991) Distribution of birds amongst habitats: theory and relevance to conservation. *Bird Population Studies* (eds C. Perrins, J.-D. Lebreton & G.J.M. Hirons), pp. 317–345. Oxford University Press, Oxford.
- Brooke, M. (1979) Differences in the quality of territories held by wheatears (*Oenanthe oenanthe*). *Journal of Animal Ecology*, **48**, 21–32.
- Brown, J.L. (1969) Territorial behavior and population regulation in birds. *Wilson Bulletin*, **81**, 293–329.
- Darley, J.A., Scott, D.M. & Taylor, N.K. (1977) Effects of age, sex, and breeding success on site fidelity of gray catbirds. *Bird Banding*, **48**, 145–151.
- Drilling, N.E. & Thompson, C.F. (1988) Natal and breeding dispersal in house wrens (*Troglodytes aedon*). *Auk*, **105**, 480–491.
- Gauthreaux, S.A. (1982) The ecology and evolution of avian migratory systems. *Avian Biology, Vol. IV* (eds D.S. Farner, J.R. King & K.C. Parks), pp. 93–197. Academic Press, New York.
- Gavin, T.A. & Bollinger, E.K. (1988) Reproductive correlates of breeding-site fidelity in bobolinks (*Dolichonyx orizyvorus*). *Ecology*, **69**, 96–103.
- Gezelius, L., Grahn, M., Källander, H. & Karlsson, J. (1984) Habitat-related differences in clutch size of the pied flycatcher *Ficedula hypoleuca*. *Annales Zoologici Fennici*, **21**, 209–212.
- Greenwood, P.J. & Harvey, P.H. (1976) The adaptive significance of variation in breeding area fidelity of the blackbird (*Turdus merula L.*). *Journal of Animal Ecology*, **45**, 887–898.
- Greenwood, P.J. & Harvey, P.H. (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, **13**, 1–21.
- Haartman, L. von (1949) Der Trauerfliegenschnäpper. I. Ortstreue und Rassenbildung. *Acta Zoologica Fennica*, **56**, 31–92.
- Harvey, P.H., Greenwood, P.J. & Perrins, C.M. (1979) Breeding area fidelity of great tits (*Parus major*). *Journal of Animal Ecology*, **48**, 305–313.
- Harvey, P.H., Greenwood, P.J., Campbell, B. & Stenning, M.J. (1984) Breeding dispersal of the pied flycatcher *Ficedula hypoleuca*. *Journal of Animal Ecology*, **53**, 727–736.
- Hogstad, O. (1988) Age-related increase in wing length of male willow warbler *Phylloscopus trochilus*. *Fauna Norvegica Series C Cinclus*, **8**, 116–118.
- Holmes, R.T. & Sherry T.W. (1992) Site fidelity of migratory warblers in temperate breeding and neotropical wintering areas: implications for population dynamics, habitat selection and conservation. *Ecology and Conservation of Neotropical Migrant Landbirds* (eds J.M. Hagan III & D.W. Johnston) Smithsonian Institution Press, Washington D.C.
- Howe, R.W., Davis, G.J. & Mosca, V. (1991) The demographic significance of 'sink' populations. *Biological Conservation*, **57**, 239–255.
- Jakober, H. & Stauber, W. (1989) Beeinflussen Bruterefolg und Alter die Ortstreue des Neuntöters (*Lanius collurio*)? *Die Vogelwarte*, **35**, 32–36.
- Jacobsson, S. (1988) Territorial fidelity of willow warbler (*Phylloscopus trochilus*) males and success in competition over territories. *Behavioral Ecology and Sociobiology*, **22**, 79–84.
- Johnson, A.R., Wiens, J.A., Milne, B.T. & Crist, T.O. (1992) Animal movement and population dynamics in heterogeneous landscapes. *Landscape Ecology*, **7**, 63–75.

- Kluijver, H.N. & Tinbergen, L. (1953) Territory and the regulation of density in titmice. *Archives néerlandaises de Zoologie*, **10**, 265–289.
- Krebs, J.R. (1971) Territory and breeding density in the great tit, *Parus major* L. *Ecology*, **52**, 2–22.
- Labhardt, A. (1988) Siedlungsstruktur von Braunkehlchen-Populationen auf zwei Höhenstufen der Westschweizer Voralpen. *Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg*, **51**, 139–158.
- Lanyon, S.M. & Thompson, C.F. (1986) Site fidelity and habitat quality as determinants of settlement pattern in male painted bunting. *Condor*, **88**, 206–210.
- Lawn, M.R. (1982) Pairing systems and site tenacity of the willow warbler *Phylloscopus trochilus* in southern England. *Ornis Scandinavica*, **13**, 193–199.
- Manly, B.F. (1990) *Randomization and Monte Carlo Methods in Biology*. Chapman and Hall, London.
- Matthysen, E. (1990) Behavioral and ecological correlates of territory quality in the Eurasian nuthatch *Sitta europea*. *Auk*, **107**, 86–95.
- Mikkonen, A.V. (1983) Breeding site tenacity of the chaffinch *Fringilla coelebs* and the brambling *F. montefringilla* in northern Finland. *Ornis Scandinavica*, **14**, 36–47.
- Nyholm, N.E.I. (1986) Birth area fidelity and age at first breeding in a northern population of pied flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica*, **17**, 249–252.
- Nyholm, N.E. & Myhrberg, H.E. (1983) Breeding area fidelity of the pied flycatcher *Ficedula hypoleuca* at Ammarnäs, Swedish Lapland. *Ornis Fennica*, **60**, 22–27.
- Pärt, T. & Gustafsson, L. (1989) Breeding dispersal in the collared flycatcher (*Ficedula albicollis*): possible causes and reproductive consequences. *Journal of Animal Ecology*, **58**, 305–320.
- Pulliam, H.R., Dunning, J.B. & Jianguo, L. (1992) Population dynamics in complex landscapes: a case study. *Ecological Applications*, **2**, 165–177.
- Reijnen, R. & Foppen, R. (1994) The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for willow warblers (*Phylloscopus trochilus*) breeding close to a highway. *Journal of Applied Ecology*, **31**, 85–94.
- Rheinwald, G. & Gutscher, H. (1969) Dispersion und Ortstreue der Mehlschwalbe *Delichon urbica*. *Die Vogelwelt*, **90**, 121–141.
- Smith, J.N.M. (1988) Determinants of lifetime reproduction success in song sparrow. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (ed. T.H. Clutton-Brock), pp. 154–172. University of Chicago Press, Chicago.
- Solonen, T. (1979) Population dynamics of a population of the garden warbler in southern Finland. *Ornis Fennica*, **56**, 3–12.
- Tiainen, J. (1983) Dynamics of a local population of the willow warbler *Phylloscopus trochilus* in southern Finland. *Ornis Scandinavica*, **14**, 1–15.
- Ulfstrand, S., Alatola, R.V., Carlson, A. & Lundberg, A. (1981) Habitat distribution and body size of the great tit *Parus major*. *Ibis*, **123**, 494–499.
- Verboom, J., Schotman, A., Opdam, P. & Metz, J.H.J. (1991) European nuthatch metapopulations in fragmented agricultural landscape. *Oikos*, **61**, 149–156.
- Villard, M.-A. (1991) *Spatio-temporal dynamics of forest bird patch populations in agricultural landscapes*. PhD Thesis, Department of Biology, Carleton University, Ottawa.
- Weatherhead, P.J. & Boak, K.A. (1986) Site infidelity in song sparrows. *Journal of Animal Ecology*, **34**, 1299–1310.
- Winkel, W. & Frantzen, M. (1991) Zur Populationsdynamik der Blaumeise *Parus caeruleus*, langfristige Studien bei Braunschweig. *Journal für Ornithologie*, **132**, 81–96.

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