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Effects of habitat fragmentation on the red squirrel, *Sciurus vulgaris* L.

B. Verboom and R. van Apeldoorn
Department of Landscape Ecology, Research Institute for Nature Management, P.O. Box 46, 39.56 ZR Leersum, The Netherlands

Abstract

The effects of woodlot size and isolation, in relation to habitat fragmentation, on the distribution of the red squirrel were studied. In The Netherlands, 50 woodlots (0.55 – 13.78 ha) were surveyed in an agricultural landscape for the presence of red squirrel. In 26 woodlots squirrel dreys (nests) were found. Logit regression analysis showed that woodlot size and the area per woodlot covered with coniferous trees were the best predictors of squirrel presence. Addition of isolation variables by means of a stepwise forward regression method showed significant effects of the distance to a large, permanently inhabited wood and the amount of surrounding wood. No effect was found for the distance to the nearest woodlot (> 0.5 ha). The model could be further improved by adding a measure of the amount of hedgerows surrounding a woodlot.

Introduction

Animal species use landscapes on different scales. The medium-sized European badger (*Meles meles*) and most birds of prey, for example, roam the whole landscape in search for food. For them, a landscape is a mosaic of more or less suitable habitat elements. On the other hand, small mammals, such as voles and forest-interior birds, are confined to a restricted number of habitat types. For these species a landscape consists of suitable habitat patches separated by unsuitable habitat. Each species will have its own specific response to changes in its landscape.

According to the metapopulation concept (Levins 1970), the probability for a subpopulation to become extinct decreases as patch size is reduced and increases with isolation of patches. On the other hand, probability depends on dispersal capabilities of the species and on distances between patches. Moreover, landscape elements like roads, hedgerows and ditch verges may (positively or negatively) influence dispersal movements between occupied and empty patches. In a metapopulation both local extinction and recolonization events occur continuously. When the recolonization rate of patches cannot keep up with the rate of local extinction, the metapopulation itself becomes extinct and the species disappears from the landscape (Opdam 1988). Species with spatially separated habitat patches are assumed to be most affected by landscape changes resulting in habitat fragmentation, especially when they have a low dispersal rate.

Several studies during the last 20 years have focused on the impact of fragmentation on forest species in agricultural landscapes. Van Dorp and Opdam (1987) found significant effects of woodlot size and isolation on size and diversity of forest bird communities. Similar effects were found for invertebrates (e.g. Brönmark 1985; Soesbergen and

Fig. I. Location of the study area in The Netherlands.

Mabelis 1989). For small mammals, Smith (1974) and Gottfried (1979) found a relationship between the proportion of occupied patches, the isolation of patches and the density of subpopulations for pikas ***(Ochotona princeps)*** and white-footed mice ***(Peromyscus leucopus).*** Getz ***et al.*** (1978) found *Microtus pennsylvanicus* mainly in habitat patches which were connected with roadsides of interstate highways. These roadsides formed important landscape elements for the range expansion of the species. For chipmunks ***(Tamias striatus),*** fence rows formed crucial corridors for recolonizing empty woodlots (Henderson ***et al.*** 1985).

Here we investigate effects of habitat fragmentation on the red squirrel ***(Sciurus vulgaris*** L.). The red squirrel is smaller than the grey squirrel ***(Sciurus carolinensis),*** which does not occur in The Netherlands. Body and tail measure 21-25 and 15-20 cm respectively. The color varies from red dark brown or almost black, with white underparts. The red squirrel is active during the day and spends most of its time in trees, especially conifer trees, searching for seeds. Dreys or nests are usually built high in the crowns of conifers or, less frequently, in deciduous trees. In The Netherlands the species is common in the forested part of the country. Mature coniferous and mixed forests are preferred as habitat. Pure deciduous wood is inhabited less frequently. Red squirrel habitat in The Netherlands has become more and more dissected into small fragments, especially outside the larger forest tracts. During the last 25 years, the number of small woodlots (0.5– 10 ha) has more than doubled, while the total amount of wood has remained approximately the same.

We will relate the distribution of the red squirrel to woodlot size, to several variables pertaining to isolation of the woodlots, and to differences in habitat quality.

Methods

The area of investigation (Fig. 1) is situated in Twente (province of Overijssel, The Netherlands). The approximately 150 km^2 area consists of 7 large woods from 30-200 ha in size, many small woodlots less than 14 ha in size and maize fields and pastures. In part of the area there is a dense network of hedgerows.

There were 60 woodlots of more than 0.5 ha, and all of these were checked for the presence orabsence of red squirrels. Only 50 contained suitable squirrel habitat and these were used for the analysis. These woodlots ranged from 0.55–13.78 ha in size. The remaining woodlots consisted of unsuitable habitat (that is, they were alder carrs). The size limit of 0.5 ha is well below the home range size of red squirrel. In Belgium, for example, Wauters and Dhondt (1986) found home range size ranged between 1.52-3.59 ha in large forests with a species composition comparable to our woodlots.

The large woods (> 30 ha) were not studied, be, cause they are inhabited permanently, according to data of the National Forest Service. They are assumed to act as sources of squirrels for the area. The area (per woodlot) covered by coniferous trees has been used to represent differences in habitat quality (Table 1). Coniferous trees are the most suitable trees for building dreys, and they provide high energy food nearly all year (Corbet and Southern 1977; Wauters and Dhondt 1987). In our woodlots the Scots pine ***(Pinussylvestris)*** is the dominant conifer.

In order to analyze the effects of patch size and

Table 1. Variables pertaining to habitat quality, patch size and isolation. R2 = percentage of variance accounted for by a variable.

habitat quality

CCON area per woodlot covered by coniferous trees (ha)

patch size

AR area of woodlot (ha)

isolation

DW distance from nearest woodlot larger than 0.5 ha (m)
DLW distance from nearest woodlot larger than 30 ha (m)
W2–4 amount of wood surrounding a woodlot within 200-400 m
W4–6 amount of wood surrounding a woodlot within 400-600 m
W2–6 amount of wood surrounding a woodlot within 200-600 m
HR2–6 amount of hedgerow surrounding a woodlot within 200-600 m

	CCON	AR	DW	DLW	W2–4	W4–6	W2–6	HR2–6
min	0	0.55	40	40	0	0	0	0
max	1.4	13.78	700	3500	8	10	9	11
mean	0.9	3.34	230	843	1.9	2.8	2.1	3.3
sd	1.62	3.14	179.9	914.2	2.30	2.80	2.38	2.03
R2	31	22	0	1	4	0	2	5

isolation on the distribution of red squirrels, woodlot size, interpatch distance, distance to the nearest large and permanently inhabited woodlot and density of surrounding woods and hedgerows were calculated from maps at a scale of 1:25,000 (Table 1). The density of surrounding woodland was calculated by placing donut-shaped areas at 200-400, 400-600 and 200-600 m from the center of a woodlot, dividing these into 20 sectors, and counting the area of woodlots and hedgerows in each sector. A sector was scored if at least 25% of the area was covered by woods (equalling 1.9, 3.1 and 5.1 ha respectively). For the hedgerow density, a 200-600 m donut area was used, and a sector was scored if it contained at least 250 m of hedgerow, with at least 50 m present within 200-400 m of the center of the woodlot.

Woodlots were examined for dreys. This method proved to be fast and accurate for detecting the presence of red squirrels, and also for estimating relative population densities. Differences in drey density are known to be strongly correlated with differences in squirrel density (Don 1985; Wauters and Dhondt 1988).

Surveys were made in November 1988, when there was a very small chance to mistake a squirrel drey for a bird nest. Since one squirrel builds up to 4 to 5 dreys (Wauters and Dhondt 1988), two inhabited dreys were assumed to indicate squirrel presence. Inhabited dreys are more or less spherical, compact structures with an average diameter of approximately 30 cm. They are easily distinguished from unused dreys, which are untidy and often misshapen.

The variation in the dependent variable of the presence/absence data was analyzed with logit regression analysis (Jongman *et al.* 1987), using the standard statistical package Genstat (Genstat 5 committee 1987). Because frequency distributions of the independent variables were skew, they were transformed logarithmically. Linearity of all independent variables in relation to the dependent variable was assumed. For clarity, we use the term variance instead of the technical term deviance.

First, a model was fitted with each of the independent variables separately. Test runs indicated that patch size and area of woodlot covered with coniferous trees reduced the variance of the dependent variable more than any of the isolation variables (Table 1). A basic model was constructed with both of these parameters. By means of a stepwise forward regression method this model was extended with one or more variables, until addition of a variable no longer significantly reduced the residual variance. The level of significance used was $P = 0.05$.

Results

Of the 50 woodlots analyzed, 26 (52%) were inhabited by red squirrels. The probability of occurrence was greater in larger woodlots and in woodlots with more coniferous trees (Figs. 2 and 3). Both vari-

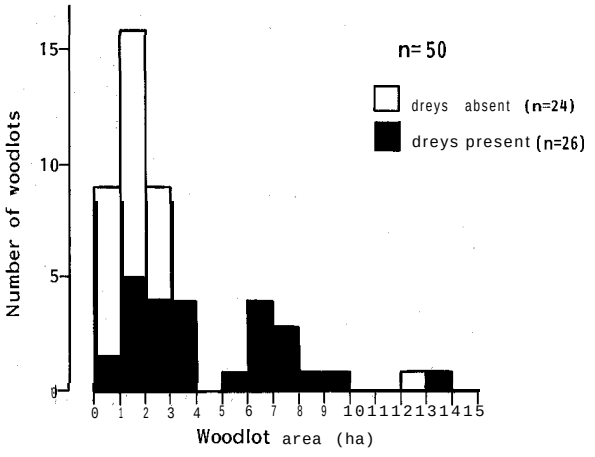

Fig. 2. Distribution of woodlots over size classes (ha), with absence and presence of dreys shown separately. Note: the minimum size limit is 0.5 ha.

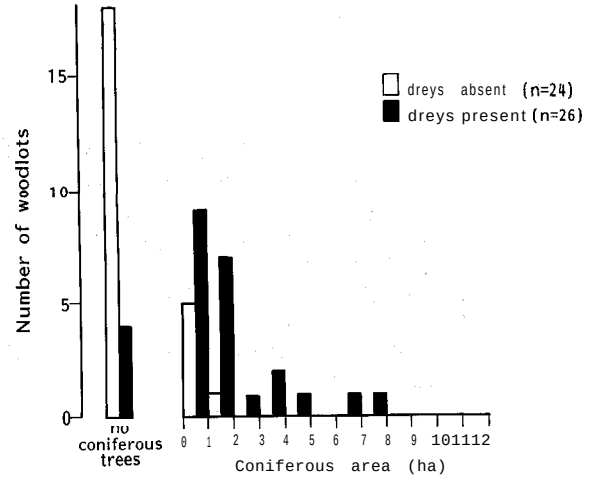

Fig. 3. Distribution of woodlots over classes of area covered by coniferous trees (ha); absence and presence of dreys are separately shown.

ables together explain 35% of the variance ($P < 0.005$; Table 2).

The remaining variables all pertained to isolation of the woodlots. Distance to woods larger than 30 ha (DLW) yielded maximal reduction of the remaining variance (11 %, $P < 0.025$; Table 2). However, DLW could be replaced by any of the other variables reflecting the amount of woodland surrounding a woodlot (W2−4, W4−6, W2−6), without a substantial drop in the percentage of the variance explained by the variable (Table 2). The

Table 2. Logit regression models of presence/absence data. R2 = percentage of variance accounted for by a model.

	R2	significance of the last variable
CCON + AR	35	***+
CCON + AR + DLW(-)	46	**
CCON + AR + W2−4	45	*
CCON + AR + W4−6	43	*
CCON + AR + W2−6	42	*
CCON + AR + DW(-)		N.S.
CCON + AR + DLW(-) + HR2−6	53	*
CCON + AR + W2−4 + HR2−6	53	*
CCON + AR + W4−6 + HR2−6	52	*
CCON + AR + W2−6 + HR2−6	51	*

* $p < 0.05$; ** $p < 0.025$; *** $p < 0.005$; N.S. = not significant; + overall significance of both variables

only exception was the distance to the nearest woodlots larger than 0.5 ha (DW). Although DLW and DW were strongly correlated ($r = 0.70$), addition of DW had no significant effect ($P > 0.05$; Table 2). This difference may imply that the presence of a permanently inhabited source of squirrels has more effect on the presence of dreys than the presence of potentially suitable (and often smaller) woodlots.

The model could be improved further by adding a measure of hedgerow or corridor density (HR2−6; Table 2). With this addition, variance was reduced by 7% ($P < 0.05$) when DLW was included in the model, and by 8 and 9% when DLW was replaced by W2−4, W4−6, W2−6 ($P < 0.05$; Table 2). The four variables together explained 51−53% of the variance, one-third of which was accounted for by variables representing degree of isolation.

Conclusions and discussion

The basic model consisted of two variables, the area per woodlot covered by coniferous trees and the total woodlot area, the first being a part of the second. The importance of these two variables cannot be determined here separately. The factor that is really important for squirrel presence is the habi-

tat quality of a woodlot, since it determines the total number of individuals a woodlot can accommodate. The percentage of the woodlot with conifers is an indirect measure of habitat quality. Conifers provide year-round food and materials and support for dreys. The deciduous part of a woodlot will provide seeds mainly during the summer and autumn. Thus, we expect relatively high squirrel densities in coniferous woods or in the coniferous portions of mixed woodlots (Wauters and Dhondt 1987). We also expect larger home ranges in deciduous woods (Tonkin 1983; Wauters and Dhondt 1986). While in northwestern Europe, oak (*Quercus robur*) is used for dreys (Tonkin 1983; Wauters and Dhondt, in press), only a few dreys were found in oak in this study. We did not study home ranges of the squirrels.

Small woodlots tend to be uninhabited more often than larger woodlots and some vacant woodlots may have been too small to accommodate red squirrels. Home range of this species varies from 1.5 ha (Wauters and Dhondt 1986) to 13.4 ha (Corbet and Southern 1977), and distances crossed daily in large forests range from 61 m or less in winter to 107 m in summer (Lemnel 1967, in Corbet and Southern 1977). Even so, the two smallest inhabited woodlots measured 0.72 and 0.88 ha. Of course, there is a possibility that some squirrel home ranges consist of more than one small woodlot.

Populations in small woodlots can become extinct due to stochastic events. A group of small populations can be considered to compose a metapopulation, which is a dynamic system of extinctions and recolonizations. Van Dorp and Opdam (1987) have shown that the European nuthatch (*Sitta europaea*) in the Gelderse Vallei in The Netherlands forms a metapopulation. In a three-year study in 47 woodlots, they found that local extinction occurred 11 times and recolonization 6 times. On the average, 25 (53%) of the woodlots were occupied at any one time. Also for small mammals regular local extinction and recolonization are found on real islands (for *Microtus agrestis*; Pokki 1981) and in woodlots as well (for *Clethrionomys glareolus*; Geuse *et al.* 1985). In our survey, 7 of 25 woodlots smaller than 2 ha were inhabited, and in two of the vacant woodlots the remains of old dreys were observed.

We conclude that red squirrel populations are affected by the fragmentation of habitat. The probability of red squirrel occurrence significantly increases when a woodlot is situated close to a large, permanently inhabited wood, or when the amount of surrounding woods or the amount of hedgerow increases.

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References

Brönmark, C. 1985. Freshwater snail diversity: effects of pond area, habitat heterogeneity and isolation. Oecologia 67: 127-131.

Corbet, G.B. and Southern, H.N. (eds.) 1977. The handbook of British mammals. Blackwell Scientific Publications, London.

Don, B.A. 1985. The use of drey counts to estimate Grey squirrel populations. J. Zool., Lond. 206: 282-286.

Genstat 5 committee 1987. Genstat 5 Reference Manual. Oxford University Press, Oxford.

Getz, L.L., Cole F.R. and Gates D.L. 1978. Interstate roadsides as dispersal routes for *Microtuspennsylvanicus*. J. Mammal. 59: 208-212.

Geuse, P., Bauchau, V. and Le Boulengé, E. 1985. Distribution and population dynamics of bank voles and wood mice in a patchy woodland habitat in central Belgium. Acta Zool. Fennica 173: 65-68.

Gottfried, B.M. 1979. Small mammal populations in woodland islands. Am. Midl. Nat. 102: 105-112.

Henderson, M.T., Merriam, G. and Wegner, J. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. Biol. Conserv. 31: 95-105.

Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R. 1987. Data analysis in community and landscape ecology. Centre for Agricultural Publishing and Documentation (Pudoc), Wageningen.

Levins, R. 1970. Extinction. *In*: Some mathematical questions in biology. Lectures on Mathematics in the Life Sciences Vol. 2: 75-101. Am. Math.-Sot., Rhode Island.

Opdam, P. 1988. Populations in fragmented landscape. *In*: Schreiber, K.-F. (ed.). Connectivity in Landscape Ecology. Proceedings of the 2nd International Seminar of the "Inter-

national Association for Landscape Ecology", Münstersche Geografische Arbeiten 29, Münster.

Pokki, J. 1981. Distribution, demography and dispersal of the field vole, *Microtus agrestis* (L.), in the Tvärminne archipelago, Finland. Acta Zool. Fennica 164: 1-48.

Smith, G.T. 1974. The distribution and dispersal of Pikas: consequences of insular population structure. Ecology 55: 1112–1119.

Soesbergen, M. and Mabelis, A. 1989. Evertebraten in een versnipperd landschap. *In:* Insektenfauna en Natuurbeheer. Wetenschappelijke Mededeling 192, K.N.N .V., Utrecht.

Tonkin, J.M. 1983. Red squirrel ecology. PhD thesis, University of Bradford, Bradford.

Van Dorp, D. and Opdam, P.F.M. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. Landsc. Ecol. 1: 59-73.

Wauters, L.A. and Dhondt, A.A. 1986. Dichtheid en home ranges van een populatie eekhoorns *Sciurus vulgaris* L., 1758 in België. Lutra 29: 243-260 (with English summary).

Wauters, L.A. and Dhondt, A.A. 1987. Activity budget and foraging behaviour of the red squirrel *(Sciurus vulgaris* Linnaeus, 1758) in a coniferous habitat. Z. Säugetierk. 52: 341–353.

Wauters, L.A. and Dhondt, A.A. 1988. The use of red squirrel *(Sciurus vulgaris)* dreys to estimate population density. J. Zool. 214: 179– 187.

Wauters, L.A. and Dhondt, A.A. Nest-use by red squirrels *(Sciurus vulgaris* Linnaeus, 1758). Mammalia: in press.