

Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels

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In heterogeneous habitats with limited resources, spacing behaviour will affect individual variation in breeding success and density of populations, and is thus of general interest to ecologists. We investigated how red squirrels *Sciurus vulgaris* adapt their social organisation to fine-grained heterogeneity in habitat quality, studying spacing behaviour, habitat use and population dynamics in a forest in north Italy, characterised by a mosaic of high-quality (chestnut-pine) and poor-quality patches. We compared the data with those from more homogeneous broadleaf and mixed woodlands with similar overall tree seed abundance ("stable" habitats). Squirrels lived at lower densities (pre-breeding density $0.39\text{--}0.58\text{ ha}^{-1}$) than in "stable" habitats, although breeding rate was not reduced. Female breeding success was related to being primiparous as yearlings, and increased with body mass and proportion high-quality habitat in the home range. Persistency rate of females was as in stable habitats. It was higher than male persistency, but immigration and recruitment rates were male biased, resulting in even sex-ratio. All residents occupied high-quality patches, and no subadults established a permanent home range in poor-quality habitat. Home range and core-area size was typically larger in males than in females and a male's core-area overlapped those of other males and of females. Female core-areas were overlapped by males but not, or very little, by other females (intrasexual territoriality). Home ranges, or core-areas, were not smaller than in "stable" habitats, nor did we find a higher degree of core-area overlap. We conclude that in patchy habitats dominant, resident red squirrels exclude dispersing animals from preferred, high-quality habitat, producing a spacing pattern referred to as ideal despotic distribution, and that poor patches were only used temporarily by transient individuals, resulting in a reduction of density in comparison to populations in "stable" habitats.

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In resource limited systems with a high degree of spatial variation in habitat quality, the habitat use and social organisation of resident animals is mainly affected by the distribution and defensibility of critical resources (Andrewartha and Birch 1954, Lomnicki 1980, Wauters and Lens 1995). Spacing behaviour and habitat use, especially of adult breeding females, will not only influence individual variation in reproductive success, but also overall population growth and density (Bujalska

1973, Zammuto and Millar 1985, Clutton-Brock et al. 1987, Boyce and Boyce 1988, Wauters and Dhondt 1995, Wauters and Lens 1995, Wauters et al. 1995). Therefore, understanding relationships between spatial variation of food supplies and spacing behaviour and reproductive output is of general interest to ecologists.

Holarctic tree squirrels are ideal model organisms to study these relationships: distribution and availability of critical resources, high-energy tree seeds, can be

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measured accurately at the level of the individual home range since, and the animal's body size, diurnal habits, average lifetime and the range of population densities at which they occur, allows detailed analysis of their life-history traits and social organisation (Smith 1968, Havera and Nixon 1978, Farentinos 1979, Don 1983, Gurnell 1984, Wauters and Dhondt 1992, 1995, 1998, Larsen and Boutin 1994, Lurz et al. 1997, 2000, Wauters 2000). Moreover, since tree squirrels have a promiscuous or polygynous mating system (Smith 1968, Koford 1982, Wauters et al. 1990, Koprowski 1992, 1993a, b, 1998), use of space often differs between the sexes, since males and females have different behavioural strategies to increase reproductive success and, in some cases, use resources differently (Koprowski 1992, 1993a, b, Wauters and Dhondt 1992, 1995, Wauters et al. 1994a, 1995). This is not the case for American pine squirrels *Tamiasciurus hudsonicus* and Douglas squirrels *Tamiasciurus douglasii* where both sexes defend small, individual year-round territories containing one or more middens (larderhoards of pine or spruce cones) in high-quality pine or spruce forests (Smith 1968, Kemp and Keith 1970, Larsen and Boutin 1994). Only when a female is in oestrus, neighbouring males leave their territory to chase the female and interact aggressively to obtain copulations (Smith 1968, Koford 1982, Koprowski 1998). In contrast, the species belonging to the genus *Sciurus* have a social system that consists of overlapping individual home ranges, with extensive overlap between males and females, and varying degrees of intrasexual defense of smaller core-areas among adult, breeding females, so-called intrasexual territoriality (Farentinos 1972, Donohoe and Beal 1972, Havera and Nixon 1978, Don 1983, Wauters and Dhondt 1992, Wauters et al. 1994a, 1995, Wauters and Gurnell 1999, Lurz et al. 2000). Eastern grey squirrels, *Sciurus carolinensis* are an exception, forming female kin-groups, with daughters settling on or near the mother's home range, in high-quality deciduous woodlands (Koprowski 1996).

In populations of Holarctic tree squirrels, demographic processes largely depend on seasonal and annual variation in tree seed crops (Gurnell 1983, 1987, 1996, Wauters and Dhondt 1990, 1998, Wauters and Lens 1995, Lurz and Garson 1998). Therefore the spatial distribution of food resources in the habitat, the degree of habitat heterogeneity, and the temporal variation and predictability of food will strongly affect the costs and benefits associated with spacing behaviour and dispersal. This has been well documented for Eurasian red squirrels *Sciurus vulgaris* L. by comparing social organisation, habitat use and dispersal behaviour of populations occurring in high-quality conifer and mixed, deciduous woodlands in Belgium (so-called "stable populations", Lurz et al. 1997) and in poorer quality conifer plantations in northern England, characterised by a high degree of temporal and spatial

variation in habitat quality (Wauters and Dhondt 1992, 1993, 1995, 1998, Wauters et al. 1994b, 1995, Lurz et al. 1997, 2000, Lurz and Garson 1998).

When temporal variation in food availability is limited, but spatial variation is pronounced, we expect a strong selection on red squirrels to establish residency in high-quality patches within the habitat, and, especially breeding females, to have a high degree of site-fidelity (see Wauters et al. 1995). Both these traits will influence spacing behaviour of adults and thus social organisation. Such conditions of spatial heterogeneity of tree seed availability, with little annual variation in the size of seed crops, occur in the southern part of the red squirrel's distribution range (Wauters and Gurnell 1999, Cagnin et al. 2000). In large parts of Lombardy and Piedmont, northern Italy, the edge of the upper Po plain and the lower elevations of the Pre-Alps (between 250 and ca 1000 m a.s.l.) are largely covered with quite extensive mixed forests dominated by sweet chestnut *Castanea sativa* often mixed with Scots pine *Pinus sylvestris*. With decreasing elevation the proportion of black locust *Robinia pseudoacacia* an imported species of North American origin, increases. Black locust is an invasive species and often forms large blocks of pure or mixed stands in valley bottoms or flat ground. Since black locust seeds or flowers or rarely utilised by red squirrels, most woodlands in this area form habitats with a marked spatial gradient in resource availability, but, because of relatively little annual variation in seed crops of chestnut and Scots pine, with little temporal variation in food supplies.

In this paper we describe space and habitat use by red squirrels in a mixed forest dominated by black locust, sweet chestnut and Scots pine, with a high degree of spatial heterogeneity. In particular, we investigated: 1) squirrel densities, persistence of adult squirrels and female breeding success, 2) the spacing pattern of both sexes, 3) possible factors that might explain the observed pattern of spacing behaviour, such as food availability and quality, the intensity of intrasexual competition, and an individual squirrel's condition (body mass), and 4) avoidance or selection of particular habitat types in different seasons.

Material and methods

Study area

Red squirrels were monitored from July 1996 to October 1999 within a 31 ha area of mature, mixed woodland at Parco Pineta, an extensive mixed forest of 3000 ha on the northern edge of the upper Po plain in Lombardy, north Italy (8°57'E, 45°45'N). The study area in which red squirrels were radio-tracked consisted of a heterogeneous forest with a small-grained structure, dominated by deciduous trees, mainly black locust

Robinia pseudoacacia (25%), sweet chestnut *Castanea sativa* (20%), oaks *Quercus robur*, *Q. petraea* (9%), and hornbeam *Carpinus betulus* (5%), with Scots pine *Pinus sylvestris* (19%), and plantations of white pine *Pinus strobus* and Norway spruce *Picea abies* covering ca 17% of the study area. The understorey was diverse, with hazel *Coryllus avellana* mixed with young trees of black locust, sweet chestnut and birdcherry *Prunus avium* and with some blackberry *Sambucus nigra* and hawthorn *Crataegus monogyna*.

Trapping and handling squirrels

Trapping was carried out for at least five days bi-monthly, from July 1996 to October 1999, on a 22 ha trapping grid with 26 trap stations (1.3 traps ha⁻¹), using ground-placed Tomahawk "squirrel" traps baited with sunflower seeds and hazelnuts. Each trapped squirrel was individually marked using numbered metal ear-tags, and weighed to the nearest 5 g using a Pesola spring-balance, and the length of the right hind foot (without the nail) was measured (0.5 mm) with a thin ruler (Wauters and Dhondt 1989, Wauters and Gurnell 1999). Sex and age were recorded (Wauters and Dhondt 1989, 1993, Wauters and Gurnell 1999). Subadult males had abdominal testes and a small, unstained scrotum, subadult females have a very small vulva and the nipples were still invisible. Adult males have scrotal testes when sexually active, or abdominal testes but sometimes a dark-stained scrotum when sexually inactive. Nulliparous adult females have external genitalia and nipples similar to subadults, primiparous or multiparous females have a slightly larger vulva and visible nipples (Wauters and Lens 1995). Female squirrels are in oestrus for ca 24 h per breeding-cycle, but post-oestrus (from oestrus to parturition, 38–42 d) can easily be recognized because the vulva remains slightly swollen and has a longitudinal scar. Young red squirrels are weaned between 10 and 12 weeks old (Gurnell 1987). Hence, we scored a female's reproductive status as: 1) anoestrus (vulva small, no longitudinal opening) or oestrus (or post-oestrus: vulva partly or strongly swollen with longitudinal opening), early in the breeding season; 2) lactating (nipples large, milk excretion could be stimulated) or not lactating (nipples small) later on (Wauters and Dhondt 1995, Wauters and Lens 1995, Wauters et al. 1995). The majority of lactating females were fitted with radio-collars to locate breeding nests, and to determine whether litters were lost. Breeding success was also monitored by regular recaptures of previously lactating females to check their reproductive condition: a female was considered to have lost its litter when, prior to the earliest possible date of weaning, it shifted its nest site and no young were found in the nest, and/or when the nipples were no longer swollen (Wauters and Lens 1995).

Population parameters

We use the minimum number of animals known to be alive (MNA), from trapping, radiotracking or observations, at each trapping period as our estimate of population size. Since on one side of the trapping grid the woodland continued, squirrel density was estimated using an edge-correction, by assuming that the area trapped extended 100 m (average range radius of female red squirrel) beyond the edge of the grid. This area of 31 ha corresponded with the size of the total area used by radiotagged resident squirrels. All subadult and adult squirrels captured for the first time after March 1997 were considered immigrants. Recruits were new animals not captured previously (adults, subadults and juveniles), thus including locally born juveniles as well as immigrants born elsewhere, that stayed resident on the study area for at least six months. A recruitment index was calculated as the number of recruits per resident adult present in spring of each year (after Wauters et al. 1994b). Local annual survival rate (from t to $t + 1$) was estimated as (number of animals present in July of year t and still alive in June $t + 1$)/no. animals present July of year t).

Radio tracking and space use analysis

Red squirrels were radio tagged over 3-month periods within each season. Seasonal variation in squirrel home ranges and patterns of habitat use was investigated for the following periods: spring, March–May, summer-autumn, July–October, and winter, December–February. All adults resident on the study area were radio tagged in 1997 and 1998 allowing good estimates of space use patterns and habitat use. Locations were determined by following the radio signal until the squirrel was seen or pinpointed by signal strength and direction (Wauters and Dhondt 1992). At each fix, a squirrel's location was plotted (to the nearest 10 m in relation to a mapped grid with scale 1:2500), and the activity (1 = active, 2 = in a nest), and position (on the ground or in a tree, and where appropriate the tree species) were recorded. For home range analyses, between 30 and 40 radio-locations (fixes) were collected for each squirrel, which proved sufficient to adequately describe a squirrel's home range (Wauters and Dhondt 1992). Mononuclear 70% core-area estimates were used to describe an animal's activity centre (Wauters and Dhondt 1992, Wauters and Gurnell 1999) and to calculate the food resources available for each individual squirrel.

All data on home range size, home range use, and overlap of home ranges were analysed using the RANGES V program (Kenward and Hodder 1995). For each squirrel, in each period, the following parameters were calculated: 1) total home range area (100% of

the point-fixes) using the convex polygon method (MCP = minimum convex polygon), 2) mononuclear core-area estimates based on 70% core-areas (all squirrels, except a single male, had mononuclear core-areas as determined by a single inflection point in the slope of the utilisation distribution, and the 70% core-area best described an animal's activity centre), and 3) core-area overlap, expressed as percentage of overlap of a squirrel's core-area with the core-area of all other squirrels (Wauters and Dhondt 1992).

Estimating home range food availability

Since woodland structure was heterogeneous at a fine-grained level, we calculated the availability of tree seeds for each squirrel's home range separately and we used this as a measure of home range quality. To do this we first determined woodland composition by establishing one 20×20 m (400 m^2) vegetation quadrat in each 1 ha across the study area ($n = 19$). In each vegetation quadrat, we estimated canopy, understorey and ground cover in one of five categories ($< 20\%$, $21\text{--}40\%$, $41\text{--}60\%$, $61\text{--}80\%$, $> 80\%$). The number of trees of each tree species were counted, and the diameter at breast-height (DBH in cm) of each tree was measured. The number of understorey species and the proportion of hazel in the understorey were also recorded. We then estimated seed food availability of those tree species whose seeds are regularly eaten by squirrels (i.e. seeds from sweet chestnut, oak, hornbeam, and hazel, and fallen and consumed cones from Scots pine and white pine). Fruit fall from trees was monitored from July 1996 to June 1999. We used 1 m^2 seed quadrats placed under each tree species in each vegetation quadrat (Wauters and Dhondt 1995, Wauters and Lens 1995). This enabled us to estimate total seed production for the years 1996, 1997 and 1998. To combine data of different seed species, the numbers of seeds m^{-2} were converted to energy values (kJ m^{-2}). To estimate seed energy values, 100 seeds from each tree species were collected and the pericarp of each seed removed. The fresh weight of the remaining endocarp, the part consumed by seed predators such as squirrels, was determined for each seed species to the nearest mg. The samples were then dried to dry weight (to nearest mg) and crushed and pressed into pellets of known weight. The pellets were burnt in a Semi-micro bomb calorimeter (Parr, type 1425), previously calibrated using benzoic acid, to obtain their caloric values (kJ g^{-1}). We used the information of the relative canopy cover of each tree species in each vegetation quadrat and the seed energy production of each tree species to estimate seed food energy availability in each vegetation quadrat. We then expressed the home range food availability for each squirrel (HRQ) as the mean food abundance ($\text{kJ } 400 \text{ m}^{-2}$) of all vegetation quadrats

within the 70% core-area of the squirrel's range. Seeds and fruits produced in the summer-autumn of year t were considered available for the squirrels during the following "squirrel year" (see Wauters and Lens 1995), i.e. from July of year t to June of year $t + 1$.

Since red squirrels mainly fed on seeds of Scots pine and sweet chestnut (Wauters et al. unpubl.), we also used the sum of the proportions of Scots pines, mixed Norway spruce-Scots pine stands, and sweet chestnut of all vegetation quadrats within the 70% core-area as an index of habitat quality of the squirrel's home range.

Data analyses

The time spent on each tree species or on the ground was expressed as a percentage of the total hours of active behaviour observed in each season for each individual squirrel. These data were used to calculate the squirrel's habitat niche. Niche breadths (B_i) for two niche components (B_s = substrate: ground or tree, B_t = tree species) were calculated using Levin's formula $B_i = [1/\sum P_j^2(n)]$, where P_j is the proportion of observations in the j th resource state of the niche component and n equals the total number of resource states (Hurlbert 1978). Changes in habitat utilisation between seasons and habitat preference of red squirrels were assessed using compositional analysis (Aebischer et al. 1993). Compositional analysis takes the log-ratio differences of used (here radio locations) and available habitat proportions to determine habitat-use preferences (Lurz and Garson 1998, Lurz et al. 2000). In the initial step a Wilks' lambda statistic is calculated: a statistically significant χ^2 -value ($p < 0.05$, with DF = number of habitat types $- 1$) indicates a non-random use of the available habitat types (Aebischer et al. 1993). The second step produces a matrix of pairs of compared habitat types in which negative values imply avoidance of the numerator habitat type by comparison with the denominator habitat type, whilst positive values imply selection. The statistical significance of these comparisons are assessed by computing t -values (Aebischer et al. 1993). We used the proportions of trees within the whole study area to determine the following six categories of potentially available habitat types: Scots pine (SP, 19%), white pine and Norway spruce (CON, 17%), chestnut (20%), oak (9%), hornbeam (5%), others, mainly black locust (30%).

Proportions (p) were transformed using arcsine $\sqrt{p}$ when used in multivariate parametric tests.

We used logistic regression (Hosmer and Lemeshow 1989) to examine the relationship between habitat structure around the trap-site and the probability of trapping a resident squirrel. The dependent binary variable (Y_i) was scored 0 for traps where no squirrels were caught or a single capture occurred, it was scored 1 when more than two captures, of at least one resident

squirrel, occurred. The form of the logistic regression model was:

$$P(Y_i = 1) = \exp G(x_i) / 1 + \exp G(x_i)$$

where $P(Y_i = 1)$ refers to the probability of the binary variable being equal to 1.0, and where $G(x_i)$ includes the Y-intercept and regression coefficients associated with a series of variables: % canopy cover, % hazel understorey, seed productivity (kJ), proportion pine-spruce-chestnut, proportion black locust. Multivariate models were calculated by stepwise logistic regression with p -value < 0.05 set as the screening criteria for the selection of candidate variables (Hosmer and Lemeshow 1989).

Results

Food availability

Woodland structure varied greatly between the different vegetation quadrats and the number of seeds of several tree species varied widely among seed quadrats (see CV in Table 1), indicating that food availability was very heterogeneous throughout the woodland. Total seed production, in terms of energy-content of available high-quality food resources, was lowest in 1996, intermediate in 1997 and highest in 1998 (Table 1). Differences in food abundance per sampling plot between 1996 and 1997 (paired t -test $t = 3.249$, $n = 19$, $p = 0.0045$), and between 1996 and 1998 (paired t -test $t = 2.774$, $n = 19$, $p = 0.013$) were statistically significant, while that between 1997 and 1998 was not (paired t -test $t = 1.794$, $n = 19$, $p = 0.09$). Seed production (Table 1) was significantly higher in 1998 than in other years for chestnuts (One-way ANOVA and Tukey-test for comparison of means, with year as factor: $F = 9.98$, $DF = 2$, 30 , $p = 0.0005$), and a similar tendency existed for Scots pine cones ($F = 2.91$, $DF = 2$, 21 , $p = 0.077$). Acorns were more abundant in 1997 than in the other years ($F = 4.42$, $DF = 2$, 36 , $p = 0.019$), while there was no significant difference between years in the produc-

Table 1. Annual variation in tree seed production (number of seeds m^{-2} , mean and coefficient of variance, CV %, expressed as % of the mean) of different tree species and over the whole study area (in $10^6 J ha^{-1}$).

Tree species (n)	Mean (CV %)		
	1996	1997	1998
Scots pine (8)	13.8 (38)	19.0 (86)	29.9 (54)
Oak (13)	10.6 (67)	122.2 (140)	33.1 (121)
Hornbeam (5)	461.2 (84)	426.3 (89)	417.0 (130)
Chestnut (11)	44.1 (32)	64.2 (41)	111.2 (50)
Hazelnut (10)	9.0 (84)	3.4 (75)	6.9 (83)
Total food abundance (MJ ha^{-1})	6804 (106)	10943 (104)	15750 (131)

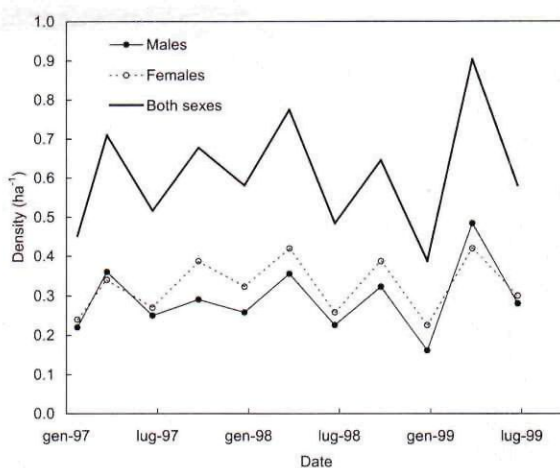


Fig. 1. Changes in red squirrel density over the entire study period.

tion of hornbeam seeds and hazelnuts (Table 1, hornbeam $F = 0.01$, $DF = 2$, 12 , $p = 0.99$, hazelnut $F = 2.51$, $DF = 2$, 27 , $p = 0.10$).

Squirrel demography

Red squirrel numbers fluctuated seasonally, with little annual variation. Numbers typically increased in April–May and September–October, as a result of seasonal reproduction and immigration (Fig. 1). They decreased from June to September, and again during late-autumn and winter due to emigration and mortality, mainly of juvenile animals. Pre-breeding winter density of resident adults changed little between years (from 0.39 to 0.58 squirrels ha^{-1} , Fig. 1), and so did maximum spring densities, when both adults and juveniles occurred (from 0.71 to 0.90 ha^{-1} , a 27% difference between lowest April-density of 1997, and highest of 1999, Fig. 1). Spring density tended to increase with tree seed productivity of the preceding year. Over the three years, the number of resident adult males in the pre-breeding population (January–March) varied between six and eight, and the number of adult females between seven and ten (0.23–0.32 ha^{-1} , Fig. 1). In summer there was even less annual variation: from seven to eight resident adults of either sex (Fig. 1, Table 2).

Multivariate logistic regression was applied to data on trapping success from April 1997 to April 1999. When considered singly, both proportion of pine-spruce-chestnut (high-quality habitat: $\chi^2 = 19.95$, $DF = 1$, $p = 0.0001$) and proportion of black locust (negative effect: $\chi^2 = 9.73$, $DF = 1$, $p = 0.002$) were significant factors in predicting trapping success. The other variables were not significant (all $p > 0.1$). The stepwise procedure selected only the proportion of high-quality

Table 2. Mean annual home range size (MCP) and 70% core-area size estimates (mean $\pm$ SD) and percentage of core-area overlap (mean $\pm$ SD) for adult and subadult red squirrels at Parco Pineta. Sample size: males (1997, $n = 7$, 1998, $n = 8$), females (1997, $n = 7$, 1998, $n = 8$). Significance of differences in home range size and core-area size between years and sexes was calculated using a Two-way ANOVA (all $DF = 1$, 26).

Home range estimate	Males (ha)	Females (ha)	Mean % overlap (range number of overlappers)			
			M with MM	M with FF	F with MM	F with FF
1997						
MCP	7.57 $\pm$ 3.42	2.70 $\pm$ 0.80				
Core-area	3.32 $\pm$ 1.75	1.06 $\pm$ 0.38	16 $\pm$ 16 (0–2)	38 $\pm$ 36 (1–3)	93 $\pm$ 16 (1–3)	4 $\pm$ 4 (0–1)
1998						
MCP	7.26 $\pm$ 3.41	4.31 $\pm$ 2.13				
Core-area	2.73 $\pm$ 1.20	1.46 $\pm$ 0.75	21 $\pm$ 33 (0–2)	32 $\pm$ 30 (1–3)	48 $\pm$ 42 (1–3)	8 $\pm$ 10 (0–1)
Two-way ANOVA		Home range size			Core-area size	
Year-effect		$F = 0.49$ $p = 0.49$			$F = 0.05$ $p = 0.82$	
Sex-effect		$F = 18.2$ $p = 0.0002$			$F = 18.3$ $p = 0.0002$	
Year $\times$ sex interaction		$F = 1.10$ $p = 0.30$			$F = 1.46$ $p = 0.24$	

habitat for inclusion in a multivariate predictive model, that explained 66% of the observed deviance ($G = -1.4 + 13.5$ [proportion high-quality habitat]). Adding proportion black locust (change in $\chi^2 = 1.26$, $DF = 1$, $p = 0.26$) did not significantly improve the fit of the model. Three subadult squirrels, two males and a female, were only caught in black locust patches. Two of them were only trapped once (dispersers), while a subadult male was radiotagged and behaved as a floater (*sensu* Wauters and Dhondt 1992) for ca 40 d, after which its radiosignal was lost and the squirrel was never recaptured.

We tested local annual survival rates (persistence), from July of year t to June of year $t + 1$, for a year and a sex effect and a year $\times$ sex interaction using a 2-way G-test. G-values were adjusted for small sample sizes using William's correction (Sokal and Rohlf 1995). There was no significant interaction, and no year effect (Fig. 2a, year $\times$ sex $G = 1.858$, $DF = 2$, $p > 0.3$, year $G = 1.791$, $DF = 2$, $p > 0.3$), but there was a significant sex effect (Fig. 2a, sex $G = 3.868$, $DF = 1$, $p = 0.046$), with females having a higher local annual survival than males.

Between July 1997 and June 1998, six male and three female immigrants were caught, and another seven males and one female immigrant from July 1998 to June 1999. Overall, 76% of immigrants were males and 24% females, which differed significantly from a 1:1 sex-ratio ($\chi^2 = 4.77$, $DF = 1$, $p = 0.029$).

The effects of year and season on breeding rate, proportion of adult females that successfully weaned offspring, were also compared using a 2-way G-test with William's correction. There was no significant year $\times$ season interaction, and no significant effect of either year or season (Fig. 2b, year $\times$ season $G = 1.322$, $DF = 2$, year $G = 0.340$, $DF = 2$, season $G = 0.842$, $DF = 1$, all $p > 0.3$). Recruitment rates of males were high in both years (0.63 in 1997–98, 0.57 in 1998–99), those of females were high in 1997–98 (0.63), but low

the following year (0.13). This corresponded with higher local survival of resident females in 1998–99 than in 1997–98.

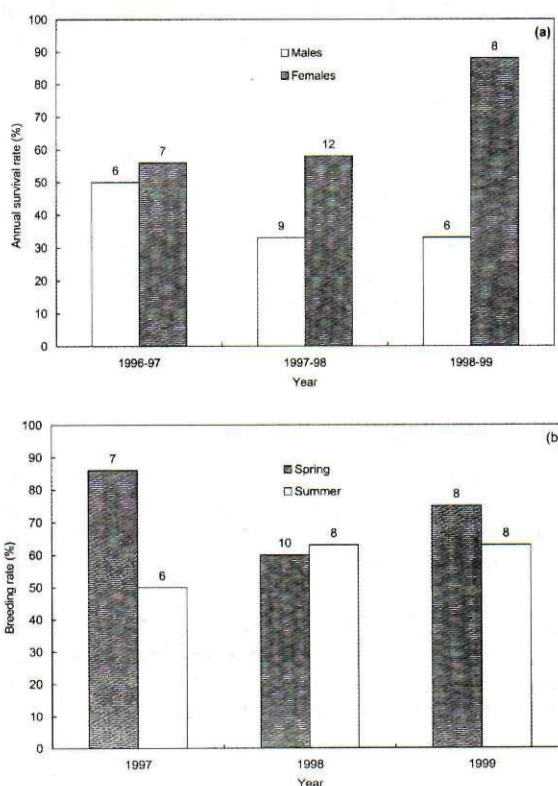


Fig. 2. (a) Annual local survival rates (%) according to sex and year. For 1996–97 the annual survival rate was calculated from the proportion of squirrels present in December 1996 that were still alive in June 1997. Numbers above bars indicate the number of red squirrels present at the start of each period. (b) Breeding rate (% successfully lactating females) according to season and year. Numbers above bars indicate the number of adult females present on the study area in each period.

At the individual level, breeding success was expressed as the proportion of reproductive events a female successfully weaned offspring (number of breeding seasons with weaned offspring divided by total number of breeding seasons alive on the study site as yearling or adult). Breeding success of 12 female red squirrels was positively correlated with habitat quality of the home range ($r = 0.839$, $p = 0.0006$), and with body mass ($r = 0.777$, $p = 0.0029$). Females that bred as yearlings (primiparous females) had a significantly higher breeding success than yearlings that did not breed (mean $\pm$ SD: primiparous yearlings, $n = 7$, 0.87 ± 0.19 , nulliparous yearlings, $n = 5$, 0.47 ± 0.28 , $t = 2.933$, $DF = 10$, $p = 0.015$), but also the habitat quality of their home range was better (primiparous yearlings 0.75 ± 0.19 , nulliparous yearlings 0.52 ± 0.12 , $t = 2.340$, $n = 10$, $p = 0.041$). In a multiple ANCOVA model (Proc GLM, Anon. 1989), both habitat quality and body mass significantly affected a female's breeding success (partial $p < 0.05$), while the reproductive performance as yearling (primiparous vs nulliparous) did not explain any additional variation in breeding success (partial $p = 0.35$).

We therefore calculated a stepwise forward linear regression model with breeding success as dependent variable, and habitat quality and body mass as independent variables. Both variables were significant at the 5% level, and together explained 79% of individual variation in breeding success (partial effects: habitat quality $F = 11.59$, $DF = 1$, 9 , $p = 0.008$, partial $R^2 = 0.64$; body mass $F = 6.53$, $DF = 1$, 9 , $p = 0.031$, partial $R^2 = 0.15$). Thus, female red squirrels produced more often offspring when they had a high proportion of Scots pine and sweet chestnut in their home range (habitat quality) and when they had a higher body mass.

Home range analysis

Seasonal variation in home range size and range use, core-area size, was statistically not significant (Two-way ANOVA: season effect $F = 1.53$, $p = 0.23$ for home range size, $F = 1.19$, $p = 0.32$ for core-area size, all $DF = 2$, 34). In all seasons, males had larger 100% MCP ranges (Two-way ANOVA sex effect $F = 20.89$, $DF = 1$, 34 , $p < 0.001$, sex-season interaction $F = 2.25$, $DF = 2$, 34 , $p = 0.12$) and larger 70% core-areas than females (sex effect $F = 23.83$, $DF = 1$, 34 , $p < 0.001$, sex-season interaction $F = 0.94$, $DF = 2$, 34 , $p = 0.40$). Home ranges (MCP) and core-areas of males were ca 2–2.5 times larger than those of females (Fig. 3). Both sexes used dreys, built in Scots pine, Norway spruce or oak, and dens, mainly found in natural cavities of chestnut trees, for resting and sleeping, or, in case of lactating females, as nursery nests. The number of nests did not differ with sex, but changed with season and both males and females used more nests in winter than

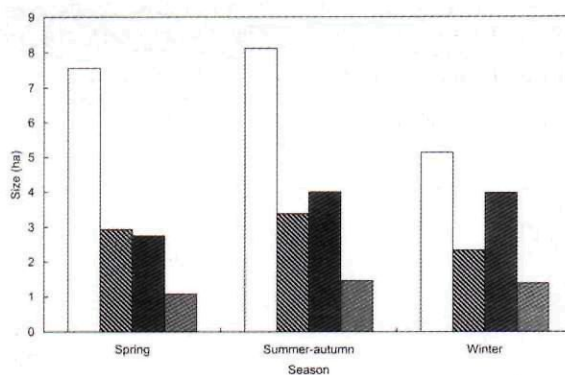


Fig. 3. Seasonal home range size estimates (mean $\pm$ 1 SD) for red squirrels. Males ($n = 5$, 7 and 6 in different seasons); MCP = open bars, 70% core-area = hatched bars, females ($n = 7$, 8 and 7 in different seasons): MCP = shaded bars, 70% core-area = light-shaded bars.

in the other seasons (Fig. 4). Adult females used less dreys in spring, when most of them were lactating and were confined to a single nursing nest for several weeks.

In order to have estimates of annual home range size (MCP), core-area size and core-area overlap of all red squirrels resident on the study site in 1997 and in 1998, we combined radiotracking data of animals monitored in spring and those monitored in summer-autumn. Since we showed earlier there was no significant seasonal variation in range size, this procedure did not cause any bias in our results. There were no differences in mean home range size and mean core-area size of male or female red squirrels between years (Table 2). This was confirmed comparing the range size at the individual level for those squirrels that were radio-tracked both in 1997 and in 1998 ($n = 7$, 2 males, 5 females, paired t -test: MCP $t = 1.62$, $p = 0.16$, core-area size $t = 0.54$, $p = 0.61$). In both years, males used larger

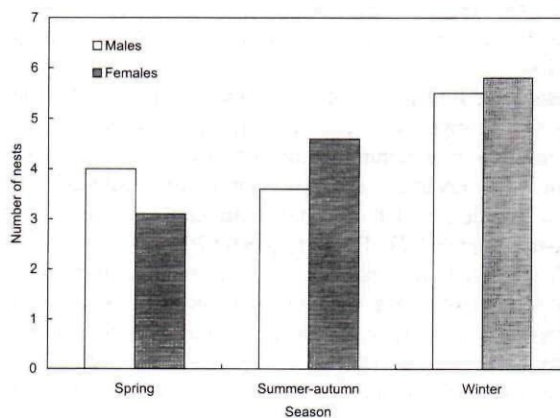


Fig. 4. Seasonal variation in the number of nests used (mean) by radiotagged red squirrels. Males = open bars, females = shaded bars. Two-way ANOVA: season effect $F = 3.97$, $DF = 2$, 24 , $p = 0.032$, sex effect $F = 0.06$, $DF = 1$, 24 , $p = 0.88$, season-sex interaction $F = 1.31$, $DF = 2$, 24 , $p = 0.29$.

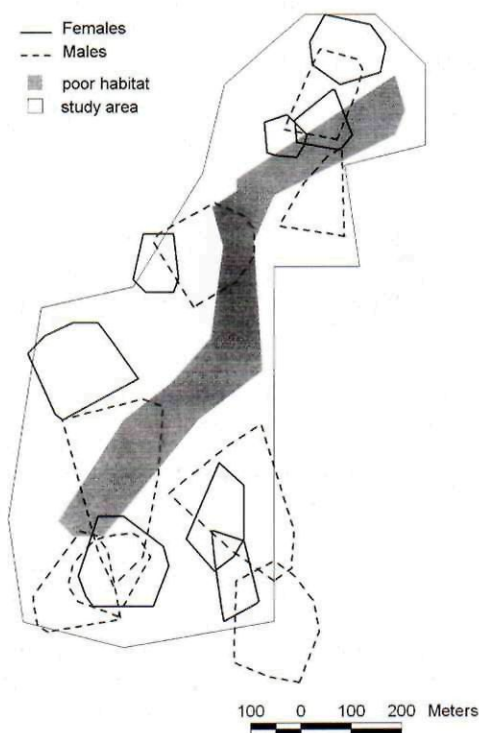


Fig. 5. Core-areas of resident male (dotted lines) and female (full lines) red squirrels in 1998. Shaded area is the poor-quality habitat dominated by black locust.

home ranges and larger core-areas than females (Table 2). Individual variation in total home range size and core-area size were strongly and positively correlated, indicating that squirrels with larger home ranges also used larger core-areas than those having smaller home ranges ($r = 0.936$, $n = 30$, $p < 0.0001$). The core-areas were concentrated in woodland patches dominated by Scots pine or chestnut, while areas with predominantly black locust were avoided (Fig. 5). Patterns of core-area overlap were similar in both years (Table 2). For males there was no significant difference in the amount of intra- and intersexual core-area overlap, hence a male's core-area was overlapped to a similar degree by other males than by females (Table 2, Wilcoxon matched-pairs signed-ranks test: 1997, $p = 0.12$, 1998, $p = 0.26$). The core-areas of adult females, in contrast, were more strongly overlapped by males than by other females (Table 2, Wilcoxon test: 1997, $p = 0.018$, 1998, $p = 0.012$). About half of the resident females did not overlap with any other female, while the others had their core-area slightly overlapped by only one squirrel of the same sex (Table 2, Fig. 5), indicating the existence of female intrasexual territoriality (Wauters and Dhondt 1992).

Individual variation in home range size of male and female red squirrels was further analysed using radio-location data of 13 individual males and 10 individual

females tracked between April 1997 and October 1998. The relationship between home range size (dependent variable) and home range quality, habitat quality, body mass, % overlap with males, % overlap with females, and the proportion of conifers (Scots pine, white pine and Norway spruce) was investigated using a multiple linear regression model, applying a stepwise backward procedure to select significant parameters (Proc REG, Anon. 1989). Individual variation in home range size (100% MCP) of males was significantly predicted by the proportion of conifers in the home range, and range size was found to increase the higher the proportion of conifers (selected regression model $F = 7.57$, $DF = 1, 11$, $p = 0.019$, $R^2 = 0.41$, home range size = $4.2 (\pm 1.3) + 5.7 (\pm 2.1)$ proportion conifers). None of the other variables significantly improved the fit of the model (partial $r < 0.3$, $p > 0.2$ in all cases). For females, individual variation in body mass explained 64% of variation in home range size, with heavier females using smaller home ranges than those of lower body mass (selected regression model $F = 14.31$, $DF = 1, 8$, $p = 0.0054$, $R^2 = 0.64$, home range size = $25.2 (\pm 5.7) - 0.07 (\pm 0.02)$ body mass). None of the other variables tested significantly improved the fit of the model (partial $r < 0.2$, $p > 0.3$ in all cases).

Habitat use and niche-width

Male and female red squirrels spent similar proportions of their active time on the ground in the different seasons and for both sexes the proportion of time spent on the ground varied with season (Fig. 6a: Two-way ANOVA: season effect $F = 5.08$, $DF = 2, 26$, $p = 0.014$, sex effect $F = 2.58$, $DF = 1, 26$, $p = 0.12$, season-sex interaction $F = 0.24$, $DF = 2, 26$, $p = 0.79$). Both sexes were found relatively more often on the ground in winter than in the other seasons. Consequently, niche-width for substrate differed significantly between seasons. There was also a significant differences for the niche-width dimension tree species between seasons (Fig. 6b: Two-way ANOVA, season effect $F = 4.72$, $DF = 2, 26$, $p = 0.018$). Niche-width was smallest in winter, and increased in spring and summer-autumn (Fig. 6b). There was no sex-difference in niche-width for tree species (Two-way ANOVA: sex effect $F = 1.13$, $DF = 1, 26$, $p = 0.30$, season-sex interaction $F = 0.43$, $DF = 2, 26$, $p = 0.66$).

Habitat use of red squirrels was not random in either season (Wilk's lambda test, spring, $n = 15$, $\chi^2 = 46.30$, summer-autumn, $n = 17$, $\chi^2 = 25.00$, winter, $n = 16$, $\chi^2 = 38.68$, all $DF = 5$, all $p < 0.001$). Overall, there was a strong relationship between seasonal food availability in the different tree species and habitat use. In spring, squirrels showed a significant preference for oak over all other tree species except Scots pine, which was second in use (Table 3). This corresponded with a

prevalence in the spring diet of pine flowers, buds and shoots and of oak flowers and caterpillars. Squirrels were regularly observed in chestnut trees while still feeding on chestnuts recovered from their caches, and some animals fed regularly on flower buds and young shoots of Norway spruce in the plantations. Hornbeam was avoided with respect to all other species and so was black locust (main species of the category "others", Table 3).

In summer-autumn squirrels showed a strong preference for Scots pine, when they fed intensively on immature (summer) and maturing pine seeds (autumn). They also foraged in hornbeam more often than expected and, from September–October onwards, were often found in chestnuts. Hornbeam seeds were an important food supply in summer, early autumn, while chestnuts were heavily fed upon from October onwards when they started to mature but were still on the trees. However, differences in preferences between hornbeam, chestnut, other tree species and oak were not significant (Table 3). In winter, habitat selectivity was more pronounced, with still Scots pine significantly preferred over all other tree species (Table 3). Also chestnut and conifers were selected, while oak, hornbeam and other tree species were avoided (Table 3: SP >> chestnut = CON > [others = oak > hornbeam]). Scots pine cones were still a major food supply in winter. Many chest-

nuts were recovered from the forest floor, but consumed – in a safer place – a nearby chestnut tree, explaining the frequent use of this tree species. In plantations, squirrels also fed on the partly open cones of white spruce. Occasionally squirrels were observed in oaks, foraging on dead branches for insects or fungi.

Discussion

In patchy habitats, with a strong spatial gradient in the availability of critical resources, there will be strong selection on individual squirrels to establish a home range in high-quality patches, where densities will be close to carrying capacity (Gurnell 1987, Wauters and Dhondt 1992, 1998, Lurz et al. 2000). Therefore, tree squirrels might adapt their social organisation to fine-grained heterogeneity in the distribution of primary food resources in three ways: 1) reducing home range size, and core-area size as a response to locally high densities; 2) not reducing range size, but increasing the amount of core-area overlap in high-density patches; or 3) adopting a settlement pattern across the different habitat types with individuals occurring in habitats according to the ideal despotic distribution (Fretwell and Lucas 1970), in which case we expect dominant, breeding individuals occupying the high-quality patches, and subordinate, non-breeding squirrels the lower quality patches. In the first two cases, we expect overall population density to be similar as in more homogeneous habitats with a comparable tree seed productivity. In the third case, densities in the high-quality patches will be similar as that found in homogeneous, high-quality woodlands, but squirrel density over the entire study area will be significantly lower. The degree of difference will depend on the number of squirrels that can settle in the low-quality patches.

Food availability, squirrel density and habitat use

Habitat use differed from random in all seasons, and niche width was smallest in autumn-winter, when the availability of high-energy tree seeds is highest, and increased in spring and summer, when squirrels fed more intensively on secondary food-items of lower energy content. This pattern was consistent with that of conspecific occurring in both high-quality habitats with relatively limited spatial and temporal variation in food availability, further called "stable" habitats, or habitats with a high degree of temporal and spatial variation in tree seed abundance, further called "variable" habitats (Wauters and Dhondt 1987, Lurz and Garson 1998, Lurz et al. 1997, 2000). Compositional analysis showed that the poorest quality habitat (black locust dominated patches) was avoided in all seasons, and this was confirmed by the negative effect of proportion of black

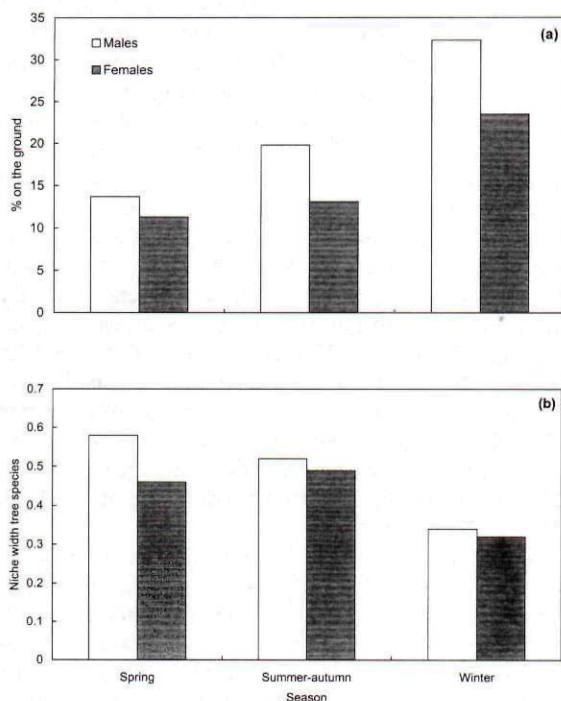


Fig. 6. Habitat use by male and female red squirrels. (a) % foraging on the ground, (b) niche-width index for tree species (mean).

Table 3. Mean log-ratio differences (± 1 SE) between used and available habitat compositions for three periods at Parco Pineta. Levels of significance: $^{\circ} 0.1 > p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Habitat types (numerator)	Habitat types (denominator)				
	CON	Chestnut	Oak	Hornbeam	Others
(a) Spring (n = 15)					
SP	1.357 $\pm$ 0.755 $^{\circ}$	0.965 $\pm$ 0.307	-0.226 $\pm$ 0.288	5.913 $\pm$ 0.776 ***	2.860 $\pm$ 0.472 ***
CON	—	-0.391 $\pm$ 0.731	-1.583 $\pm$ 0.668 *	4.555 $\pm$ 1.017 ***	1.505 $\pm$ 0.565 *
Chestnut	—	—	-1.191 $\pm$ 0.225 ***	4.947 $\pm$ 0.852 ***	1.894 $\pm$ 0.411 ***
Oak	—	—	—	6.139 $\pm$ 0.747 ***	3.087 $\pm$ 0.339 ***
Hornbeam	—	—	—	—	-3.051 $\pm$ 0.851 **
(b) Summer-autumn (n = 17)					
SP	3.642 $\pm$ 0.951 **	1.261 $\pm$ 0.663 $^{\circ}$	2.731 $\pm$ 0.722 **	1.009 $\pm$ 1.157	1.972 $\pm$ 0.533 **
CON	—	-2.381 $\pm$ 0.964 *	0.912 $\pm$ 1.176	-2.632 $\pm$ 1.376 $^{\circ}$	-1.670 $\pm$ 1.038
Chestnut	—	—	1.470 $\pm$ 0.831 $^{\circ}$	-0.250 $\pm$ 1.257	0.712 $\pm$ 0.825
Oak	—	—	—	-1.722 $\pm$ 1.336	-0.759 $\pm$ 1.016
Hornbeam	—	—	—	—	0.963 $\pm$ 0.995
(c) Winter (n = 16)					
SP	1.242 $\pm$ 0.544 *	1.186 $\pm$ 0.243 **	4.419 $\pm$ 0.842 ***	6.339 $\pm$ 0.714 ***	3.353 $\pm$ 0.652 ***
CON	—	-0.056 $\pm$ 0.615	3.178 $\pm$ 1.188 **	5.097 $\pm$ 0.818 ***	2.111 $\pm$ 0.950 *
Chestnut	—	—	3.232 $\pm$ 0.819 **	5.153 $\pm$ 0.758 ***	2.166 $\pm$ 0.563 **
Oak	—	—	—	1.921 $\pm$ 1.013 $^{\circ}$	-1.066 $\pm$ 1.024
Hornbeam	—	—	—	—	-2.987 $\pm$ 1.022 $^{\circ}$

locust at trap sites on trapping success. Thus resident, adult red squirrels settled and intensively used the high-quality patches, mainly those dominated by sweet chestnut and Scots pine, and avoided poor-quality habitat patches, that were only used temporarily by dispersing (transient) squirrel.

We could compare the tree seed productivity estimates in our study site with estimates derived from data on seed crop sizes of oak, beech, and hazelnut in mixed deciduous forests in Belgium and the U.K., and of spruce and pine cone crops in mixed conifer woodlands in Belgium and England, and large man-made conifer plantations in northern England (Wauters and Lens 1995, Kenward et al. 1998, Lurz et al. 2000, Wauters et al. 2000). Total tree seed productivity was lowest in man-made conifer forests in northern England, the variable habitat (ca 26–36 MJ ha⁻¹), where also red squirrel densities were low (0 in poor-quality patches in years with poor cone crops, and 0.29 squirrels ha⁻¹ pre-breeding density and 0.34 to 0.46 ha⁻¹ post-breeding density, Lurz et al. 1995, 2000, Wauters et al. 2000). Similar fluctuations in red squirrel densities were found in most years in large patchy conifer forests of Norway spruce and Scots pine in Sweden (Andrén and Lemnell 1992). Scots and/or Corsican pine *Pinus nigra* dominated woodlands in southern England and in Belgium had a much higher productivity (from ca 500 to 5600 MJ ha⁻¹), and pre-breeding squirrel densities ranging from 0.8 to 1.3 ha⁻¹, with even a long-term average of 3.4 ha⁻¹ in a 6 ha mature, high-quality Scots pine woodland on a small island (Wauters and Dhondt 1990, Wauters and Lens 1995, Kenward et al. 1998). The highest, absolute energy-values of tree seed crops were those estimated for mixed deciduous woodlands and mixed woodlands dominated by oak, beech and Scots

pine (ca 2500–20 000 MJ ha⁻¹, with extremes of over 50 000 MJ ha⁻¹ in mast years of acorn or beechnuts production), corresponding with red squirrel pre-breeding densities ranging between 0.6 and 1.0 squirrels ha⁻¹ in southern England, and 0.7–1.7 in Belgium (Wauters and Dhondt 1990, 1998, Kenward and Holm 1993, Wauters and Lens 1995, Kenward et al. 1998). In the Belgian woodlands, summer densities of adult red squirrels varied from 0.80 to 1.29 ha⁻¹ and adult female densities from 0.43 to 0.60 ha⁻¹ (Wauters et al. 1994b). The size of the tree seed crop in our study area (6800–15 700 MJ ha⁻¹), mainly determined by the abundance of chestnuts, acorns and Scots pine cones, fell within the range observed for mixed woodlands dominated by broadleaf trees in other countries. However, red squirrel densities were lower: pre-breeding densities ranged between 0.39 and 0.58 ha⁻¹, ca 40% less than those registered in England and 44–66% less than in stable habitats in Belgium. Adult summer densities, which remained stable around 0.5 squirrels ha⁻¹, were about one third lower than in continuous Belgian woodlands, and comparable with values found in small woodlands in fragmented landscapes (Wauters et al. 1994a, b). Densities of adult females, the best index of the number of red squirrels resident within the woodland, fluctuated from 0.23 to 0.32 ha⁻¹, hence slightly lower than in British oak-hazel woods (long-term average of 0.33 adult females in spring, Kenward et al. 1998), and 50% lower than in the Belgian population. They fell within the range of female summer densities in woodland fragments in Belgium (0.2–0.32 ha⁻¹, Wauters et al. 1994a, b). Hence, our data on squirrel densities agree with predictions of the ideal despotic distribution hypothesis.

Survival, breeding and recruitment

Estimates of red squirrel survival and breeding in broadleaf and mixed Scots pine dominated woodlands vary markedly according to time of the year, food availability and adult density (Wauters and Dhondt 1990, Wauters et al. 1994b, Wauters and Lens 1995). For example, the frequency of lactating adult females in spring or in summer in deciduous woods in Belgium ranged from 0 to 80%, and from 25 to 80% in mixed coniferous woodlands (Wauters and Dhondt 1990, Wauters and Lens 1995). In the "variable" habitat in northern England, breeding rates fluctuated between 38 and 45% in spring, and 33–68% in summer (Wauters et al. 2000). There was only little annual variation in the availability of primary food resources and in adult squirrel density over the three years we monitored our population, and, consequently, there was little annual variation in the frequency of lactating females, with more frequent spring (60–86%) than summer breeding (50–63%). For comparison with literature data from woodlands with a comparable productivity of primary food resources, we calculated an annual breeding rate (frequency of lactating adult females in spring and summer season). Annual breeding rate in our population ranged from 61 to 69%, which was slightly higher than long-term estimates from oak-hazel woods in southern England (mean $\pm$ SE = $51 \pm 6\%$) and deciduous woods ("stable" habitat) in Belgium (mean 52%, range 39–67%), and similar to those from Scots or Corsican pine dominated woodlands (England $64 \pm 7\%$, Belgium, mean 60%, range 54–64%, Wauters and Dhondt 1990, Wauters et al. 1994b, Kenward et al. 1998).

Average litter sizes for red squirrels in Belgium ranged from 1.7 to 2.7 weaned young per breeding female, and 0.8–1.7 juveniles per adult female (Wauters et al. 1994b), while in southern England comparable estimates were found (oak-hazel woods: mean $\pm$ SE = 1.11 ± 0.14 , range 0.5–1.8 juveniles per adult female, Scots pine woods 1.57 ± 0.16 , range 0.8–2.3 juveniles per adult female, Kenward et al. 1998). Litter sizes in our population in north Italy, of ca 1.5–2 weaned young per breeding female, and 0.8–1.5 per adult female, fall into this range. Thus, average annual reproductive output in our population was not lower than that found in Belgium or southern England. Therefore, the lower densities could not be explained by a reduction in the reproductive rate of the red squirrel population.

Red squirrel survival varies according to age, with the annual survival being higher in adults than juveniles or subadults (Gurnell 1987, Wauters and Dhondt 1990, Wauters et al. 1994b, Kenward et al. 1998). In so-called stable habitats, there is no difference between the local survival of adult male and female red squirrels (annual survival rates in deciduous and conifer woodlands in

Belgium 0.57–0.72, and 0.50–0.76 respectively, Wauters and Dhondt 1990, Wauters et al. 1994b), or their persistency rates (on average 0.55 and 0.67 in oak-hazel and Scots pine woods in southern England, Kenward et al. 1998). However, in "variable" habitat, annual local survival rate of females (0.57–0.71) was significantly higher than that of males (0.22–0.50, Wauters et al. 2000). In the population studied here, annual survival rate of adult females (0.56–0.87) was comparable with that found in high-density populations in Belgium and southern England, while local survival of adult males (0.33–0.50) was much lower. However, more male than female immigrants occurred on our trapping grid, and, over the whole study period, recruitment of males into the population was higher than female recruitment. Hence, there was a higher turnover rate in the male than in the female population, similar to that documented for red squirrels in "variable" habitats (Lurz et al. 1997, 2000). As a result, adult sex-ratios did not differ from equal (1:1 sex-ratio) in our population. For comparison, recruitment rates, of immigrants and locally born juveniles combined, were within the range found in "stable" populations in Belgium (0.33–0.66 in our population against 0.41–0.57 in deciduous woodland in Belgium, from Wauters et al. 1994b).

Finally, recruitment rates were in balance to replace losses to the population due to mortality and emigration. However, they were not sufficiently high to have, at least temporarily, a marked density increase, with subadult animals behaving as floaters (except a single subadult male, monitored for ca 40 d), or settling in poorer quality habitats, as occurred after good breeding in populations in "stable" habitats in Belgium (Wauters and Dhondt 1989, 1992, Wauters and Lens 1995). Thus, no floaters remained for several months and no subordinate squirrels established residency in this population, neither in the poor-quality, nor in high-quality habitat patches.

To summarize, the demographic processes (breeding rate, adult survival rate, recruitment rate) in the Italian red squirrel population, characterised by a high degree of spatial variability in the abundance of primary food resources, were comparable with estimates from high-density populations occurring in relatively homogeneous "stable" habitats in Belgium and southern England. They differed in the degree of sex-biased local survival of adult red squirrels (female biased), and subadult recruitment rate (male biased) which showed a pattern as in "variable" man-made conifer plantations in northern England (Lurz et al. 1997, 2000, Wauters et al. 2000). However, the reduction in local survival of adult males is not sufficient to explain the lower densities, of both sexes, in our population with respect to the densities found in Belgium and southern England, suggesting a direct relationship between the spatial distribution of primary food resources and red squirrel space use.

Spacing behaviour

The general spacing pattern at Parco Pineta, north Italy, was similar to that in other red squirrel populations on the British Isles, in Belgium and in Sweden (Wauters and Dhondt 1992, Andrén and Delin 1994, Wauters et al. 1994a, Lurz et al. 2000). Adult males used larger home ranges than females and their core-areas overlapped with those of females and with those of neighbouring males. The core-areas of adult females were small and nearly exclusive with respect to other females, confirming the existence of intrasexual territoriality in this sex (Wauters and Dhondt 1992, Wauters et al. 1994a, Lurz et al. 2000). Male red squirrels at Parco Pineta used home ranges that were ca 1.2–1.8 times larger than in mixed “stable” deciduous woodlands in Belgium, and 1.9–2.4 times larger than in conifer dominated woods. Home ranges of adult females were of similar size as in the oak-beech woods in Belgium (0.9–1.4 times larger), and slightly larger than in the “stable” coniferous woodland (1.4–1.5 times; Wauters and Dhondt 1992, 1998). As in Belgium woods, and in contrast with red squirrels in “variable” habitats in northern England, nearly all adult animals used a single core-area, indicating that in high-quality habitat single patches contained sufficient food resources to sustain a squirrel year-round (Wauters and Dhondt 1992, Lurz et al. 2000). Male 70% core-areas were nearly of similar size as in broadleaf woodland in Belgium (1.1–1.2 times larger), but ca 1.5 times larger than in the coniferous wood. Female core-areas were of similar size when density in the broadleaf woodland in Belgium was low, but ca 1.8 times larger when density was high (Wauters and Dhondt 1992, 1998). They were of similar size as those of females living in the “stable” coniferous habitat in Belgium. Thus, compared with conspecifics in habitats with similar overall tree seed abundance, red squirrels in our population did not respond to habitat patchiness by reducing home range, or core-area size. These results, and reduced adult density, disagree with predictions of the first hypothesis, allowing us to conclude that red squirrels do not adapt their social organisation to fine-grained habitat patchiness, in terms of primary food resources, by reducing home range and/or core-area size. For comparison, male and female home range size in “variable” habitats in northern England were, respectively 2–2.5 and ca 2 times larger than in the population studied here, which was related to core-areas being multinuclear in the large, “variable” conifer plantations (Lurz et al. 2000). However, core-areas (85% multinuclear core-area, Lurz et al. 2000) were of similar size as in Italy for both sexes. In patchy, natural conifer forests in Sweden, home ranges of females were even 5–6 times larger, those of males > 10 times larger than in north Italy (Andrén and Delin 1994). Interestingly, total home range size in males, and core-area size and intrasexual

core-area overlap in females in our population were similar to those found in one of the fragmented mixed woodlands in Belgium, with also a comparable density of resident red squirrels (site K, Wauters et al. 1994a, b).

Our detailed estimates of home range quality (energy content of tree seeds within an animal's core-area) were not correlated with individual variation in home range or core-area size, or with parameters of female breeding success. We argue that such detailed estimates are of little use in small-grained heterogeneous habitats, because they take into account the energy supplied by seed species that are only consumed in a brief period of time (in our case white pine seeds, hazelnuts and hornbeam seeds), or on which squirrels only feed occasionally (e.g. acorns). In fact, we found that simple indices of habitat quality in the home range (proportion of sweet chestnut, Scots pine, and Norway spruce, the latter was added because it occurred in very small patches surrounded by Scots pine or interspersed with the latter), were more reliable indicators: “habitat quality” was positively correlated with female breeding success, and with primiparity, as was the case in other populations of red squirrels and in North American pine squirrels (Wauters and Dhondt 1989, 1995, Becker et al. 1998). Moreover, female body mass tended to be positively correlated with habitat quality in the home range (see also Wauters and Dhondt 1989, 1995), and females of high body mass tended to use smaller ranges than those of lower body mass. The two females that used large home ranges, comparable with those of males, were in fact yearlings that were apparently still exploring quite large areas and did not produce offspring.

Finally, red squirrels of both sexes had their core-area overlapped by fewer conspecifics of the same sex than in the “stable” habitats in Belgium, while patterns of intersexual core-area overlap were similar (Wauters and Dhondt 1992). Moreover, the degree of intrasexual territoriality in adult females in our study population was the highest recorded (lowest % of female-female overlap: means 24–30% in Belgium, 8–14% for multinuclear core-areas in woodland fragments in Belgium, 12–27% for multinuclear core-areas in northern England, 4–8% in our population; Wauters and Dhondt 1992, Wauters et al. 1994a, Lurz et al. 2000). Likewise, the % of male-male core-area overlap was the lowest recorded. Hence, red squirrels in the small-grained patchy forest in north Italy did not adapt their spacing behaviour to small-scale habitat heterogeneity by increasing the amount of core-area overlap in high-quality habitat patches. We can, therefore, reject the second hypothesis stated at the beginning of the discussion.

We conclude that the data on red squirrel home range distribution, core-area overlap and density presented here indicate that dominant residents (“territory” owners) are able to exclude dispersing animals

from preferred, high-quality habitat, producing a spacing pattern referred to as ideal despotic distribution (Fretwell and Lucas 1970). Theoretically, surplus (settled subadult and yearling squirrels, and floaters) individuals might settle or temporarily use the less preferred habitat patches, at least in years with high food abundance, resulting in an increase of overall population density (e.g. Andrén and Lemnell 1992). In our study site, however, black locust seeds were not consumed by red squirrels and thus availability of edible tree seeds in the poor-quality habitat patches was limited to some hazelnuts in the understorey and the seeds of a few hornbeam trees, and, consequently, very low in all years. This made it impossible for animals to establish a home range in these patches, resulting in a considerable reduction of red squirrel population density, in comparison to populations in "stable" habitats. In fact, when only the high-quality habitat was considered, our summer densities ($0.7\text{--}0.8$ residents ha^{-1}) were similar to those in British oak-hazel woods and in deciduous woodland in Belgium during years of medium to good tree seed crops (Wauters and Lens 1995, Kenward et al. 1998).

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References

- Aebischer, N. J., Robertson, P. A. and Kenward, R. E. 1993. Compositional analysis of habitat use from radio-tracking data. – *Ecology* 74: 1313–1325.
- Andrén, H. and Lemnell, P. A. 1992. Population fluctuations and habitat selection in the Eurasian red squirrel *Sciurus vulgaris*. – *Ecography* 15: 303–307.
- Andrén, H. and Delin, A. 1994. Habitat selection in the Eurasian red squirrel, *Sciurus vulgaris*, in relation to forest fragmentation. – *Oikos* 70: 43–48.
- Andrewartha, H. G. and Birch, L. C. 1954. The distribution and abundance of animals. – Univ. of Chicago Press.
- Anon. 1989. SAS STAT users guide. – SAS Inst., Cary, NC.
- Becker, C. D., Boutin, S. and Larsen, K. W. 1998. Constraints on first reproduction in North American red squirrels. – *Oikos* 81: 81–92.
- Boyce, C. C. K. and Boyce, J. L. 1988. Population biology of *Microtus arvalis*. I. Lifetime reproductive success of solitary and grouped breeding females. – *J. Anim. Ecol.* 57: 711–722.
- Bujalska, G. 1973. The role of spacing behaviour among females in the regulation of reproduction in the bank vole. – *J. Reprod. Fert.* 19: 465–474.
- Cagnin, M. et al. 2000. Habitat use and population density of the red squirrel, *Sciurus vulgaris meridionalis*, in the Sila Grande mountain range (Calabria, south Italy). – *Ital. J. Zool.* 67: 81–87.
- Clutton-Brock, T. H. et al. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. – *J. Anim. Ecol.* 56: 53–67.
- Don, B. A. C. 1983. Home range characteristics and correlates in tree squirrels. – *Mammal Rev.* 13: 123–132.
- Donohoe, R. W. and Beal, R. O. 1972. Squirrel behaviour determined by radio-telemetry. – *Ohio Fish and Wildl. Rep.* 2: 1–20.
- Farentinos, R. C. 1972. Social dominance and mating activity in the tassel-eared squirrel (*Sciurus aberti ferreus*). – *Anim. Behav.* 20: 316–326.
- Farentinos, R. C. 1979. Seasonal changes in home range size of tassel-eared squirrels. – *Southwest Nat.* 24: 49–62.
- Fretwell, S. D. and Lucas, H. L. Jr 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. – *Acta Biotheor.* 19: 16–36.
- Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. – *Mammal Rev.* 13: 133–148.
- Gurnell, J. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. – *Anim. Behav.* 32: 1119–1131.
- Gurnell, J. 1987. The natural history of squirrels. – Christopher Helm, London.
- Gurnell, J. 1996. The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. – *J. Appl. Ecol.* 33: 325–338.
- Havera, S. P. and Nixon, H. M. 1978. Interaction among adult female fox squirrels during the winter breeding season. – *Trans. Ill. State Acad. Sci.* 71: 24–38.
- Hosmer, D. W. and Lemeshow, S. 1989. Applied logistic regression. – Wiley.
- Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. – *Ecology* 59: 67–77.
- Kemp, G. A. and Keith, L. B. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. – *Ecology* 51: 763–779.
- Kenward, R. E. and Holm, J. L. 1993. On the replacement of the red squirrel in Britain: a phytotoxic explanation. – *Proc. R. Soc. Lond. B* 251: 187–197.
- Kenward, R. E. and Hodder, K. H. 1995. Ranges V: an analysis system for biological location data. – ITE, Furzebrook.
- Kenward, R. E. et al. 1998. Comparative demography of red squirrels (*Sciurus vulgaris*) and grey squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. – *J. Zool. (Lond.)* 244: 7–21.
- Koford, R. R. 1982. Mating system of a territorial tree squirrel (*Tamiasciurus douglasii*) in California. – *J. Mammal.* 63: 274–283.
- Koprowski, J. L. 1992. Removal of copulatory plugs by female tree squirrels. – *J. Mammal.* 73: 572–576.
- Koprowski, J. L. 1993a. Alternative reproductive tactics in male eastern gray squirrels: "making the best of a bad job". – *Behav. Ecol.* 4: 165–171.
- Koprowski, J. L. 1993b. Behavioral tactics, dominance, and copulatory success among male fox squirrels. – *Ethol. Ecol. Evol.* 5: 169–176.
- Koprowski, J. L. 1996. Natal philopatry, communal nesting, and kinship in fox squirrels and gray squirrels. – *J. Mammal.* 77: 1006–1016.
- Koprowski, J. L. 1998. Conflict between the sexes: a review of social and mating systems of the tree squirrels. – In: Steele, M. A., Meritt, J. F. and Zegers, D. A. (eds), *Ecology and evolutionary biology of tree squirrels*. Spec. Publ. of the Virginia Mus. of Nat. Hist. 6: 33–41.
- Larsen, K. W. and Boutin, S. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. – *Ecology* 75: 214–223.
- Lomnicki, A. 1980. Regulation of population density due to individual differences and patchy environment. – *Oikos* 35: 185–193.
- Lurz, P. W. W. and Garson, P. J. 1998. Seasonal changes in ranging behaviour and habitat choice by red squirrels (*Sciurus vulgaris*) in conifer plantations in northern Eng-

- land. – In: Steele, M. A., Meritt, J. F. and Zegers, D. A. (eds), Ecology and evolutionary biology of tree squirrels. Spec. Publ. of the Virginia Mus. of Nat. Hist. 6: 79–85.
- Lurz, P. W. W., Garson, P. J. and Rushton, S. P. 1995. The ecology of squirrels in spruce dominated plantations: implications for forest management. – For. Ecol. Manage. 79: 79–90.
- Lurz, P. W. W., Garson, P. J. and Wauters, L. A. 1997. Effects of temporal and spatial variation in habitat quality on red squirrel dispersal behaviour. – Anim. Behav. 54: 427–435.
- Lurz, P. W. W., Garson, P. J. and Wauters, L. A. 2000. Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels, *Sciurus vulgaris* L. – J. Zool. (Lond.) 251: 167–178.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. – Ecol. Monogr. 38: 30–63.
- Sokal, R. R. and Rohlf, F. J. 1995. Biometry, 3rd ed. – Freeman.
- Wauters, L. A. 2000. Squirrels – medium-sized granivores in woodland habitats. – In: Halle, S. and Stenseth, N. C. (eds), Activity patterns in small mammals: a comparative ecological approach. Ecol. Stud. 141, Springer, pp. 131–143.
- 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. Säugetierkd. 52: 341–352.
- Wauters, L. A. and Dhondt, A. A. 1989. Body weight, longevity and reproductive success in red squirrels (*Sciurus vulgaris*). – J. Anim. Ecol. 58: 637–651.
- Wauters, L. A. and Dhondt, A. A. 1990. Red squirrel population dynamics in different habitats. – Z. Säugetierkd. 55: 161–175.
- Wauters, L. A. and Dhondt, A. A. 1992. Spacing behaviour of the red squirrel, *Sciurus vulgaris*: variation between habitats and the sexes. – Anim. Behav. 43: 297–311.
- Wauters, L. A. and Dhondt, A. A. 1993. Immigration patterns and success in red squirrels. – Behav. Ecol. Sociobiol. 33: 159–167.
- Wauters, L. A. and Dhondt, A. A. 1995. Components of lifetime reproductive success of female Eurasian red squirrels. – Oikos 72: 402–410.
- Wauters, L. A. and Lens, L. 1995. Effects of food availability and density on red squirrel (*Sciurus vulgaris*) reproduction. – Ecology 76: 2460–2469.
- Wauters, L. A. and Dhondt, A. A. 1998. Variation in spacing behavior of Eurasian red squirrels, *Sciurus vulgaris* in winter: effects of density and food abundance. – In: Steele, M. A., Meritt, J. F. and Zegers, D. A. (eds), Ecology and evolutionary biology of tree squirrels. Spec. Publ. of the Virginia Mus. of Nat. Hist. 6: 71–77.
- Wauters, L. A. and Gurnell, J. 1999. The mechanism of replacement of red by grey squirrels: a test of the interference competition hypothesis. – Ethology 105: 1053–1071.
- Wauters, L. A., Dhondt, A. A. and De Vos, R. 1990. Factors affecting male mating success in red squirrels *Sciurus vulgaris*. – Ethol. Ecol. Evol. 2: 195–204.
- Wauters, L., Casale, P. and Dhondt, A. A. 1994a. Space use and dispersal of red squirrels in fragmented habitats. – Oikos 69: 140–146.
- Wauters, L. A. et al. 1994b. The effects of habitat fragmentation on demography and on the loss of genetic variation in the red squirrel. – Proc. R. Soc. Lond. B 255: 107–111.
- Wauters, L. A., Lens, L. and Dhondt, A. A. 1995. Variation in territory fidelity and territory shifts among red squirrel, *Sciurus vulgaris*, females. – Anim. Behav. 49: 187–193.
- Wauters, L. A., Lurz, P. W. W. and Gurnell, J. 2000. The effects of interspecific competition by grey squirrels (*Sciurus carolinensis*) on the space use and population dynamics of red squirrels (*S. vulgaris*) in conifer plantations. – Ecol. Res. 15: 271–284.
- Zammuto, R. M. and Millar, J. S. 1985. Environment predictability, variability and *Spermophilus columbianus* life history over an elevation gradient. – Ecology 66: 1784–1794.

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