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## Interspecific competition between native Eurasian red squirrels and alien grey squirrels: does resource partitioning occur?

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**Abstract** In heterogeneous environments, differential niche selection by two competing species will result in niche partitioning so that individuals of each species can maximise their fitness under different sets of environmental variables. Thus, niche partitioning is considered essential to allow co-existence of ecologically related species. To assess whether niche partitioning was occurring between native red squirrels and alien grey squirrels living together in a 13-ha high-quality mixed deciduous woodland in north Italy, we investigated temporal and spatial patterns in their activity and foraging behaviour between 1996 and 1998. We used live trapping and radio-tracking to study numbers, distribution and behaviour of squirrels. Daily and seasonal temporal activity patterns, and activity on the ground and in the trees, were similar in the two species. However, grey squirrels were more tree specialists and had a narrower tree-species niche width than red squirrels, in particular making greater use of oak. Other studies of red and grey squirrels in allopatry show that the two species differ in the extent they utilise oak. Overall, tree-species niche overlap was about 70%. Grey squirrels had larger home ranges than red squirrels. Home ranges and core areas of both species were larger in males than females. Also, intraspecific home range and core-area overlap patterns were similar to those found in allopatric populations of these species. Overall, there was no evidence that the use of space of one species was affected by the other. Our results show that there was no niche partitioning of activity or foraging behaviour in time or space during the study. This suggests that, at moderate grey-squirrel densities,

red squirrels are unable to avoid competition with grey squirrels, and that competition for food and/or space will occur when these resources become limiting.

**Keywords** *Sciurus vulgaris* · *S. carolinensis* · Exclusion competition · Resource partitioning · Activity pattern

### Introduction

In natural communities, species that occupy a similar ecological niche will compete with one another for resources that are in limited supply. This interspecific competition will negatively affect fecundity, growth or survival of one, or both species, and its effects are considered to be density-dependent (e.g. May 1973; Rosenzweig 1981). Both theoretical and experimental studies on interspecific competition conclude that niche differentiation, dissimilarity in activity patterns, foraging behaviour (food choice) or habitat use among competing species, are necessary for competitive coexistence in communities influenced by density-dependent processes (MacArthur and Levins 1964; May 1973; Schoener 1974; Brown 1989a, b). Hence, each mechanism of coexistence is composed of two essential features: a heterogeneous environment and an evolutionary trade-off between the abilities of the coexisting species to utilise various parts of that environment. Since these two features may provide each species with a set of behavioural adaptations that will give it an advantage over its competitor under different environmental conditions, each species will reproduce and maintain a non-decreasing population size (Brown et al. 1994).

In small mammals, the important role of competitive relationships between coexisting species in organising desert rodent communities has been widely demonstrated, especially for gerbils (e.g. Ambramsky et al. 1990; Mitchell et al. 1990; Kotler et al. 1993) and pocket mice (e.g. Hoover et al. 1977; Brown 1989a, b; Ziv and Smallwood 2000). In tree squirrels and gliding squirrels, niche partitioning has mainly been studied in tropical

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and subtropical forests where as many as nine different species may occur sympatrically (Emmons 1980). The two guilds are separated along a temporal niche axis, with gliding squirrels exclusively nocturnal and true tree squirrels diurnal (Muul and Lim 1978). Moreover, within each guild, species living in the same forest use different microhabitats (Lee et al. 1986; Viljoen 1986; Tamura 1993), or differ markedly in body size and food choice, from small-sized seed or fruit specialists, to large-sized generalists feeding on leaves, bark, sap, twigs, buds, flowers, fruits and insects (Emmons 1980; Viljoen 1986). Sympatric populations of coexisting Holarctic tree-squirrel species also show resource partitioning. *Tamiasciurus hudsonicus* and *T. douglasii* defend individual territories not only against conspecifics but also against the other species (Smith 1968, 1981). Sympatric American red squirrels (*T. hudsonicus*) and eastern grey squirrels (*Sciurus carolinensis*) exhibit differences in fine-scale habitat selection (Riege 1991). Thus, although niche overlap is considerable in most natural communities of tree squirrels, there appears to be enough habitat or food resource partitioning to give each species an advantage over its competitor under certain environmental conditions. Hence, coexistence among sympatric tree squirrels is the result of: (1) the existence of habitat heterogeneity, and (2) the evolutionary adaptations, of each single species, to a specific combination of environmental conditions (Brown 1989a, b).

When an alien species is introduced into the range of an ecologically similar species that has evolved without a high degree of interspecific competition with other members of the community, the lack of niche differentiation may result in competitive exclusion of the "weaker" species (e.g. Connell 1961). This is the case for the diurnal Eurasian red squirrel (*S. vulgaris*), which is the only tree-squirrel species throughout large parts of its range, sharing its arboreal habits only over parts of its range with nocturnal flying squirrels (*Pteromys volans*) or with hibernating, nocturnal dormice (Gliridae) (Gurnell 1987; Mitchell-Jones et al. 1999). The introduction of the eastern grey squirrel (*S. carolinensis*) to the British Isles and parts of northern Italy, and the subsequent rapid increase of its distribution range, coincided with a dramatic decline of the range of the native red squirrel (e.g. Gurnell and Pepper 1993; Wauters et al. 1997). The grey squirrel has now replaced the red squirrel over much of its range in Britain and in the fragmented landscapes it currently occupies in Piedmont, northern Italy (Gurnell and Pepper 1993; Wauters et al. 1997). In mixed deciduous woodlands, one of the major habitat types in Europe where species replacement occurred, resource preferences of allopatric populations of red and grey squirrels are very similar. Both species are typically day-active, with activity patterns that change from unimodal to bimodal with season and, to some degree, with latitude (ambient temperature). Activity patterns are further adapted to food availability and quality, and thus to the rate of energy intake (reviewed in Wauters 2000). They have home ranges of similar size and feed on the same food types (Moller

1983; Gurnell 1987, 1996a; Wauters and Dhondt 1989, 1992; Wauters et al. 1992; Kenward et al. 1998). Both species depend heavily on large seeds of broadleaf trees or shrubs, such as sweet chestnut (*Castanea sativa*), beech (*Fagus sylvatica*), oak (*Quercus* sp.), walnut (*Juglans regia*) and hazel (*Coryllus avellana*), from late summer throughout autumn and winter, and intensively use small seeds of maple (*Acer* sp.) and hornbeam (*Carpinus betulus*) in summer. In late winter and spring, red and grey squirrels consume previously cached tree seeds (chestnuts, beechnuts, walnuts, hazelnuts and acorns) and feed on temporary food items of low energy content, such as buds, shoots and flowers of different tree species, in particular oak, and on insects and fungi (review in Moller 1983; see also Gurnell 1987; Wauters et al. 1992, 1995, 2001; Wauters and Casale 1996; Kenward et al. 1998). Hence, there is a strong potential for interspecific competition in broadleaf woodlands where both species co-occur.

The aim of this paper is to determine whether niche partitioning occurs among coexisting red and grey squirrels in a mixed deciduous woodland. In particular, we studied niche width and niche overlap of the two species along the three major niche dimensions: (1) time, monitoring the circadian activity patterns of both species, (2) habitat use, and (3) space use, estimating home-range size and core-area overlap.

If resource partitioning occurs along each of these niche dimensions, we predict that: (1) red squirrels will avoid grey squirrels in time, concentrating their activity in other periods of the circadian cycle; (2) tree-species selection will differ markedly between both species, resulting in a low degree of habitat niche overlap; and (3) red squirrels will avoid areas of high grey-squirrel density, and interspecific core-area overlap will be less than intraspecific overlap.

## Methods

### Study area

Squirrels were studied at Borgo Cornalese, a mature mixed deciduous woodland of 13 ha within a 17-ha castle park, near Turin, Piedmont, north Italy (7°44'E, 44°55'N), from July 1996 to October 1998. The woodland was dominated by oaks (*Quercus robur*, *Q. petraea*), hornbeam, field maple and sycamore (*Acer campestre*, *A. pseudoplatanus*) and ash (*Fraxinus excelsior*), with some bird cherry (*Prunus avium*), lime (*Tilia cordata*) and alder (*Alnus glutinosa*). In addition, some exotic tree species had been planted: particularly walnut (*J. regia*) and black walnut (*J. nigra*). A single block of planted white pine (*Pinus strobus*) covered about 8% of the study area (Table 1). The understorey was dominated by blackberry (*Sambucus nigra*) with some hazel, and the ground vegetation consisted of forbs and grasses. In comparison with other mixed broadleaf woodlands containing red and/or grey squirrels (Gurnell 1996a; Kenward et al. 1998), food availability (annual tree-seed production) was higher than average in 1997 (8125 MJ ha<sup>-1</sup>) and slightly below average in 1998 (3050 MJ ha<sup>-1</sup>, Gurnell et al. 2001). The first grey squirrels colonised the woodland in spring 1996. The grey-squirrel population expanded quickly and numbers increased threefold from March 1997 to May 1998 (1.9 ha<sup>-1</sup>). By September 1998, grey squirrels had become more

**Table 1** Selection indices ( $w_i$ ) for different tree species ( $i$ ) for red and grey squirrels in spring/summer and autumn/winter. The log-likelihood  $G$ -test is based on the null hypothesis that squirrels were randomly selecting habitats in proportion to availability (in

all cases  $df=1$ ,  $P<0.0001$ ). A value of  $w_i=1$  indicates no selection; a value  $>1$  indicates preference and a value  $<1$  indicates avoidance; + or – after  $w_i$  indicates that  $w_i$  is significantly larger (selection) or smaller than 1.0 (avoidance), respectively (see Methods)

Tree species (% cover)	Proportion available ( $p_{ir}$ ) red	Proportion available ( $p_{ig}$ ) grey	Spring/summer				Autumn/winter			
			Red squirrels		Grey squirrels		Red squirrels		Grey squirrels	
			$w_i$	Use	$w_i$	Use	$w_i$	Use	$w_i$	Use
Maple (26)	0.26	0.23	0.45 (–)	0.12	0.13 (–)	0.03	0.35 (–)	0.09	0.31 (–)	0.07
White pine (8)	0.11	0.03	0.85	0.09	1.15	0.03	0.65	0.07	0.39	0.01
Ash (15)	0.13	0.18	0.26 (–)	0.03	0.33 (–)	0.06	0.22 (–)	0.03	0.39 (–)	0.07
Walnut (5)	0.06	0.07	1.33	0.08	1.41	0.10	2.46 (+)	0.15	0.84	0.06
Oak (18)	0.17	0.20	2.42 (+)	0.41	3.15 (+)	0.63	2.43 (+)	0.43	3.16 (+)	0.63
Hornbeam (19)	0.17	0.22	0.70	0.12	0.18 (–)	0.04	0.57 (–)	0.08	0.32 (–)	0.07
Hazel (3)	0.03	0.03	0.89	0.03	0.82	0.02	1.68	0.06	1.17	0.04
Others (6)	0.07	0.04	1.71 (+)	0.12	2.09 (+)	0.09	1.44	0.09	1.32	0.05
G			151.5		253.9		188.7		169.3	

abundant than red squirrels (1.6 and 1.5  $ha^{-1}$  respectively (Wauters and Gurnell 1999; Gurnell et al. 2001). With respect to other populations in deciduous woodlands in Europe, these densities can be considered high for red squirrels but still below carrying capacity for grey squirrels (Kenward and Holm 1993; Gurnell 1996a; Kenward et al. 1998).

#### Trapping and handling squirrels

A total of 20 (1.6  $ha^{-1}$ ) Tomahawk “squirrel” traps (Tomahawk, Wis.), baited with sunflower seeds and hazelnuts, were randomly placed on the ground or against tree trunks, throughout the woodland. Trapping was carried out bimonthly, for at least 5 days, from July 1996 to October 1998. A trapped squirrel was put into a handling bag, individually marked, using numbered metal ear-tags (type 1003 S National Band and Tag, Newport, Ky.), 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. Sex and age were recorded (Wauters and Dhondt 1995).

#### Radio-tracking

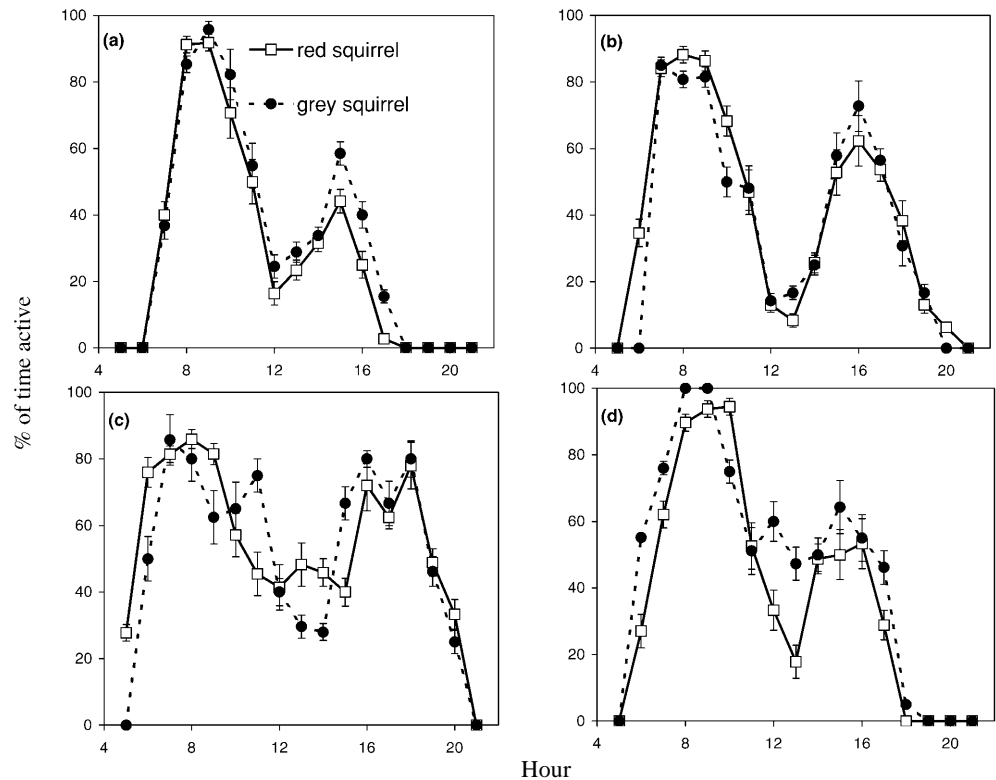
Both red and grey squirrels were radio-tagged (TW-4 transmitter with adjustable necklace size, Biotrack, Wareham, UK, and TXP-1 transmitter with adjustable necklace size, Televilt, Sweden) over 3-month periods, coinciding with the seasons (winter=December to February; spring=March to May; summer=June to August; autumn=September to November). All adults of both species were radio-tagged in summer/autumn of 1997 and 1998, allowing exact estimates of their space-use patterns. 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 5×5 m (25  $m^2$ ) on detailed maps (scale 1:2500) of the study sites, and X (from west to east) and Y (from north to south) co-ordinates were assigned; the exact time (summer hour schedule), its activity (1 active, 2 in a nest), whether on the ground or in the 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). Each nest location was used only once when determining ranges, in order to avoid artificial clustering of fixes. All data on home-range size, home-range use, and overlap of home ranges were calculated using the RANGES V program (Kenward and Hodder 1995). The utilisation distribution of fixes was analysed to determine, for each squirrel species, the proportion of animals with a single (mononu-

clear core areas) activity centre and with more than one activity centre (multinuclear core areas) within the home range. For each individual, the position of a single inflection point (mononuclear core area), or several inflection points (multinuclear core area) in the slope of the utilisation distribution was determined (Kenward and Hodder 1995; Wauters et al. 2000). For both species, the most squirrels had mononuclear core areas; few animals had a second, smaller core area (proportion with mononuclear core areas: red squirrels 14 out of 18, 78%; grey squirrels 12 out of 15, 80%; Fisher Exact test  $P=0.61$ ). The mean percentage of fixes included in the major core area did not differ between species and was close to 70% (mean±SD: red squirrels 74±9%, grey squirrels 73±9%, Mann-Whitney  $U$ -test:  $U=128$ ,  $P=0.80$ ). Therefore, a mononuclear 70% core-area estimate was calculated to represent each squirrel's activity centre. For each squirrel, the following data were calculated: (1) total home-range size using the convex polygon method (MCP, including 100% of the point-fixes); (2) mononuclear 70% core-area estimates; (3) core-area overlap, expressed as percentage of overlap of a squirrel's core area with the core area of all other squirrels of both species (Wauters and Dhondt 1992; Kenward and Hodder 1995).

#### Foraging behaviour and activity pattern

The activity pattern of red squirrels was studied by focal sampling (Wauters et al. 1992, 2001): a focal squirrel was first located using radio-telemetry and then continuously observed, using 10×50 binoculars when necessary, for 20–60 min. Observations were interrupted when the squirrel's behaviour indicated it was aware of the observer's presence. During an observation period, we continuously recorded the focal squirrel's activity (Wauters and Gurnell 1999). Data were analysed seasonally: within each season, the length of observation time per individual red squirrel varied from 120 to 260 min. Here, we focus on the habitat niche. Two habitat niche dimensions were considered: substrate (ground or tree,  $n=2$  categories) and tree species (sycamore, ash, white pine, walnut or black walnut, oak, hornbeam, shrubs – mainly hazel or blackberry – and category “others”,  $n=8$  categories). During continuous observations of radiotagged red squirrels, the time an individual remained on the ground or in a tree (tree species) was measured in minutes. When point-fixes of both squirrel species were used, each fix position was assigned to ground or tree (dimension substrate) and to a tree or shrub species (dimension tree species). On a single day, we sampled each individual only once or twice. In the latter case, one fix was taken in the morning, the other in the afternoon to exclude dependency of the data of the same squirrel. Number of fixes available for individual red and grey squirrels ranged between 30 and 56 fixes per season.

**Fig. 1** Percentage of time spent active in 1-h intervals (mean $\pm$ SD) for red squirrels and grey squirrels in the study area; sample sizes ( $n$ ), total number of fixes for red and grey squirrels, respectively; **a** winter  $n=630, 591$ ; **b** spring  $n=788, 360$ ; **c** summer  $n=630, 498$ ; **d** autumn  $n=752, 400$



Niche width of individual squirrels for each of the two niche components (substrate= $B_s$ , tree species= $B_t$ ) was calculated using Levin's formula:  $B_i=1/\sum p_i^2(n)$ , where  $p_i$  is the proportion of observations in the  $i^{\text{th}}$  category of the resource and  $n$  equals the number of resource states, thus the number of categories that are considered (Hurlbert 1978). Hence,  $0 \leq B_i \leq 1$ . Niche overlap between red and grey squirrels ( $NO_{rg}$ ), for each niche component, was calculated using a measure of proportional overlap:  $NO_{rg}=\sum (\text{minimum } p_{ir}, p_{ig})$ , which is the sum, over all categories (resource states), of the minima of the relative frequencies of observations (Hurlbert 1978). Thus  $NO_{rg}$  also ranges between 0 and 1.

The daily activity pattern, averaged over seasons (winter=December to February, spring=March to May, summer=June to August, autumn=September to November), was calculated from all data (combining all squirrels) collected within that season using radio-tracking. For each 1-h period (e.g. from 0600 to 0659 hours), the proportion of time spent active ( $A_i$ ) was calculated using the formula:  $A_i=(\text{number of active fixes during period } i/\text{number of active and non-active fixes during period } i)$ . We compared the seasonal activity pattern of red and grey squirrels, testing for differences in the distribution of time spent active per hour ( $A_i$ ) over all hours that activity occurred (Fig. 1). We correlated the proportion of time active in each 1-h period of red squirrels with that of grey squirrels using non-parametric Spearman rank-correlation (Sokal and Rohlf 1995).

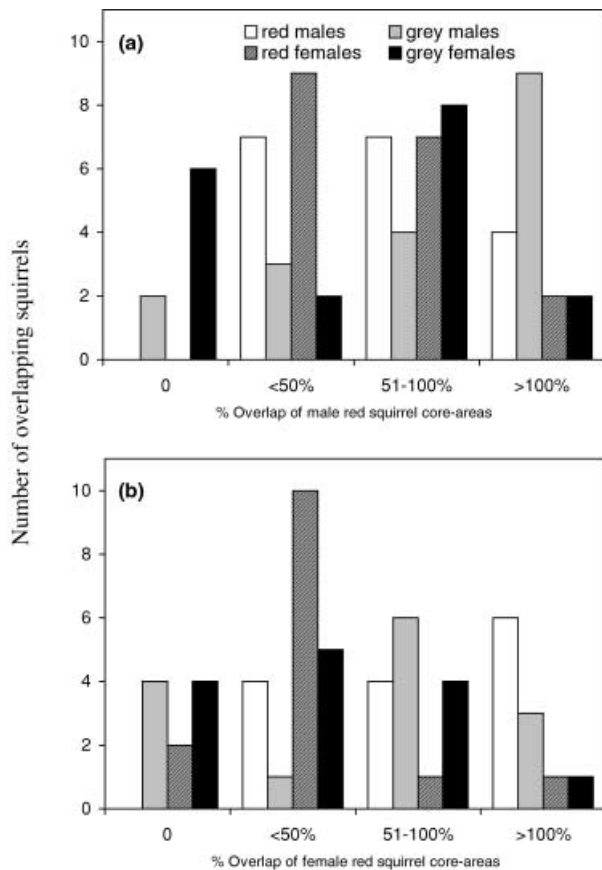
#### Statistical analyses

All continuous variables analysed at the level of the individual squirrel were normally distributed (Shapiro-Wilk test,  $P>0.1$ , SAS 1989). One-way ANOVA, with niche width of individual red squirrels as dependent variable, was used to test for seasonal variation in niche components, and means were compared with a post-hoc Tukey test corrected for unequal sample size (Proc glm, SAS 1989). When only the species effect (red vs grey squirrel) was examined, a two-tailed Student  $t$ -test was calculated (Proc ttest, SAS 1989). Home-range data, with the size of an individual squirrel's home range or core area as dependent variable, were analysed

with multi-way ANOVAs, computed with Proc glm (SAS 1989). If not otherwise specified, data are presented as means $\pm$ 1 SD.

For each niche component, substrate and tree species, the total number of observations of each squirrel species in each resource state were used as counts in a multiway  $G$ -test (Sokal and Rohlf 1995), to test the effects of squirrel species, season and a species by season interaction on habitat use. In a second step, we examined levels of selection for each tree species ( $i$ ) by red and grey squirrels in spring/summer and autumn/winter, respectively. The selection index ( $w_i$ ) was derived from  $w_i=u_i/a_i$ , where  $u_i$ =the sample proportion of radiotrack fixes (use) and  $a_i$ =the proportion of total tree species available. The null hypothesis, that squirrels were randomly selecting habitats in proportion to availability, was tested using a log-likelihood  $G$ -test. A value of  $w_i=1$  indicates no selection; a value  $>1$  indicates preference and a value  $<1$  indicates avoidance. Each  $w_i$  value has been tested to see if it is significantly different to 1.0 by computing a chi-square statistic from  $(w_i-1)/SE(w_i)^2$  with  $df=1$ , and with a Bonferonni adjustment, i.e. here the significance level  $\alpha=(0.05/8)=0.00625$  (Manly et al. 1993). We determined the habitat available to each squirrel species by calculating the proportion of each tree species within the area of the 100% MCP of all radiotracked individuals of that species (red squirrels= $a_{ir}$  for tree species  $i$ , grey squirrels= $a_{ig}$  for tree species  $i$ ).

We investigated spatial separation between the two species by comparing the proportion of intra- and interspecific core-area overlap, pooling the 1997 and 1998 data. Core-area overlap was divided into four categories: no overlap, less than 50%, between 50 and 100%, and more than 100% overlap. We compared the frequency of core-area overlap with conspecifics against that with grey squirrels, for male and female red squirrels separately (Fig. 2), using Goodness-of-fit tests with William's correction (Sokal and Rohlf 1995).



**Fig. 2** Frequency distribution of the % of core-area overlap of red squirrels (**a** males, **b** females) with other conspecifics and with grey squirrels in 1998

## Results

### Red- and grey-squirrel activity pattern

Correlations between the proportion of time active in each 1-h period of red squirrels and grey squirrels were significant for all seasons (Fig. 1). Hence, both species had their activity peaks and resting periods during the same hours of the day (Fig. 1: winter,  $n=15$ ,  $r_s=0.985$ ; spring,  $n=17$ ,  $r_s=0.924$ ; summer,  $n=17$ ,  $r_s=0.738$ ; autumn,  $n=15$ ,  $r_s=0.889$ ; all  $P<0.001$ ).

### Red-squirrel habitat use based on observations

Habitat use of red squirrels changed with season (data pooled for autumn and winter to increase number of sampled squirrels). Red squirrels spent on average significantly more time on the ground in spring ( $n=11$ ,  $18.5\pm 8.7\%$ ) and in autumn/winter ( $n=14$ ,  $25.0\pm 7.9\%$ ) than in summer ( $n=12$ ,  $8.6\pm 3.8\%$ ). Consequently, niche width for substrate was significantly smaller in summer than in the other seasons (summer  $0.59\pm 0.04$ , spring  $0.72\pm 0.11$ , and autumn/winter  $0.80\pm 0.09$ ,  $F=17.9$ ,  $df=2$ ,  $34$ ,  $P=0.0001$ ). In the trees, red squirrels foraged more as

generalists, having a large niche width in summer when feeding on small, early-maturing seeds of many tree species. Niche width for tree species was most reduced in spring (spring  $0.33\pm 0.09$ , summer  $0.50\pm 0.13$ , and autumn/winter  $0.41\pm 0.14$ ,  $F=5.22$ ,  $df=2$ ,  $34$ ,  $P=0.011$ ), when red squirrels heavily utilised oaks to feed on oak flowers and caterpillars (Wauters et al. 2001).

### Comparing habitat use of red and grey squirrels

Only a few radiotagged grey squirrels were monitored in spring. Therefore, point-fix data on habitat use were pooled for spring and summer. Of all red squirrels sightings, 27% ( $n=411$ ) were on the ground in spring/summer, and 37% in autumn/winter ( $n=439$ ). For grey squirrels, this was respectively, 29% ( $n=286$ ) and 43% ( $n=300$ ). Seasonal changes were similar for the two species (two-way  $G$ -test, season by species interaction  $G=0.38$ ,  $df=1$ ,  $P=0.54$ ), with both red and grey squirrels observed more frequently on the ground in autumn/winter than in spring/summer (season effect  $G=22.1$ ,  $df=1$ ,  $P<0.0001$ ). There was no significant difference in the proportion of time spent on the ground between the two squirrel species (species effect  $G=2.81$ ,  $df=1$ ,  $P=0.09$ ). Average niche width estimates were, for red and grey squirrels respectively,  $0.82\pm 0.10$  ( $n=15$  individuals) and  $0.85\pm 0.07$  ( $n=7$ ) in spring/summer, and  $0.92\pm 0.09$  ( $n=13$ ) and  $0.95\pm 0.04$  ( $n=7$ ) in autumn/winter. In both seasons, niche overlap for substrate was very high (spring/summer  $NO_{rg}=0.98$ , autumn/winter  $NO_{rg}=0.94$ ).

For the tree species niche component, there was a significant season by tree species by squirrel species interaction (three-way  $G$ -test,  $G=14.8$ ,  $df=7$ ,  $P=0.038$ ), indicating that the relative frequencies of use of different tree species by red and grey squirrels changed with season. Therefore, we calculated a two-way  $G$ -test for spring/summer and autumn/winter separately. In both seasons, the tree species available in the study area were used in different proportions (tree species effect: spring/summer  $G=500.7$ , autumn/winter  $G=433.0$ , in all cases  $df=7$ ,  $P<0.0001$ ), and there was a significant difference between red and grey squirrels in the relative use of the different tree species (tree by squirrel species interaction: spring/summer  $G=43.9$ , autumn/winter  $G=34.9$ , in all cases  $df=7$ ,  $P<0.001$ ).

Both red and grey squirrels were selective in their habitat use throughout the year ( $G$ -tests, Table 1). In spring/summer, both squirrel species showed a significant selection for oaks and the category "others", with red squirrels feeding on the flowers of lime, whereas grey squirrels foraged in horse chestnuts (*Aesculus hippocastanum*) (Wauters et al. 2001 and unpublished data). Grey squirrels foraged on oak buds, oak flowers and caterpillars found on the leaves more frequently than red squirrels (63% against 41% of observations). Both species avoided maple and ash (Table 1). Grey squirrels also avoided hornbeam, but red squirrels used hornbeam according to availability, feeding on early-maturing horn-

**Table 2** Home-range size and core-area size (mean±SD) of male and female red squirrels and grey squirrels in the study area, in 1997 and 1998. Sample sizes, number of radio-tracked squirrels in parentheses for 1997 and 1998, respectively

Year		Red squirrels		Grey squirrels	
		Males (8, 10)	Females (6, 8)	Males (6, 8)	Females (2, 7)
1997	Home-range size (ha)	3.20±0.88	2.44±0.72	4.52±0.92	3.69±1.39
	Core-area size (ha)	1.48±0.55	1.04±0.49	2.25±0.88	1.45±0.35
1998	Home-range size (ha)	2.43±0.44	1.74±0.57	3.73±1.25	1.80±1.50
	Core-area size (ha)	1.10±0.42	0.89±0.37	1.61±1.08	0.69±0.58

beam seeds in summer (Wauters et al. 2001). Thus habitat use for the niche component “tree species” was similar for red and grey squirrels in spring/summer. However, the greater use of oak trees by grey squirrels resulted in them having a significantly narrower niche width, thus being more habitat specialists, than red squirrels (red squirrels  $0.46\pm 0.18$ , grey squirrels  $0.28\pm 0.07$ , Student *t*-test  $t=2.62$ ,  $df=20$ ,  $P=0.016$ ). In autumn/winter, both red and grey squirrels used trees with small seeds less than expected by chance (maple, ash and hornbeam), but red squirrels positively selected walnut trees while greys did not (Table 1). Although both species had a significant preference for oak trees (Table 1), grey squirrels foraged in oaks more frequently than reds (63% against 43%, Table 1). Consequently, niche width of grey squirrels in autumn/winter was again smaller than that of red squirrels (red squirrels  $0.43\pm 0.13$ , grey squirrels  $0.24\pm 0.09$ , Student *t*-test  $t=3.60$ ,  $df=18$ ,  $P=0.002$ ). In both seasons, niche overlap was around 70% (spring/summer  $NO_{rg}=0.73$ , autumn/winter  $NO_{rg}=0.69$ ).

#### Space-use patterns of red and grey squirrels

As described in the Methods section, most individuals of both species had a single activity centre within their home range, best described by the 70% mononuclear core area. Grey squirrels had larger home ranges than red squirrels and mean home-range size of both species was larger in 1997, when densities were lower, than in 1998, when grey-squirrel densities had increased (Table 2). Moreover, males of both species typically used larger home ranges than females (three-way ANOVA: year-effect  $F=11.4$ ,  $P=0.002$ ; species-effect  $F=10.1$ ,  $P=0.003$ ; sex-effect  $F=15.0$ ,  $P=0.0003$ ; all  $df=1, 48$ ; all interaction-terms  $P>0.1$ ). Therefore we separated the sexes and tested for differences between red and grey squirrel home-range size and core-area size for males and females (Table 2). Since some of the squirrels were monitored in both years, separate analyses were carried out for 1997 and 1998 (Table 2). Male grey squirrels had larger home ranges than male red squirrels in both years (1997:  $t=2.72$ ,  $df=12$ ,  $P=0.02$ ; 1998:  $t=2.81$ ,  $df=16$ ,  $P=0.01$ ), but there were no differences in female home-range size between the two species (1997:  $t=1.76$ ,  $df=6$ ,  $P=0.13$ ; 1998:  $t=0.12$ ,  $df=13$ ,  $P=0.91$ ). In 1997, only two adult female grey squirrels were present, whose home ranges were slightly larger than of red squirrel females, but in 1998, many of the yearling female grey squirrels used small ranges (Gurnell et al. 2001) and the mean

range size of both species was similar (Table 2). There was no significant difference in core-area size between red and grey squirrels (Table 2, three-way ANOVA: species-effect  $F=3.44$ ,  $df=1, 48$ ,  $P=0.07$ ). The 70% core areas were larger in males than females and, for both species and sexes, core areas were larger in 1997 than in 1998 (Table 2, three-way ANOVA: year-effect  $F=5.92$ ,  $P=0.019$ ; sex-effect  $F=10.4$ ,  $P=0.002$ ; all  $df=1, 48$ ; all interaction-terms  $P>0.1$ ).

The core areas of a high proportion of male red squirrels were strongly overlapped (>50%) by both other male red squirrels and male grey squirrels ( $G=6.20$ ,  $df=3$ ,  $P=0.10$ , Fig. 2a). Male red squirrel core areas were more frequently aggregated around core areas of females of their own species than around core areas of female grey squirrels. Six out of 18 male red squirrels had no core-area overlap with female grey squirrels, while all had their core area overlapped by at least 1 female red squirrel ( $G=10.3$ ,  $df=3$ ,  $P=0.016$ , Fig. 2a). For female red squirrels, there was no significant difference between intra- and interspecific core-area overlap patterns, either with males, or with other females (comparison with male red vs male grey squirrels:  $G=6.99$ ,  $df=3$ ,  $P=0.07$ ; female red vs female grey squirrels:  $G=4.01$ ,  $df=3$ ,  $P=0.26$ , Fig. 2b). These results confirm pair-wise comparisons of core-area overlap for individual red squirrels (the core-area overlap for a specific red squirrel with other red squirrels vs grey squirrels, see Wauters and Gurnell 1999) and show that interspecific core-area overlap is similar to red squirrel intraspecific core-area overlap in both sexes. Thus, although some male and female red squirrels that intensively used the white-pine woodland patch (L.A. Wauters, J. Gurnell, A. Martinoli, G. Tosi, unpublished data) had core areas that were not overlapped by any grey squirrels, there was no home-range niche partitioning between the two squirrel species.

## Discussion

### Time of activity of red and grey squirrels

The activity rhythm of co-occurring red and grey squirrels in our study area was similar to that described for other populations in Europe and North America respectively, where the congener did not occur (Wauters and Gurnell 1999; review in Wauters 2000). Although there is a high degree of asynchronicity in the timing of activity among individuals of both species, the activity of red and grey squirrels peaked in the same daylight hours (see

also Wauters and Gurnell 1999). Thus, we found no effects of the presence of grey squirrels, at current densities, on the activity pattern of red squirrels, indicating that there was no temporal niche partitioning between the two species.

#### Habitat niche overlap between red and grey squirrels

The utilisation pattern of high-quality food patches was similar for red and grey squirrels, with most individuals having a single activity centre within their home range. Other characteristics of habitat use differed between the two squirrel species, and this resulted partly from differences in their preferences for different tree species. Red squirrels occupied the whole woodland, including the white-pine stand, while grey squirrels, at the current density, only occurred in broadleaf woodland and did not enter the area planted with pine. This explains why some male and female red squirrels had core areas that were not overlapped by congeners (see Fig. 2). We showed elsewhere that the settlement of grey squirrels was not affected by the presence or local density of resident red squirrels (Gurnell et al. 2001), and that small changes in home-range use from one year to the next (core-area shifts) of some red squirrels were independent from grey-squirrel space use, but were related to the settlement of subadult conspecifics (Wauters and Gurnell 1999). As grey-squirrel densities increase, we would expect the grey squirrels to enter the pine area; they readily utilise stands of pine trees in Britain (Gurnell 1996b; Smith and Gurnell 1997). By late July/August, red squirrels were feeding intensively on early-maturing hornbeam seeds, whereas grey squirrels primarily foraged on maturing acorns, although some fed on hornbeam seeds in late summer (see also Wauters et al. 2001). This points to a difference in food preference between the species, but since grey squirrels are known to readily feed on hornbeam seeds (Moller 1983), we believe that they are likely to increase their feeding on these seeds in years when acorns are poor. Our study period was too short to investigate effects of annual changes in tree seed crops, and thus food resource availability, on the amount of habitat niche overlap between the two species. However, the relatively short period of time in which replacement of red by grey squirrels takes place in broadleaf woodlands makes it unlikely that niche partitioning will occur when food resources are more limited. In any case, in mixed deciduous woods with oaks, grey squirrels have an advantage over red squirrels: they are able to utilise and digest acorns more efficiently than red squirrels (Kenward and Holm 1993). Consequently, in single-species situations (allopatric red and grey squirrel populations), in oak-hazel woods in Britain, population growth of grey squirrels was positively affected by the size of the previous year's acorn crop, while red-squirrel breeding and density did not fluctuate in relation to the size of the acorn crop, but increased when hazelnuts were abundant (Kenward and Holm 1993; Gurnell

1996a; Kenward et al. 1998). In our study area, hazel occurred only in a few patches and the majority of hazelnuts were already consumed by late summer/early autumn by several different seed predator species including edible dormouse (*Myoxis glis*), hazel dormouse (*Muscardinus avellarius*), woodmouse (*Apodemus sylvaticus*), great spotted woodpecker (*Picoides major*), nuthatch (*Sitta europea*), as well as both squirrel species (Wauters et al. 2001, unpublished data). Red squirrels fed intensively on walnuts and black walnuts in autumn/winter and cached large numbers of them for use in late winter/spring (Wauters et al. 2001, 2002). Although they positively selected walnut trees in autumn/winter, when grey squirrels did not, the latter regularly fed on walnuts and black walnuts. Overall, there was a high degree of habitat niche overlap, and we believe that the differences we have described result from individual species food preferences rather than niche segregation as a result of interspecific competition. This is supported by the fact that red squirrels did not show any major shifts in their diet in the presence of grey squirrels compared to non-sympatric populations (Wauters et al. 2001).

In spring and early summer, both squirrel species feed on a large variety of food items, and in summer, tree species niche width is larger than in other seasons. Most of these food resources (buds, shoots, tree flowers, caterpillars, fungi or insects found on or under the bark of dying branches) are seasonal and abundant: thus squirrels can easily consume them, but only during a limited period of time. Hence it is unlikely that competition for such resources will affect a squirrel's fitness. However, one limited, high-energy food resource is of extreme importance in late winter and throughout spring: scatterhoarded tree seeds (Wauters et al. 1995; Wauters and Casale 1996). Both squirrel species spend a lot of time on the ground in winter and spring and red squirrels fed intensively on cached seeds from January to April. We have shown that, as spring progressed, seed caches become depleted and the energy intake in spring of red squirrels that were strongly overlapped by grey squirrels was reduced with respect to that of red squirrels not or only slightly overlapped by congeners (Wauters et al. 2002). Thus, cache pilfering by grey squirrels seemed to be an important mechanism of interspecific resource competition and was made possible because of the lack of niche separation in space and habitat use between the two species.

#### Spatial niche overlap between red and grey squirrels

The intraspecific core-area overlap pattern for each squirrel species in our population, where both species co-occurred, was similar to the typical space-use pattern in allopatric populations, for grey squirrels as well as for red squirrels (e.g. Kenward 1985; Koprowski 1996 for grey squirrels, Wauters and Dhondt 1992; Wauters and Gurnell 1999 for red squirrels). Thus, spacing behaviour of red squirrels was characterised by a low degree of intrasexual core-area overlap between adult females

(intrasexual territoriality, Wauters and Dhondt 1992), by a high degree of intrasexual core-area overlap amongst adult males and by a high degree of intersexual overlap. The decrease in home-range size from 1997 to 1998 was consistent with red squirrels reducing their home range when densities increase (Wauters and Dhondt 1992, 1998). The spacing pattern and home-range size of grey squirrels in this expanding population was similar to stable populations in the United Kingdom, occurring in oak-hazel woods with a rich food supply, except for the very small ranges used by yearlings (Kenward 1985; Gurnell et al. 2001). Also, home ranges of male grey squirrels were larger than those of male red squirrels, which is consistent with the mating behaviour and male mating strategies of both species in relation to local female densities (e.g. Kenward 1985; Wauters et al. 1990; Koprowski 1993). In females, in contrast, we found no significant difference in home-range size, or core-area size, between red and grey squirrels. This agreed with the hypothesis of Wauters and Dhondt (1992) that spacing behaviour and home-range (core-area) size of female tree squirrels is mainly determined by the distribution and abundance of primary food resources, linked to local female densities (Wauters and Dhondt 1992, 1998; Lurz et al. 2000). Thus home range and core-area size of co-occurring red and grey squirrels of either sex were determined by the intraspecific social organisation pattern and not by interspecific interactions. Finally, patterns of intra- and interspecific core-area overlap confirmed that interspecific core-area overlap is similar to red squirrel intraspecific core-area overlap in both sexes (Wauters and Gurnell 1999). Hence, red squirrels did not obtain a true spatial segregation, and there was no partitioning of the space niche between the two squirrel species. This implies that, as grey squirrels become more abundant, the amount of interspecific spatial overlap will increase, suggesting that an increase in grey-squirrel numbers will augment the intensity of competition for limited resources (see also Wauters and Gurnell 1999).

#### Absence of niche partitioning and exclusion competition

Although grey squirrels are larger than red squirrels, there was no evidence of interference competition between the adults of the two species (Wauters and Gurnell 1999). However, we have discussed elsewhere that the presence of grey squirrels appears to reduce the recruitment of young red squirrels into the population, and that the body-growth rate of young red squirrels is also slightly lower than in allopatric red-squirrel populations (Wauters et al. 2000, 2001). Both red and grey squirrels have social organisations based on dominance hierarchies within and between sexes, and the primary determinant of dominance is age, and adults significantly outrank young of both sexes (Thompson 1978; Allen and Asprey 1986; Wauters and Dhondt 1989, 1992). In autumn, many animals, especially young of the year, disperse and there is a reorganisation in the population. Dis-

persal rate tends to be inversely related to food availability (Gurnell 1987). So, in addition to the effects of cache pilfering during winter and spring, we hypothesise that small, young red squirrels find it difficult to locate a place to settle in the population in the autumn, when grey squirrels are present, and thus the population of red squirrels will decline over time. This hypothesis requires further testing.

We conclude from our data on activity patterns and habitat niche width and niche overlap between red and grey squirrels that, even in mixed woodlands with a high tree species diversity, there was no small-scale habitat partitioning between the two species. Hence, in contrast to natural communities of sympatric tree squirrels, we found no evidence for niche partitioning between native red and alien grey squirrels in any of the niche parameters. This suggests that the red squirrel, although a flexible species, will not be capable of successfully adapting its ecological niche to avoid competition with the grey squirrel when resources become limiting.

#### Implications for red-squirrel conservation

Biological invasions, the expansion of species outside their natural distribution range as a result of human interference, are currently a major risk for the loss of biodiversity, second only to large-scale habitat destruction (Mack et al. 2000). Numerous examples exist of alien birds or mammal species causing extinction of native wildlife, especially in island situations, through predation, herbivory (causing changes in habitat structure), hybridisation, or as vectors for infectious diseases (e.g. Atkinson 1996; Cunningham 1996; Simberloff 1996; Mack et al. 2000). Cases in which alien mammal species compete for resources or aggressively interact with (closely) related native species are less frequent (e.g. escaped American mink (*Mustela vison*) with endangered European mink (*Mustela lutreola*) and otter (*Lutra lutra*); lagomorphs, Eastern cottontail (*Sylvilagus floridanus*) with New England cottontail (*Sylvilagus transitionalis*) (Lever 1994; Kauhala 1996; Probert and Litvaitis 1996). However, the extinction of red squirrels over wide areas in Britain, Ireland and parts of Piedmont, north Italy, following the spread of the introduced grey squirrel, is the best documented case of species replacement caused by interspecific exclusion competition. The rate at which replacement will occur mainly depends on factors that facilitate the spread of the alien species (reviewed by Lever 1994). For grey squirrels, major factors are landscape structure (connectivity between good habitats) and abundant food supplies. In the range currently occupied by grey squirrels in Piedmont, an abundant food supply is available in most years in mixed deciduous woods, where grey-squirrel population increase and subsequent red-squirrel extinction takes place in a brief period of time (a few years, Genovesi and Bertolino 2001). Therefore, the increase in grey-squirrel numbers in our study site, and its small size (13 ha woodland) will



presumably lead to local extinction of red squirrels in only few years time.

Thus, the greater use of acorns by grey squirrels and the lack of niche differentiation between native red squirrels and alien grey squirrels in deciduous woodlands in northern Italy confirm earlier findings from single-species studies carried out in deciduous woods in Britain: co-existence of both species in these habitats is of short duration due to grey squirrels having a competitive advantage, which results in local extinction of red squirrels (Gurnell 1987, 1996a; Kenward and Holm 1993; Kenward et al. 1998). Moreover, spatially explicit population models of grey-squirrel expansion in north Italy predict an increasing rate of spread in the next decades, with a dramatic increase of population size after colonisation of continuous broadleaf forests of the Prealps in Piedmont (Lurz et al. 2001). The results of our study, linked with these model predictions, have serious implications for red-squirrel conservation in Italy, and in Europe as a whole (see Genovesi and Bertolino 2001; Lurz et al. 2001).

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