Behav Ecol Sociobiol (2002) 51:360–367
DOI 10.1007/s00265-001-0446-y

ORIGINAL ARTICLE

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# Interspecific competition in tree squirrels: do introduced grey squirrels (*Sciurus carolinensis*) deplete tree seeds hoarded by red squirrels (*S. vulgaris*)?

Received: 15 June 2001 / Revised: 24 September 2001 / Accepted: 28 November 2001 / Published online: 22 January 2002
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**Abstract** Red squirrels (*Sciurus vulgaris*) and introduced eastern grey squirrels (*S. carolinensis*) scatterhoard seeds of broadleaf trees. Scatterhoarded seeds are an essential resource in spring and their consumption increases red-squirrel fitness. We examined whether grey squirrels partly deplete the high-energy food resources cached by red squirrels, reducing their consumption, in two ways: (1) at the population level, comparing energy intake of feeding on cached seeds between a study site with red and grey squirrels and one with only red squirrels present; and (2) at the individual level, in the study site where species co-exist, relating hoard recovery of red squirrels to the amount of core-area overlap with grey squirrels. There were no significant site differences in the mean daily energy intake of red squirrels feeding on seeds recovered from caches. However, in the red-grey site, during spring, red squirrels that had a high percentage of their home-range core area overlapped by grey squirrels had a lower daily energy intake than low-overlap red squirrels. Body mass of red squirrels in spring was negatively correlated with the percentage of interspecific core-area overlap, but not with core-area overlap with other red squirrels. Our data suggest that interspecific competition for scatterhoarded seeds, with grey squirrels pilfering red squirrels' food caches, caused a reduced energy intake in red squirrels with a high degree of interspecific core-area overlap, and reduced body mass in spring. Therefore, cache pilfering is likely to reduce reproductive output in red squirrels, and thus play a role in the replacement of red by grey squirrels.

**Keywords** Interspecific competition · Squirrels · Hoarding behaviour · Cache pilfering · Food-energy intake

Communicated by T. Czeschlik

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## Introduction

Food hoarding or caching is considered to be advantageous because it serves to: (1) increase the availability of high-energy food items during periods of food scarcity, and (2) decrease the possibility that naive foragers, animals that did not do the caching, will find the cached food (Jacobs and Liman 1991; Smith and Reichman 1984; Stapanian and Smith 1984). Holarctic tree squirrels of the genus *Sciurus* scatterhoard tree seeds in autumn, caching one or a few food items in each storage site throughout the home range, to retrieve and consume the cached seeds during the following winter and spring (Hayashida 1989; Stapanian and Smith 1984; Tamura and Shibasaki 1996; Wauters and Casale 1996). In deciduous woodlands, Eurasian red squirrels (*Sciurus vulgaris*) and eastern grey squirrels (*S. carolinensis*) depend greatly on cached food resources during late winter and spring (Gurnell 1987; Thompson and Thompson 1980; Wauters et al. 1992), and in red squirrels living in mixed woodlands, individual variation in several fitness components was positively correlated with variation in recovery activity of scatterhoarded tree seeds (Wauters et al. 1995). A consequence is that there might be a reduction in availability of scatterhoards as a result of increased cache pilfering when squirrel densities are high with grey squirrels present. This could lead to a reduction in body condition of red squirrels in spring and a lower chance of females reproducing successfully (Wauters and Dhondt 1989; Wauters et al. 1993). These effects may result at the population level, in a reduced recruitment rate of juvenile and subadult red squirrels, occurring in conifer forests where the two squirrel species co-exist (Wauters et al. 2000).

Although tree squirrels are capable of remembering the location of seeds they hoarded (Jacobs and Liman 1991), they cache the seeds in a spatial pattern that should increase the probability that the caching animal will find and retrieve the stored food (Stapanian and Smith 1984, 1986). However, naive squirrels or other seed predators (e.g. wood mice) are known to find buried nuts by odour and “steal” them, and about 12–33% of hidden seeds are retrieved by intra- and interspecific competitors (Jacobs and Liman 1991; Rice-Oxley 1993; Tamura and Shibasaki 1996; Tamura et al. 1999; Thompson and Thompson 1980). Such intra- and interspecific competition for scatterhoards is likely to become more intense when squirrel densities are high, with more core-area overlap between neighbouring animals (Rice-Oxley 1993; Wauters and Dhondt 1998). Therefore, in woodlands where red squirrels co-exist with grey squirrels, interspecific competition for scatterhoarded tree seeds is likely to be high. Thus, pilfering by grey squirrels of food cached by red squirrels may contribute to the competitive exclusion of red by grey squirrels in Britain and northern Italy, especially in deciduous woods particularly favoured by grey squirrels (Gurnell and Pepper 1993; Wauters and Gurnell 1999; Wauters et al. 1997).

Here we report on a study that examined interspecific competition for scatterhoarded nuts in broadleaf woodlands where both red and grey squirrels live. The general hypothesis tested is that grey squirrels partly deplete the high-energy food resources cached by red squirrels, which reduces the consumption of cached tree seeds by red squirrels in winter and spring. We studied the effects of competition for food caches at two levels: (1) the population level, investigating whether the amount of time spent recovering and consuming cached food, and the corresponding energy intake, by red squirrels is less in a study area with red and grey squirrels present compared to an area with only red squirrels; and (2) the individual level, comparing hoarding and hoard-recovery behaviour in the study area where both species co-exist, between red squirrels with the core area of their home range strongly overlapped by several grey squirrels and those with little core-area overlap. We thus assume, based on their activity budget, foraging behaviour and food choice (Wauters and Dhondt 1987; Wauters et al. 1992, 2001), that red squirrels select cached tree seeds, and will only feed on secondary food items when the cost of searching and retrieving cached seeds exceeds the benefits (see Methods).

At the population level, we predict that energy intake by red squirrels from consuming cached food in winter and spring will be higher in the red-only than in the red-grey site, and the ratio of recovered seed energy per year to seed energy cached per year will be higher in the red-only site. Alternatively, if red squirrels adapt their hoarding to the presence of grey squirrels, and to increased competition for mature tree seeds in autumn, we expect that red squirrels will increase the quantity of seeds cached, measured by energy content, to avoid scramble competition for mature nuts and seeds (whether still in the trees, or fallen on the ground), where grey squirrels co-exist. If this tactic is successful, there will be no decrease in the amount of energy intake by recovering cached food in the red-grey compared to the red-only site, and the ratio of seed energy recovered per year to seed energy cached per year is similar in both sites.

At the individual level, we predict that, if grey squirrels gradually deplete seeds cached by red squirrels with overlapping core areas, those red squirrels that have a high percentage of core-area overlap with the congener will have a lower energy intake from feeding on cached food resources than their conspecifics that have little core-area overlap with grey squirrels. In contrast, if pilfering does not occur, or if red squirrels steal cached seeds similarly to what they lose from their own caches being pilfered, there will be no difference between sites in the ratio of recovered seed energy per year to cached seed energy per year, and there will be no relationship between the amount of energy intake from retrieving cached seeds and the amount of interspecific core-area overlap. Alternatively, if red squirrels adapt hoarding to the presence of grey squirrels, we expect that, where grey squirrels co-exist: (1) red squirrels overlapped by several grey squirrels will spend more time caching than conspecifics with little interspecific core-area overlap and, as a consequence, (2) there will be no association between the amount of core-area overlap with the congener on the energy intake by red squirrels of cached seed.

To test these predictions, we studied spacing behaviour (home-range size, core-area overlap), activity budget and feeding behaviour of individually marked red and grey squirrels from August 1997 to June 1998 in two study sites in Italy; one had red squirrels only (red-only site), and the other had both species (red-grey site). Because of the limited number of sympatric populations of red and grey squirrels in northern Italy, and because of the labour-intensive nature of the field observations and time constraints, we were unable to replicate the red-grey and red-only study sites in this study (see also Wauters et al. 2001). Therefore, in addition to analysing the data at the population level, we have considered in detail behaviour at the individual level.

## Methods

### Red-squirrel hoarding and foraging

In Europe, both red squirrels and introduced eastern grey squirrels scatterhoard seeds of broadleaf trees, such as walnuts (*Juglans regia*), black walnuts (*J. nigra*), sweet chestnuts (*Castanea sativa*), acorns (*Quercus* spp.), beechnuts (*Fagus sylvatica*) and hazelnuts (*Corylus avellana*), and red squirrels also store single cones of Scots (*Pinus sylvestris*) and Corsican pine (*P. nigra*) and fungi (Gurnell 1987; Lurz and South 1998; Sulkava and Nyholm 1987; Wauters and Dhondt 1987; Wauters et al. 1992, 1995). Consumption of scatterhoarded tree seeds covers about 20–50% of a red squirrel's daily energy intake during November/April, peaking in February/April (Wauters and Casale 1996). The rest of their late winter-spring diet consists of food items that are temporarily abundant but lower in energy and nutrient content than tree seeds: young shoots, leaf and flower buds of deciduous trees and conifers, tree flowers, bark-growing fungi and insects (Gurnell 1987; Moller 1983; Wauters and Dhondt 1987; Wauters et al. 1992). Red squirrels select tree seeds over other food and animals that fed intensively on cached seeds lost less weight during spring/early summer and had a higher probability to survive this season, when energy-rich food supplies are scarce, than conspecifics feeding less on scatterhoarded seeds (Wauters et al. 1995). In the longer term, both survival (longevity) and female reproductive success increased with consumption of cached tree seeds (Wauters et al. 1995). Thus, individual red-squirrel fitness is positively affected by the amount of cached food it can consume during January/April.

## Study sites

We monitored caching and cache-recovery behaviour of red squirrels from August 1997 to June 1998 in two mature, mixed woodlands in North Italy that were high-quality habitats for both red and grey squirrels. One study site (red-only, 22 ha) had only red squirrels and was in Parco Pineta, an extensive mixed forest of 3,000 ha on the northern edge of the upper Po plain in Lombardy, North Italy (8°57′E, 45°45′N). It was dominated by deciduous trees, mainly black locust (*Robinia pseudoacacia*) (25%), sweet chestnut (*Castanea sativa*) (20%), Scots pine (*P. sylvestris*) (19%), oaks (*Quercus robur*, *Q. petraea*) (9%) and hornbeam (*Carpinus betulus*) (5%), with plantations of white pine (*P. strobus*) and Norway spruce (*Picea abies*) covering about 17% of the study area. Understorey was diverse, mainly hazel (*Coryllus avellana*) and blackberry (*Sambucus nigra*). The second study site (red-grey, 13 ha), had both red and grey squirrels, and consisted of a mature, mixed deciduous woodland at Borgo Cornalese in the Po plain in Piedmont, North Italy (7°44′E, 44°55′N). It was dominated by oaks (18%), hornbeam (19%), field maple and sycamore (*Acer campestris*, *A. pseudoplatanus*) (26%) and ash (*Fraxinus excelsior*) (15%),with some birdcherry (*Prunus avium*), lime (*Tilia cordata*) and alder (*Alnus glutinosa*). Walnuts of sparsely planted *J. regia* and *J. nigra* were important food resources for both squirrel species. There was also a single block of planted white pine, which covered about 8% of the study area. Understorey was dominated by blackberry with some hazel. Estimates of food availability and population densities of red squirrels at both study sites and of grey squirrels at the red-grey site are presented elsewhere (Wauters and Gurnell 1999; Wauters et al. 2001).

## Trapping, handling and radiotracking squirrels

Trapping occurred bimonthly, for at least 5 days, from July 1996 to October 1998. Squirrels were livetrapped, individually marked with ear tags, and their sex and age were determined (Wauters and Dhondt 1989; Wauters and Gurnell 1999). Body mass was measured at each recapture to the nearest 5 g using a Pesola spring balance. All adult red and grey squirrels were radiotagged over 3- to 6-month periods in 1997 and 1998 and we determined space use and activity patterns of both species (Wauters and Gurnell 1999). 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), and X (west to east) and Y (south to north) co-ordinates were assigned; the exact time (summer hour schedule), the squirrel's 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 home range (Wauters and Dhondt 1992). 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). For each species, most animals had a single activity centre (mononuclear core-areas, Kenward and Hodder 1995) and the mean percentage of fixes included in the core area did not differ between species (mean±SD: red squirrels 74±9%, grey squirrels 73±9%). 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 minimum convex polygon method (MCP, including 100% of the point-fixes); (2) mononuclear 70% core-area estimates; (3) intraspecific core-area overlap, expressed as the sum of the percentage of overlap of a red squirrel's core area with core areas of all other red squirrels; (4) interspecific core-area overlap, expressed as the sum of the percentage of overlap with core areas of all grey squirrels (Kenward and Hodder 1995; Wauters and Dhondt 1992; Wauters et al. 2000). Thus, core-area overlap can exceed 100% if a squirrel's core area is overlapped by many other squirrels.

## Monitoring behaviour

We studied the activity budget of radiotagged red squirrels, observing their behaviour for 20–60 min with 10×50 binoculars (Wauters and Gurnell 1999; Wauters et al. 1992). The total time an individual was observed during autumn, winter or spring varied from 63 to 334 min in the red-only site, and 81 to 201 min in the red-grey site. We assigned behaviour to one of nine categories (see Wauters et al. 1992). Here we concentrate on caching behaviour, i.e. taking a tree seed (chestnut, walnut, black walnut or hazelnut) from a tree or from the ground, transporting and caching it, and recovering cached food. Recovery activity is characterised by a squirrel jumping and sniffing the ground in a restricted area (<100 $m^2$) while searching for cached food, and subsequently digging up and consuming cached seeds (Wauters et al. 1995). This behaviour also includes unsuccessful searching. Time allocated by each squirrel to caching ("caching activity") and recovering and consuming cached food ("recovery activity") per day was calculated by multiplying, respectively, the proportions of active time it was observed hoarding and recovering cached food by the mean time active per day (Wauters et al. 1995). In each study site, time active per day (MTA), averaged over monthly periods, was calculated by combining all radiotrack data from all squirrels collected that month (Wauters et al. 2001).

Caching occurred over a total of ca. 120 days per year (September/December in red-only, August/November in red-grey site). Recovering and consuming cached seeds was monitored during winter (mainly January/February) and spring (mainly March/April), totalling 120 days for red squirrels observed both seasons. For each seed species, mean time spent caching (min $seed^{-1}$) was calculated across all squirrels, per study area. We also calculated mean time feeding per seed species, using 20 complete observations of feeding bouts by different red squirrels. Time feeding was measured from the moment the food item was found until the remains were dropped (Wauters et al. 1992).

For each seed species, the number of seeds hoarded per day was estimated by dividing the time spent hoarding per day, of the different seeds, by the time needed to hoard a single seed. Energy content of seeds cached in a single day per individual squirrel was computed by multiplying the number of hoarded seeds by their energy content and summing over all different seed species. This measure of cached seed energy was then multiplied by 120 to derive an estimate of total seed energy cached $year^{-1}$ (kJ $year^{-1}$) for each individual red squirrel. Likewise, daily energy intake by individual red squirrels of consuming cached seeds (kJ $day^{-1}$) was calculated by multiplying the number of cached seeds, per seed species, consumed per day by the energy value per seed. Dry weight of edible parts of a seed (mean± SD) and energy content per seed (mean± SD) are, respectively, 3,700±350 mg and 66.2±6.3 kJ for chestnuts, 3,450±275 mg and 103.1±10.4 kJ for walnuts, 2,760±144 mg and 89.9±6.3 kJ for black walnuts, and 805±15 mg and 20.7±2.7 kJ for hazelnuts (Wauters et al. 2001).

### Statistical analyses

Statistical analyses were conducted using SAS (SAS 1989) with a nominal significance level of 0.05. All the continuous variables that were investigated were normally distributed (Shapiro-Wilk test, $P>0.2$), and assumptions for parametric tests were met in most cases. When this was not the case (small sample size), the non-parametric Mann-Whitney *U*-test was used. Testing for an effect of study site, sex (males vs females) and a site-sex interaction on caching and recovery activity, using unbalanced two-way ANOVA, there was no significant sex effect (males vs females, all $P>0.6$), and no significant site*sex interaction (all $P>0.4$) on the two dependent variables tested. Therefore, in analyses, data from males and females are pooled and two-tailed Student *t*-tests are used to investigate the effect of study site on each single dependent variable. Recovery activity was analysed for winter and spring separately, because some red squirrels were monitored in both seasons.

## Results

### Time spent caching and time spent feeding for different seeds

Red squirrels spent on average 1.4 min ($n$=21 seeds, coefficient of variation, CV=25%) on caching a single hazelnut, 1.5 min ($n$=30, CV=40%) for chestnuts, 2.3 min ($n$=16, CV=33%) for walnuts, and 2.4 min ($n$=8, CV=38%) for black walnuts. Time spent feeding on a single seed ($n$=20 seeds in all cases) averaged 4.9 min (CV=27%) for hazelnuts, 7.7 min (CV=20%) for chestnuts, 15.3 min (CV=27%) for walnuts, and 30.7 min (CV=32%) for black walnuts.

Grey squirrels are less arboreal than reds and search more often for food on the ground (Kenward and Tonkin 1986; Wauters et al. 1992), but there was little difference in the way red and grey squirrels cache and retrieve scatterhoarded seeds. Occasional observations of caching grey squirrels showed they mainly cached acorns, black walnuts and walnuts, while most hazelnuts were already consumed in late summer, when still maturing. However, grey squirrels were observed retrieving cached hazelnuts and walnuts that had been cached by red squirrels in winter. Thus, seed pilfering by grey squirrels occurred.

### Comparisons of caching and recovery activity at the population level

In the red-only site, red squirrels cached mainly chestnuts, and to a lesser extent hazelnuts and walnuts (Table 1). Some squirrels occasionally cached Scots pine cones or acorns (<3%), but these were not included in analyses. In the red-grey site, walnuts were cached most intensively, and black walnuts and hazelnuts less frequently. A few red squirrels also cached acorns, but this occurred rarely (<3%), and acorns were not included in the analyses. The total seed energy cached over the entire caching period (Table 1) did not differ between sites ($t_{26}$=1.39, $P$=0.17) and variation among squirrels in the number of different seeds that were cached was large (Table 1).

Neither in winter (January/February) nor in spring (March/April) were there significant differences between sites in daily energy intake of red squirrels feeding on seeds recovered from caches (winter $t_{28}$=0.75, $P$=0.46; spring $t_{26}$=0.99, $P$=0.33; Table 2 a). In a similar way to caching activity, there were large individual differences in recovery activity among red squirrels in both study sites (Table 2 a).

For animals monitored both seasons (13 in red-only site, 9 in red-grey site), the number of cached seeds recovered over the entire period that red squirrels fed on scatterhoards was nearly twice the amount in the red-only site as in the red-grey site (Mann-Whitney *U*-test $z$=–2.27, $P$=0.02; Table 2 b). However, total energy intake for individual squirrels feeding on cached seeds in the red-only site was not greater than in the red-grey site

**Table 1** Caching activity in both study sites ($n$ number of red squirrels monitored; *CV* coefficient of variation expressed as percentage of mean)

| Variable | Red-only site ($n$=15) | | Red-grey site ($n$=13) | |
|---|---|---|---|---|
| | Mean (%CV) | Range | Mean (%CV) | Range |
| Time hoarding day$^{-1}$ (min) | | | | |
| All species combined | 12.7 (50) | 2.2–25.8 | 23.6 (62) | 7.5–50.1 |
| Chestnuts/black walnuts[a] | 9.4 (56) | 2.2–21.1 | 4.8 (204) | 0–35.5 |
| Hazelnuts | 1.9 (126) | 0–7.0 | 2.1 (133) | 0–8.5 |
| Walnuts | 1.4 (236) | 0–9.4 | 16.7 (81) | 0–45.3 |
| Number of seeds hoarded year$^{-1}$ | | | | |
| All species combined | 767 (49) | 133–1441 | 737 (68) | 94–1684 |
| Chestnuts/black walnuts[a] | 576 (56) | 133–1298 | 121 (234) | 0–1013 |
| Hazelnuts | 134 (125) | 0–485 | 79 (127) | 0–279 |
| Walnuts | 57 (233) | 0–379 | 538 (88) | 0–1623 |
| Seed energy hoarded year$^{-1}$ (kJ) | | | | |
| All species combined | 46539 (51) | 8770–86173 | 66288 (74) | 9370–167807 |
| Chestnuts/black walnuts[a] | 38046 (56) | 8770–85687 | 10870 (234) | 0–91187 |
| Hazelnuts | 2808 (125) | 0–10190 | 1654 (127) | 0–5853 |
| Walnuts | 5685 (234) | 0–37899 | 53764 (88) | 0–162347 |

[a] Chestnuts in red-only site, black walnuts in red-grey site

**Table 2** Recovery activity in both study sites (*n* number of red squirrels monitored; *CV* coefficient of variation expressed as a percentage of mean). Time of recovery activity day$^{-1}$ and energy intake by feeding on recovered seeds (seed energy recovered day$^{-1}$) for winter and spring separately. Recovery activity calculated over the entire period in which recovering of cached seeds was most intense (January to April): time of recovery activity day$^{-1}$, total number of cached seeds recovered and total energy intake by feeding on recovered seeds (seed-energy recovered year$^{-1}$)

| Variable | Red-only study area | | | Red-grey study area | | |
|---|---|---|---|---|---|---|
| | *n* | Mean (%CV) | Range | *n* | Mean (%CV) | Range |
| Time recovering day$^{-1}$ (min) | | | | | | |
| Winter | 16 | 44.5 (53) | 8.4–102.1 | 14 | 52.4 (20) | 32.8–68.6 |
| Spring | 15 | 65 (60) | 24.4–156.0 | 13 | 94.4 (41) | 33.5–185.5 |
| Seed energy recovered day$^{-1}$ (kJ) | | | | | | |
| Winter | 16 | 298 (49) | 71–666 | 14 | 335 (34) | 165–547 |
| Spring | 15 | 463 (55) | 167–992 | 13 | 373 (59) | 127–901 |
| Time recovering day$^{-1}$ (min) | 13 | 56.6 (45) | 21.5–107.1 | 9 | 71.8 (38) | 33.2–126.8 |
| Seeds recovered year$^{-1}$ | 13 | 1009 (54) | 312–2070 | 9 | 535 (41) | 250–975 |
| Seed-energy recovered year$^{-1}$ (kJ) | 13 | 46424 (40) | 21968–81757 | 9 | 43709 (43) | 12911–78417 |

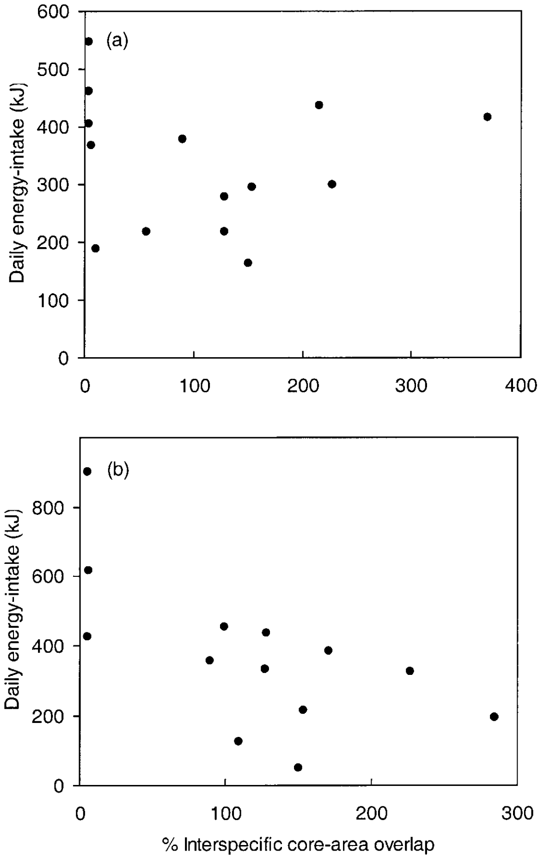

**Fig. 1a, b** Relationship between the % of core-area overlap of red by grey squirrels and the daily energy intake (kJ) of consumption of recovered seeds by red squirrels. **a** Winter, **b** spring. *Dots* indicate individual red squirrels monitored in each season

($t_{20}$=0.33, *P*=0.74; Table 2 b). This was because red squirrels in the red-only site retrieved mainly chestnuts, which had lower seed-energy content than walnuts, the main species recovered by red squirrels in the red-grey site. Nevertheless, the average ratio of seed energy recovered per year on seed energy cached per year in the red-only site was 99.8% (46,424 kJ/46,539 kJ) and that in the red-grey site was only 66% (43,709 kJ/66,288 kJ). Thus recovery rate by red squirrels was higher in the red-only than in the red-grey site.

### Comparisons at the individual level within the red-grey study area

Our previous analyses assumed that grey squirrels' home ranges were randomly distributed over the entire red-grey study site, with little individual variation in the degree of core-area overlap of grey squirrels with red squirrels. However, data on space use of both species show that this was not the case. Most grey squirrels occupied northern, western and central parts of the study site where many red squirrels had core areas (Wauters and Gurnell 1999). Interspecific core-area overlap was low or non-existent for some red squirrels in the south-eastern section (<50%; Fig. 1), but high for others (90–350%; Fig. 1). On average, core-area overlap of a red squirrel with conspecifics of the same or of the other sex did not differ significantly with the amount of interspecific core-area overlap with grey squirrels of either sex (Wauters and Gurnell 1999). Neither the amount of intraspecific core-area overlap among red squirrels, nor that of interspecific core-area overlap with grey squirrels were significantly correlated with the energy content of seed cached by individual red squirrels (respectively *r*=–0.20, *P*=0.54, *r*=–0.56, *P*=0.06, *n*=12, in both cases).

In winter, average daily energy intake from the consumption of recovered seeds was not related to percentage of interspecific core-area overlap (*r*=–0.07, *n*=14, *P*=0.81; Fig. 1a). However, in spring, when caches became gradually depleted, high-overlap red squirrels exhibited lower daily energy intake than low-overlap squirrels (*r*=–0.65, *n*=13, *P*=0.02; Fig. 1b). Also, spring body mass of red squirrels was negatively correlated with the percentage of interspecific core-area overlap (*r*=–0.56 *n*=13, *P*=0.05). Spring body mass was correlated with daily energy intake (*r*=0.55, *n*=13, *P*=0.05). The amount

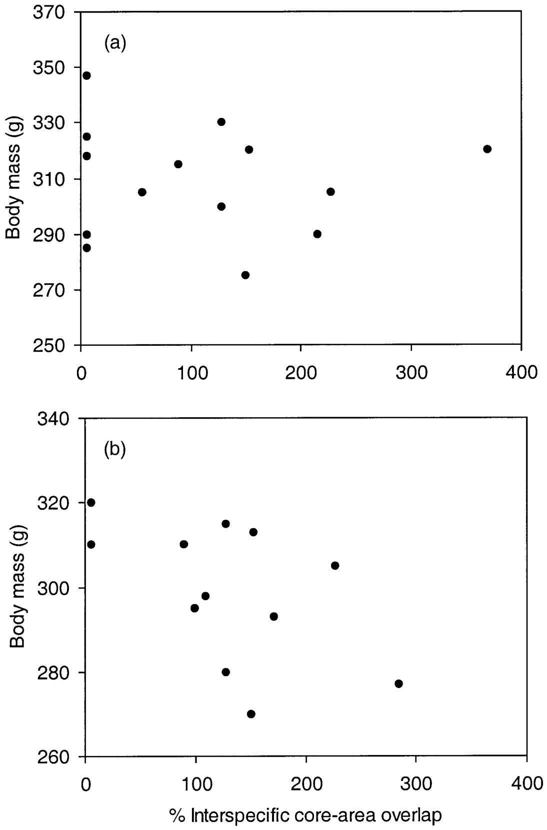

**Fig. 2** Relationship between the % of interspecific core-area overlap of red by grey squirrels and red-squirrel body mass in **a** winter, **b** spring. *Dots* indicate individual red squirrels monitored in each season

of intraspecific core-area overlap among red squirrels was not correlated with either daily energy intake from recovered seeds, or spring body mass (respectively $r=-0.25$, $r=0.13$, $n=13$, $P>0.4$ in both cases). In a stepwise multiple linear regression model, only % overlap with grey squirrels contributed significantly to explaining individual variation in spring body mass of red squirrels [body mass=312(±7)–0.104(±0.05)% interspecific core-area overlap, $R^2=0.31$, $F=5.01$, $df=1$, 11, $P=0.05$; Fig. 2b], while the partial effects of daily energy intake ($r_p=0.24$, $P=0.31$) and % core-area overlap with other red squirrels ($r_p=0.39$, $P=0.12$) were not significant. In winter, however, autumn-winter body mass of red squirrels was not correlated with either core-area overlap with grey squirrels (Fig. 2a), other red squirrels, or daily energy intake ($n=14$, $r=-0.09$, $P=0.75$; $r=-0.29$, $P=0.32$; and $r=-0.19$, $P=0.52$, respectively).

Finally, for nine red squirrels monitored over the whole period of hoard recovery (winter and spring), total energy intake of cached seeds was negatively correlated with the amount of interspecific core-area overlap ($r=-0.69$, $P=0.04$).

## Discussion

### The importance of food caching in our study populations

In the present study, red squirrels scatterhoarded fewer seeds than in mixed woodlands in Belgium (Wauters and Casale 1996). However, because the main cached seed species were larger with higher energy content per seed than in Belgian woodlands, the total food energy stored was highest in the Italian populations (22,700–36,300 kJ year$^{-1}$ in Belgium, 46,500–66,300 kJ year$^{-1}$ in Italy, see also Wauters and Casale 1996). Belgian red squirrels consumed about 80% of the seeds they cached (i.e. 1,900–2,200 seeds), sufficient to cover daily energy requirements for an average of 43 and 68 days in coniferous and deciduous woodland, respectively (Wauters and Casale 1996). Using an estimated daily energy consumption of 700 kJ in both red-only and red-grey study sites over winter/early spring (from Wauters et al. 2001), consumption of scatterhoarded seeds would have been sufficient to fulfil daily energy demands for about 62–66 days. Thus, as for other squirrel populations, stored seeds were an important food supply for red squirrels at both study sites in winter and early spring, covering on average about 50% of their total energy requirements from January to the end of April. During this period, red squirrels at both study sites integrated their diet of high-energy scatterhoarded tree seeds with fungi growing on dying oak branches, mature maple and ash seeds, leaf and flower buds in winter, and with young shoots and flowers of oak, maple, Scots pine and Norway spruce, and insects in spring (Wauters et al. 2001)

### Do red squirrels adapt their caching behaviour to the presence of grey squirrels?

Red squirrels did not store more seed energy where grey squirrels co-exist, mainly because of large individual variation among squirrels' hoarding activity. Hence, at the population level, our results do not agree with the first prediction of the alternative hypothesis that red squirrels increase the amount of food energy cached in the presence of the congener. Moreover, in the red-grey site, red squirrels that shared large parts of their home range with several grey squirrels (high interspecific core-area overlap) did not increase caching, as measured by the energy content of scatterhoarded seeds.

Finally, red squirrels retrieved nearly all seeds cached in the red-only site (99.8%), but less (66%) in the red-grey site. Since grey squirrels were observed stealing hazelnuts and walnuts cached by red squirrels, this decrease in the red-grey site seems to result from the depletion of red-squirrel caches by grey squirrels as spring progresses. Thus, cache pilfering by grey squirrels occurred, decreasing the proportion of cached seeds retrieved by red squirrels. Hence, our data failed to support the hypothesis that red squirrels adapt their scatterhoarding behaviour to the presence and potential cache pilfering of grey squirrels.

### Do grey squirrels steal and partly deplete food caches of red squirrels?

Our comparisons at the population level were equivocal with regard to the predictions of the hypothesis that grey squirrels partly deplete the energy-rich food caches of red squirrels. Red squirrels without congeners did not have a higher daily energy intake from consuming cached seeds than their conspecifics co-occurring with grey squirrels. However, in spring, when caches were progressively depleted, red squirrels in the red-only site tended to consume on average 100 kJ $day^{-1}$ more of cached seed energy than conspecifics in the red-grey site. But overall, the population of red squirrels that co-occurred with grey squirrels did not consume less energy by recovering cached seeds than the red-squirrel population in the study site without grey squirrels.

Nevertheless, these inter-site comparisons of cache-recovery behaviour were affected by the spatial distribution and density of the grey squirrels at the red-grey study site. In particular: (1) grey-squirrel densities were low (about 1.7 $ha^{-1}$ in summer 1998, Wauters and Gurnell 1999); (2) grey squirrels were not uniformly distributed over the study area, but were concentrated in the oak-dominated section; and (3) interspecific overlap of individual red squirrels by grey squirrels varied markedly. There are several lines of evidence to support the idea that grey squirrels steal and progressively deplete seeds cached by red squirrels; these come from comparisons made at the level of the individual. First, recovery activity did not differ between red squirrels that were overlapped by few grey squirrels and those overlapped by several grey squirrels in winter. Second, the percentage of interspecific core-area overlap for red squirrels monitored in spring was negatively correlated with daily energy intake from retrieving cached seeds in spring, as one would expect if depletion of red-squirrels caches by pilfering increases with time. Third, over the entire period of cache recovery (January/April), red squirrels with little interspecific core-area overlap had higher energy intake by eating scatterhoarded seeds than red squirrels more strongly overlapped by grey squirrels. Fourth, energy consumption of cached seeds was not correlated with intraspecific (thus with other red squirrels) core-area overlap. These results suggest that in woodlands were both species co-exist, even at current low grey-squirrel densities, red squirrels that share most of their home-range core area with greys are faced with a more rapid depletion of cached food resources than their conspecifics that have little core-area overlap with grey squirrels. In contrast, the amount of core-area overlap with other red squirrels did not cause a reduction in cached food intake, indicating that intraspecific competition for scatterhoarded seeds was less strong than interspecific competition.

We conclude that interspecific competition for high-energy scatterhoarded seeds in winter and spring, with grey squirrels pilfering red squirrels' food caches, is the most likely cause of the reduced energy intake in red squirrels with a high degree of interspecific core-area overlap. Such pilfering not only significantly reduced the body mass of red squirrels in spring, suggesting it probably reduces red-squirrel fitness (Wauters et al. 1995), but is also likely to increase with increasing grey-squirrel densities. Grey squirrels originated in the extensive, deciduous forests in eastern North America and they are well adapted to deciduous or mixed forest, in Europe reaching densities 5–6 times higher than red squirrels (Gurnell 1987; Gurnell and Pepper 1993). Recent studies indicate that a key factor in the replacement of red by grey squirrels is a decrease in rate of recruitment of juvenile red squirrels when grey squirrels are present (Wauters and Gurnell 1999; Wauters et al. 2000, 2001). Thus, in deciduous woodlands in Italy and probably also in Britain, competition from grey squirrels for cached seed leading to a reduction in red-squirrel fitness in spring, is likely to be a major mechanism of the replacement of red by grey squirrels.

**Acknowledgements** We thank Xavier de Maistre and Caterina Gromis de Trana for allowing us to work on their estate and for their personal support and interest in the project. We are also grateful to the Consorzio Parco Pineta di Appiano Gentile e Tradate for permission to use the regional park as study site. Constructive comments by four anonymous referees greatly helped to improve the manuscript. L. Wauters was financed by a TMR grant (no. ERBFMBICT 960662) from the Commission of the European Union. Methods of trapping and handling animals comply with the current Italian laws, and trapping and marking of squirrels was carried out under licence no. DGR 80-37850 (1994) of the Region of Piedmont, and licence no. DGR 22194 (1996) of the Region of Lombardy.

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