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A REVIEW OF THE COMPETITIVE EFFECTS OF ALIEN GREY SQUIRRELS ON BEHAVIOUR, ACTIVITY AND HABITAT USE OF RED SQUIRRELS IN MIXED, DECIDUOUS WOODLAND IN ITALY

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ABSTRACT – The introduction of alien species can cause competitive exclusion of ecologically similar native species when there is no niche differentiation between them. Such invasive species can constitute a serious threat to biodiversity in the region where they have been introduced, causing extinction or decline of native species through competition. A well-documented case is widescale replacement of native Eurasian red squirrel (*Sciurus vulgaris*) by introduced eastern grey squirrel (*Sciurus carolinensis*) on the British Isles and parts of northern Italy. Rapid increase of grey squirrel’s distribution range, coincided with a dramatic decline of the native red squirrel’s range, and grey squirrels have now replaced red squirrels over much of Britain and in fragmented landscapes in Piedmont, northern Italy. In this review, we consider the evidence that has been obtained from studies on compettive effects of grey squirrels on activity, habitat use, foraging behaviour and food choice of individual red squirrels in broadleaf woodlands in North-west Italy. In these habitats, there is no evidence for niche partitioning between red and grey squirrels in any of the niche parameters examined, suggesting that red squirrels are unable to adapt to avoid competition with the congener when resources become limiting. Interspecific competition seems to occur mainly for food resources that affect fitness of squirrels at crucial periods of the year, such as cached tree seeds in winter and spring. Also, the greater use of acorns by grey squirrels gives the invasive species an advantage over red squirrels in mixed deciduous woods, especially with a preponderance of oaks. This is supported by studies in Britain and Italy that show that co-existence of the two species in mixed deciduous woodlands is of short duration (e.g. less than 3-5 years) with grey squirrels advantaged in resource exploitation competition, resulting in the local extinction of red squirrels. Based on these findings and modelling studies, a dramatic increase in grey squirrel population size in north Italy is predicted, once they spread into the continuous deciduous forests in the Prealps in Piedmont and Lombardy. This has serious implications for red squirrel conservation in Italy, and in Europe as a whole.

Key words: *Sciurus vulgaris*, *Sciurus carolinensis*, interspecific competition, niche differentiation, resource exploitation, activity pattern, habitat use

RIASSUNTO – ***Effetti della competizione sul comportamento, ritmi di attività e uso dell’habitat indotti dalla specie alloctona scoiattolo grigio sullo scoiattolo comune, in boschi misti di latifoglie.*** L’introduzione di specie alloctone può indurre il fenomeno dell’esclusione competitiva a spese di specie autoctone, in particolare se manca una netta separazione di nicchia ecologica. Pertanto specie invasive possono costituire un serio pericolo per la conservazione della biodiversità nelle aree di introduzione, causando l'estinzione locale o il declino delle popolazioni di specie autoctone. Casi ben documentati di questo fenomeno di sostituzione su larga scala, da parte dello Scoiattolo grigio (*Sciurus carolinensis*) a scapito dello Scoiattolo comune (*Sciurus vulgaris*), si sono verificati sia in Gran Bretagna sia in alcune parti del nord Italia. Il rapido incremento della distribuzione dello scoiattolo grigio, coincide con un forte declino dell'areale dello scoiattolo comune in gran parte della Gran Bretagna e nord Italia (Piemonte). Nel presente lavoro vengono considerati i dati ottenuti dagli studi volti alla valutazione degli effetti della competizione sul comportamento, ritmi di attività, uso dell'habitat, foraggiamento e sulla dieta indotti dallo scoiattolo grigio sullo scoiattolo comune, in boschi misti di latifoglie. In tali habitat non ci sono evidenze che ci sia separazione di nicchia tra le due specie per ognuno dei parametri analizzasuggerendo quindi che lo scoiattolo comune non è in grado di evitare la competizione con la specie congenerica, in particolare quando le risorse divengono limitanti. La competizione interspecifica sembra manifestarsi principalmente per le risorse alimentari, come il consumo, durante l'inverno e la primavera, dei semi immagazzinati che, durante i periodi "critici" stagionali, influenzano la sopravvivenza e/o il successo riproduttivo. Inoltre, il maggior consumo di ghiande da parte dello scoiattolo grigio fornisce alla specie alloctona un vantaggio trofico nei boschi decidui, in particolare con predominanza di querce. Questo è supportato dai dati degli studi condotti in Gran Bretagna e in Italia, che mostrano una coesistenza temporalmente ridotta delle due specie nei boschi di latifoglie misti (meno di 3-5 anni), con lo scoiattolo grigio che risulta avvantaggiato nella competizione per l'utilizzo delle risorse, comportando la conseguente estinzione locale dello scoiattolo comune. In relazione a tali dati e all'elaborazione di modelli predittivi, è ipotizzabile un massiccio incremento della consistenza delle popolazioni di scoiattolo grigio in nord Italia, in particolare a partire dall'insediamento della specie nelle estese foreste di latifoglie in ambiente prealpino. Tale scenario indurrà a una più attenta valutazione inerente la conservazione dello scoiattolo comune in Italia e nell'intera Europa.

Parole chiave: *Sciurus vulgaris, Sciurus carolinensis,* competizione interspecifica, differenziazione della nicchia, uso delle risorse, attività, uso dell'habitat

INTRODUCTION

Competition occurs when resource availability is limited and one organism has a negative effect on another by controlling access to and/or by consuming that resource (after Keddy, 1989). It follows that competition acts principally at the level of the individual and can adversely affect reproduction (e.g. by delaying reproduction or reducing reproductive output thus lowering lifetime reproductive success), survival, dispersal (e.g. by increasing the likelihood of emigration), activity in time and space, and habitat use (e.g. by reducing access to high quality habitats patches). Within a species, these effects at the individual level may be translated into effects at the population level (so-called intraspecific competition), by affecting one or more population processes (e.g. reproductive rate, survival rate, recruitment rate), which results in reduced per capita growth rate at a given density. Finally, interspecific competition, which acts at the level of the community level, will shape community structure (e.g. number and relative abundance of species) and realised niche width (Schoener, 1974; Rosenzweig, 1981; Brown, 1989).

Niche differentiation (e.g. by a dissimilarity in foraging behaviour, food, habitat use or activity patterns) among potentially competing species is necessary for competitive coexistence to occur within communities (e.g. May, 1973; Rosenzweig, 1981). However, in situations where two (or more) similar species occur but niche differentiation has not evolved, competitive exclusion of one species by the other is the likely outcome. This situation arises when a foreign or alien species is deliberately or inadvertently introduced into a community. Such invasive species can constitute a serious threat to biodiversity in the region where they have been introduced, causing the extinction or decline of native species through competition or predation (e.g. Lodge, 1993; Williamson, 1996; Lovei, 1997; Wilcove *et al.*, 1998; IUCN, 2000).

A well-documented case is the widescale replacement of the native Eurasian red squirrel (*Sciurus vulgaris*) by the introduced eastern grey squirrel (*Sciurus carolinensis*) on the British Isles and parts of northern Italy. The rapid increase of the grey squirrel's distribution range, coincided with a dramatic decline of the range of the native red squirrel, and 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; Gurnell, 1996a; Wauters *et al.*, 1997a, b; Genovesi and Bertolino, 2001, Lurz *et al.*, 2001). Although the grey squirrels (adult body mass 500 to 650g) is larger than the red squirrel (250 to 400 g), red and grey squirrels behave and live in very similar ways (Gurnell, 1987, 1996a). However, and despite >100 years since grey squirrels were introduced into Britain, and >50 years into Italy, little progress on identifying the processes involved in the ecological replacement of red by grey squirrels had been made until recently (see Williamson, 1996). In this paper, we consider the evidence that has been obtained from studies on the effects of grey squirrels on the activity, habitat use, foraging behaviour and food choice of individual red squirrels in broadleaf woodlands in North-west Italy.

STUDY SITES

For full descriptions of the study sites see Gurnell *et al.* (2001, 2004) and (Wauters *et al.*, 2002a, b). In short, research on sympatric red and grey squirrels was carried out 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*, *Quercus petraea*), hornbeam (*Carpinus betulus*), field maple and sycamore (*Acer campestris, A. pseudoplatanus*), and ash (*Fraxinus excelsior)*, with some bird cherry (*Prunus avium*), lime (*Tilia cordata*), and alder (*Alnus glutinosa*), walnut (*Juglans regia*), black walnut (*Juglans nigra*) and planted white pine (*Pinus strobus*). The understorey was dominated by blackberry (*Sambucus nigra*) with some hazel (*Coryllus avellana*), and the ground vegetation consists of forbs and grasses. The first grey squirrels colonised this woodland in spring 1996. The grey squirrel population expanded quickly and numbers increased three-fold from March 1997 to May 1998 (1.9 ha^{-1}). By September 1998, grey squirrels had become more abundant than red squirrels (1.6 and 1.5 ha^{-1} respectively, Wauters and Gurnell, 1999; Gurnell *et al.*, 2001, 2004); these densities can be considered high for red squirrels but below carrying capacity for grey squirrels (Kenward and Holm, 1993; Wauters and Lens, 1995; Gurnell, 1996b; Kenward *et al.*, 1998). The size of tree-seed crops was comparable with other mixed broadleaf woodlands in Europe containing red and/or grey squirrels. Research on red squirrels without grey squirrels present (the “red-only” control site) was carried at Parco Pineta, a 22 ha area within an extensive mixed forest (3000 ha) on the northern edge of the upper Po plain in Lombardy, North Italy (8°57’ E, 45°45’ N). The woodland was dominated by black locust (*Robinia pseudoacacia*), sweet chestnut (*Castanea sativa*), Scots pine (*Pinus sylvestris*), oaks, hornbeam and Norway spruce (*Picea abies*), with some white pine. The understorey was diverse but mainly consisted of hazel and blackberry. Red squirrel densities were lower than in the “red-grey” site (pre-breeding density approximated 0.4-0.6 ha^{-1}; Gurnell *et al.*, 2004).

METHODS

The methods used to study squirrels and their food supplies involved capture, mark and release of animals through a programme of live trapping, radiotracking individual red and grey squirrels to determine activity patterns, nest use, habitat utilization and range area in each season of the year (winter - December to February; spring - March to May; summer - June to August; autumn - September to November), and direct focal sampling of the behaviour of individuals for periods of up to 260 minutes across all daylight hours throughout the study. Activity patterns and behaviour were analysed in terms of one hour periods (e.g. 10.00-10.59) throughout the day. Tree seed availability was measured across the sites and within each squirrel home range as an indicator of home range quality. All these methods have been described in detail elsewhere (e.g. Wauters and Gurnell, 1999; Gurnell *et al.*, 2001, 2004; Wauters *et al.*, 2001, 2002a, b).

RESULTS AND DISCUSSION

1. Aggressive and mating behaviours

There was a very slight increase in the amount of time that red squirrels interacted with other red squirrels when greys were present, but there were no differences in the proportions of aggressive and non-aggressive encounters between red squirrels at the red-only and red-grey sites. Overall there were slightly more non-aggressive than aggressive encounters with most male-male and female-female encounters being aggressive whereas most male-female encounters were not (Wauters and Gurnell, 1999). More importantly, we did not see red squirrels aggressively chasing grey squirrels at the red-grey site, and only one aggressive chase by a lactating grey squirrel female on an adult female red squirrel. All other interspecific encounters were non-aggressive. Thus there was no evidence of red squirrels changing their behaviour towards other red squirrels when grey squirrels were present, or of grey squirrels behaving aggressively towards red squirrels. Moreover, grey squirrels did not interfere with the mating chases of red squirrels, and all oestrus, female red squirrels observed in mating chases produced young (Wauters and Gurnell, 1999). Because there is no evidence of interference competition in the form of overt aggression by the larger grey squirrel towards the smaller red squirrel, it follows that any niche partitioning is likely to result from a subtle avoidance of one species by the other, or by one species utilizing more of shared resources than the other.

2. Activity patterns

Like all tree squirrels, both red and grey squirrels are day-active with activity patterns that change from unimodal to bimodal from winter to summer and, to some degree, with latitude (ambient temperature) (Tonkin, 1983; Gurnell, 1987; Wauters and Dhondt, 1987; Wauters *et al.,* 1992). Activity patterns are further related to food availability and quality, and thus to the rate of energy-intake (reviewed in Wauters, 2000). Correlations between the proportion of time active of red and grey squirrels in each 1-hour observation period were significant for all seasons. Therefore, and although the timing of activity among individuals of both species was often asynchronous, both species had activity peaks and resting periods during the same hours of the day (Fig. 1; Wauters and Gurnell, 1999; Wauters *et al.,* 2002a). In addition, the activity rhythm of co-occurring red and grey squirrels was similar to that described for allopatric populations in Europe (red squirrels) and North America (grey squirrels) (Wauters and Gurnell, 1999; reviewed by Wauters, 2000). Thus, we found no evidence that the presence of grey squirrels affected the activity pattern of red squirrels, indicating there is no temporal niche partitioning between the two species.

3. Habitat use and foraging behaviour

In allopatry, red and grey squirrels feed on similar food types in a similar manner (Thompson and Thompson 1980; Korschgen, 1981; Moller, 1983; Tonkin, 1984; Ludolf, 1986; Gurnell, 1987; Wauters and Dhondt, 1987; Holm 1991; Wauters *et al.,* 1992; Magris and Gurnell, 2002). Both species heavily depend on large seeds of broadleaf trees or shrubs such as sweet chestnut, beech, oak, walnut and hazel from late summer throughout autumn and winter, and intensively use small seeds of maple and hornbeam 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 or 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; Lurz and South, 1998). Hence, we expect interspecific competition for food resources to occur in broadleaf woodlands where both species co-occur, particularly in conditions when resources are limited (e.g. high squirrel densities, poor tree seed crops).

Habitat use of red and grey squirrels changed with the season. In the red-

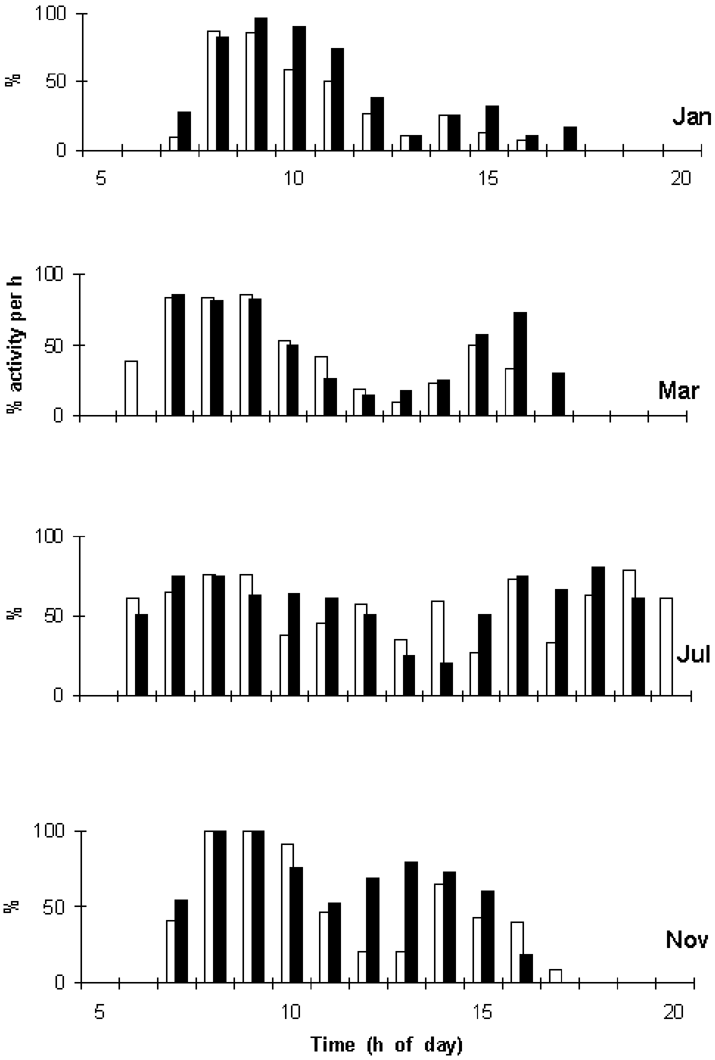

Figure 1 – The daily activity pattern of red squirrels (open bars) and grey squirrels (shaded bars) in different months (one month shown for each season) in the Borgo Cornalese study site, northern Italy (from Wauters and Gurnell, 1999).

grey site, red squirrels spent about 27% of active time on the ground in spring-summer and 37% in autumn-winter; likewise grey squirrels forage less on the ground in spring-summer (29%) than in autumn-winter (43%; Wauters *et al.,* 2002a). In summer, tree-species niche width was larger than in the other seasons, and squirrels fed on small, early maturing seeds of many tree species. Niche width for tree species was most reduced in spring, when red squirrels heavily use oaks to feed on oak flowers and caterpillars (Wauters *et* *al.*, 2001, 2002a). Thus, seasonal changes were comparable for the two species, with both red and grey squirrels observed more frequently on the ground in autumn-winter than in spring-summer. Consequently, Hurlbert nicheoverlap indices, NO (ranging from 0 when there is no niche-overlap to 1.0 the niche of both species is identical, Hurlbert, 1978) for substrate (ground versus trees) were high (spring-summer NOrg = 0.98, autumn-winter NOrg = 0.94; Wauters *et al.*, 2002a).

Both species were selective in their use of habitat throughout the year. For example, there were significant differences between red and grey squirrels in the relative use of the different tree species in different seasons (Tab. 1). In spring-summer, red squirrels showed a significant selection for oaks and were often found feeding on the flowers of lime; grey squirrels also preferred oak and foraged in horse chestnuts (*Aesculus hyppocastanum*) more than expected by chance (Wauters *et al.*, 2001, 2002a and unpubl.). However, grey squirrels fed on oak buds, oak flowers and catterpillars found on the leaves more frequently than red squirrels (63% against 41% of observations). In spring and summer, grey squirrels avoided hornbeam, but red squirrels used hornbeam according to availability (Tab. 1). Thus habitat use for the niche component 'tree species' was similar for red and grey squirrels in springsummer. However, the greater use of oak trees by grey squirrels resulted in a significantly narrower niche width than red squirrels (red squirrels 0.46 ± 0.18, grey squirrels 0.28 ± 0.07, from Wauters *et al.*, 2002a) suggesting they are habitat specialists more than red squirrels. By late July-

Table 1 - Selection indices (wi) 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 wi =1 indicates no selection, a value >1 indicates preference and a value <1 indicates avoidance. A (+) or a (-) after wi indicates that wi is significantly larger (selection) or smaller than 1 (avoidance) respectively (from Wauters *et al.*, 2002a).

	Spring-summer				Autumn-winter			
	Red squirrels		Grey squirrels		Red squirrels		Grey squirrels	
Tree species (% cover)	w_i	use	w_i	use	w_i	use	w_i	use
Maple (26)	0.45 (-)	0.12	0.13 (-)	0.03	0.35 (-)	0.09	0.31(-)	0.07
White pine(8)	0.85	0.09	1.15	0.03	0.65	0.07	0.39	0.01
Ash (15)	0.26 (-)	0.03	0.33 (-)	0.06	0.22 (-)	0.03	0.39 (-)	0.07
Walnut (5)	1.33	0.08	1.41	0.10	2.46 (+)	0.15	0.84	0.06
Oak (18)	2.42 (+)	0.41	3.15 (+)	0.63	2.43 (+)	0.43	3.16 (+)	0.63
Hornbeam (19)	0.70	0.12	0.18 (-)	0.04	0.57 (-)	0.08	0.32 (-)	0.07
Hazel (3)	0.89	0.03	0.82	0.02	1.68	0.06	1.17	0.04
Others (6)	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	

August, red squirrels fed intensively on early maturing hornbeam seeds, whereas grey squirrels primarily foraged on maturing acorns, although some fed on hornbeam seeds in late summer (Wauters *et al.*, 2001). This points to a difference in food preference between the species, but, since grey squirrels in other woodlands 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 crops are poor, and/or when their densities increase. The study by Wauters *et al.* (2001, 2002a) was too short to investigate effects of annual changes in tree seed crops, thus food resource availability, or fluctuating squirrel densities 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 general, the studies show that, both squirrel species feed on a large variety of food items in spring and early summer, and tree species niche width is larger in summer than in other seasons. Most of these spring-early summer food resources (buds, shoots, tree flowers, caterpillars, fungi or insects found on or under the bark of dying branches) are abundant but their availability is limited in time. Hence it is unlikely that competition for such resources in spring and summer affect the squirrels' fitness. Both congeners used small-seeded trees less than expected by chance (maple, ash and hornbeam) in autumn-winter and showed a preference for oak although grey squirrels foraged in oaks more frequently than reds (63% against 43%, Tab. 1), and consequently, niche width of grey squirrels was again smaller than that of red squirrels (grey squirrels 0.24 ± 0.09, red squirrels 0.43 ± 0.13, from Wauters *et al.*, 2002a). Red squirrels selected walnut trees (Tab. 1) and cached large numbers of them for use in late winter-spring (Wauters *et al.*, 2001, 2002b). Grey squirrels also regularly fed on walnuts and black walnuts but did not use walnut trees more than expected. Overall, there was a high degree of habitat niche overlap in the mixed species study site (around 70%), and we suggest that the differences described result from individual species food preferences rather than niche segregation as a result of interspecific competition (Wauters *et al.*, 2002a). This view is supported by the fact that red squirrels do not show any major shifts in their diet in the presence of grey squirrels compared to non-sympatric populations (Wauters *et al.*, 2001).

Finally, studies of allopatric as well as sympatric grey and red squirrels in Europe indicate that the grey squirrels species feeds on acorns more intensively than red squirrels (Moller, 1983; Gurnell, 1987; Wauters and Dhondt, 1987; Wauters *et al.*, 1992; Kenward and Holm, 1993). There is also some evidence that grey squirrels may be able to utilise and digest acorns more efficiently than red squirrels (Kenward and Holm, 1993). Together with the fact that grey squirrels usually live at densities two to four or more times high than red squirrels in deciduous woodland

(Gurnell 1987; Gurnell *et al.,* 2004; Wauters *et al.,* 2004), this giving them an advantage over red squirrels in mixed deciduous woods containing a preponderance of oak trees. Intensive feeding on acorns by grey squirrels is a form of exploitation competition of a food-resource shared with red squirrels, but it also implies that the invasive species will require alternative food supplies when acorn-crops are depleted (as succeeds in many years by late winter, Gurnell 1993) or in woodlands without oak. Since grey squirrels also occupy mixed deciduous woods with no or few oaks and replace the native congener also in these habitats (e.g. Wauters *et al.,* 1997a, b), they must have a competitive advantage in all types of broadleaf woods.

4. Competition for cached food

Both red and grey squirrels scatterhoard seeds of broadleaf trees in autumn, and recover a large amount of their caches between early winter and late spring (Gurnell, 1987; Thompson and Thompson, 1980; Stapanian and Smith, 1984; Wauters and Casale, 1996; Tamura *et al.,* 1999; Steele *et al.,* 2004). Red squirrels prefer tree seeds to other foods, and animals that feed intensively on cached seeds loose less weight and survive better over spring-early summer than those that do not (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). To assess whether grey squirrels deplete seeds cached by red squirrels we compared energy-intake from feeding on cached seeds between the red-only and red-grey study sites; and related hoard recovery by red squirrels to the amount of core-area overlap with grey squirrels in the mixed species site (Wauters *et al.,* 2002b). Red squirrels cached similar quantities of seeds, in terms of total seed energy-content at both the red-only and red-grey sites. There was no evidence, therefore, that red squirrels stored more seed-energy when grey squirrels were present, and in this respect they do not appear to adapt to the presence of the congener. Their daily energy-intake from feeding on cached was also similar in winter (January – February) and spring (March – April) (Wauters *et al.,* 2002b). However, the number of cached seeds squirrels recovered over the January-April period was nearly twice the amount in the red-only site than in the red-grey site. In energy terms, this resulted in a 99.8% recovery of cached seed per year in the red-only site compared with 66% in the red-grey site (Wauters *et al.,* 2002b). Since grey squirrels were observed stealing hazelnuts and walnuts cached by red squirrels, this decrease at the red-grey site seemed 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. Furthermore, the average daily energy-intake per red squirrel from the consumption of recovered seeds in winter was not related to the percentage of interspecific core-area overlap with grey squirrels (r = -0.07, n = 14, P = 0.81; Fig. 2a). However, in spring, when caches became depleted,

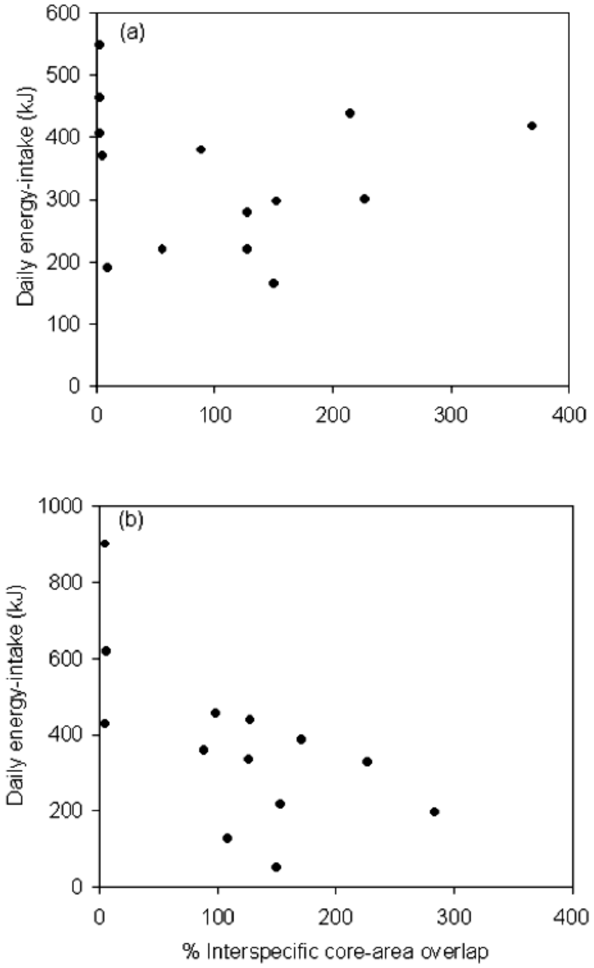

Figure 2a, b – Relationship between the % of core-area overalp of red by grey squirrels and the daily energy intake (kJ) of consumption of recovered seeds by red squirrels: (a) winter, (b) spring. Dots indicate individual red squirrels monitored in each season (after Wauters *et al.*, 2002b).

there was a significant negative association between daily energy intake by red squirrels and percentage interspecific core area overlap (r = -0.65, n = 13, P = 0.02; Fig. 2b). This was associated with a reduced body mass) in spring (Wauters *et al.*, 2002b). This is what we expected would occur if depletion of red squirrels caches by pilfering grey squirrels increased through time. We should note that energy consumption of cached seeds by red squirrels in this study was not associated with intraspecific (red-red) percentage core-area overlap. These studies show that, in woodlands were both species coexist, and even at relatively low grey squirrel densities, red squirrels that share most of their home range core-area with grey squirrels have to contend with a more rapid depletion of cached food resources than those that have little core-area overlap. Also, intraspecific competition for scatterhoarded seeds was less intense than interspecific competition. Since pilfering significantly reduced the body mass of red squirrels in spring, it probably reduced red squirrel fitness (see Wauters *et al.,* 1995); hence, it is likely to be an important mechanism in the replacement of red by grey squirrels.

CONCLUSIONS

We conclude from these studies on activity patterns, behaviour, diet, habitat niche width and niche overlap of red and grey squirrels in deciduous woodlands with a high tree species diversity that there is no small-scale habitat partitioning between the two species. Hence, in contrast with natural communities of sympatric tree squirrels (e.g. Emmons, 1980), there is no evidence for niche partitioning between red and grey squirrels in any of the niche parameters examined. This suggests that the red squirrel is unable to adapt to avoid competition with the grey squirrel when resources become limiting and this has a detrimental effect on red squirrel fecundity, residency and recruitment (Gurnell *et al.,* 2004). Interspecific competition seems to occur mainly for those food resources that affect the fitness of squirrels at crucial periods of the year, such as cached tree seeds in winter and spring. Also, the greater use of acorns by grey squirrels gives the invasive species an advantage over red squirrels in mixed deciduous woods, especially with a preponderance of oaks. This is supported by studies in Britain and Italy that show that co-existence of the two species in mixed deciduous woodlands is of short duration (e.g. less than 3-5 years) because grey squirrels have a competitive advantage that results in the local extinction of red squirrels (Gurnell, 1987, 1996a; Kenward and Holm, 1993; Skelcher 1993; Wauters *et al.,* 1997a; Kenward *et al.,* 1998). Based on these findings and modelling studies, it is predicted that there will be a dramatic increase in grey squirrel population size in north Italy once they spread into the continuous deciduous forests in the Prealps in Piedmont and parts of Lombardy (Lurz *et al.,* 2001; Tattoni *et al.*, 2005). This has serious implications for red squirrel conservation in Italy, and in Europe as a whole (Genovesi and Bertolino, 2001; Bertolino and Genovesi, 2003).

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