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The foraging behaviour and diet of red squirrels *Sciurus vulgaris* receiving supplemental feeding

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The effect of *ad libitum* supplemental feeding upon the diet and foraging behaviour of red squirrels *Sciurus vulgaris* was studied in a coniferous habitat during May 1994 - July 1996. Although supplemental feeding in the form of peanuts was widely available, the animals continued to exploit natural foods such as pine seed, buds and flowers. The degree to which pine seed was exploited was a function of pine cone availability. In contrast, peanut consumption was not correlated with peanut availability, but was determined by the abundance of pine cones. During late winter and spring when seed was becoming scarce, peanuts contributed 30-56% of the dietary items. In addition, increasing amounts of alternative 'low energy' foods such as buds and flowers were also exploited. These foods are calcium rich and their ingestion would compensate for the high phosphorus content of peanuts. The nutritional composition of peanuts appears to have restricted the degree to which they could be included in the diet. Nevertheless peanuts were an important dietary component, and seasonally contributed 25-181% of the animals' basic daily energy requirements. Supplemental feeding was associated with relatively large amounts of activity occurring on the ground (annual mean estimates were 47 and 50% of total foraging time). The animals continued to exhibit 'scatter-hoarding' behaviour, with peanuts accounting for 90% of the identified cached items. This stored resource could satisfy 344 (1994/95) and 198 (1995/96) days of the animals' basic energy requirements.

Key words: diet, foraging behaviour, red squirrel, Sciurus vulgaris, supplemental feeding

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The abundance of tree seeds is a major influencing factor on red squirrel *Sciurus vulgaris* population density (Andrén & Lemnell 1992, Lurz, Garson & Rushton 1995), reproductive success (Kenward & Holm 1993, Wauters & Lens 1995) and survival rates (Gurnell 1983, Wauters & Lens 1995). Tree seed availability varies seasonally and between years (Mollar 1983), and in years when seed is relatively scarce, a marked decline in red squirrel numbers can occur (Gurnell 1983, 1987). Red squirrels scatter-hoard excess foods and these stores are used to overcome periods of food scarcity (Tittensor 1975, Wauters, Swinnen & Dhondt 1992). An intensive use of high-energy cached food items in spring has been shown to be positively correlated with several fitness components in natural populations of red squirrels (Wauters, Suhonen & Dhondt 1995).

During the last sixty years, the geographical distribution of the red squirrel has retracted sharply on mainland Britain. This is largely a result of inter-specific competition with the introduced North American grey squirrel *Sciurus carolinensis* (Lloyd 1983, Skelcher 1997). Research has shown that differences in foraging efficiency are involved in the replacement of red by grey squirrels (Kenward & Holm 1993, Skelcher 1997). In an attempt to divorce red squirrel populations from variation in natural food supplies and competition from grey squirrels the use of supplemental feeding programmes using specialised 'red only' hoppers has been suggested (Gurnell & Pepper 1993, Pepper 1993, JNCC 1996).

The effect of supplemental feeding upon red squirrel reproduction, survival and patterns of population density have been studied in detail (J.L. Holm, unpubl. data 1991, P.W.W. Lurz, unpubl. data 1995, Magris, Morris & Gurnell 1997). However, the extent to which supplemental feeding influences dietary composition and foraging behaviour has not been examined fully. The present paper details the effect of long term *ad libitum* supplemental feeding upon the diet, foraging and scatter-hoarding behaviours of red squirrels in a coniferous habitat. The importance of the relative nutritional values of natural and supplemental foods upon dietary composition is examined. Finally, the potential implications of providing supplemental feeding in woodlands containing sympatric red and grey squirrel populations are outlined.

Methods

A 40-ha study area was selected within the National Trust reserve at Formby, West Lancashire, England. The woodland was dominated by mature stands of Scots *Pinus sylvestris* and Corsican pine *Pinus nigra*. These blocks were interspersed by small patches of lodgepole pine *Pinus contorta* and sycamore *Acer pseudoplatanus* dominated mixed deciduous scrub. The reserve received approximately 250,000 visitors each year, many of whom came specifically to feed the red squirrels. The general public often either brought supplemental foods with them or purchased peanuts at the reserve office where in excess of 2,500 kg were sold annually. This form of supplemental feeding had been taking place for over a decade prior to my study.

Focal sampling of randomly selected animals was carried out each month from May 1994 until July 1996 to quantify squirrel foraging behaviour. Squirrels within the reserve had been individually marked with a tattoo number in their right ear as part of a parallel live-trapping programme which was examining reproductive output and changes in body condition. Unfortunately these marks could not be read on a foraging animal and consequently the identity of each focal animal was not known. However, as the site contained a large adult population with a density of 3.7 ± 0.11 (SE) animals/ha, (N = 4 years; C.M. Shuttleworth, unpubl. data 1997) pseudo-replication of samples is unlikely to have been significant. Behaviour was divided into the following categories:

- Searching: Searching the immediate surroundings, e.g. moving aside foliage or fallen leaves;
- Travelling: Moving at speed through the tree canopy or across the woodland floor;
- Feeding: Handling and consuming food items;
- Caching: Burying food items;
- Cache recovery: Unearthing a buried or cached food item;
- Grooming: Cleaning or scratching the coat;
- Aggression: Tail waving, aggressive vocalisations, chasing behaviour;
- Resting: Periods of inactivity between bouts of foraging;
- Other: Sniffing at branches, scent marking (face wiping and anal dragging).

A focal sampling technique similar to those employed by Tonkin (1983) and Wauters & Dhondt (1987) was used. An individual was randomly selected and its behaviour recorded until it was either lost or disturbed by the observer. During each period of observation, the animal's behaviour and foraging position (ground, trunk or canopy) were noted every 30 seconds. Periods of data lasting less than five minutes were not used in further analysis, and individual observations were limited to a maximum of three hours. The total duration of sample times averaged 1,120 ± 80 (SE) minutes (range: 660-2,110 minutes) per month and the number of foraging red squirrels observed ranged within 30-78.

Within each month the relative amounts of time which the animals spent active on the ground or in the woodland canopy were determined. Similarly, the proportion of time devoted to different activities, such as searching for food could also be calculated. During the focal sampling, every food item which was consumed, cached or unearthed was recorded and identified if possible. For analytical purposes, items where classified under general headings such as 'Cone', 'Bud' and 'Unidentified', hence both fungal mycelium and fruiting bodies were combined as 'Fungi'. Collection of these data allowed changes in dietary composition to be monitored through the seasons. Variation in the diet could then be compared with the relative availability and abundance of different food types.

Estimates of cone production were made by counting the fallen and exploited cones within fixed quadrats of 4 and 20 m^2 (see Gurnell & Pepper 1994). The volume of supplemental foods sold on the reserve was correlated to visitor numbers ($r = 0.866$, $N = 8$, $P < 0.02$), and consequently monthly total visitor numbers were used as an index of peanut availability. Determining the chemical and calorific content of different food items was beyond the scope of the study and consequently these data were obtained from the published literature (Evans 1960, Wauters & Casale 1996). The energy values of foods were used to assess the relative importance of different foods in satisfying the animals daily energy requirements. The total calorific value of the items cached annually was calculated from the number of each food type cached per hour and the seasonal duration of daily activity. Activity patterns varied seasonally: 5 hours (December-February), 9 hours (March-May), 11 hours (June-August) and 8 hours (September-November) (C.M. Shuttleworth, unpubl. data 1996).

Results

Foraging behaviour

The population showed pronounced seasonal changes in foraging behaviour with 47-50% of annual activity spent on the ground. The proportion of daily foraging time spent in the woodland canopy peaked during the late summer and autumn months (Fig. 1), and was strongly correlated with the number of pine cones found eaten per squirrel ($r_s = 0.49$, $N = 24$, $P < 0.01$). An increasing amount of time spent foraging in the canopy was associated with a higher proportion of feeding behaviour ($r_s = 0.75$, $N = 24$, $P < 0.01$) and reduced searching activity ($r_s = -0.37$, $N = 24$, $P < 0.05$) by the animals whilst they were in the trees. As the proportion of time spent active in the canopy declined, the frequency of resting / grooming ($r_s = -0.39$, $N = 24$, $P < 0.05$) shown by animals whilst in the woodland canopy increased (Fig. 2). There was also a tendency for animals to travel less when in the canopy within months when they were spending a large amount of their time in the trees (see Fig. 2) although this was not statistically significant ($r_s = -0.11$, $N = 24$, $P > 0.05$). The availability of pine seed was relatively high during these times.

During the months when the red squirrels spent the lowest amount of time in the canopy it was observed that whilst in the canopy the animals consumed fewer cones per hour than at other times of the year ($r_s = -0.48$, $N = 24$, $P < 0.05$). Casual observations indicated that the remaining cone crop had progressively become smaller and more fragmented. In the summer and autumn months when the availability of both seed and supplemental foods was high, the squirrels spent a relatively large amount of their foraging time in the tree tops, and seed made up the largest proportion of the diet (Fig. 3). The proportion of foraging time spent on the ground appeared to be independent

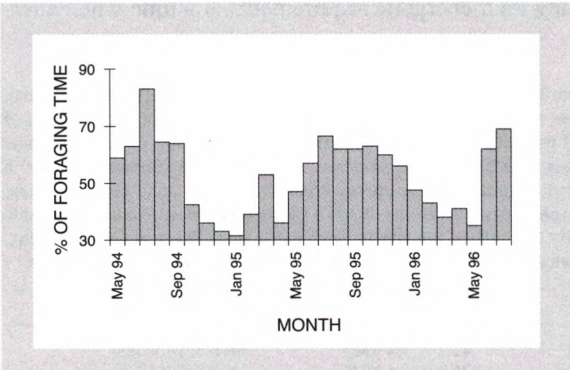

Figure 1. Monthly percentage of total foraging time spent in the woodland canopy during May 1994 - July 1996.

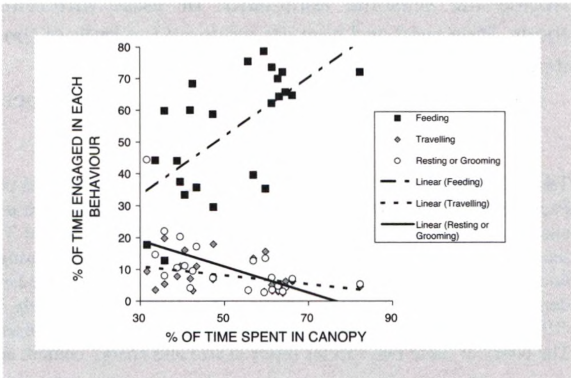

Figure 2. Behaviour of foraging animals in relation to the amount of time spent in the woodland canopy. The y-axis provides the proportion of time that animals spent engaged in various behaviours whilst in the tree tops. Three regression lines are plotted: Feeding: $y = 5.1 + 0.93x$, $r^2 = 0.42$; Travelling: $y = 15.3 - 0.14x$, $r^2 = 0.13$; and Resting: $y = 31.5 - 0.41x$, $r^2 = 0.36$.

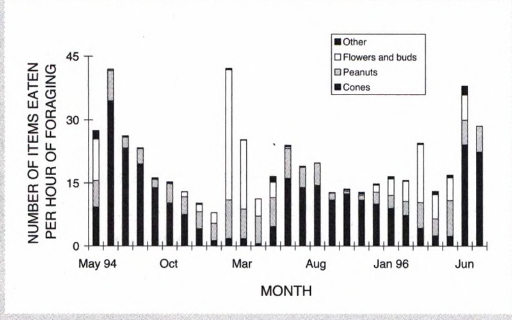

Figure 3. Monthly changes in the diet of red squirrels during May 1994 - July 1996.

of the abundance of peanuts (r_s = -0.25, N = 24, N.S.). However, the proportion of time that animals spent feeding whilst they were on the woodland floor was greatest in the summer months (22 ± 4% (SE), N = 8 months) than in the other seasons (Autumn: 8%, Winter: 11%, Spring: 15%; Mann-Whitney U-test: U = 19; P < 0.05). The summer months coincided with the peak in the abundance of peanuts, a factor which enabled the animals to obtain peanuts more rapidly and to spend a larger proportion of their time feeding.

Dietary composition

Natural foods accounted for the bulk of the items consumed by the red squirrels (see Fig. 3). Conifer seed, shoots, buds and flowers were all exploited, with fungi (22 species), and a small amount of animal matter in the form of insects, e.g. *Andricus kollari* and *Andriscus quercuscalcis* grubs, bone and bird's eggs also being taken. Dietary composition reflected the seasonal abundance of these different foods. Pine seed and peanuts made up the bulk of the items in the diet (see Fig. 3).

The consumption (number of items handled per hour) of both pine cones (seed) (one way ANOVA: $F_{3,23}$ = 22.52, P < 0.001) and peanuts (one way ANOVA: $F_{3,23}$ = 6.86, P < 0.02) was highly seasonal. Utilisation of seed peaked in the summer and autumn months when cones accounted for 70% of the total number of identified food items exploited. Through these two seasons, conifer seed provided the animals with the largest proportion of their energy intake (Table 1, see Fig. 3). Conifer seed was very heavily exploited and data from cone quadrats showed that the squirrels consumed 96.7 and 99.5% of the cone crop in 1994/95 and 1995/96, respectively. Casual observations indicated that very few two-year-old cones remained in the canopy in the early summer. In late winter and spring when pine seed was scarce, peanut intake increased (see Table 1), and contributed up to 56.6% of the items consumed (see Fig. 3). The number of peanuts consumed in each month was not correlated with the availability of peanuts (r_s = 0.1, N = 24, P > 0.05). Despite the increased abundance of peanuts during the summer, the reduction in the proportion of foraging time spent on the forest floor (see Fig. 1) was more strongly influenced by the peak in the availability of pine seed at that time (see Fig. 3).

The animals not only responded to a late winter/spring decline in the availability of conifer seed by consuming more peanuts, but also included more alternative natural foods such as tree buds and flowers in the diet (see Fig. 3). When buds were being selected in earnest, relatively large amounts were consumed, e.g. 120 in 25 minutes. Conifer buds are relatively bulky foods which are low in energy (19 kJ/g dry weight) and the energetic returns per gram fresh weight obtained from buds would be considerably lower than those of tree seed or peanuts. However, the large volumes consumed in late winter/spring would have assisted the animals in obtaining their energetic requirements at a time when alter-

Table 1. Amount of energy derived from peanuts and pine seed per hour (kJ) of foraging time (± SE; % of daily energy requirements). Peanut energy was estimated from the number of peanuts eaten per hour ∗ 0.36 g dry weight ∗ 31.8 kJ per g dry weight. The amount of energy obtained from pine seed was calculated using a value of 3.48 kJ per cone. The amount of energy obtained from peanuts and pine seed was calculated using seasonal activity patterns during spring: 9 hours (March-May); summer: 11 hours (June-August), autumn: 8 hours (September- November); and winter: 5 hours (December-February). Estimates of the energy content of peanuts and pine seed were derived from Evans (1960) and Wauters et al. (1992), respectively. Daily energy requirements of 365 kJ were taken from Wauters & Casale (1996). Only 2% of the study area was Lodgepole pine and consequently the bulk of the conifer seed came from Scots or Corsican pine. The cones of these two species differ in size and energy content and hence the 3.48 kJ per cone should be viewed as a broad estimate.

Year	Item	Spring	Summer	Autumn	Winter
1	Peanuts	78.5 ± 1.7 (177)	50.9 ± 15.7 (140)	41.1 ± 9.4 (82)	66.1 ± 19.1 (83)
1	Pine seed	8.0 ± 3.8 (18)	89.5 ± 3.6 (246)	36.9 ± 6.4 (74)	8.4 ± 2.9 (11)
2	Peanuts	71.2 ± 8.5 (160)	65.7 ± 15.3 (181)	12.7 ± 3.4 (25)	35.9 ± 1.7 (45)
2	Pine seed	10.6 ± 2.1 (24)	52.2 ± 2.1 (144)	40.3 ± 1.7 (81)	30.5 ± 2.9 (38)

native 'high energy' foods such as tree seeds were scarce.

In Belgium, it has been estimated that red squirrels require 305-365 kJ of energy per day (Wauters et al. 1992, Wauters & Casale 1996). The Formby animals are significantly larger (mean shin length 74 mm) than those found in the Belgian studies (mean shin length 72 mm) and their energy requirements are therefore likely to be closer to the upper value of 365 kJ. At Formby there was considerable seasonal variation in rates of energy acquisition from peanuts and tree seed (see Table 1). These figures suggest that animals would be required to forage for 2.6-6.9 hours in order to satisfy their energy needs. The exploitation of buds and flowers by red squirrels during late winter and spring would have enabled the animals to obtain their energy requirements more rapidly than the percent energy figures in Table 1 suggest.

Scatter-hoarding behaviour

Red squirrels at Formby continued to show the scatter-hoarding strategy typical of the species (see Rice-Oxley 1993, Wauters & Casale 1996). Pine cones, peanuts, walnuts and hazelnuts were all buried, whilst fruit, fungi and bones were cached in the canopy. Such items were wedged in the forks formed by small branches and twigs. Flowers, buds and shoots were only very occasionally cached in the canopy. Fallen cones, those discarded or accidentally dropped by feeding animals were frequently cached in addition to those deliberately removed from the canopy and carried down to the ground.

There was a strong seasonal pattern in the frequency with which items were cached (number of items per hour; one way ANOVA: $F_{3,23} = 3.37$, $P < 0.05$) and recovered (one way ANOVA: $F_{3,23} = 14.47$, $P < 0.001$) per unit foraging time (Figs. 4 and 5). Caching peaked in the autumn and winter months but declined through and into the spring and summer (Table 2). In contrast, cache recovery was most frequent in the winter and spring. Peanuts made up the bulk of the identified items which were cached, and over two years accounted for 90.0 ± 2.7 % (SE) (N = 24) of the identified items. The recovering rate of peanuts (mean: 0.73 ± 0.10 (SE) per hour, N = 24 months) was lower than the caching rate (mean: 1.54 ± 0.27 (SE) per hour, N = 24 months; Wilcoxon's test for matched pairs: T = 62, $P < 0.002$). In contrast, the mean rates of cone caching (mean: 0.14 ± 0.04 (SE) per hour, N =24) and recovery (mean: 0.12 ± 0.02 (SE) per hour, N = 24) were similar (Wilcoxon's test for matched pairs: T = 92, $P > 0.05$).

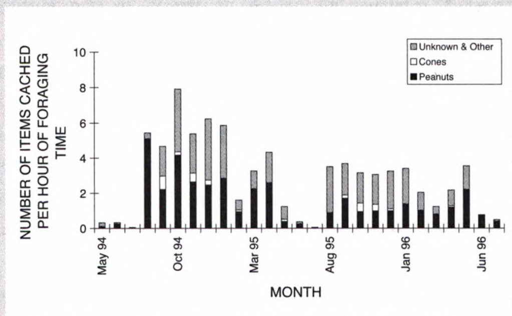

Figure 4. Number of items cached per hour of foraging time during May 1994 - July 1996.

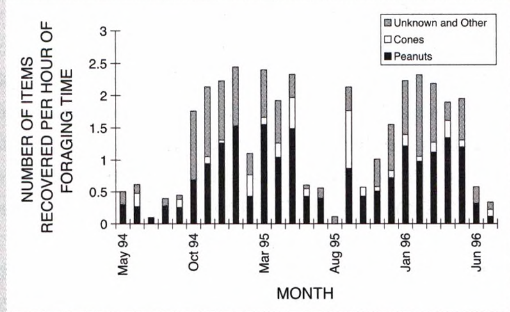

Figure 5. Number of items recovered per hour of foraging time during May 1994 - July 1996.

The relative frequencies with which different foods were cached or recovered showed specific seasonal patterns. The majority of pine cones were cached (number of items per hour) in the autumn and winter months (one way ANOVA: $F_{3,23} = 16.85$, $P < 0.001$). Cones were still relatively abundant in the canopy at this time. Cone recovery tended to occur later in the year during the spring months, however, this seasonal variation was not statistically significant (one way ANOVA: $F_{3,23} = 2.49$, $P = 0.085$). The frequency with which cones were uncached increased as the

Table 2. Number of items cached or recovered per hour of foraging time (± SE) during the seasons described in the legend of Table 1.

Year		Spring	Summer	Autumn	Winter
1	Cache	2.9 ± 0.9	3.4 ± 1.9	6.0 ± 1.0	4.6 ± 1.5
1	Recover	2.2 ± 0.1	0.4 ± 0.1	1.5 ± 0.5	1.6 ± 0.3
2	Cache	2.5 ± 0.7	1.3 ± 1.1	3.2 ± 0.1	3.0 ± 0.4
2	Recover	2.0 ± 0.1	0.2 ± 0.0	1.0 ± 0.2	2.0 ± 0.2

number of cones consumed within the canopy declined ($r = -0.356$, $N = 24$, $P < 0.05$).

Combining the frequency of caching (see Table 2) and information on the duration of daily activity patterns through the year suggests that each individual would have cached 12,280 and 7,060 items over the course of the two respective years of study. The volume of cached peanuts alone (90% of identified items) would represent a stored energy resource of 125,921 kJ and 72,436 kJ. These stores would satisfy the animals basic energy requirements for between 344 and 198 days.

Discussion

In the two years of study, the Formby red squirrels spent a lower proportion of their active time within the woodland canopy (1994: 50%; 1995: 53%) than has been recorded in studies elsewhere (67%, Tonkin 1983; 90%, Wauters & Dhondt 1987). The presence of supplemental foods on the woodland floor will have contributed to this difference. However, it was the abundance of pine seed rather than peanuts which was the primary influence upon foraging behaviour. Foraging in the canopy was a function of the abundance of pine seed rather than availability of peanuts. This finding is likely to be a function of the relative chemical compositions of these foods.

The nutritional composition of foods has been shown to be an important factor governing the dietary composition of tree squirrels (Rajala & Lampio 1963, Havera & Smith 1979, Capretta, Farentinos, Littlefield & Potter 1980). Both pine seed and peanuts satisfy the 10-12% crude protein and 16-17% crude fat 'minimum maintenance' requirements of red squirrels which were determined by Pulliainen (1984). However, peanuts contain high levels of both fat (ca 45% dry weight) and phosphorus, as well as enzymes which inhibit the absorption of amino acids (Evans 1960, J. Gurnell, G. Peck, H. Pepper & J. Davies, unpubl. data 1990). The chemical composition of peanuts is likely to have restricted the volume which the animals could consume. Similar problems with the nutritional value of supplemental foods have been reported in other tree squirrel studies (Vartio 1949, Havera & Nixon 1980, Klenner & Krebs 1991). They may explain why the animals at Formby continued to use low energy 'secondary' natural foods, e.g. buds, flowers and fungi (see Fig. 1) particularly in late winter when pine seed was scarce. Conifer buds are a valuable source of calcium and their inclusion in the diet would help restore any nutritional imbalance produced by increased consumption of phosphorus rich peanuts. Limits upon peanut use would also explain why a larger proportion of cached cones was recovered relative to the lower recovery rate of peanuts (see Figs. 4 and 5).

It is clear that despite their nutritional limitations, supplemental foods such as peanuts and sunflower seeds are a valuable energy source for red squirrels, and in one study provided 40-50% of the 305-365 kJ daily requirements of red squirrels (Magris et al. 1997). In my study, peanuts provided the animals with 25-181% of their basic daily energy requirements. The chemical composition of such foods is, however, likely to restrict the effectiveness of feeding regimes. This has been illustrated where supplemental feeding has failed to prevent red squirrel population declines when tree seed is scarce (P.W.W. Lurz, unpubl. data 1995, Shuttleworth 1997). In habitats where red and grey squirrels are sympatric the caching behaviour of red squirrels will also be a factor to note when considering use of feeding programmes.

The results of focal sampling suggest that each individual would have cached between 7,060 and 12,280 items, respectively, in the two full years of study. This volume of food is considerably larger than the 2,300 cached items recorded by Wauters & Casale (1996) in a coniferous population which did not receive supplemental feeding. At Formby, approximately 90% of the identified cached items were peanuts (11.4 kJ per item), whereas caches in the study area used by Wauters & Casale (1996) consisted of 1,208 cones from Scots and Corsican pine (3.48 kJ per item), 650 acorns from oak *Quercus robur* (22.47 kJ per item) and 465 nuts from beech *Fagus sylvatica* (3.14 kJ per item). Consequently, in energy terms, the animals receiving supplemental foods cached 4-7 times as much as those in the Belgian study.

The scatter-hoarding behaviour of supplementary fed animals has implications for the effective use of 'red only' feeding hoppers. These designs restrict direct access to supplemental foods by grey squirrels (Pepper 1993, Gurnell & Pepper 1993), but they do not prevent the animals from exploiting the caches of red squirrels. The problem of cache piracy may be exacerbated by the spatial distribution of the caches. For example, Rice-Oxley (1993) found that 63% of all items collected, but not immediately consumed, by red squirrels from feeding hoppers (N = 266) were cached within 12 m of the hopper. This behaviour effectively concentrates the cached resource therefore making the location of such material easier. The exploitation of supplemental foods by grey squirrels would obviously be counter productive. It is therefore essential that systematic grey squirrel control is integrated into supplemental feeding programmes.

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