Space use and foraging movements in the American red squirrel
(Tamiasciurus hudsonicus)

Simon Benhamou *

C.N.R.S. - I.N.C. F-13402 Marseille Cedex 20, France
Accepted 20 September 1995

Abstract

This study deals with the movements of two American red squirrels (Tamiasciurus hudsonicus) in their home ranges from late spring to early autumn in a deciduous-coniferous forest in Québec. During 70 six-hour tracking sessions, the type of behaviour exhibited at any place, and its terrestrial or arboreal occurrence, were recorded. Spatio-temporal structure of the squirrels' home ranges were analysed in relation to vegetation type and food availability. Although American red squirrels are known to be mainly adapted to coniferous forests, they also exploit deciduous areas when these areas become productive. Half of the squirrels' activity time was devoted to feeding or to searching for food, and a third was devoted to moving about. Movements were performed mainly on the ground, with a rate of about 0.5 km per activity hour, and appeared to be mainly organized around the locations of food caches and food-providing sites.

Keywords: Caching; Foraging; Home range; Movement; Red squirrel; Territory

1. Introduction

The American red squirrel (Tamiasciurus hudsonicus) is a medium-size, diurnal, solitary, year-round active, and usually territorial rodent. It is widespread in boreal forests of northern America, and it specializes in exploiting coniferous cones, although numerous seeds and buds of deciduous trees, berries and fungi are also present in its diet to a large extent in mixed woodlands (e.g., C.C. Smith, 1968, 1970; M.C. Smith, 1968; Ferron et al., 1986). One particularly interesting aspect of space use and foraging of red squirrels is that most movements are centred around food caches (Gurnell, 1984), which are exploited during the winter and spring, and made during summer and autumn.

Depending on whether food items are cached together in a main cache or scattered one by one in
numerous caches, animals are usually classified as larder- or scatter-hoarders (e.g., see Smith and Reichman, 1984). In dry northwestern coniferous forests, red squirrels typically exhibit larder-hoarding: each individual fills one single underground cache, called a midden, on which a large amount of scales, cores and remnants of eaten cones accumulate (as the squirrel usually consumes the cones while perched just above the midden), in the centre of its territory (M.C. Smith, 1968; Rusch and Reeder, 1978). The midden seems maintain the high humidity required for conserving conifer cones in suitable conditions (Finley, 1969). C.C. Smith (1968, 1981) interpreted territoriality in red squirrels as enabling the resident individual to have an exclusive access to the food available on its territory (in so far as the territory defense is efficient), and showed that the social organization of red squirrels defending individual territories around a large central cache would be the most economic way to share space and resources among the squirrel population. In wet eastern coniferous forests, however, conifer cones do not require midden storage, and red squirrels exhibit an intermediate form of caching lying somewhere between larder-hoarding and scatter-hoarding: most caches contain only a small number of food items, and are usually distributed throughout the territory (Hurly and Robertson, 1990; Dempsey and Keppie, 1993). In pure deciduous forests, red squirrels were often shown to be non-territorial (Layne, 1954; Rusch and Reeder, 1978) probably because of the presence of grey squirrels (Sciurus carolinensis) which would pilfer the deciduous seeds harvested by red squirrels (see also Riege, 1991). Lair (1984) showed that, in a mixed coniferous-deciduous forest in Québec, where grey squirrels are absent, red squirrels are territorial, at least during the whole period when cacheable food is available (see also Kemp and Keith, 1970), and exhibit the intermediate form of caching described above.

The field work of the present study was conducted in the same deciduous-coniferous forest in Québec. My aim was to determine how a red squirrel uses space and organizes its movements in relation to the locations of food caches. In this area, the eastern chipmunk (Tamias striatus) was the only species which could, and only to a slight extent, compete for food with red squirrels. It was therefore possible to study how an individual red squirrel freely (i.e., without interspecific competition from grey squirrels) allocates its foraging and caching effort between coniferous and deciduous areas.

Numerous studies have already focused on space use and foraging at the population level (see the papers previously cited; for more recent accounts, see Sullivan, 1990; Klenner and Krebs, 1991; Klenner, 1991; Koford, 1992; Sullivan and Klenner, 1992). These studies are interesting from the ecological point of view, but give little information on the behavioural strategies actually used at the individual level. As I was particularly interested in determining how a red squirrel can modify its space use and foraging behaviour to track environmental changes, I deliberately chose to focus on one single individual during the whole field study (in fact two individuals had to be studied successively; see Materials and methods). I acknowledge that this is somewhat unusual, but concentrating all the time available on one or a few individuals rather than dissipating it among many was the only means of getting accurate information on individual movement behaviour in a species whose gross behavioural and ecological traits are now well known at the population level. Obviously, this can provide only a limited sample of the behavioural patterns displayed by this species. Nevertheless, studies conducted in eastern Canada have shown that there exists considerable intra-individual rather than inter-individual variations in the behaviour of this species (Ferron et al., 1986; Hurly and Robertson, 1990; Dempsey and Keppie, 1993). The behavioural patterns observed in the present study are therefore likely to represent a large part of the whole set of patterns displayed by this species in the eastern part of its range.
2. Materials and methods

The study area was a 2.2 hectare mixed deciduous-coniferous woodlot located in the ‘Station forestière expérimentale de Duchesnay’, about 50 km northwest of Québec city. A first individual, an adult female which resided on the study area, was tracked from 19 May 1989, just after most snow thawed, to 7 July 1989, the day before she died accidentally. The study area was afterwards occupied by transient squirrels, and then definitely by a young adult female which was tracked from 9 August 1989 to 3 October 1989.

At the beginning of the study, about 500 tapes, labelled with a two-letter code, were tied around tree-trunks. The study area was accurately mapped by recording the relative locations of the marked trees, using a sighting system (enabling bearings of trees to be measured to the nearest half-degree) together with a thirty-meter measuring tape (enabling distances between trees to be measured to the nearest half-meter). The species names of the marked trees were systematically noted to sample the vegetation structure. Four vegetation areas were distinguished (Fig. 1): CF (conifers), YB (yellow birch), SM (sugar maple), and RM (red maple). The main tree species were balsam fir (Abies balsamea), black spruce (Picea mariana), white spruce (P. glauca), red spruce (P. rubens), yellow birch (Betula alleghaniensis), canoe birch (B. papyrifera), sugar maple (Acer saccharum), red maple (A. rubrum), striped maple (A. pensylvanicum), mountain maple (A. spicatum), and American beech (Fagus grandifolia).

The focal squirrel was tagged with a radio-transmitter set in a neck-collar serving as a loop antenna. The whole apparatus weighted about 8 g. Radio-tracking was performed on foot with one receiver, allowing the animal to be relocated when it disappeared from sight. The squirrel quickly got used to the presence of the observer who could stay at a few meters from it. Its successive locations were accurately recorded (to the nearest meter and second) by direct sighting with reference to the closest labelled trees, and its behaviour was systematically noted. Nine main behavioural classes were used: (1) random searching (moving very slowly with the nose close to the ground without

Fig. 1. Vegetation structure (trees) of the study area (175 m by 150 m). CF: mainly balsam fir, black spruce and white spruce; partly yellow birch and red maple; scarcely red spruce. YB: mainly yellow birch; partly canoe birch, sugar and red maples, and conifers; scarcely American beech and striped maple. SM: mainly sugar maple; partly red maple, yellow birch and American beech; scarcely conifers and mountain maple. RM: mainly red maple; partly yellow birch, scarcely conifers. The study area was delimited in the southwest by a forestry road that the resident squirrel crossed very rarely.
discovering anything; in most occurrences, this behaviour was likely to correspond to searching for food unsuccessfully); (2) foraging (searching for food successfully or feeding); (3) caching (carrying food to a given cache or caching on the spot); (4) hoarding nest material (collecting and carrying it to an arboreal or underground nest); (5) exploring burrows; (6) territorial warning calls; (7) social interactions; (8) resting (either directly observed or assumed when the squirrel disappeared in an arboreal nest hole or in an underground burrow during more than 10 min); and (9) moving about (mere locomotory behaviour between two specific activity points; unknown behaviour, when the squirrel was concealed by the vegetation, was also assigned to this class). Another behaviour, vigilance (with or without calls), was systematically noted but not analysed because it appeared to be both non-exclusive (it was often performed during feeding) and not specific (it was often impossible to determine whether it was triggered by the observer, a conspecific, a predator, or anything else). The terrestrial or arboreal occurrence of behaviours was systematically recorded.

Tracking sessions started at dawn and lasted about six hours (until midday), corresponding to the period of the highest activity in red squirrels (C.C. Smith, 1968; personal observations). All observations (time, location, behaviour and occurrence level) were dictated in real time into a tape recorder. The successive locations of the squirrel were later transcribed into a computer using a digitizing table with the map of the study area serving as background, and the corresponding times and behavioural codes were transcribed using the keyboard. The whole time period during which the squirrel was accurately located by sight was referred to as the recording time. Activity time was computed as the recording time minus the resting time.

From a behavioural point of view, two periods were distinguished for the first squirrel: (a) late spring, from May 19th to June 17th, during which the squirrel fed almost only on old conifer cones from caches; and (b) early summer, from June 18th to July 7th, during which the squirrel had to search for scattered single seeds because most caches had been emptied (a cache was sometimes discovered by chance). In contrast, the whole study period of the second squirrel (August 9th to October 3rd) was not partitioned because no major behavioural changes were observed during this period.

To determine the space use exhibited by squirrels both qualitatively and quantitatively, the whole study area was divided into $5 \times 5$ m$^2$ quadrats. Every quadrat was assigned to one of the four vegetation areas (CF, YB, SM, or RM; see Fig. 1) and the time spent by each of the two squirrels in each quadrat was computed. Home ranges were determined empirically by counting the number of $5 \times 5$ m$^2$ quadrats in which a given minimum time was spent. Three measurements were taken. The first concerned the 'total size' of the home ranges (maximum observed, except for the very scarce

<table>
<thead>
<tr>
<th>Squirrel</th>
<th>No. of sessions</th>
<th>Track time (h)</th>
<th>Recording time (h)</th>
<th>Activity time (h)</th>
<th>Travelled distance (km)</th>
<th>Activity time in trees</th>
<th>Distance in trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>la</td>
<td>21</td>
<td>125</td>
<td>88</td>
<td>60</td>
<td>29</td>
<td>13% (0-37)</td>
<td>3% (0-21)</td>
</tr>
<tr>
<td>lb</td>
<td>16</td>
<td>91</td>
<td>55</td>
<td>45</td>
<td>20</td>
<td>15% (3-42)</td>
<td>3% (0-10)</td>
</tr>
<tr>
<td>2</td>
<td>33</td>
<td>182</td>
<td>149</td>
<td>143</td>
<td>76</td>
<td>53% (23-75)</td>
<td>13% (1-32)</td>
</tr>
</tbody>
</table>
sallies beyond the forestry road), i.e., the area encompassing 100% of the activity time (computed from the total number of the quadrats which had been at least visited once). The second and the third concerned the ‘usual’ home range size and the ‘core area’ size, determined as the minimum areas containing 95% and 50%, respectively, of the activity time (computed from the minimum number of the most visited quadrats necessary to reach the corresponding percentage of the activity time).

3. Results

3.1. General activity

The global activity times and distances travelled by the two squirrels are given in Table 1. They travelled about 500 meters per activity hour, and moved mainly on the ground. The increase in time spent and distance travelled in trees observed from squirrel #1 to squirrel #2 corresponded to a shift in the food available with the maturation of yellow birch fruit in mid-July, and of conifer cones and sugar maple seeds in mid-August: before the trees became productive (squirrel #1), only 3% of the distance was travelled in trees, and 1/7 of the activity time was spent in trees, whereas the distance travelled in trees reached 13%, and half of the activity time was spent in trees when the trees became productive (squirrel #2). About half of the activity time was spent foraging and a third moving about (Table 2). Squirrels allocated only little activity time to other behaviours.

3.2. Space use pattern

During late spring (squirrel #1a) the activity was mainly concentrated in CF where most of the cone caches were located. From mid-June (squirrel #1b), known caches were empty and the activity was less concentrated in CF as the squirrel wandered in a larger area to search for scattered seeds. Later, the maturation of birch fruit (mid-July) and sugar maple seeds (mid-August) caused the part of the activity time spent in YB and SM to increase (squirrel #2). The part spent in CF remained the largest, however, because the squirrel also started foraging on maturing conifer cones from mid-August onwards (Table 3).

The two squirrels did not exploit their home range uniformly but highly concentrated their activity in some particular areas (Table 3; Fig. 2). In the three cases considered (#1a, #1b and #2), the ratios between the total size and the usual size of the home range was greater than 2. During late spring, the focal squirrel (#1a) spent 95% of its activity time in an area less than a half-hectare, mainly in CF,

<table>
<thead>
<tr>
<th>Squirrel</th>
<th>Random searching</th>
<th>Feeding and searching for food</th>
<th>Caching food</th>
<th>Hoarding nest materials</th>
<th>Exploring burrows</th>
<th>Moving about</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>0% (0–8)</td>
<td>51% (24–72)</td>
<td>0% (0–8)</td>
<td>2% (0–7)</td>
<td>0% (0–1)</td>
<td>34% (22–66)</td>
</tr>
<tr>
<td>1b</td>
<td>5% (1–16)</td>
<td>51% (18–69)</td>
<td>0% (0–1)</td>
<td>2% (0–7)</td>
<td>0% (0–0)</td>
<td>33% (21–49)</td>
</tr>
<tr>
<td>2</td>
<td>9% (1–24)</td>
<td>51% (27–67)</td>
<td>4% (0–24)</td>
<td>0% (0–6)</td>
<td>5% (0–14)</td>
<td>28% (13–72)</td>
</tr>
</tbody>
</table>
Table 3
Space use and home range sizes

<table>
<thead>
<tr>
<th>Squirrel</th>
<th>CF</th>
<th>YB</th>
<th>SM</th>
<th>RM</th>
<th>100%</th>
<th>95%</th>
<th>50%</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>81%</td>
<td>18%</td>
<td>1%</td>
<td>&lt;1%</td>
<td>1.18 ha</td>
<td>0.47 ha (2.3 s)</td>
<td>500 m² (42 s)</td>
</tr>
<tr>
<td>1b</td>
<td>70%</td>
<td>24%</td>
<td>6%</td>
<td>&lt;1%</td>
<td>1.81 ha</td>
<td>0.78 ha (1.5 s)</td>
<td>1300 m² (17 s)</td>
</tr>
<tr>
<td>2</td>
<td>55%</td>
<td>37%</td>
<td>8%</td>
<td>&lt;1%</td>
<td>1.74 ha</td>
<td>0.68 ha (1.7 s)</td>
<td>825 m² (22 s)</td>
</tr>
</tbody>
</table>

The first four columns give the mean percentage of activity time spent in coniferous (CF), yellow birch (YB), sugar maple (SM) and red maple (RM) areas. The last three columns give the minimum areas encompassing 100%, 95% and 50% of the activity time. The values in parentheses refer to the minimum mean times per activity hour which must be spent in a given quadrat to allow it to belong to the minimum area encompassing either 95% or 50% of the activity time.

and 50% in an area of 500 m² only. The core area was compact and located almost exclusively in CF. When this squirrel had to begin randomly searching for scattered seeds because the food caches had been emptied (#1b), the area where it spent 95% of its activity time increased over 3/4 hectare, including a large deciduous part, and 50% of its activity was spent in an area of 1300 m². The core area was not compact any more, and less intensively used (as the core area increased, the mean percentage of the activity time spent per quadrat of the core area decreased). In spite of its scattered pattern, it was however located mainly in CF. The squirrel #2 established its home range on the study area at a moment when new resources occurred at numerous locations. Nevertheless, its space use pattern was not very different from that of squirrel #1b. It spent 95% of its activity time in an area of about 2/3 hectare, including a large deciduous part, and 50% in an area of 825 m². In this case too, the core area was not compact, but scattered mainly in CF. The nests were not located centrally in the home range. They were used mainly for rest and the activity time around them was low.

3.3. Territoriality, social interactions and mating

Red squirrels are able to produce various calls (C.C. Smith, 1978; Lair, 1990). One of them, the ‘rattle’, is often produced spontaneously without a triggering stimulus, and is considered as an advertisement call used by the territory owner to repel potential intruders. The territories of squirrels #1 and #2 were determined from the spontaneous rattles they produced (Fig. 2). A rattle was considered as spontaneous if it lasted about 2 s and was not followed by vigilance behaviour or by social interactions. The spatial patterns of the locations of the spontaneous rattles reflected the space use patterns, indicating that these calls were produced regularly by squirrels (average rate 8.77, 7.13 and 3.55 calls per activity hour for squirrels #1a, #1b and #2, respectively), independently of their locations. This system of global territorial defense by advertisement calls appeared both inexpensive, the territorial owner did not have to patrol along territorial boundaries, and efficient, the social interactions being scarce and lasting usually a few minutes (observed on 2 out of 21 sessions for squirrel #1a, 3 out of 16 sessions for squirrel #1b, and 5 out of 33 sessions for squirrel #2: in all these occurrences, the intruder was driven out of the focal squirrel’s territory; however, on some occasions the focal squirrel was observed not to react to the presence of an intruder in YB or SM).

Mating in red squirrels occurs only once or twice a year: in early spring and for half of the females again in early summer (Lair, 1985), females being in estrus only a few hours on each occurrence. Squirrel #1 was in estrus on June 28th. During this day, her behaviour was unique. Early in the morning, and later, she performed several forays out of her own territory, probably to inform male squirrels owning neighbouring territories that she was in estrus. After each of these external forays,
she was found moving with a male squirrel on her territory. Copulation acts occurred on her territory, at least twice during the session, in CF.

3.4. Foraging behaviour

During late spring (squirrel #1a), foraging behaviour was fully organized around the locations of underground food caches (Fig. 3). Only one or a few caches were used each day. A total of 58 main
Fig. 3. Examples of foraging (left) and caching (right) movement patterns. The locations of the nests used during the session, if any, are labelled with black dots (#1: arboreal nests; #2: burrow). The represented area is the same as in Figs. 1 and 2 (175 m by 150 m). Squirrel #1a, on a session during which it foraged on a cache of old conifer cones (located 75 m SE from the nest; activity time: 3 h 34 min, travelled distance: 2.22 km), and on another session during which it carried 42 old conifer cones from an old cache to a new one located 30 m NW away (activity time: 4 h 05 min, travelled distance: 3.40 km); Squirrel #1b, on a session during which it searched for scattered seeds (activity time: 4 h 50 min, travelled distance: 2.48 km), and on another session during which it scattered 20 old conifer cones from an old cache (see arrow; activity time: 1 h 27 min, travelled distance: 1.29 km); Squirrel #2, on a session during which it foraged for immediate consumption (activity time: 4 h 06 min, travelled distance: 1.97 km), and on another session during which it constituted a new cache of 17 new conifer cones mainly collected on a place located 54 m SE away (activity time: 4 h 52 min; travelled distance: 2.83 km).
caches, where the squirrel went and picked up at least 3 food items, were identified (the cache holes located within 4 m from each other were considered as a single cache because most close holes were connected underground). All caches contained conifer cones and were located in CF, or in a few cases, in YB but within 5 m from the limits of CF. The squirrel ate each cone on the spot, usually on the ground but sometimes perched on a nearby tree. It often returned several times to the same cache to take another cone. Most of the time devoted to foraging was taken up by feeding. Only very short distances were travelled either for searching for food successfully (17 m per activity hour) or for random searching (13 m per activity hour).

In contrast, during early summer (squirrel #1b) most caches were empty, and the squirrel spent a large amount of time searching for scattered seeds (Fig. 3). The percentage of time spent foraging was similar (half of the activity time) but the time actually devoted to feeding was lower because the squirrel spent more time searching for food. The distances travelled searching successfully for food were larger (28 m per activity hour), as were the distances travelled for random searching (36 m per activity hour).

During late summer and early autumn (squirrel #2), the time spent foraging, and the distances travelled searching successfully for food (28 m per activity hour) or for random searching (45 m per activity hour) were similar to those measured in early summer (squirrel #1b). There were however two major differences: foraging occurred mainly in trees rather than on the ground, since almost all the food (except mushrooms and berries, which were scarce on the study area) was found in trees, and a large amount of the food harvested was not used for immediate feeding but for caching. Sometimes, however, squirrel #2 spent a whole session without caching. During this type of session, the movement pattern was similar to that which was exhibited by squirrel #1b (Fig. 3).

3.5. Caching behaviour

Three types of food, conifer cones, birch fruit and mushrooms, were observed to be cached. Conifer cones and birch fruit were stored separately in underground burrows. In contrast, mushrooms were stored for drying in trees as single items, but this later type of food was scarce and hence cached infrequently. The fact that squirrel #1a was only observed foraging on caches of conifer cones would suggest that caches of yellow birch fruit were exploited early.

Squirrel #1 sometimes transported the old conifer cones from an old cache to a new cache (Fig. 3). This particular form of caching behaviour was observed four times during the first period (#1a), involving four different old caches and four different new caches: on 8 m (about 30 cones), 11 m (about 25 cones), 30 m (about 40 cones), and 28 m (about 10 cones), and twice during the second period (#1b), from two old caches (about 20 and 15 cones, respectively) to numerous new caches scattered around the old ones. The motivation of this behaviour is unknown in most cases (sometimes, it occurred just after a social interaction with another squirrel).

Squirrel #2 cached new conifer cones and birch fruit. Usually, it started knocking the food items (either birch fruit or conifer cones) down from one tree or a small group of close trees of the same species. Afterwards (usually not the same day), it collected the dropped food items one by one on the ground, and transported them once at a time to a more or less distant underground cache (located up to 54 m from the collecting area; Fig. 3). Birch fruit and conifer cones were always observed to be stored in different caches, but sometimes the squirrel made one cache of birch fruit and one cache of conifer cones on the same day. In most cases concerning caching of birch fruit, a small percentage of
items were individually buried directly on the spot a few cm into the soil. In some occasions, the squirrel was also observed to directly collect a food item in a tree (either birch fruit or conifer cone) and to go and store it in an underground cache. Twenty-five caches containing at least three items were identified by observing the caching behaviour of squirrel #2: 13 were made of birch fruit and 12 of conifer cones. Some of these caches contained numerous items: up to almost 100 conifer cones and up to almost 200 birch fruit items. Most of the caches (including the largest ones) were filled in a few hours, on the same day, and were located in CF. Additionally, 7 new caches of 3 to 23 old conifer cones were made by transferring 68 cones up to 40 m from one old cache on one day. This behaviour occurred after squirrel #2 discovered and pursued out of its territory another squirrel feeding on the old cache. Two other new caches of 4 and 8 old conifer cones were made from two other old caches on two other days. The day after it was made, a cache of about 60 birch fruit items was emptied by the squirrel which buried the birch fruit individually a few cm into the soil, scattered in the immediate surroundings of the cache.

A very striking aspect of caching behaviour was that, in most cases, even if the distance was very large, squirrels were observed to run directly between the collecting place and the caching place with a very high speed in both directions (sometimes the mean speed was greater than 5 km/h), jumping over obstacles like in a steeple-chase, even though the distant place and the landmarks surrounding it could not be perceived from the other one. Similarly, squirrels could be sometimes observed gathering nest material and going directly to the nest located far away from the gathering place even though the nest and the landmarks surrounding it were not perceptible from the gathering place, and the squirrels had not returned to their nest for several hours.

4. Discussion

This study showed that the amount of movement performed was stable during the whole period, about 0.5 km per activity hour, as were the fractions of time devoted to foraging and to moving about (about one half and one third of the activity time, respectively) in spite of considerable variations in the availability of food and in the type of food available. The two squirrels moved mainly on the ground, even when most of the available food was found in trees. Although red squirrels are mainly adapted to coniferous forests (C.C. Smith, 1970), they appeared to be sufficiently opportunistic to efficiently exploit deciduous areas, at least in the absence of grey squirrels. Thus, in the coniferous-deciduous area involved in the present study, the two squirrels always spent most of their activity time in CF but there was an increasing part of time which was spent in YB, and to a less extent in SM, when these areas had become productive.

Caching behaviour strongly affected a squirrel’s activity pattern. During late spring, feeding occurred almost exclusively from caches of old conifer cones, and most activity time was concentrated in the area where caches were located. As the caches became empty in early summer, foraging consisted in searching for randomly scattered food items, involving a considerable variation in the spatio-temporal structure of the home range. During this period, the squirrel was often observed to exhibit area-concentrated searching once it had discovered a food item in the ground; it slowed down to a very low speed, walking with the nose on the ground along a sinuous path. This behaviour is known to increase the probability of discovering further food items when they occur in patches (see Benhamou and Bovet, 1989; Benhamou, 1992, 1994). Later, in late summer and early autumn, caches
were made. Caching behaviour, strictly speaking, took only 4% on average of the activity time. In fact, this percentage took into account only the time spent carrying food to a given cache or individual caching on the spot (scarce). During the same period, much time was spent foraging for caching (searching for food to cache and knocking the food items from the trees to the ground) and moving back to a given foraging area after each caching. This indicates that the percentage of the activity time actually allocated to caching behaviour was more considerable.

In dry western coniferous forests, the American red squirrel is a typical larder-hoarding species. In the wet coniferous-deciduous forest involved in the present study, it was observed to exhibit an intermediate form of caching between larder-hoarding and scatter-hoarding, as in wet eastern coniferous forests. Indeed, conifer cones and most birch fruit were cached in several burrows distributed on the whole territory. Additionally, some birch fruit were buried one by one in the soil. This behaviour could be a means by which the resident squirrel survives in early summer, when all the caches have been either emptied or pilfered by other squirrels, using random searching for last year’s food until trees become productive again. With the constraint of using a midden (due to humidity requirements on storage conditions), the most efficient way to share space and resources among the squirrel population would be for each individual squirrel to settle its midden at the centre of its territory, as observed by C.C. Smith (1968, 1981). In the wet eastern coniferous and coniferous-deciduous forests, the humidity constraint of building a midden does not exist. Scattering numerous caches on the whole territory is probably even more efficient than using a central midden (Dempsey and Keppie, 1993).

In dry western coniferous forests, American red squirrels can be considered as central place foragers (Elliot, 1988) organizing their movements around central middens. In wet deciduous-coniferous forests in Québec, the absence of central middens causes space use patterns to be much more complex. Lair (1987) attempted to derive the activity centres of red squirrels’ home ranges over long periods using harmonic mean measures (Dixon and Chapman, 1980). In the present study, however, activity centres corresponded to cache locations and changed from day to day. They did not correspond to nests which were located in the periphery of the home range rather than in the core area, and were used only occasionally (for resting). Space use patterns varied in time according to the food availability. From late spring to early summer, the usual home range and the core area sizes increased dramatically, and the core area, which was very compact, tended to scatter in several units, subsequent to the disappearance of cached food. The space use pattern observed during late summer and early autumn, corresponding to a period of foraging on new items and food cache constitution, presented intermediate characteristics in terms of home range and core area sizes as well as in terms of compactness of the core area. Furthermore, even during a limited period, the space used patterns varied also in time because squirrels organized their activity successively around several food caches (or even wandered on the whole home range as squirrel #1b did). Nevertheless, it is worth noting that the territory (as revealed by territorial calls) of squirrel #2 was close to that of squirrel #1b. This means that neighbouring squirrels did not attempt to increase their own territories after squirrel #1 died (Price et al., 1986, have found similar results; notice however that in the particular area involved in the present study, there was no territorial pressure from north because no squirrel inhabited this purely deciduous area).

As most other squirrel species, the American red squirrel is a diurnal species, which probably orients in its home range mainly using visual information, whereas nocturnal macrosmatic mammals may orient using mainly olfactory information provided by their own scent-marks (Benhamou, 1989;
Jamon, 1994). Its ability to organize its activity around some particular places, such as food caches (during foraging in spring as well as during caching in late summer and autumn) and very productive trees, and its ability to return nearly directly to its nest to rest at the end of an activity phase or to bring there some material, indicates that the American red squirrel may rely on a good visual spatial memory. Recent laboratory (Jacobs and Liman, 1991; Vander Wall, 1991) and field (Devenport and Devenport, 1994) experiments on related species have demonstrated the ability of these animals to memorize locations with respect to surrounding visual landmarks. At a short scale, American red squirrels are also likely to be able to remember the locations of food caches with respect to surrounding visual landmarks. Indeed, the ability to return to a particular hidden goal, whose location has been memorized by reference to landmarks which can be perceived from both the animal’s current place and the goal location, has been demonstrated in numerous species of insects, birds and mammals, including nocturnal macrosmatic rodents (review in Benhamou and Poucet, 1996). However, red squirrels sometimes clearly exhibited the ability to return directly to a remote place (food cache or nest), even though there are no landmarks perceptible both from this place and from the animal’s current place. This type of ability appears very striking in this species whose long distance orientation performances, as revealed in homing experiments, are not very high (Bovet, 1984, 1990, 1991). Such an ability is often interpreted as a proof of a cognitive mapping of the familiar environment (e.g., Peters, 1979; Sigg and Stolba, 1981; Fabrigoule and Maurel, 1982; Boesch and Boesch, 1984). Actually, this ability can also be explained by a simpler, more parsimonious, mechanism by which the landscapes surrounding biological attraction points (food caches, productive trees) act as local systems of reference, each one coding for the locations of the others (Benhamou et al., 1990). While the present study could document a long distance orientation ability of the red squirrel within its home range, however, it does not obviously claim to address the underlying mechanism.

Acknowledgements

The field work was conducted on the ‘Station forestière expérimentale de Duchesnay’. It was supported by grant A-6639 of the ‘Natural Sciences and Engineering Council of Canada’ to Jacques Bovet. Many thanks are due to him for enabling me to work for six months in the Department of Biology of the University Laval in Québec.

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