The ecology and behaviour of female red squirrels (Sciurus vulgaris) during the breeding season in a conifer plantation

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The ecology and behaviour of female red squirrels (*Sciurus vulgaris*) during the breeding season in a conifer plantation

by

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SUMMARY

The population density, home range, activity levels and patterns and habitat utilisation of female red squirrels (*Sciurus vulgaris* L.) were studied in a 236 ha conifer plantaton of non-native species in northern Cumbria between May and June 1994.

1. Squirrels were trapped regularly in order to determine their breeding status and provide data for population density estimates.
2. Behavioural differences between 7 lactating and 5 non-lactating squirrels during the first breeding season were determined by radio telemetry. Radio tracking enabled the difference between the size of total home ranges (MCP) and core-areas of lactating and non-lactating females to be estimated. Home range and core-area overlap was also addressed.
3. Temperature sensitive radio collars were used to determine the activity levels and diurnal activity patterns of 6 lactating and 6 non-lactating females and comparisons were made.
4. A comparison of habitat availability and utilisation was made in order to identify the degree of female squirrel habitat preference and avoidance of the four tree species within the study site.
5. The population density was estimated to be 0.28/ha. Approximately 50% of the captured females were lactating.
6. No difference was found between the total home range sizes of lactating and non-lactating females.
7. Core-areas were found to be significantly smaller than total home ranges for both female categories. Core-areas were positively correlated with total home range size.
8. Lactating females had significantly smaller core-areas than non-lactating females. Core-area overlap only occurred between lactating and non-lactating females and not between individuals in the same category.
9. The total activity level of lactating females was significantly higher than that of non-lactating females. All females were more active in the morning than in the afternoon. Lactating females were more active than non-lactating females in the afternoon.
10. Female squirrels selected lodgepole pine over Sitka spruce, Norway spruce and Serbian spruce. This selection appeared to be determined by mast crops and subsequent seed availability of the tree species.

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1.0 INTRODUCTION

Mammals are unique in the balance of energy that they must attain during lactation. All of the energy provided to the young must first be consumed by the mother in addition to her own energy requirements (Hanwell & Peaker 1977, Oftedal 1984). This requirement imposes heavy physiological and behavioural demands upon females. For example, daily milk yield, as a percentage of body weight land mammals varies from 1.25% in elephants (*Loxodonta africana*) to 28% in pygmy shrews (*Sorex minutus*). As such, during lactation small mammals face a relatively short period of intense metabolic demand while large animals face a longer period of lesser demand (Hanwell & Peaker 1977).

The substrates required for the physiological demands of milk secretion and energy metabolism can be obtained from an increased rate of food intake and/or from body stores (Hanwell & Peaker 1977). Since the daily output of energy in milk is a significant proportion of the total calorific content of a small mammal it would appear that an increased food intake must be the main mechanism for supporting lactation in small mammals. Large mammals are able to utilise body reserves to a much greater extent (Hanwell & Peaker 1977). The pygmy shrew provides an example of this increased reproductive demand: it has been calculated that this species must more than double its food consumption during lactation and eat more than four times its own weight per day (Hanwell & Peaker 1977). Clutton-Brock *et al.* (1989) noted that lactation for most land mammals commonly coincides with the period of maximum food availability thus enabling such an increase in food intake.

Studies on rodents illustrate the demands of reproduction and lactation in particular. Randolph *et al.* (1977) noted that ingestion by cotton rats (*Sigmodon hispidus*) during 12 days of lactation was increased by 66% over non-reproductive rats. This figure was found to be 77% in the fox squirrel by Havera (1979) (see section 1.3.2).

Millar (1975) studied food intake and gross body composition of female white-footed mice (*Peromyscus*) and their offspring in relation to the stage of reproduction and litter size. Females were able to support offspring primarily by increased food intake and this intake was positively correlated with litter size. Food shortage was reflected in the survival and rate of growth of offspring. Kenagy *et al.* (1990) also found that daily energy expenditure of the golden-mantled ground squirrel (*Spermophilus saturatus*) was at its highest in the lactating individuals and that expenditure increased with litter size although not to the extent that was predicted.

In order to attain maximum fitness, behavioural adjustments must be made to meet the physiological demands of reproduction and maximise the success of reproductive effort through offspring nourishment. Maternal behaviour occurs in three stages (Shillito Walser 1977):

(1) Preparatory: behaviour during gestation such as nest building.
(2) Lactation: behaviour related to caring for offspring.
(3) Weaning: behaviour which helps the young to be independent.

During the second stage a number of adaptations are evident which maximise the efficiency of offspring care. Depending upon whether offspring are altricial (born naked and blind, for example rodents and insectivores), semi-altricial (born with hair but with poor locomotion and co-ordination, for example some carnivores and rodents) or precocious (well developed and able to move on their own, for example cetaceans and ungulates), appropriate levels of maternal care must be provided (Shillito Walser 1977).

Mammals with altricial young, including sciurids, actively maintain nests and are able to move young from one location to another. The female must visit the nest regularly to feed her young which leads to an increase in activity during lactation (Shillito Walser 1977). Mice, voles and rats suckle frequently and therefore spend a considerable amount of time in the nest, restricting foraging to the immediate habitat. Rabbits also forage nearby but only visit the nest to suckle once per day. Tree shrews (*Tupaia* sp.) also feed their young infrequently for 10 minute bouts every 2 days after an initial saturating post-birth feeding period (Martin 1966). Similarly, Ostfeld *et al.* (1988) found that the home ranges of breeding microtine rodents were significantly smaller than those of non-breeding females.

Hence, the activity levels of rodents with altricial offspring must be increased in order to compensate for lactation demands. Also, the home range sizes of lactating females may subsequently be increased or decreased in order to maximise energy intake. Lactating females may remain close to maternal nests in order to feed young depending upon the strategy employed by different species.

There have been few comprehensive studies on the additional energy required each day by squirrels during lactation (Gurnell 1987) and the subsequent behavioural adaptations that are related to this period of reproduction. Nonetheless, from the data provided by Linzell (1974) and Hanwell and Peaker (1977) (see section 1.3) it is clear that a high demand is placed on mammals such as squirrels. The aim of this project is to investigate some of the consequences of breeding on the behaviour of red squirrels (*Sciurus vulgaris*, Linnaeus 1758) by comparing lactating and non-lactating females within the same population.

Red squirrels can breed twice per year, the first litter being produced between February and March and the second in July. Before weaning, the altricial young depend almost exclusively on the females' milk production suggesting that energy costs to the lactating females are very high. The demands of maternal behaviour, including differences in range size, activity levels and physiology between lactating and non-lactating females are examined.

1.1 The red squirrel

1.1.1 Taxonomy and Status

The red squirrel (*Sciurus vulgaris*) belongs to the order Rodentia, family Sciuridae, subfamily Sciurinae, in which there are a total of 217 tree and ground squirrel species. The tree squirrels include the genus *Tamiasciurus* (Nearctic) and the genus *Sciurus* (Holarctic). *S.vulgaris* probably has the largest geographical range of all squirrels and consequently many subspecies have been suggested (Gurnell 1987). However, the distribution of the species is generally continuous and the taxonomic status of the subspecies is not clear (Corbet 1978; Shorten 1962).

1.1.2 Distribution

i. *Historical distribution*

Historically, the red squirrel occurred throughout Britain in both coniferous and broad-leaved woodland (Bertram & Moltu 1986), although numbers and distribution have always fluctuated widely. Such fluctuations were caused by epidemic diseases such as coccidiosis and parapoxvirus (Gurnell & Pepper 1991), food shortage, or a combination of the two (Tittensor 1977).

The introduction of conifers into Britain at the end of the 18th century led to an increase in the number of red squirrels during the second half of the 19th century. However, this increase was interrupted by a dramatic red squirrel population crash which occurred between 1920 and 1925. This was attributed to an outbreak of disease which spread through England between 1904 and 1914 and Wales, Cumberland and Scotland around 1920 (Middleton 1930; Shorten 1954; Reynolds 1981).

The red squirrel is presently isolated in areas of Ireland, Scotland, north Wales, northern England (Cumbria and Northumberland) and one or two locations in central and southern England (Gurnell 1987), including the Isle of Wight (Fig. 1).

The introduction of the grey squirrel (*Sciurus carolinensis*) from North America in the late 19th and early 20th Centuries has more recently contributed to the widespread decline of the red.

ii. *The influence of the grey squirrel*

Grey squirrels evolved in the broad-leaved forests of North America, whereas the red is found in coniferous forest throughout its range in Eurasia. Prior to the introduction of the grey squirrel, red squirrels utilised broadleaf and coniferous forest, their movements following seasonal food availability and mast crops of seed-producing trees. The apparent dominance of the grey squirrel in British broad-leaved forest may be a result of its ability to exploit deciduous food materials more efficiently. Unlike greys, red squirrels are unable to assimilate plant polyphenols (tannins) which act as digestion inhibitors in acorns (Lurz, Pers. comm.). Also, red squirrels are lighter in weight and tend to persist in lower densities.

The presence of grey squirrels appears to prevent the *return* of red squirrels to areas where they once occurred. Dense plantations of introduced conifers have partially compensated for the loss of natural red squirrel habitat providing acceptable, although lower quality areas in which competition from the grey is avoided. If the current northward spread of the grey squirrel continues there is a strong possibility that the red will be replaced in deciduous and mixed woodland throughout mainland Britain, and may eventually persist only in large areas of conifer far from oak forests (Kenward & Holm 1989). This highlights the importance of red squirrel research in forests that have not been affected by greys.

Elsewhere in Europe, the red squirrel has been unaffected by the grey which is present only in small numbers in Italy (Currado *et al., 1987)*. As a result, competitive exclusion by the grey has not imposed a limit on red squirrel niche breadth as it has in most of Britain. The decline of the red squirrel elsewhere in Europe is largely independent of grey squirrel influence, the major factors being widespread habitat destruction and epidemic disease to a lesser extent (Tittensor 1977).

1.1.3 Habitat

As an arboreal mammal, the red squirrel is well adapted to its forest habitat. Kenward

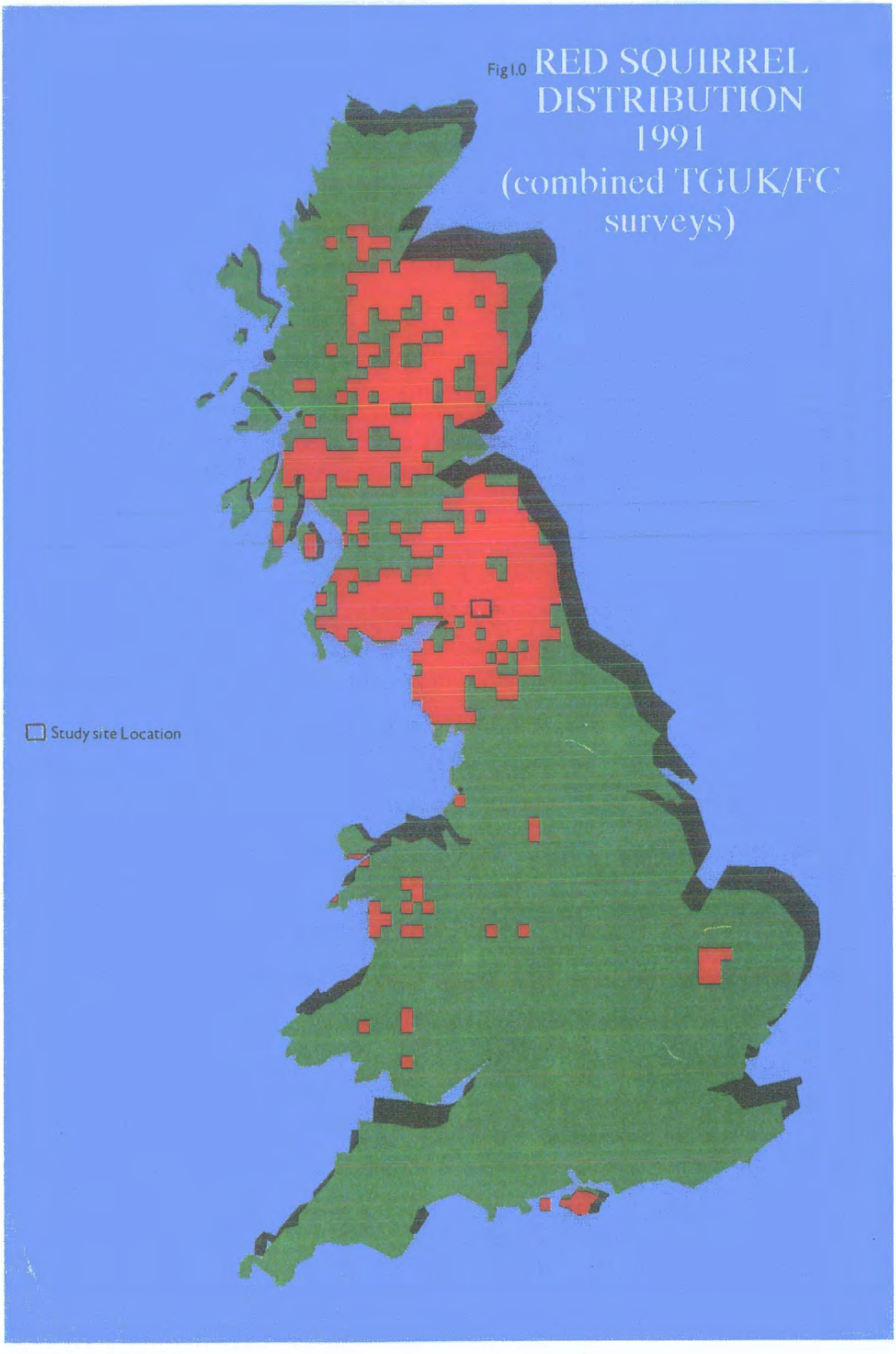


Fig 1.0 RED SQUIRREL DISTRIBUTION 1991 (combined TGUK/FC surveys)

and Tonkin (1983) stated that red squirrels spend 66% of their active time aloft in the canopy compared to only 14% for greys squirrels. Coniferous and deciduous forest are utilised to a varying extent and this consequently affects range size and habitat use. Wauters and Dhondt (1992) found range size in Belgian deciduous forest to be almost double that in coniferous forest. The difference was attributed to the more varied diet available to deciduous forest-dwelling squirrels and the predictability of tree-seed supply.

Across much of the Palaearctic red squirrels are found in boreal coniferous forests of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and Siberian pine (*Pinus* sp.) (Corbet & Southern, 1978). Broad-leaved forests are utilised in western and southern Europe where mixtures of tree species provide a more reliable year-to-year seed food supply than monocultured forests.

Red squirrel habitat in Britain is restricted almost entirely to coniferous species at present. In Scotland such conifers are represented by the remaining mature native Scots pine forests which are as yet free from grey squirrel invasion. However, the enclaves of red squirrel habitat which remain in England are dominated by non-native conifer plantations. In such habitats, squirrels are most abundant in large blocks of 50 ha or more (Tittensor 1977) where species such as Sitka spruce (*Picea sitchensis*), Norway spruce, lodgepole pine (*Pinus contorta*) and Serbian spruce (*Picea omorika*) are utilised. However, the regularity of food supply provided by each of these species varies considerably which subsequently affects squirrel densities and ranges in different forest stand mixtures.

1.1.4 Diet

Red squirrels are highly opportunistic feeders concentrating upon tree seeds, shoots, buds, flowers, bark and a range of fungi but also taking eggs, young birds, and insects when encountered (Holm 1989). Studies in Britain and elsewhere have found conifer seed to be the dominant food where available (Moller 1983) although needles, pollen and sappy tissue may also be fed upon in coniferous habitats. Seasonal variation in the diet is therefore apparent.

Tree seeds and fungi may be scatter-hoarded in the Autumn and although specific cache sites are not learned, approximate locations are recognised visually allowing final relocation by smell (Gurnell 1991). Hoarding appears to be more intense in deciduous forests than in boreal coniferous forests (Tonkin 1983).

1.1.5 Reproductive biology and behaviour

Males and females become sexually mature at 9-10 months old and breeding can take place between December-January and August-September (Gurnell 1991). Hence, two breeding peaks occur within a season leading to spring (February-April) and summer (May-August) litters with a mean size of three offspring.

Females are polyoestrous and receptive for only one day of each cycle whereas males are fecund for most of the breeding season (Gurnell 1991). Oestrous is apparent in the female by a swollen pink vulva although attraction of males is thought to occur by olfactory stimulation (Holm 1989, Gurnell 1987).

Mating behaviour appears to consist of four phases: a preliminary following period, a mating chase, copulation and post-coital behaviour (Gurnell 1987). Several authors (Tittensor 1975, Holm 1989, Gurnell 1987) have reported arboreal chases of females by one or more males culminating in successful mating by one male.

Gestation lasts for a period of 36-42 days during which time females will reline or build a 'litter drey' in which to have her young (Holm 1989). Dreys comprise an outer shell constructed from twigs and a soft insulating inner core of mosses, leaves, needles and grass (Lurz, Pers. comm.).

Young are born naked, blind and deaf and weigh between 10 and 15 g (Tittensor 1975, Holm 1989, Gurnell 1991). Lactation lasts for a period of 50-70 days but young will leave the drey on exploratory visits and begin to feed on solids after about 45 days (Tittensor 1975). Weaning occurs after 8-10 weeks when the young are 80-130 g, however, maternal protective behaviour may extend beyond weaning (Gurnell 1991).

High juvenile mortality has been reported; Tittensor (1975) states that 50-90% of juveniles do not survive beyond their first year whilst Gurnell (1991) suggests a figure of 75% to 85%. Wauters and Dhondt (1989) estimate a mortality of 40-80% due to an increased loss of weight following cessation of lactation.

1.1.6 Home range and population density

Squirrel home range, defined as the area over which an animal moves during the course of its daily activities, varies greatly in size within and between species of *Sciurus* (Table 1). Results also vary according to the method of study (Gurnell 1987) and consequently care must be taken when making comparisons. Seasonal factors may also influence squirrels' ranges which may be reduced in the summer when more focused feeding is confined to smaller areas due to limited food availability (Holm 1989). Physiological restrictions also affect range size (see section 1.2 for specific details) as do population density, habitat type, sex and age.

Table 1.1 Typical home range sizes of squirrel species

Squirrel Species	**Home range (ha)**	**Author**
Red (*S. vulgaris*)	3.90	Wauters & Dhondt (1992)
Pine (*T. hudsonicus*)	0.38	Price *et al.* (1986)
Pine (*T. hudsonicus*)	0.15	Layne (1954)
Fox (*S. niger*)	16.00	Donohoe & Beal (1972)
Western grey (*S. griseus*)	0.39	Ingles (1947)
Grey (*S. carolinensis*)	0.54	Flyger (1960)
Grey (*S. carolinensis*)	0.49	Doebel & McGuiness (1974)
Grey (*S. carolinensis*)	4.80	Kenward (1985)
Grey (*S. carolinensis*)	1.79	Kenward (1985)

Wauters and Dhondt (1992) reported mean male red squirrel home range sizes in Belgian coniferous woodland of 3.57 (N=17), 3.68 (N=16) and 4.45 (N=21) ha respectively in three consecutive years with 70% core-area sizes of 1.80, 1.65 and 2.30 ha. Female home range sizes were significantly smaller at 2.83 (N=25), 2.73 (N=39) and 2.84 (N=26) ha with core-area sizes of 1.13, 1.12 and 1.20 ha.

Mean home range sizes of other squirrel species vary considerably (Table 1.0). Those of non-territorial pine squirrels (*Tamiasciurus hudsonicus*) were 0.15 ha in a study by Layne (1954) whereas Donohoe and Beal (1972) showed fox squirrel (*S. niger*) ranges to be greater than 16 ha. Flyger (1960) found the mean home range of the grey squirrel to be 0.54 ha whilst Doebel and McGuinnes (1974) estimated it as 0.49 ha. The Western grey squirrel (*S. griseus*) showed a mean home range of 0.39 ha in a study by Ingles (1947).

Recent studies have tended to identify a core-area within the home range relative to the total area over which an animal may move (Havera and Nixon 1978, Don 1981, Koford 1982, Kenward 1982). Animals generally use space disproportionately within the boundaries of their home range. Areas receiving concentrated use are termed core-areas (Samuel *et al.* 1985). Thus, core-areas represent the regions of intense use within the total home range and provide a more useful parameter from which to make comparisons and interpretations.

Red squirrel densities also vary considerably (Table 1.2). Studies in coniferous forests have recorded densities ranging from 0.1/ha in northern Spain (Purroy & Rey 1974) and Thetford Forest, UK (Gurnell and Pepper 1988) to an exceptionally high 10/ha on the southern coast of Finland (Pulliainen 1982). Wauters and Dhondt (1985) reported a density of 1.3/ha in Belgium and Moller (1986) estimated a density of 0.33/ha in a Scots pine plantation in Scotland. Gurnell (1991) suggests that long term densities of between 0.5 and 1.5/ha are normal for both coniferous and deciduous forests, but year to year fluctuations can be large and are affected by seed supplies and weather.

Table 1.2 Typical red squirrel densities (mean number per hectare)

Location	**Habitat (coniferous/ deciduous)**	**Density (*n*/ha)**	**Author**
Spain	D	0.10	Purroy & Rey (1974)
Finland	C	10.00	Pulliainen (1982)
Belgium	C	1.30	Wauters & Dhondt (1985)
Belgium	D	0.90	Wauters & Dhondt (1985)
Scotland	C	0.33	Moller (1986)
England	C	0.10	Gurnell & Pepper (1988)
England	C	2.8/6.7	Kenward & Holm (1989)
England	C	0.80	Tittensor (1970)

1.1.7 Activity budgets and patterns

As red squirrels are diurnal, day length governs the onset and cessation of activity (Bahnak & Kramm 1977). They usually become active at first light although variations are evident with squirrels delaying the onset of activity for a number of hours in the morning. Such behaviour may result from the avoidance of adults or dominant individuals by young (Tonkin 1983), low ambient temperatures or energy conservation strategies (e.g. Deutch 1978). Periods of activity and rest alternate throughout the day although pre-noon activity is generally higher than that of the post-noon period (Tittensor 1975).

Kenward and Tonkin (1986) compared the distribution and extent of red and grey squirrel activity patterns and found that both species were active for most of the day in autumn but remained in their dreys for longer periods between January and March. They suggested that this was to conserve energy at a time of low temperatures and limited food supply. At this time both species were dependent on cached or fallen seed crop. However, red squirrels were active for longer periods than grey squirrels. They suggested that the ability of the grey squirrel to cache and recover seeds on the ground in a more efficient manner than the red squirrel reduced the need for it to forage so extensively.

Tonkin (1983) described the seasonal variation of red squirrel diurnal activity patterns noting that winter activity formed a midday peak in a typically unimodal pattern whereas spring and autumn activity displayed a bi-modal pattern with reduced activity in the midday phase. Summer activity emphasised this pattern, with a distinct midday lull to almost zero activity. Tonkin found that the winter activity phase was less than half as long as the summer activity phase.

It is important to consider individual differences when looking at aspects such as activity. This is also true at inter- and intra-population levels. For example, a number of studies conflict in the assessment of activity levels during periods of low temperatures (Naumov 1930; in Ognev 1940, Lampio 1967). Factors such as age and breeding condition should be considered in addition to environmental factors such as food supply and weather.

1.2 Conifer plantations

1.2.1 Conifer biology

Most conifers such as Norway and Sitka spruce produce seeds that ripen within one year, after which the cycle is repeated (Clapham, Tutin & Moore 1989, Farjon 1990). Species of the genus *Pinus*, such as Scots pine or lodgepole pine normally follow a two year cycle. For example, in Scots pine, flowering and pollination occurs in the spring but fertilisation and cone development do not occur until the summer of the following year. Female cones therefore take two years to ripen.

Yearly conifer seed-production varies whereby mast crops may be followed by years in which only limited seeds are produced (Anderson 1965). Masting has been attributed to factors such as climate (Matthews 1989) and an adaptive response to avoid seed predation (Gurnell 1987). Cone and seed production demand a considerable photosynthetic effort and it has been noted that stem wood production in Norway spruce may be reduced by 40% in good seed years (Koppel, Toeng & Linder 1987) after which trees may need time to recover (Lurz 1992). On average, mast crops occur every 5-6 years in Norway spruce and every 3-4 years in Scots pine (Hagner 1965, Matthews 1989) although factors such as soil conditions greatly affect the periods between large crops. Although lodgepole pine and Sitka spruce produce cone crops every year, fluctuations in the density of crops are considerable, and may peak every 3-4 years (Lurz, Pers. comm.).

1.2.2 Conifer plantations as red squirrel habitat

Conifer plantations provide a sub-optimal habitat for red squirrels. In order for a squirrel population to persist, trees must be utilised efficiently so that mast crops are exploited when they occur. Conifer seeds are considered to be the most important food for the red squirrel (Moller 1983). Pulliainen (1973) and Grönwall (1982) found spruce seed to be the preferred food item during winter, pine seeds being eaten during years of spruce cone failure. In a study of deciduous and coniferous tree-seeds eaten by small mammals, Grodziñski and Sawicka-Kapusta (1970) found calorific values to be highest among conifers.

The implications of a monoculture system whereby seed and cone production may not occur for one or more years are therefore clear. Other plant material such as conifer flowers, buds and shoots may supplement seeds during periods of reduced production (Tittensor 1975).

Scots pine and lodgepole pine provide relatively reliable crops enabling squirrels to feed on cones at various stages of ripeness throughout the season starting in the second year when green cones begin to swell and seeds develop (Sarvas 1962, Lurz 1992). Moller (1986) details the feeding ecology of red squirrels in a Scottish *Pinus sylvestris* plantation. However, species such as Norway spruce, Sitka spruce and Serbian spruce produce large crops only very occasionally which limits their value as a food item for considerable periods of time.

The fluctuation of squirrel numbers has been positively correlated with tree seed supply. Jensen (1990) noted a relationship between squirrel numbers and seed production in beech and Norway spruce in Danish forests. Andrén and Lemnell (1992) found that a red squirrel population in Sweden showed a strong correlation with the Norway spruce cone crop of the previous year during a ten year study. They suggested that the one year time-lag between the good spruce cone crop year and increased squirrel density was due to increased winter survival followed by improved reproductive success. Smith (1968) noted a 67% drop in pine squirrel numbers following a second white spruce (*Picea glauca*) crop failure. The remaining squirrels utilised spruce buds as their primary food during the winter. Nixon *et al.* (1975) found similar fluctuations in populations of grey and fox squirrels following mast crops in Ohio.

1.3. The effect of lactation on the physiology, activity pattern and home range of sciurids

Havera (1979) found that the total energy requirement of the fox squirrel during a 10 week period of lactation was 1.75 times greater than that of non-lactating females (77% more food was ingested by lactating females than non-lactating females). Similarly, Smith (1968) showed that lactating pine squirrels consumed 1.76 times more food than non-lactating individuals per day. There was a clear increase in energy demand for a period of approximately 45 days of gestation followed by a further 75 days of lactation.

Havera (1977) further analysed the body composition of lactating and non-lactating females and found fat levels to be lower in females that had finished lactating. This was possibly due to the high energy demands of lactation. He also suggested that a minimum condition level may be required before squirrels enter oestrous. Wauters and Dhondt (1989) found similar threshold weight criteria in the red squirrel whereby females that were less than 300 g in weight did not come into oestrous. Thus the energetics of the pre-oestrous period are also central to the reproductive success of the individual. Havera and Smith (1979) stated that pregnancy and lactation not only required increased food consumption, but the need for the majority of essential nutrients may be increased by two to ten times.

The implications for the energetic costs of reproduction, and in particular lactation that have been detailed above have been little studied, especially in the case of the red squirrel. However, in examining the spacing behaviour of this species, Wauters and Dhondt (1992) analysed the home range size, home range overlap and habitat use of males and females within two habitats. Within these categories they found that breeding females had significantly smaller ranges than non-breeding females in both deciduous and coniferous forest. Home range size was also significantly smaller in lactating than in non-lactating grey squirrels (Kenward 1985). Ostfeld *et al.* (1988) suggested that the more limited ranges of breeding meadow voles was caused by the occupation of superior microhabitat, allowing them to devote more energy to breeding.

Wauters and Dhondt (1989) found a similar limited home range pattern with red squirrels whereby the heaviest, more dominant females settled in the best microhabitats allowing more reduced movement for feeding. These females subsequently produced more offspring than the lighter females. Gurnell (1987) notes that the home range of the female gradually increases throughout the period of lactation.

In addition to this, Wauters and Dhondt (1992) found that food abundance was negatively correlated with home range size. More squirrels established home ranges in woodland plots with abundant food than they did in areas with scarce food which led to greater range overlap. The number of overlapping ranges was found to be lowest among females, as was the percentage overlap.

The aim of this project is to further investigate a number of the effects of lactation upon home range and activity patterns of female red squirrels by comparing lactating with non-lactating females within the same population. Core-area will also be assessed to determine whether females squirrels in Spadeadam Forest exhibit differences between the two reproductive groups. Compositional analysis will enable habitat utilisation for females to be assessed and will be analysed in relation to cone crop (ie. seed availability) for the season.

2.0 MATERIALS AND METHODS

2.1 Study site

2.1.1 Location and tenure

Spadeadam forest is situated in northern Cumbria south west of the Border Forest Park (Kielder Forest) and 15 km north east of Brampton (Fig.1). The study area is located in a section of the forest centred around Green Rigg and Foalstand Rigg covering an area of approximately 236 ha in total (Fig.2). The site lies adjacent to the 10 km^2 grid co-ordinates NGR 700 600 (O.S. Landranger series 86, 1:50 000). Historically, it represented a habitat similar to that of the North Pennine moors which lie to the south. The internationally recognised Butterburn Flow RAMSAR site is situated to the north-east. Earlier this century a conifer-planting initiative was implemented by the Forestry Commission in agreement with the Ministry of Defence (MOD) who own the land. The MOD retain the land for Royal Air Force use but lease it to the Forestry Commission in a co-operative management agreement encompassing military operations and forestry practices. Due to the nature of the RAF activities, public access is strictly controlled which subsequently minimises disturbance in the area.

2.1.2 Topography

Spadeadam Forest comprises a series of large forest blocks separated by a matrix of military roads and forestry rides (Plate 1). Within the study area the largest of these forest blocks is approximately 20 ha although adjacent blocks are separated only by narrow rides of approximately 3-15 metres. Thus contiguous forest sections, excluding fragmentation by rides, may cover an area of 100 ha before squirrel movement is limited by concrete roads.

The ground is gently undulating, the altitude ranging between approximately 240 and 285 metres. Only the surrounding valleys diverge from the relatively level landscape in the form of crags and cliff edges.

2.1.3 Climate

Given the exposed location of the site, it is frequently subjected to extreme weather systems. High winds are common and storm damage is evident in the form of blows in certain sections of the forest.

Long term climate data were obtained from the Meteorological office (Newcastle Weather Centre); the 10 year means for April, May and June in Carlisle are shown in table 2.1.

Fig 2 Aerial photograph of study site

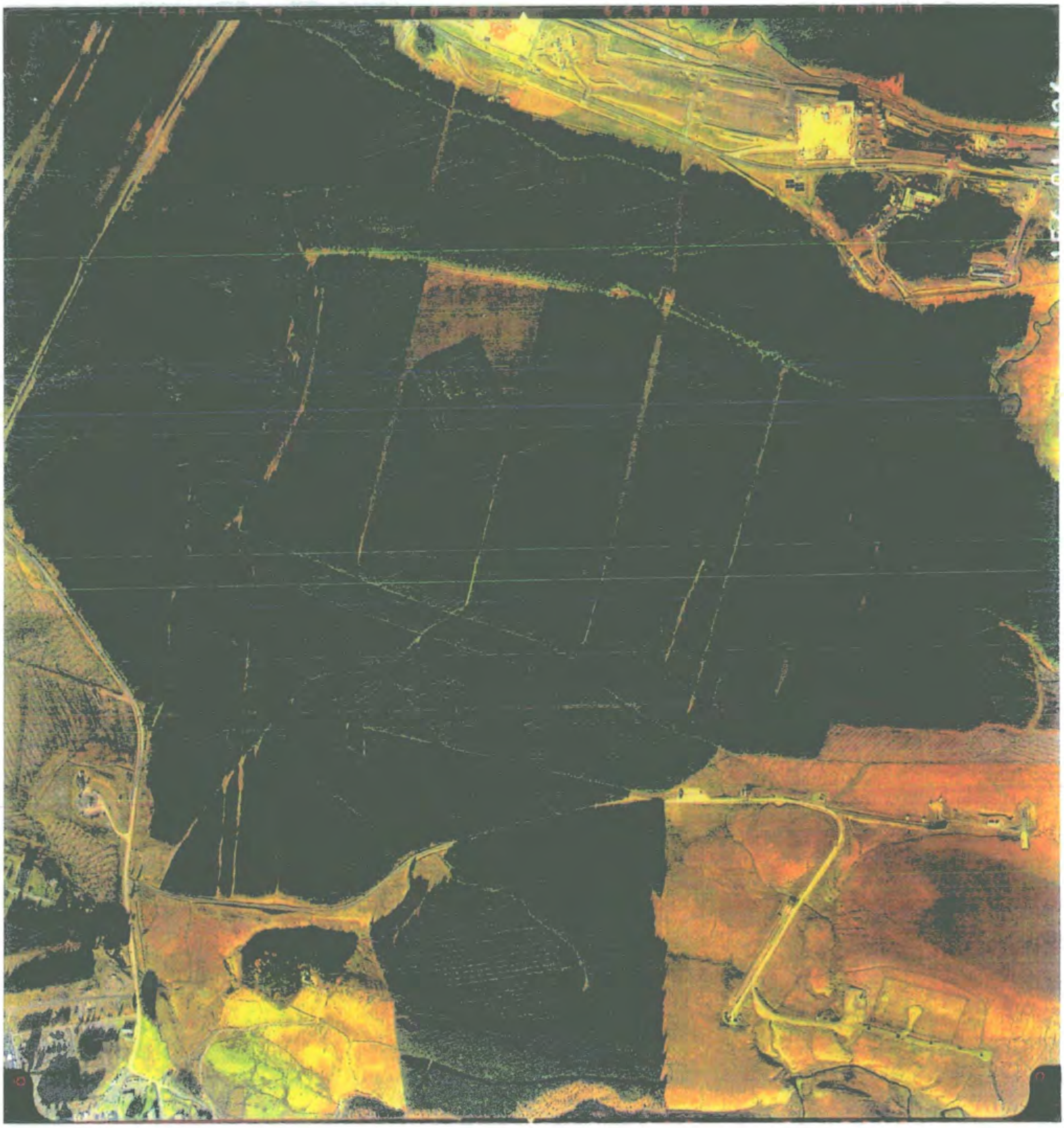


Table 2.1. Ten year mean climate data for Carlisle.

	APRIL	MAY	JUNE
Mean maximum temperature (°C)	11.4	14.8	17.5
Mean minimum temperature (°C)	3.5	6.1	9.1
Mean temperature (°C)	7.5	10.5	13.3
Rainfall (mm)	46.0	58.0	63.0
Hours of sunshine	149.0	185.0	186.0

Meteorological data for the site during the period of study was gathered at Spadeadam weather station which is situated 2 km from the study site (Table 2.2).

Table 2.2. Mean climate data for Spadeadam Forest during the months of April, May and June, 1994.

	APRIL	MAY	JUNE
Mean max. daily temperature (°C)	8.5	12.0	14.6
Mean min. daily temperature (°C)	3.6	5.7	9.7
Mean temperature (°C)	6.1	8.9	12.2
Total rainfall (24 hrs) (mm)	100.6	47.2	92.2

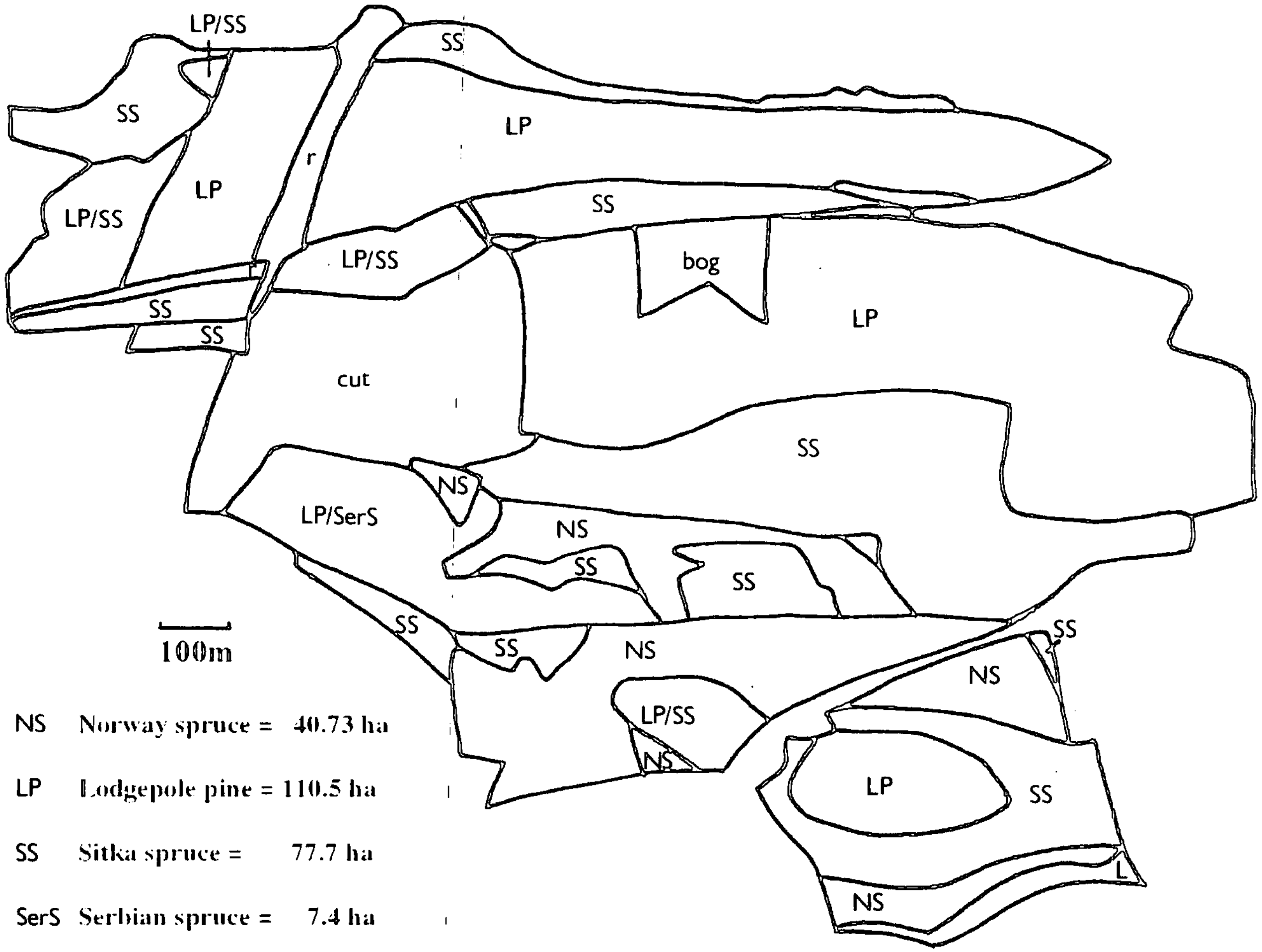
The number of days that the air temperature fell below 0°C in April, May and June, 1994 were 11,0 and 0 respectively.

2.1.4 Habitat types and ecological characteristics

Four coniferous species dominate the study site and are present in disparate proportions representing a variety of age groups (Fig.3). Lodgepole pine, covering 110.5 ha is the most abundant species followed by Sitka spruce (77 ha), Norway spruce (40.73 ha) and Serbian spruce (7.4 ha). A number of the stands comprise single tree species. However, several have been planted with two species each of which are present in an equal ratio. For example, *P. sitchensis* may be found in stands mixed equally with *P. abies* or *P. contorta*. P. omorika is found only in one stand mixed with *P. contorta*.

Planting took place throughout the site between 1954 and 1965 which indicates that tree stand ages vary from 29 to 40 years old. Most of the planting occurred between 1954 and 1958, therefore all of the trees are mature and of cone-bearing age. Conspecifics produce similar yearly cone crops (see section 1.3). Mean tree height for all species is approximately 25 metres.

Fig3 **Spadeadam Forest study site - habitat map**



NS Norway spruce = 40.73 ha

LP Lodgepole pine = 110.5 ha

SS Sitka spruce = 77.7 ha

SerS Serbian spruce = 7.4 ha

Total = 236.33 ha

r Road

Unmarked sections = unplanted

Within the forest, ground flora is particularly scarce being restricted to bryophtes due to the lack of light resulting from the dense canopy. However, the connecting rides support a variety of species ranging from xerophilic to xerophobic plants depending upon water levels at specific locations. Some locations within the site do not permit tree-planting due to the soft substrate and remain as areas of raised bog.

Principal plant species of the forest rides include primrose (*Primula vulgaris*), quaking grass (*Briza media*) purple moor grass (*Molinia caerulea*), wavy hair grass (*Deschamsia flexuosa*) bog cotton (*Eriophorum angustifolium*), harestail (*E. vaginatum*), creeping fescue (*Festuca rubra*), sheeps fescue (*F. ovina*), common bent (*Agrostis stolonifera*), and common sedge (*Carex nigra*). Rush species include *Juncus effusus, J. squarrosus* and *J. acutiflorus*. The more open areas and wider rides support crowberry (*Empetrum nigrum*), cowberry (*Vaccinium vitis-idaea*), bilberry (*V. myrtillus*), common horsetail (*Equisetum arvense*), bird's-foot trefoil (*Lotus corniculatus*) as well as undisturbed sections of blanket bog supporting *Sphagnum papillosum* and *S. magellenicum*. Less common species include heath spotted orchid (*Dactylorhiza maculata*), early purple orchid (*Orchis mascula*), sundew (*Drosera rotundifolia*), bog asphodel (*Narthecium ossifragum*) and bog rosemary (*Andromeda polifolia*).

Floristic layers are therefore restricted to tree species and ground vegetation as darkness beneath the trees and management throughout the ride network impede shrub growth.

In addition to the red squirrel, mammalian fauna include the common shrew (*Sorex araneus*), field vole (*Microtus agrestis*) and wood mouse (*Apodemus sylvaticus*) all of which must be considered as red squirrel competitors despite their limited niche overlap. The red fox (*Vulpes vulpes*) represents the only common mammalian predator of the red squirrel in this area. Pine marten (*Martes martes*) presence within the area has not yet been confirmed but may play a predatory role in the ecology of this squirrel population. Other Mustelids include stoat (*Mustela erminea*) and weasel (*Mustela nivalis*). The roe deer (*Capreolus capreolus*) and rabbit (*Oryctolagus cuniculus*) although common, are of limited importance as regards squirrel ecology.

Raptors, including the buzzard (*Buteo buteo*) and *kestrel (Falco tinnunculus*) are relatively common in the study site but the rarer goshawk (*Accipiter gentilis*) probably poses the only predatory threat to squirrels. Jays (*Garrulus glandarius*) and ravens (*Corvus corax*) which have been reported to predate on juvenile squirrels (Lurz, pers.

Comm.) are found throughout the forest. Seed-eating siskins (*Carduelis spinus*) and crossbills (*Loxia pytyopsittacus*) also demonstrate niche overlap with red squirrels.

2.2 Field techniques

2.2.1 Trapping

Live-trapping was employed in order to determine the reproductive status of females. This initially enabled the fitting of radio collars to lactating and non-lactating animals. Biometric data were taken from trapped animals on each capture with the exception of animals that were recaptured within 24 hours of the last trapping. Squirrels were trapped fortnightly so that their status could be updated. In addition to this, intensive trapping periods provided mark-recapture data so that a population estimate could be made for both sexes within the study site.

i. *The Fuller Trap*

All squirrels were captured using the Fuller Trap which is a single capture, hinged, drop-door design (Plate 2). Originally intended for mink, the trap is designed so that the animal enters freely and attempts to reach the bait area. In doing so a metal trip plate near to the rear of the trap is triggered. This releases a metal rod, which holds the door in the open position, allowing the door to drop. A spring-loaded locking bar drops simultaneously behind the door to hold it in a closed position. The traps were slightly modified by the provision of a small wooden box beyond the trip plate in order for trapped animals to shelter whilst awaiting the handling procedure. In addition to this, a front extension base provided a platform onto which squirrels could jump prior to entering the trap.

A mixed bait of sunflower seeds and peanuts was used in all traps.

ii. *Trap locations and trapping regime*

All traps were numbered and placed at a spacing of approximately 100 metres providing a density of one per hectare (see Fig.3) in a trapping area of 80 ha. Using this spacing regime, limited squirrel movements of 1 ha or less were accounted for. This ensured that all individuals within the trapping site had an equal chance of being caught. Traps were secured horizontally against the tree trunk at a height of between 1 and 2 metres.

Traps were baited approximately once per week throughout the study period so that squirrels became used to obtaining food from them. Traps were not necessarily set to catch on each of these occasions. Prior to a mark-recapture trap session, the traps were pre-baited in the early morning for five consecutive days in order to maximise capture success. This pre-baiting period was followed by a four day trapping period. On each of the four days all traps were set between 0630 and 0830 and checked between 1500 and 1800. Thus, each trap was left set for approximately 8½ hours per day. This allowed sufficient time for squirrels to visit the trap whilst at the same time not causing undue cold or hunger stress to animals that had been captured early in the day. Thus 210 trap days were used in data analysis (55 traps x 4 days) for each of two trap sessions.

iii. *Handling trapped animals*

Trapped squirrels were placed into wire mesh handling cones in order for measurements to be taken (Plate 3). Every trapped animal was sexed, weighed to an accuracy of 5 g, shin length was measured and notes were made on the reproductive status of females according to the size of the vulva (oestrous/gestation) and nipples (lactation). The trap location was also recorded for use in habitat utilisation analysis. Unmarked squirrels were collared accordingly: males were collared using a 10 g number-stamped/colour-coded metal collar covered in heatshrink plastic; females, a number of which had already been radio-collared as part of a separate study in the same site, were weighed, radio-collared and recorded as lactating or non-lactating accordingly. Juvenile squirrels were usually marked by tail-fur clipping due to the inappropriate size of the collars available.

2.2.2 Radio telemetry

i. *Equipment*

Biotrack thermistor transmitters (Biotrack, Wareham, Dorset) (see Plate 4) were utilised so that squirrel activity could be monitored using the variable pulse rate facility. Thermistor radio collars can indicate whether an animal is in a nest (warm thermistor, fast pulse) or foraging out of the nest (cool thermistor, slow pulse). The open tuned-loop brass collar is encapsulated in resin and weighs 15 g (<5% of body weight).

Mariner 57 Biotag (173 MHz) receivers were used during tracking with three-element Yagi receiving antennae. The Yagi antenna enabled accurate locations to specific trees (see section 2.2.2 ii).

The range obtained from this combination of equipment was approximately 1 km depending upon topography and the height at which the antenna was held.

ii. Telemetry techniques

Home range determination

Twelve females were tracked within the study site (n=7 lactating, n=5 non-lactating) in order to determine home range size. An attempt was made to locate each female three times per day over a ten day period providing 30 fixes per female. Kenward (1985) established that a plot of home range size against the number of point-fixes reached an asymptotic value at about 30 fixes. This number of fixes gave stable range estimates and was thus sufficient for the construction of minimum convex polygon (MCP) home ranges for this species. In some cases a period of 21 days was required in order to obtain 30 fixes as squirrels were inactive in dreys on many radio tracking occasions. Individual dreys were not recorded more than once for use in home range analysis as this would produce artificial clustering of fixes (Harris *et al.* 1990). However, such replicate fixes were noted so that drey use could be analysed.

Independence of radio fixes was ensured by allowing a minimum of one hour intervals between locations. This time sampling gave squirrels the opportunity to move across their home range area so averting serial correlation restrictions (Swihart and Slade 1985).

In order for fixes to be used in habitat utilisation calculations, the specific tree in which the squirrel was located had to be determined. Trees were circled several times pointing the directional antenna towards the canopy until location of the correct tree was certain. In this way, accurate home range fixes and specific tree use data were obtained. The following information was recorded at each fix site: female radio collar frequency number, tree species, time, activity (active or drey) and an eight figure map co-ordinate which enabled an accuracy of ±10 m.

Activity pattern determination

During the period from 17th-20th May, intensive records of activity were taken for all lactating and non-lactating females (n=12) and an additional 5 females, the status of which was unknown. Each female was recorded as active or in a drey each hour between 0500 to 1130 hrs on four consecutive days. Readings were taken at 30 minute intervals between 0500 and 0700 so that emergence time could be more accurately estimated. This provided approximately 60 activity recordings per squirrel, giving 1020 recordings for the 17 squirrels monitored. Restricting data to lactating and non-lactating females, 720 recordings were obtained. These data were then amalgamated with afternoon data which was recorded on four consecutive days between 1200 and 2000 hrs. Readings were taken every 30 minutes from approximately 1800 so that time of drey entry could be more accurately estimated. This morning and afternoon data provided a sequential activity data set throughout the squirrels' active daytime period. However, morning and afternoon records were taken in two different (consecutive) weeks.

2.2.3 Habitat utilisation

Radio-tracking data from lactating and non-lactating females were amalgamated so that female habitat use and habitat preference/avoidance could be determined. Compositional analysis (Aebischer & Robertson 1992, Aebischer *et al.* 1993a, Aebischer *et al.* 1993b) was implemented at two different scales so that a comparison of availability and utilisation results was possible: i) the tree species in which fixes were recorded were used as utilised habitat and compared with the availability of the four tree species within the entire study site; ii) Total home range MCPs were used as the habitat utilised and the entire study site as habitat available.

Cone crop estimations were provided by data collected by P. Lurz during a simultaneous study. Cone abundance was measured by counting the number of cones on the ground along a total of 28 transects (10 Norway spruce, 10 Sitka spruce and 8 lodgepole pine) each month throughout the year. Each transect followed the area between two rows of trees and were upto 70 m long and 1.5 m wide. Cones were identified and signs of squirrel feeding were noted (Plate 5). The density of each species' cone crop were then compared.

Cone crop data were compared with habitat utilisation data in order to assess correlations between food availability from each tree species and the use of each tree species by squirrels.

2.3 Data analyses

2.3.1 Trap data

In addition to continuously monitoring the lactation status of females, trapping enabled a population estimate for the study site to be made. MEGASTAT was used to calculate the Jolly-Seber (Seber 1982) and Fisher-Ford multiple mark-recapture methods with Bailey's correction in order to arrive at a population estimate for the trapping site (80 ha) from which an estimate of density was calculated for the study site.

Differences between lactating and non-lactating female body weights were compared using the Mann Whitney U test.

2.3.2 Home range

All data on home range size, home range use, overlap of home ranges and habitat utilisation and availability were analysed and calculated using the RANGES IV programme (Kenward 1990). The following components were investigated:

(1) Total home range size (100% of the fixes) of each female using the convex polygon method.

(2) A 70% core-area was calculated for each female since at the densest 70% of all fixes, a plateau emerged when percentage of area was plotted against percentage of fixes. The slope of a range's utilisation distribution was regular for nearly all squirrels. This criterion was used as an indication of transition between consistently heavily-used centre portions of the home range and outer, occasionally-used areas (Jennrich & Turner 1969, Van Winkle 1975, Anderson 1982). Mononuclear range-area analysis with the recalculated arithmetic mean as range centre was employed since all females displayed mononuclear ranges.

Kernel analysis was also used to analyse home range use on RANGES IV by producing contouring with filing of density matrices and isopleth outlines.

(3) Total home range overlaps were expressed as a percentage of overlap of a female's range with the total range of all overlapping females. Core-area overlap was analysed in the same way.

The Mann-Whitney U-test was used to determine whether there was a significant difference between the size of lactating and non-lactating female home range sizes, 70% core-areas and kernel results as data were not normally distributed.

Correlation coefficients were obtained for the home range sizes versus core-areas of both female categories.

2.3.3 Activity

The diurnal activity pattern of 17 females was investigated by considering the percentage of animals that were active during each hour of the day. Separate analyses were calculated for known-status females (N=12) so that comparisons could be made between lactating and non-lactating individuals. In this case, 'active' recordings were totalled for each female category for each hour of the day and expressed as the number of 'active' hours and as a percentage of the total number of recordings made for that hour over four days (n=24 for each category, ie. one recording for each of six squirrels per day for four days).

The Mann-Whitney U test was used to determine any difference between the overall activity levels for lactating and non-lactating females, and activity during different periods of the day between and within the female categories. Activity levels were compared with a number of factors including range size and habitat available.

2.3.4 Habitat utilisation

Habitat utilisation was analysed for all twelve squirrels simultaneously as the small sample size did not permit separate analysis for each category.

Available habitat was calculated using the RANGES IV program (Kenward 1990) and radio tracking provided utilisation data (see section 2.2.2 ii). The comparison of available and utilised habitat was calculated using compositional analysis (Aebischer & Robertson 1992, 1993, Aebischer *et al* 1993) whereby proportional habitat use by individual animals was used as a basis for analysis. Compositional analysis required an overall comparison of the proportions of radio locations in each tree species and the proportions of each tree species in the entire study site to be calculated using a multivariate analysis of log-ratio differences. If species had a utilisation proportion of zero, this was replaced by 0.001 in order to determine log-ratios. Log-ratios were calculated so that habitat compositions became independent (Aebischer 1992). Wilks'-lambda χ^2 results determined whether squirrels were utilising the habitat in a random manner. If squirrels were utilising habitat in a non-random manner (ie. showing preference for particular habitats) a *t*-test was implemented to ascertain the order of preference for each tree species. Habitats were then ranked according to relative use and significant between-rank differences were located. This process was repeated using total home range MCPs as the habitat utilised and the entire study site as habitat available.

Chi^2 goodness of fit analysis was also implemented on habitat availability and use data in order to provide a comparison with the results obtained from compositional analysis. The number of observed fixes in each habitat type for all squirrels was compared with the number of expected fixes using the study site as available habitat. It was then established whether squirrels were utilising habitat according to availability.

Habitat selection and apparent preferences were then compared with cone crop estimations (see section 2.2.3) for the year to determine the 'quality' of each tree species habitat.

3.0 RESULTS

3.1 Trapping data

3.1.1 Total capture and mark-recapture and density estimates

A total of 22 squirrels were captured in the 80 ha trapping site during the intensive four day mark-recapture session (Appendix I). Jolly-Seber (Seber 1982) mark-recapture analysis provided a population estimate of 23 squirrels. The Fisher-Ford method of analysis provided an estimate of 21 squirrels. Bailey's Correction was implemented on both tests. Squirrel densities were thus 0.3 and 0.26 per hectare for the 80 ha trapping site using data from the Jolly-Seber and Fisher-Ford analyses respectively. This data provided an extrapolated population density estimate for the study site.

3.1.2 Body weights

The body weights of females, for which the reproductive status was known, were recorded on each capture occasion (Table 3.1).

Table 3.1. Mean body weights of each lactating and non-lactating females captured during the trapping period.

Lactating females	**Weight (g)**	**Non-lactating females**	**Weight (g)**
268	346	212	300
218	370	244	282
236	300	303	306
234	320	286	333
258	325		
296	330		
207	325		
Total mean	331		305
S.D.	21.99		21.13

No significant difference was found between the body weights of lactating and non-lactating females (Mann-Whitney U test, *u*=6.5, N.S.). Of the lactating females, L218 had the highest mean body weight (370 g) and L236 had the lowest (300 g). Of the non-lactating females, the highest and lowest mean body weights were 333 g and 282 g for NL286 and NL244 respectively.

3.2 Radio telemetry

3.2.1 Home range size and use

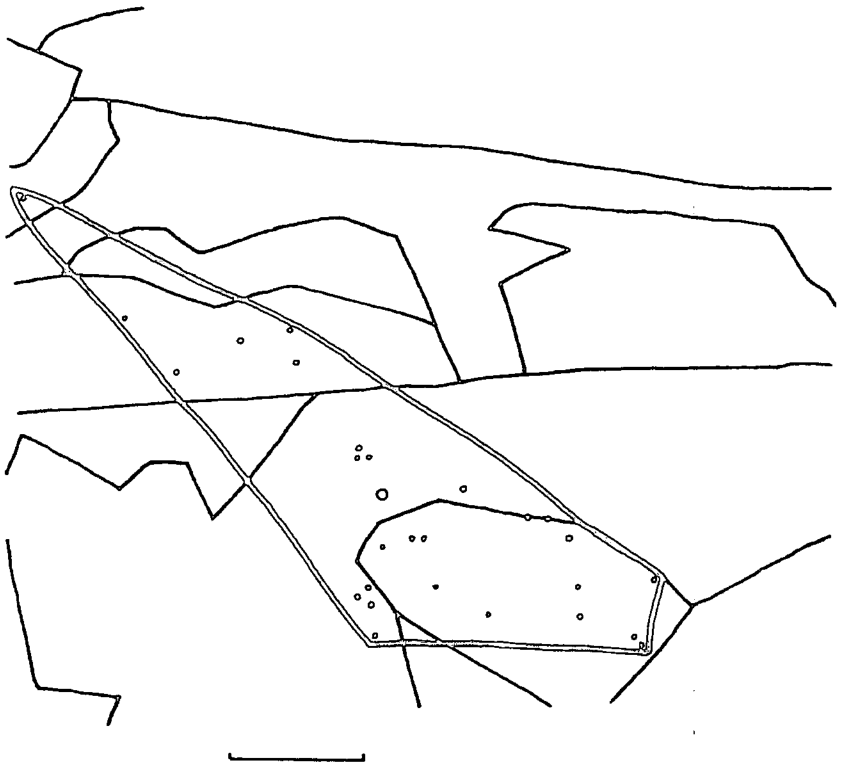
Between 28 and 30 fixes were obtained for each of the 12 females that were radio-tracked (Figs.4-15). Table 3.2 shows the calculated home range (MCP) sizes and core-areas, where the term range refers to MCP total home range, and L and NL refer to lactating and non-lactating females respectively. Figures 16 and 17 show total home range size and location within the study site and Figure 18 shows the rank order of range sizes for both female categories.

Table 3.2. Home range (MCP) and core-area sizes of lactating and non-lactating females.

Female	**Home range size (MCP) (ha)**	**Core-area size (ha)**
Lactating		
L268	7.91	3.40
L207	10.28	5.20
L218	8.49	3.10
L258	6.78	1.70
L236	9.85	3.60
L234	11.30	4.70
L8.6	6.16	2.50
Mean	8.68	3.46
S.D.	1.89	1.21
Median	8.49	3.40
Non-lactating		
NL212	17.00	5.30
NL296	30.56	14.10
NL244	15.26	6.10
NL303	4.89	2.60
NL286	19.95	5.20
Mean	17.53	6.67
S.D.	9.23	4.36
Median	17.00	5.30

Mean range size was 8.68 ha (±SD=1.89) for lactating females and 17.53 ha (±SD=9.23) for non-lactating females. The median value of range size for lactating females was 8.49 ha and that of non-lactating females was 17.0. Lactating females did not have significantly smaller home range sizes than non-lactating females (Mann-Whitney U test, *u*=7, N.S.).

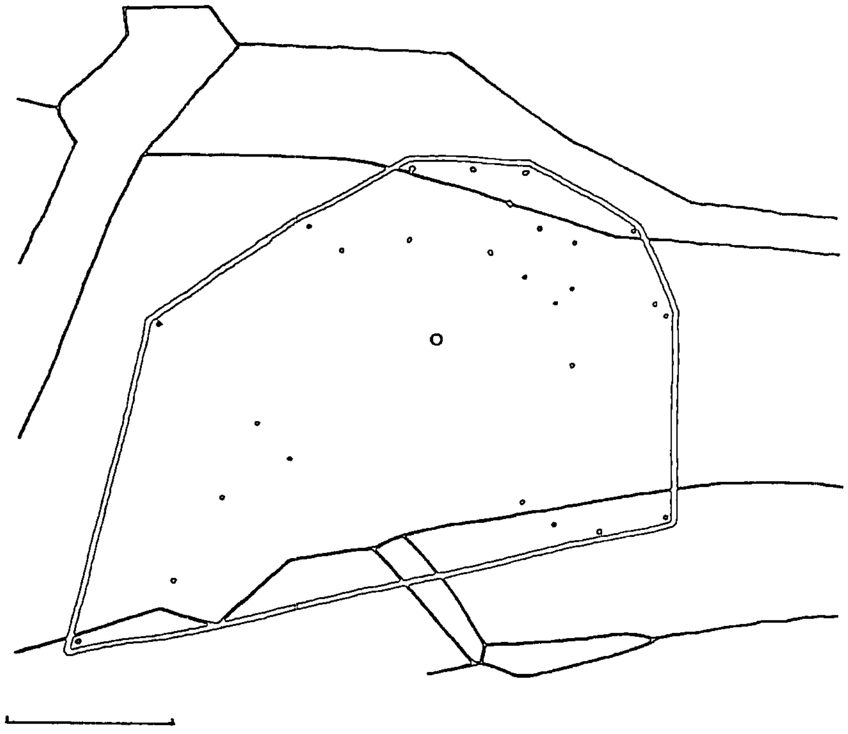
Fig4 **Total home range (MCP) and fix locations of L268**



Total home range = 7.91 ha
Core-area = 3.4 ha

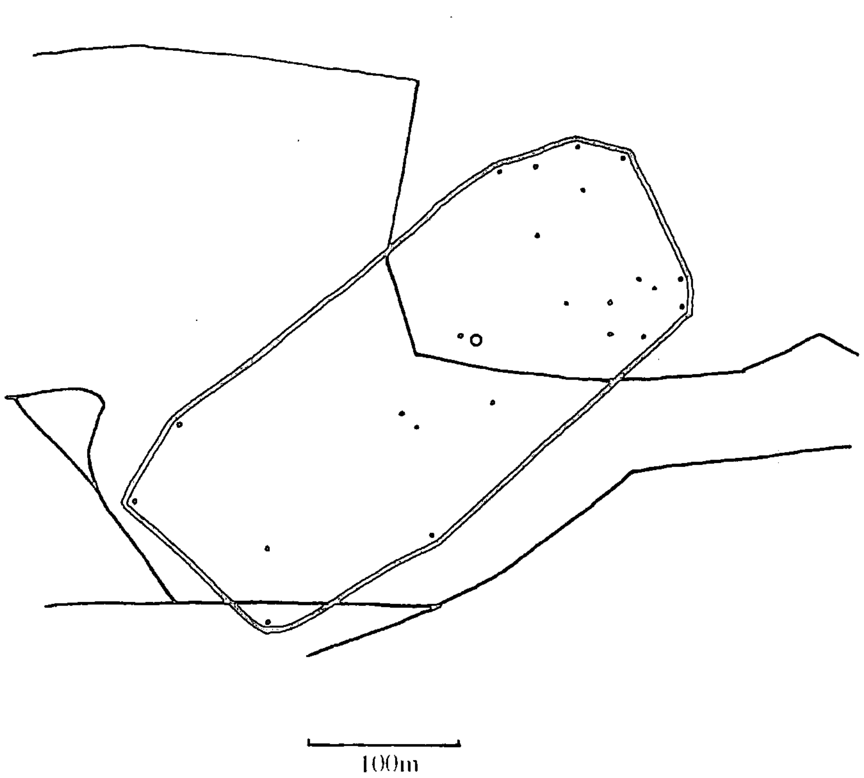
- ∘ Radio fix
- ○ Recalculated arithmetic mean

Fig5 **Total home range (MCP) and fix locations of L207**



Total home range = 10.28 ha
Core-area = 5.2 ha

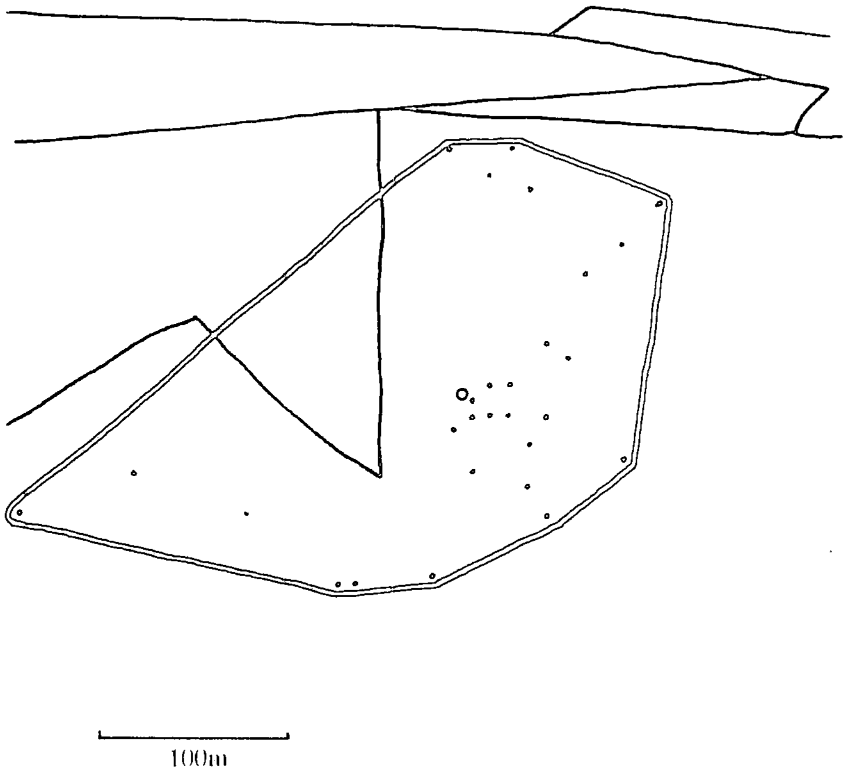
Fig6 **Total home range (MCP) and fix locations of L218**



Total home range = 8.49 ha
Core-area = 3.1 ha

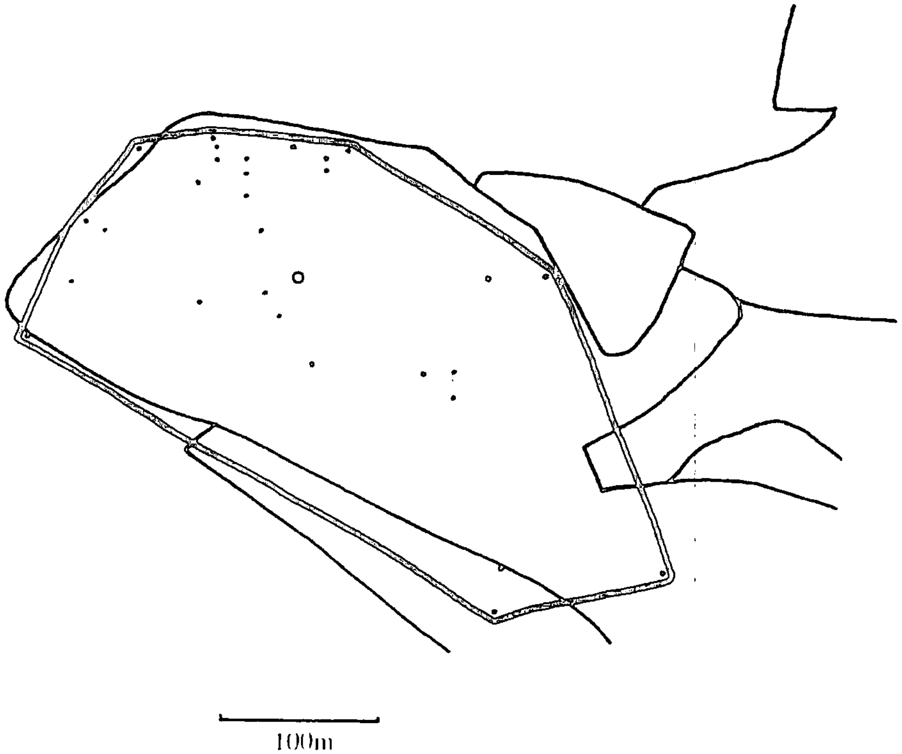
- ∘ Radio fix
- ○ Recalculated arithmetic mean

Fig7 **Total home range (MCP) and fix locations of L258**



Total home range = 6.78 ha
Core-area = 1.7 ha

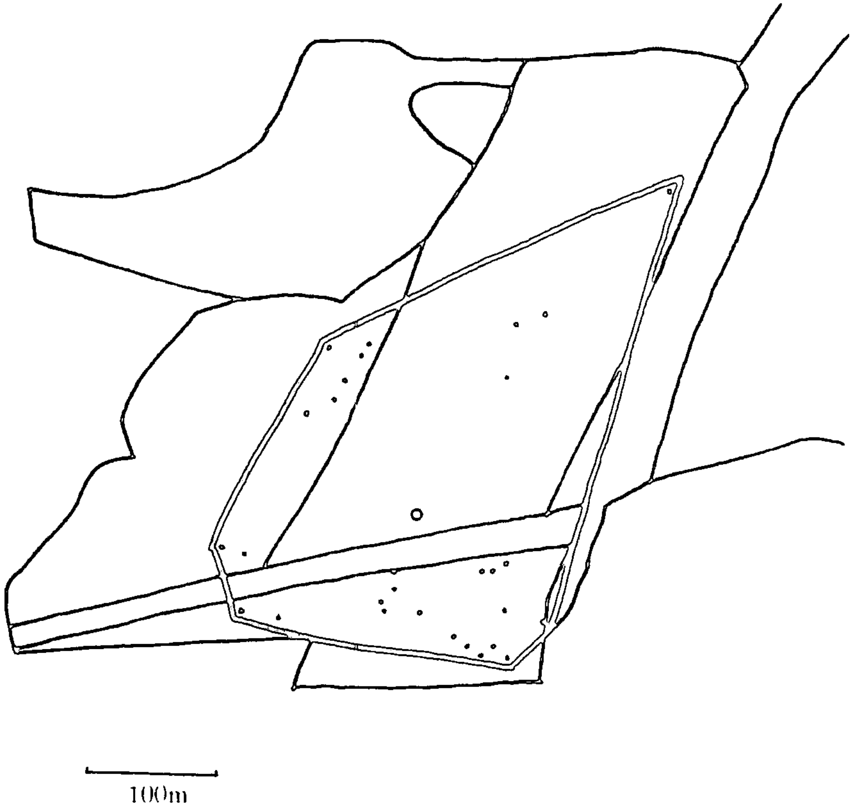
Fig8 Total home range (MCP) and fix locations of L236



Total home range = 9.85 ha
Core-area = 3.6 ha

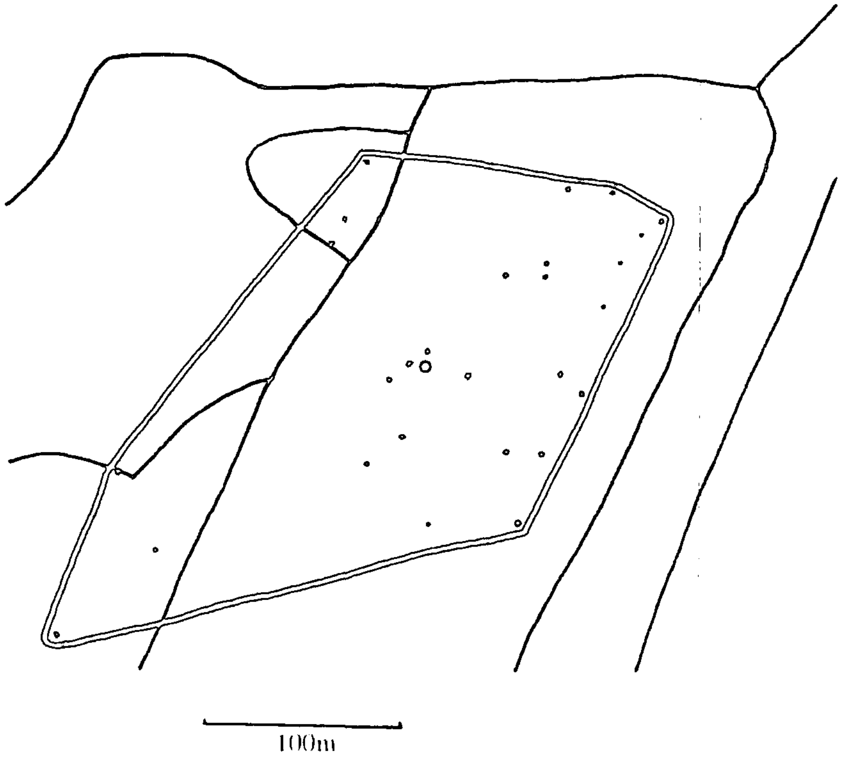
- Radio fix
- o Recalculated arithmetic mean

Fig9 Total home range (MCP) and fix locations of L234



Total home range = 11.3 ha
Core-area = 4.7 ha

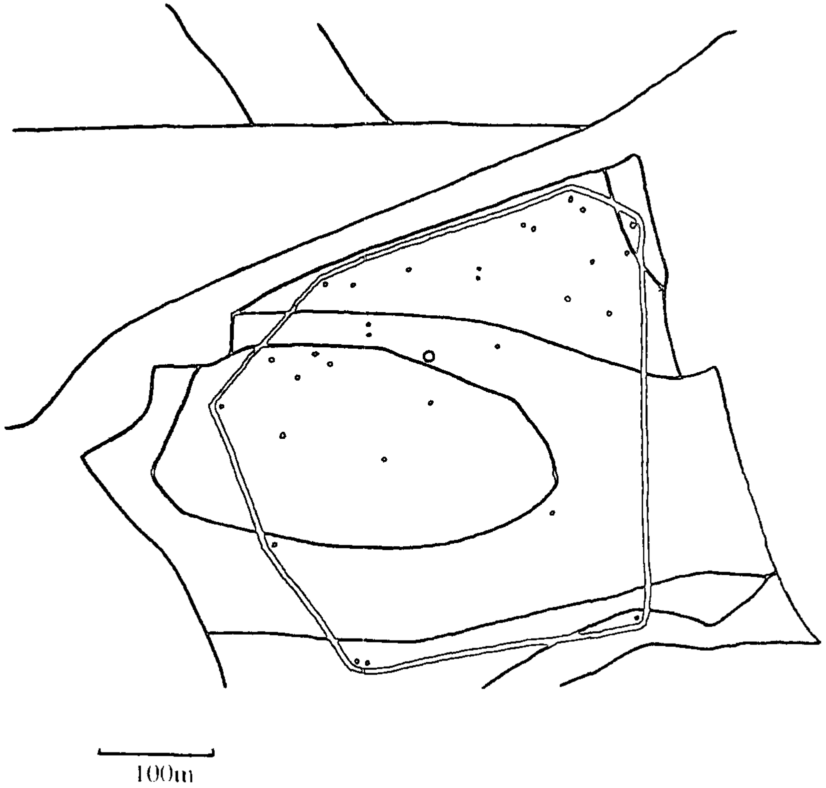
Fig10 **Total home range (MCP) and fix locations of L8.6**



Total home range = 6.16 ha
Core-area = 2.5 ha

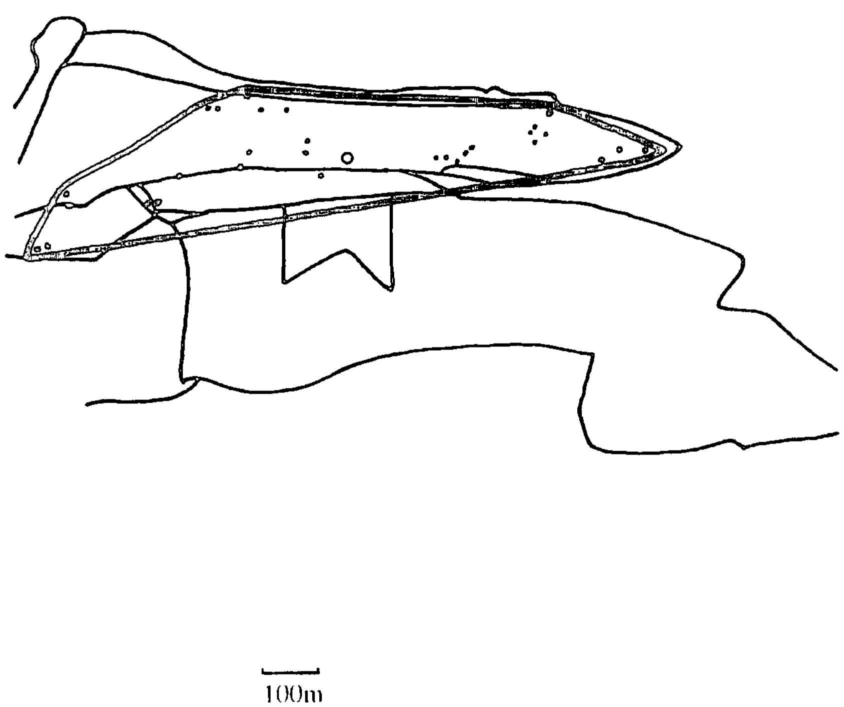
- ∘ Radio fix
- ○ Recalculated arithmetic mean

Fig11 **Total home range (MCP) and fix locations of NL212**



Total home range = 17.0 ha
Core-area = 5.3 ha

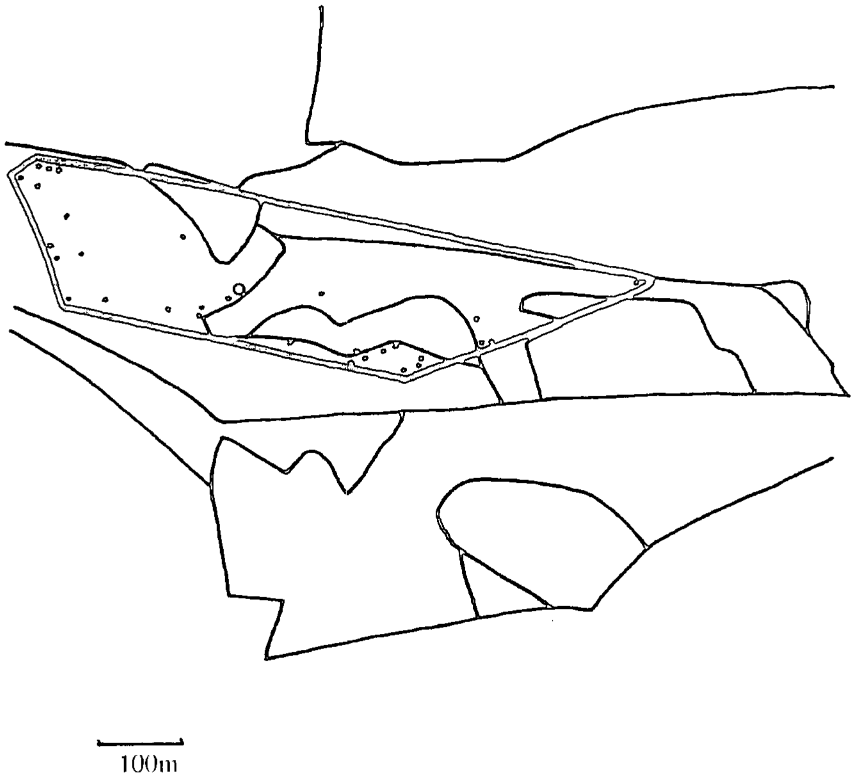
Fig 12 <u>Total home range (MCP) and fix locations of NL296</u>



Total home range = 30.56 ha
Core-area = 14.1 ha

- ◦ Radio fix
- ○ Recalculated arithmetic mean

Fig 13 <u>Total home range (MCP) and fix locations of NL244</u>



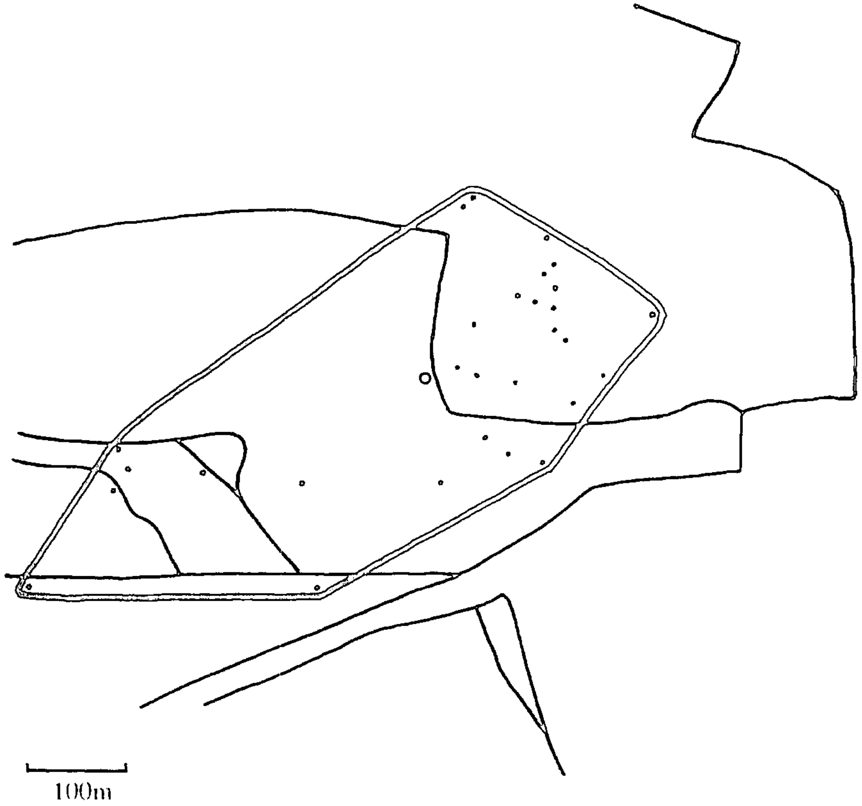
Total home range = 15.26 ha
Core-area = 6.1 ha

Fig14 **Total home range (MCP) and fix locations of NL303**

Total home range = 4.89 ha
Core-area = 2.6 ha

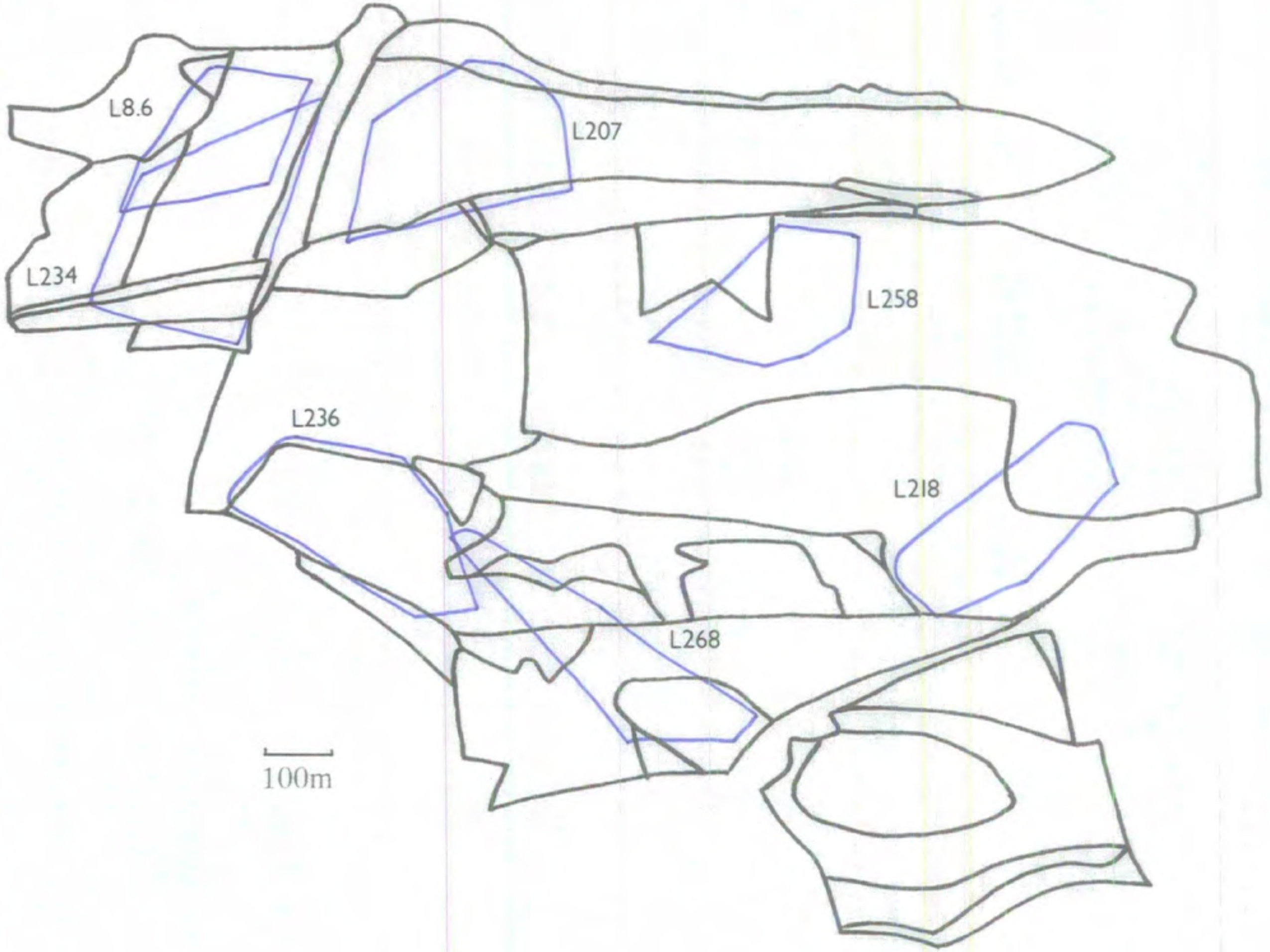
- ∘ Radio fix
- ○ Recalculated arithmetic mean

Fig15 **Total home range (MCP) and fix locations of NL286**



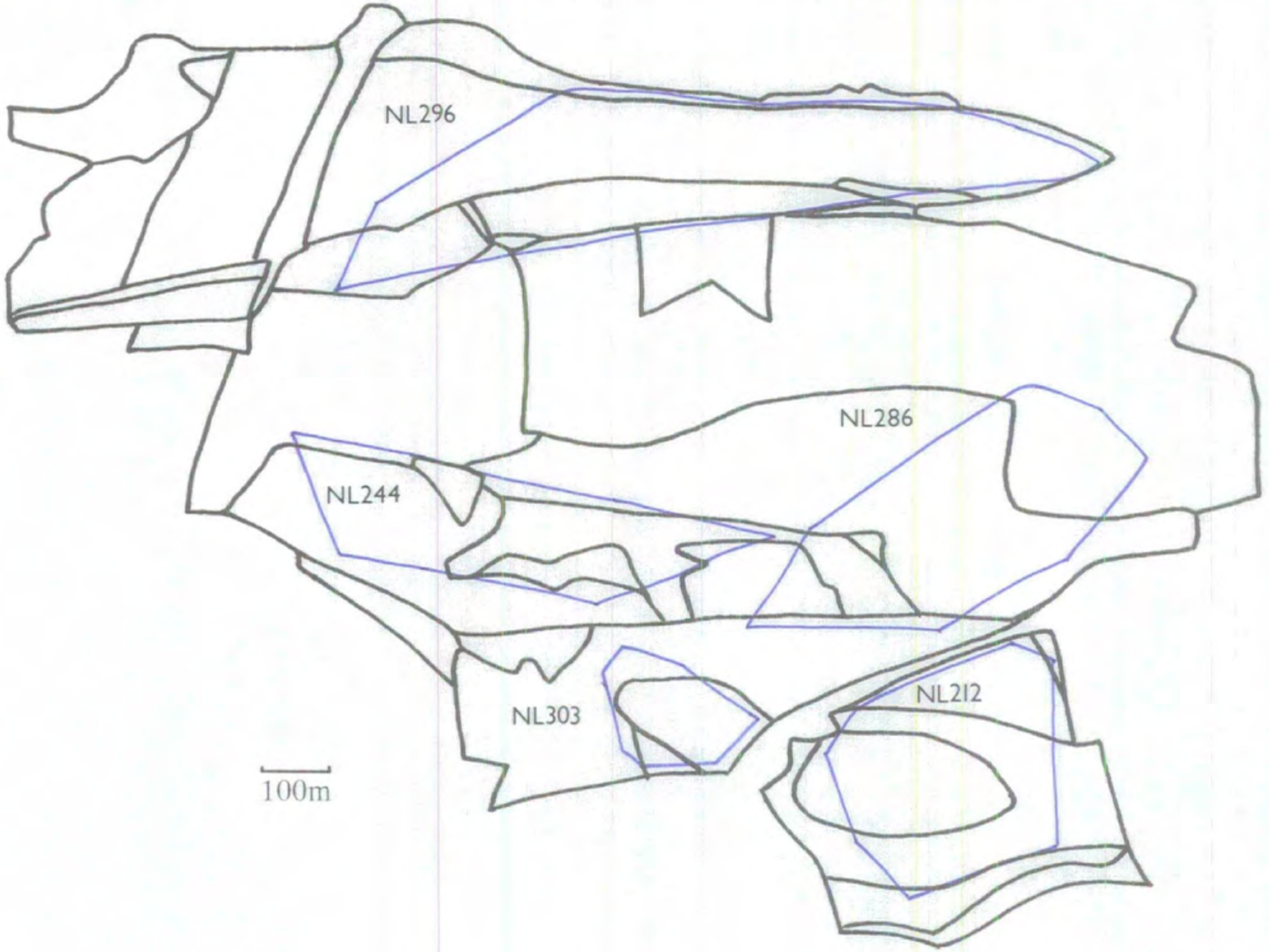
Total home range = 19.95 ha
Core-area = 5.2 ha

Fig 16 **Total home ranges (MCP) for lactating females**



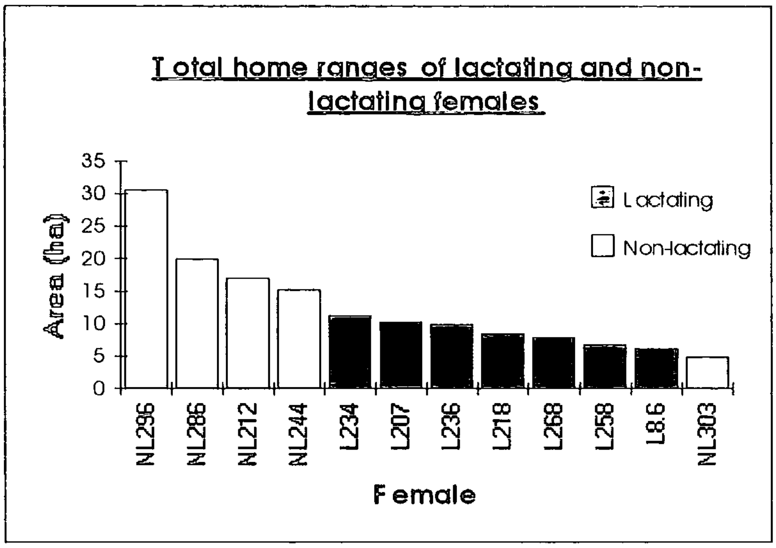
	268	207	218	258	236	234	8.6
100% minimum convex polygon (ha)	7.91	10.28	8.49	6.78	9.85	11.3	6.16
70% core-area (ha)	3.4	5.2	3.1	1.7	3.6	4.7	2.5

Figl7 **Total home ranges (MCP) for non-lactating females**



	212	296	244	303	286
100% minimum convex polygon (ha)	17.0	30.56	15.26	4.89	19.95
70% core-area (ha)	5.3	14.1	6.1	2.6	5.2

Fig.18



Core-areas were established to be the area encompassed by 70% of all fixes for eight of the females. Figure 19 shows the percentage of home range area plotted against the percentage of total fixes for each female (Fig.19). This value was therefore used for all females in identifying core-area size in which the majority of the squirrels' movements took place (Kenward 1985, Samuel *et al.* 1985).

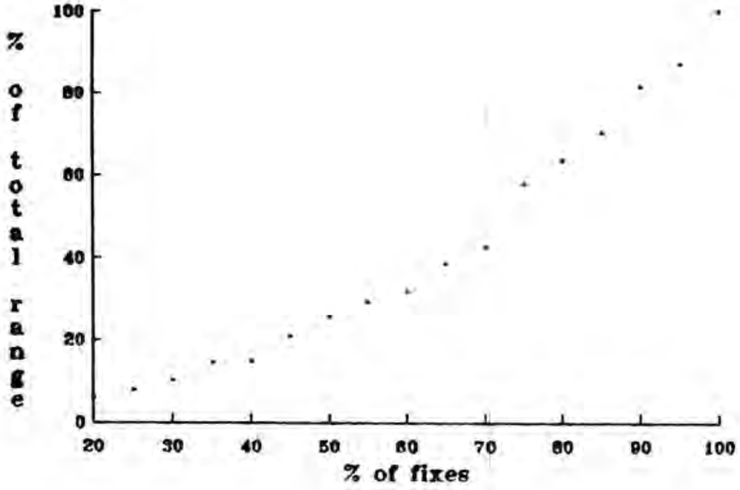
Both categories of females had core-areas that were much smaller than their total range (Figs.20 & 21). The core-areas of lactating females (*N*=7, Mean ± SD= 3.46 ±1.21) were 40% of the total range size and those of non-lactating females (*N*=5, Mean ± SD= 6.67 ±4.36) were 38% of the total range size. Thus, squirrels used part of their range very intensively, whilst range edges were visited only occasionally. A high correlation coefficient was obtained when total home range size was tested against core-area (*r*=0.927, 10 df, *N*=12). This showed that there was a significant relationship between the size of core-areas and the size of home ranges. The females with larger home ranges had core-areas that were significantly larger than those females with smaller home ranges.

Mean core-area size was 3.46 ha (±SD=1.21) for lactating females and 6.67 ha (±SD=4.36) for non-lactating females (Table 3.2). The median values for their core-areas were 3.4 ha and 5.3 ha respectively. Core-areas were significantly smaller for lactating females (Mann-Whitney U test, *u*=5, *P*<0.05) (Fig.22). Neither home range size or core-areas were significantly different between lactating and non-lactating females using the kernel method (Kenward 1990) of home range analysis (Mann-Whitney U test, *u*=7, N.S.; Mann-Whitney U test, *u*=7, N.S.). Mean ±S.D core-areas obtained by kernel analysis were 4.664±1.035 for lactating females and 8.68±5.003 for

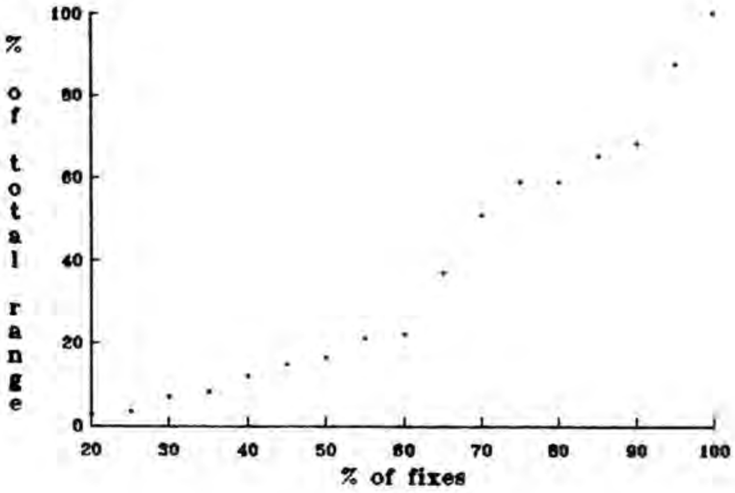
Fig 19
(3pp)

Percentage of total home range against percentage of fixes for each female showing 70% plateaus used to determine core-areas

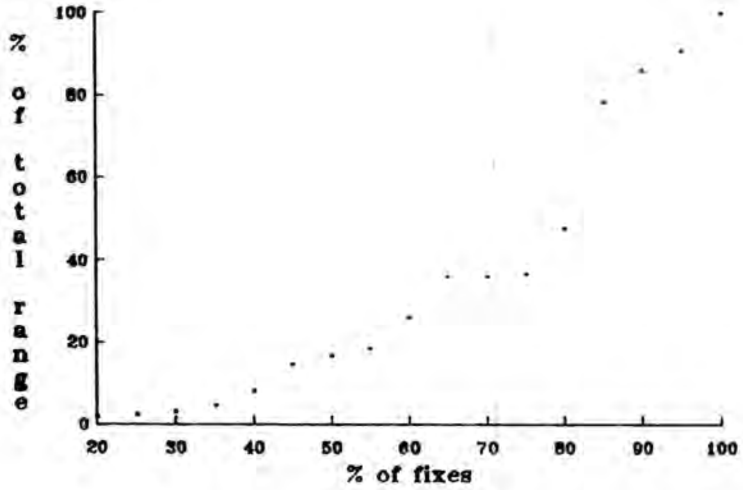
L268



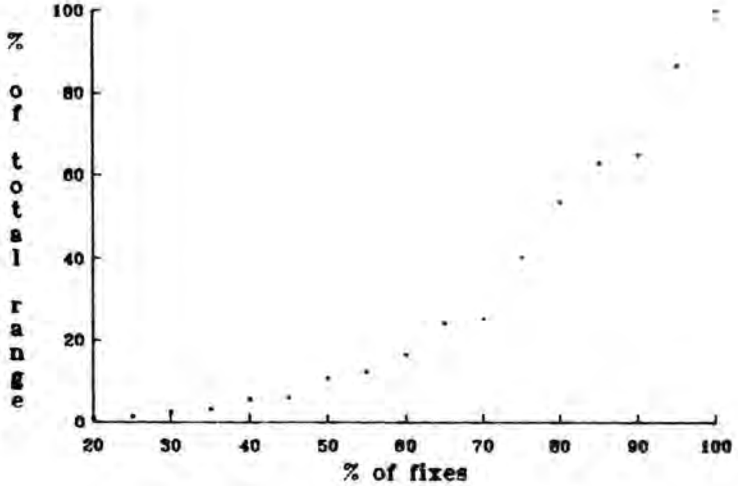
L207



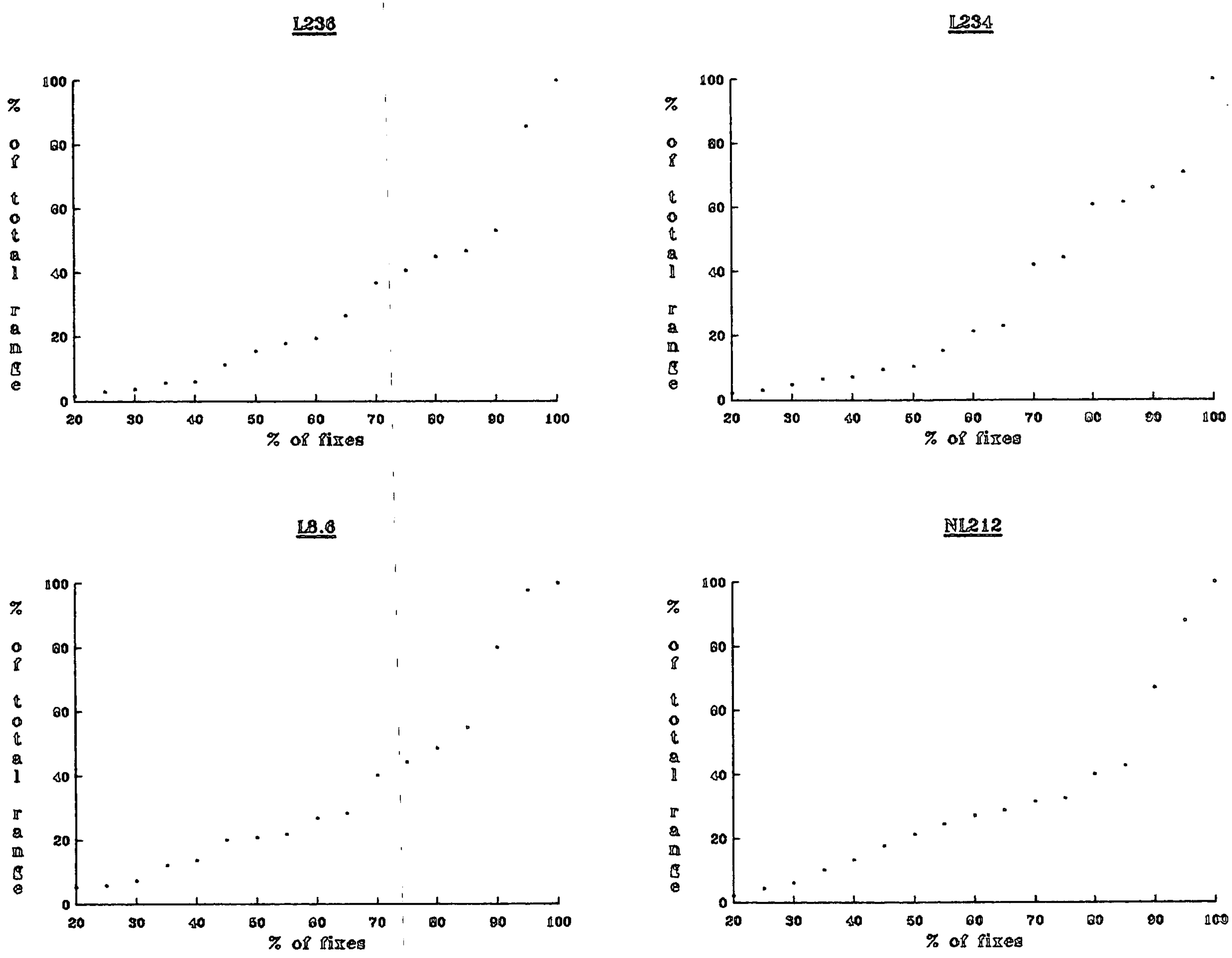
L218



L258



...19 Percentage of total home range against percentage of fixes for each female showing 70% plateaus used to determine core-areas (Cont'd)



...19 Percentage of total home range against percentage of fixes for each female showing 70% plateaus used to determine core-areas (Cont'd)

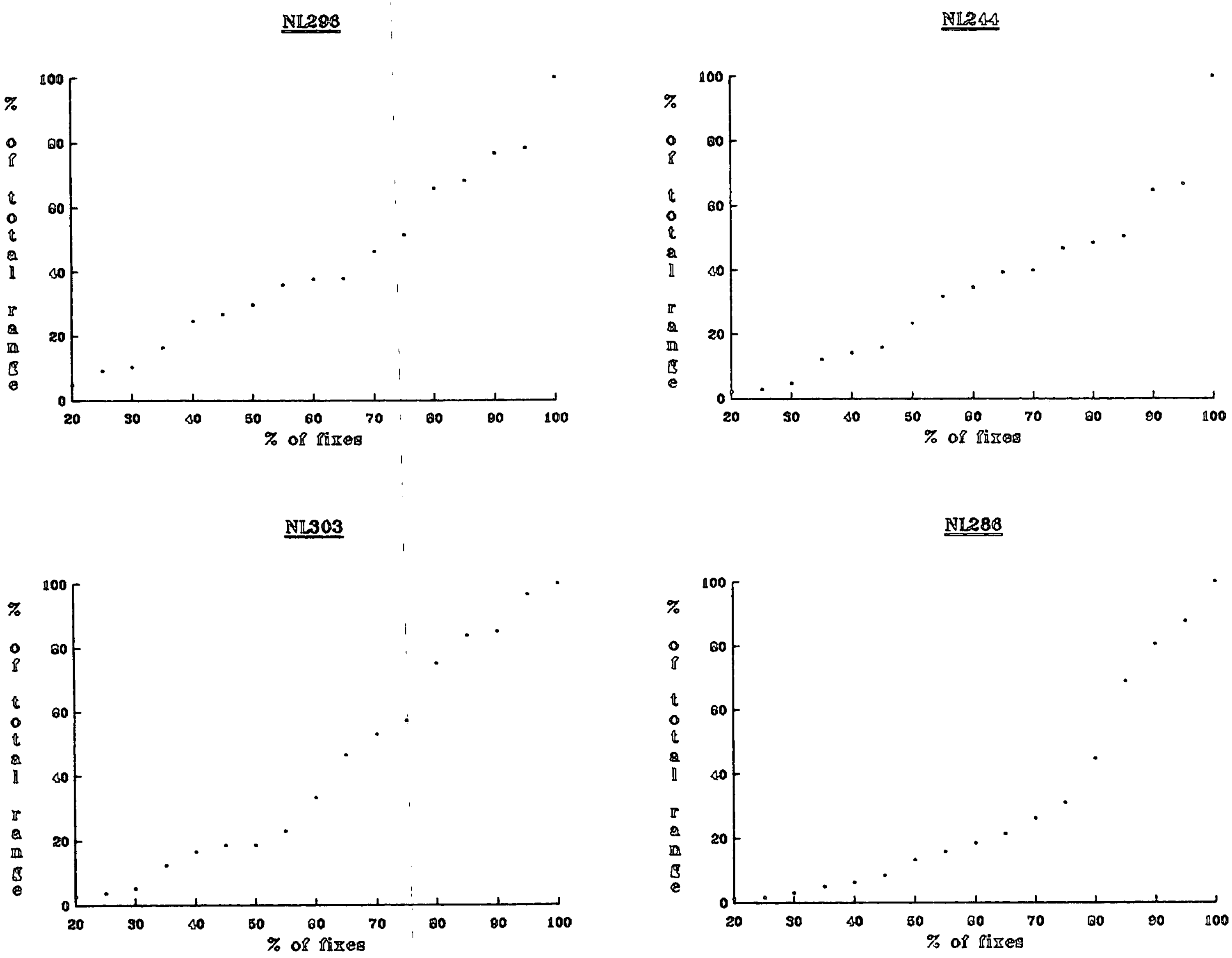
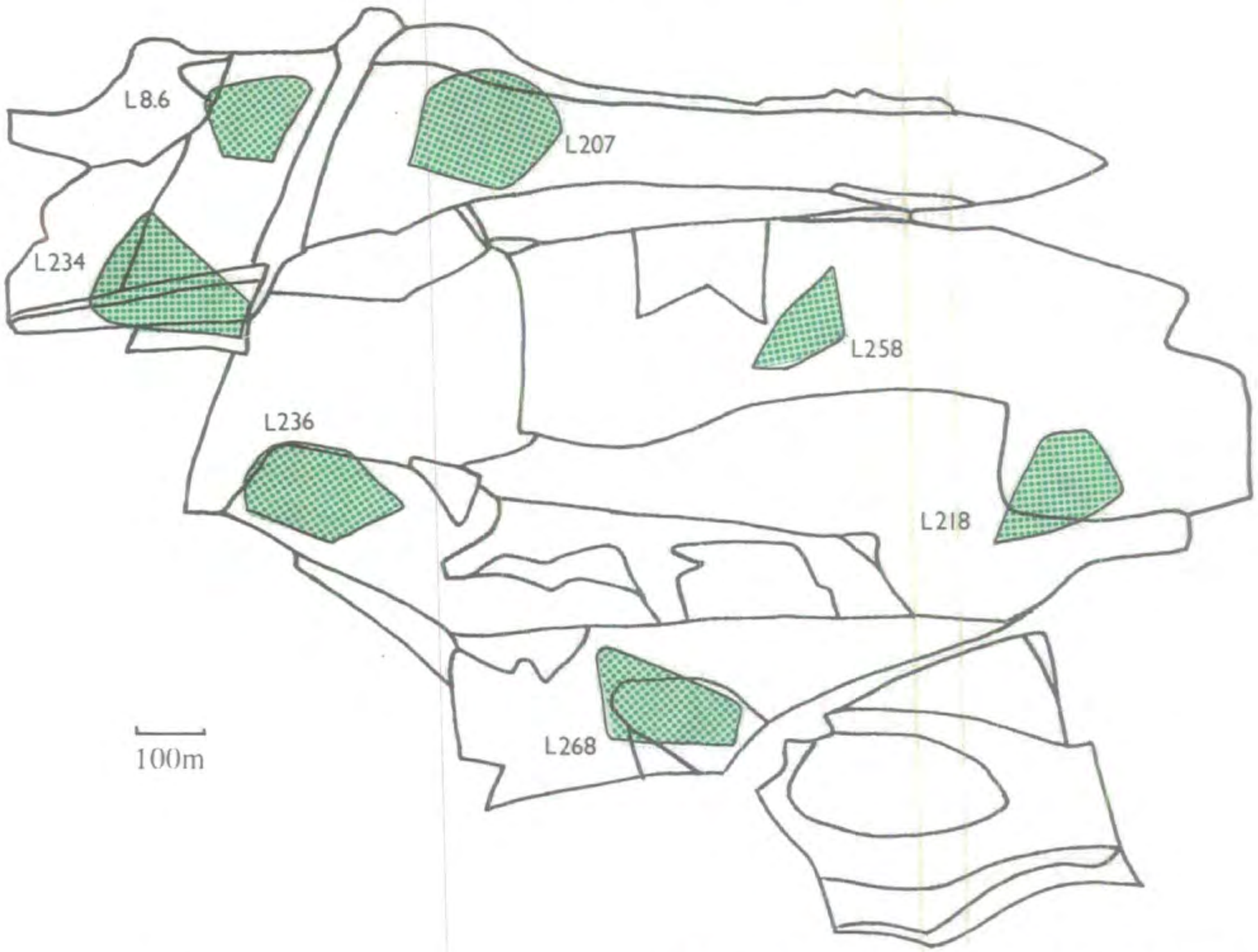
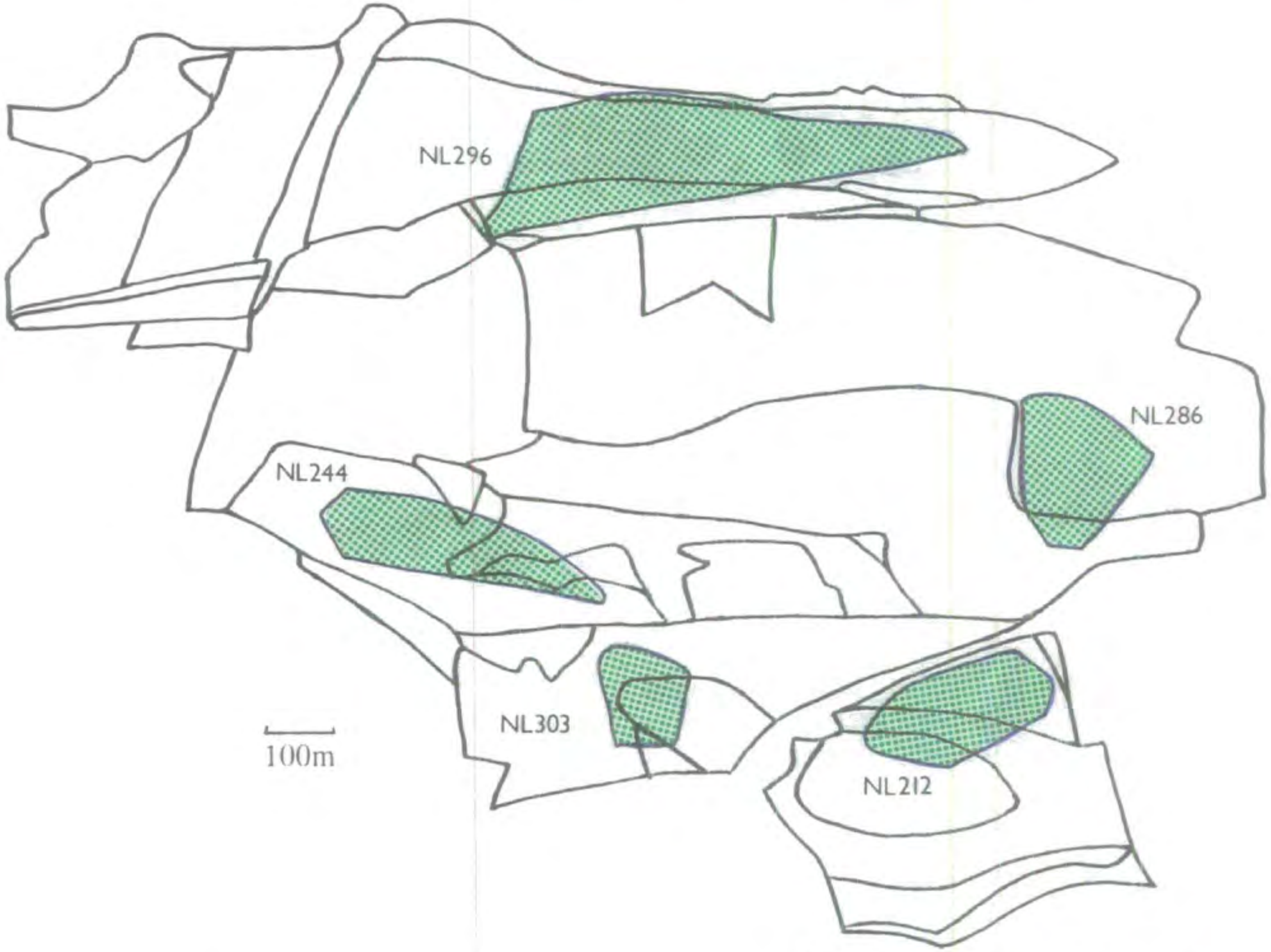


Fig 20 70% core-areas for lactating females



	268	207	218	258	236	234	8.6
70% core-area (ha)	3.4	5.2	3.1	1.7	3.6	4.7	2.5
100% minimum convex polygon (ha)	7.91	10.28	8.49	6.78	9.85	11.3	6.16

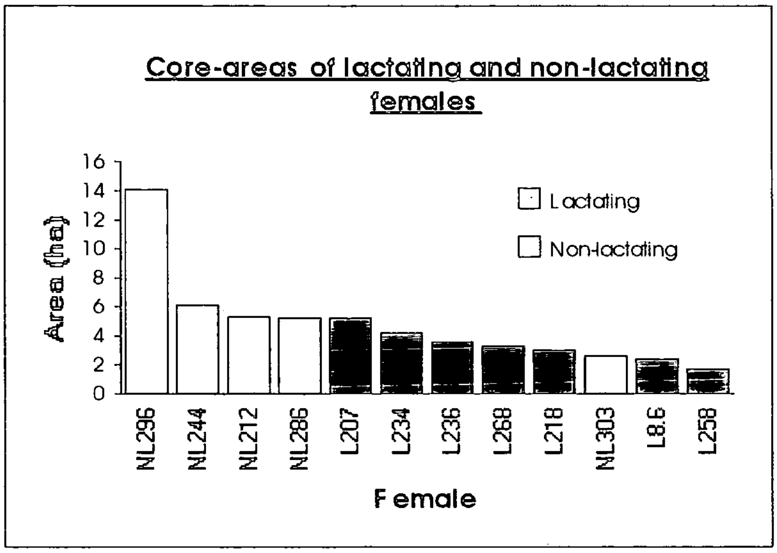
Fig21 <u>70% core-areas for non-lactating females</u>



	212	296	244	303	286
70% core-area (ha)	5.3	14.1	6.1	2.6	5.2
100% minimum convex polygon (ha)	17.0	30.56	15.26	4.89	19.95

non-lactating females.

Fig.22.



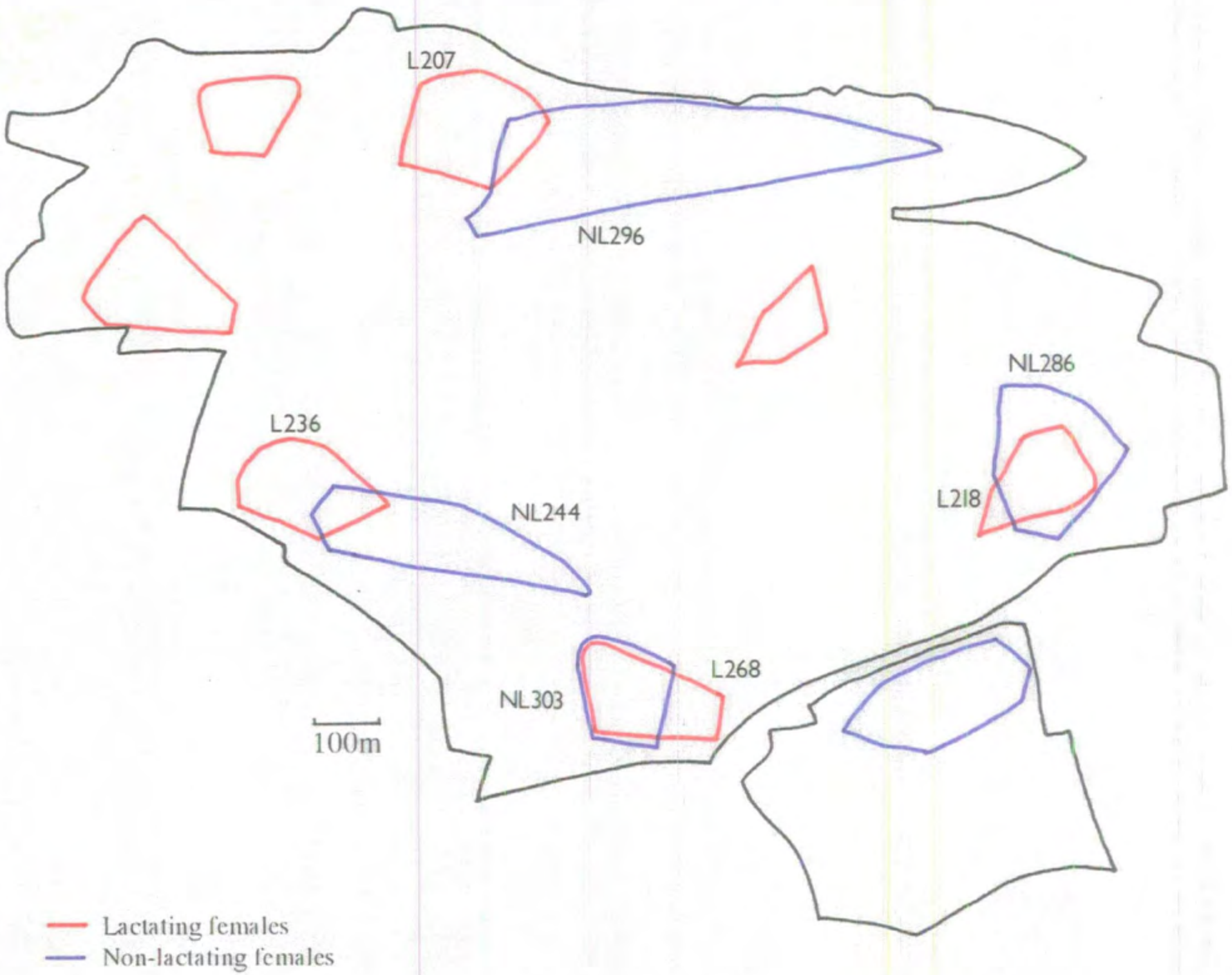
Of the lactating females, L234 had the largest home range (11.30 ha) whereas L207 showed the largest core-area size (5.2 ha). This indicates that the range of L207 was more similar in size to her core-area than was the case for L234. L207 thus utilised all sections of her range in relation to her core-area more equally than L234. The smallest range for a lactating female was that of L8.6 (6.16 ha) and the smallest core-area was that of L258 (1.7 ha). Among the non-lactating females, NL296 had the largest range and core area (30.56 ha and 14.1 ha respectively), and thus the largest home range size of all the females. NL303 had the smallest home range (4.89 ha) and core-area (2.6 ha) which was uncharacteristic of other non-lactating female range sizes. Her range and core-area were even more restricted than for the majority of lactating females.

Total home range overlap was extensive with only L258 and NL212 exhibiting exclusive ranges (Fig.23). L218 and NL286 exhibited the most extensive range overlap with 95.8% of L218's range being overlapped by 41.2% of NL286's. Within each category (lactating and non-lactating females) total range overlap only occurred extensively between L8.6 and L234 where 32.3% of the latter's core-area overlapped 45.2% of the former's.

Whilst there was no overlap of core-areas between lactating females or non-lactating females, the core-areas of lactating females overlapped those of non-lactating females to varying extents (Table 3.3, Fig.24). Four core-area overlap interactions occurred, all of which were between lactating and non-lactating females: the core-area of L286 almost entirely encompassed that of NL218. L268 and NL303 also showed extensive

Fig 23 **Total home range (MCP) overlaps of lactating and non-lactating females**

Fig 24 **Core-area overlaps of lactating and non-lactating females**



overlap, whilst the core-areas of NL296 and L207 and NL244 and L236 overlapped to a lesser extent.

Table 3.3. The percentage of overlap between the core-areas of lactating and non-lactating females. Female core-areas in rows overlap those in columns.

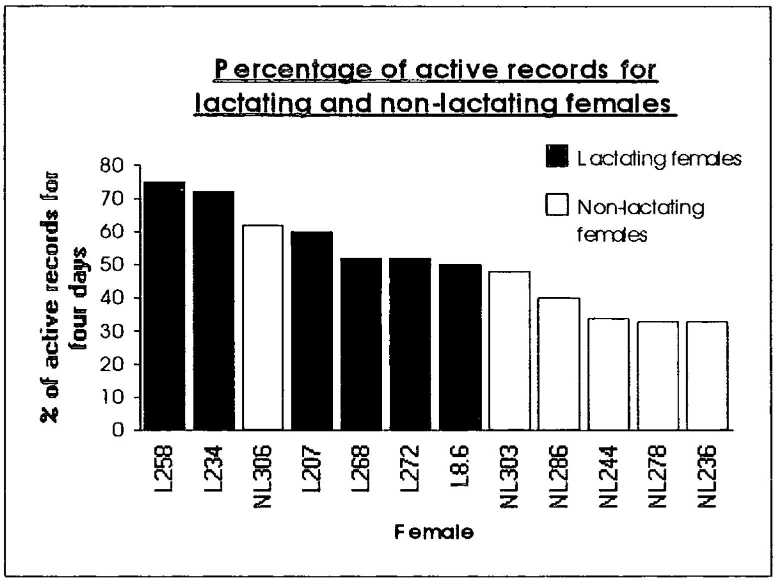
	L268	**L207**	**L218**	**L258**	**L236**	**L234**	**L8.6**	**NL212**	**NL296**	**NL244**	**NL303**	**NL286**
L268	------	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**64.3**	0.0
L207	0.0	------	0.0	0.0	0.0	0.0	0.0	0.0	**19.2**	0.0	0.0	0.0
L218	0.0	0.0	------	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**91.8**
L258	0.0	0.0	0.0	------	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
L236	0.0	0.0	0.0	0.0	------	0.0	0.0	0.0	0.0	**24.5**	0.0	0.0
L234	0.0	0.0	0.0	0.0	0.0	------	0.0	0.0	0.0	0.0	0.0	0.0
L8.6	0.0	0.0	0.0	0.0	0.0	0.0	------	0.0	0.0	0.0	0.0	0.0
NL212	0.0	0.0	0.0	0.0	0.0	0.0	0.0	------	0.0	0.0	0.0	0.0
NL296	0.0	**7.1**	0.0	0.0	0.0	0.0	0.0	0.0	------	0.0	0.0	0.0
NL244	0.0	0.0	0.0	0.0	**14.4**	0.0	0.0	0.0	0.0	------	0.0	0.0
NL303	**83.6**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	------	0.0
NL286	0.0	0.0	**54.0**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	------

3.2.2 Activity levels and patterns

Two major differences emerged between the activity of lactating and non-lactating females. Firstly, activity level, defined as the percentage of active records over four days, was higher in lactating females than in non-lactating females (Mann-Whitney U test, *u*=4, P<0.05). Secondly, lactating females were more constantly active throughout the day when compared to non-lactating females which showed a clear drop in activity after mid-day.

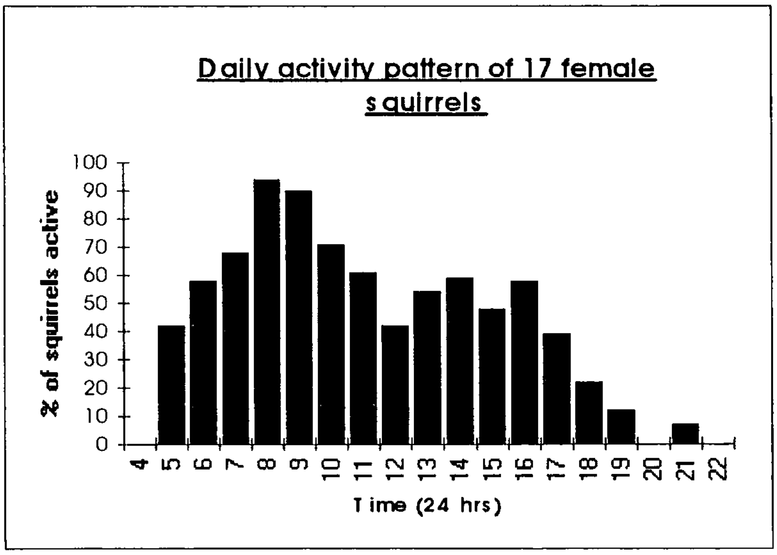
Figure 25 shows total activity records (out of 60 active and drey records in total) for lactating and non-lactating females in rank order (Appendix II). Non-lactating squirrels were less active than lactating squirrels with the exception of NL306. This female was active for 62% of the records (37 of 60) which was uncharacteristically high when compared to the other non-lactating females. L258 showed the highest activity level with 75% (45 out of 60 records) and NL236 and NL278 show the lowest with 33% (20 of 60). Mean and median values for total activity were 60.2% and 56% for lactating females and 41.7% and 37% for non-lactating females.

Fig.25



The diurnal activity pattern of 17 females (unknown lactation status) was recorded over four days which provided the largest possible squirrel sample size. A bi-modal daily activity pattern emerged when the mean percentage of squirrels active in each hour of the day was plotted (Fig.26). Activity began at 0500 hours when 42% (7 of 17) of the squirrels were active and peaked at 0800 hours when 94% (16 of 17) of the females were active. A lull in activity occurred at 1200 hours when only 42% (7 of 17) of the females were active. This was followed by a second rise in activity level which peaked at 1400 hours when 59% (10 of 17) were active . A steady decline in activity then took place until approximately 1900 hours by which time most squirrels had entered their dreys for the night.

Fig.26



Activity for combined, known-status lactating and non-lactating females (*n*=12) was calculated by counting the number of active records of each female for every hour between 0500 and 1900 hours for four days. Active records were then expressed as a percentage of total records (*n*=48 per hour) and plotted to show the diurnal activity pattern (Fig.27, Appendix III). A similar bi-modal pattern occurred although it was less pronounced than that of the 17 females (Fig.26). Times of emergence and activity cessation remained the same. Peak time of activity was 0900 hours (87.5% of records active) with the mid-day lull occurring at 1300 hours (39.6% of records active).

Fig.27

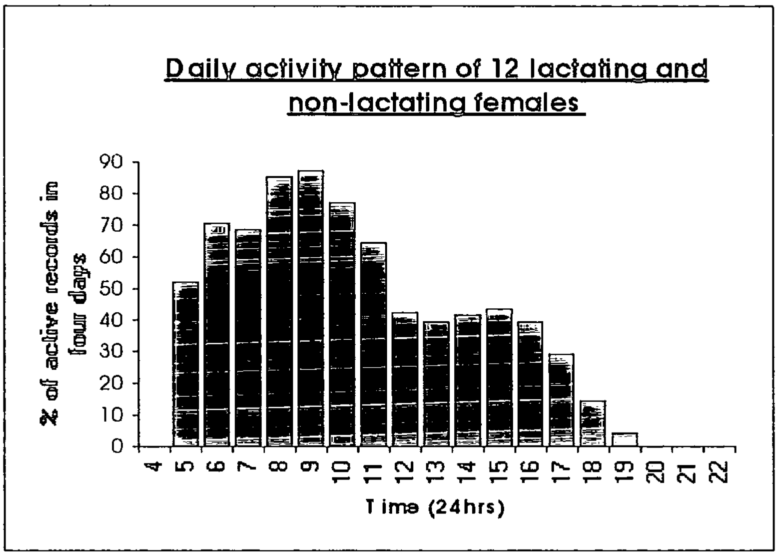
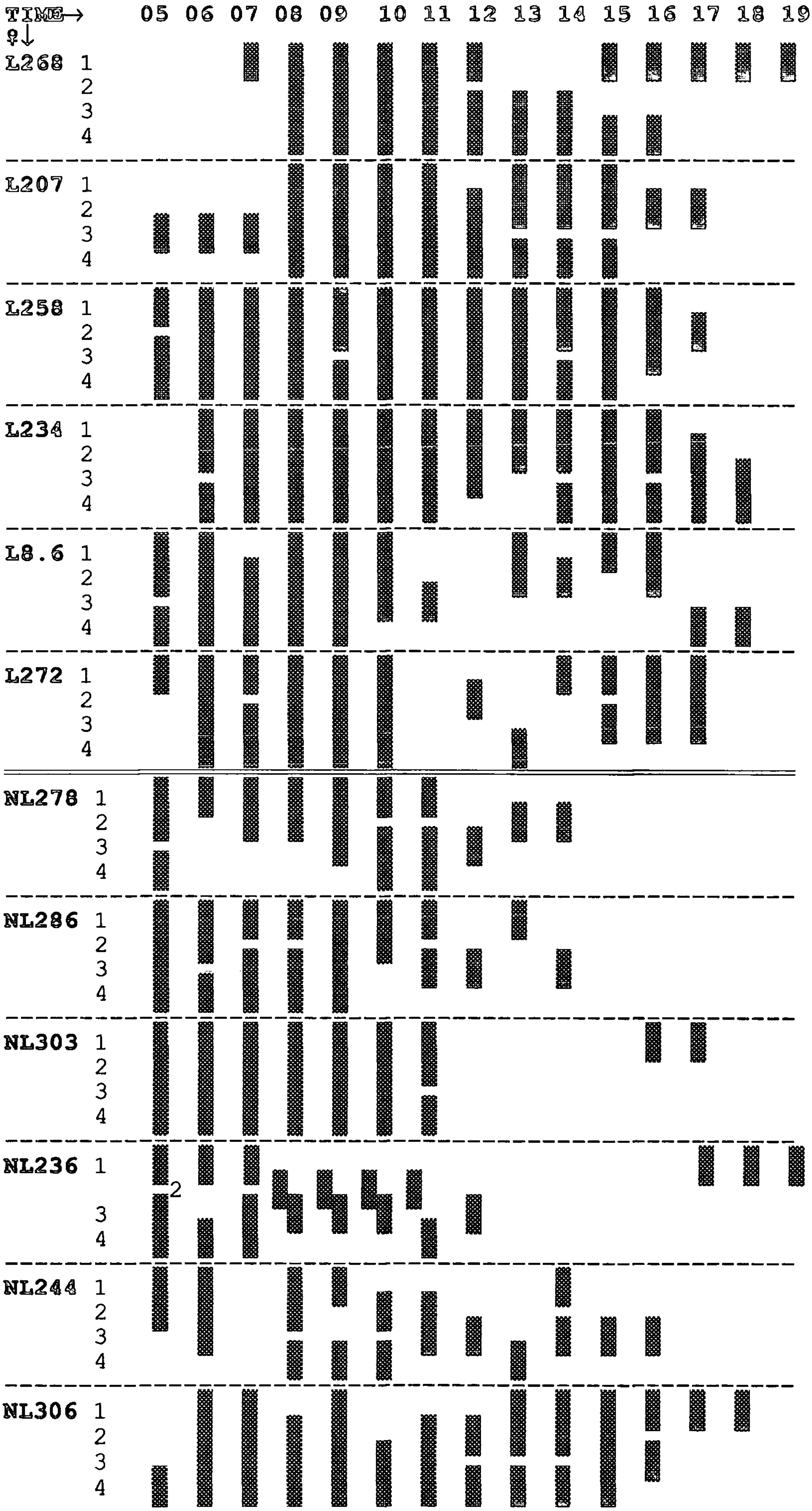


Figure 28 shows the activity patterns of each squirrel for each of the four activity recording days. Each shaded block represents an active record, blank spaces indicating a drey record. Individual variation between squirrels was apparent, as was a difference between the categories of lactating and non-lactating females. Morning activity levels (0500 -1100 hours) were not significantly different between lactating and non-lactating females (Mann Whitney U test, *u*=9.5, N.S.). However, afternoon activity levels (1200-1900 hours) were significantly higher among the lactating females than the non-lactating females (Mann Whitney U test, P<0.05, *u*=4).

Morning activity levels for lactating females were significantly higher than afternoon levels (Mann Whitney U test, P<0.05, *u*=4). The higher level of activity between 0800 and 1000 was clear as was the mid-day reduction in activity. Lactating females displayed an obvious mid-day lull which was followed by a smaller peak of activity in the early afternoon. They often remained active for long periods of time. For example, L258 showed 10 consecutive active records (between 0600 and 1500) on three out of

Fig28 Diurnal activity patterns of lactating and non-lactating females on each of four days. Each block refers to an active record; blank spaces refer to a drey record.

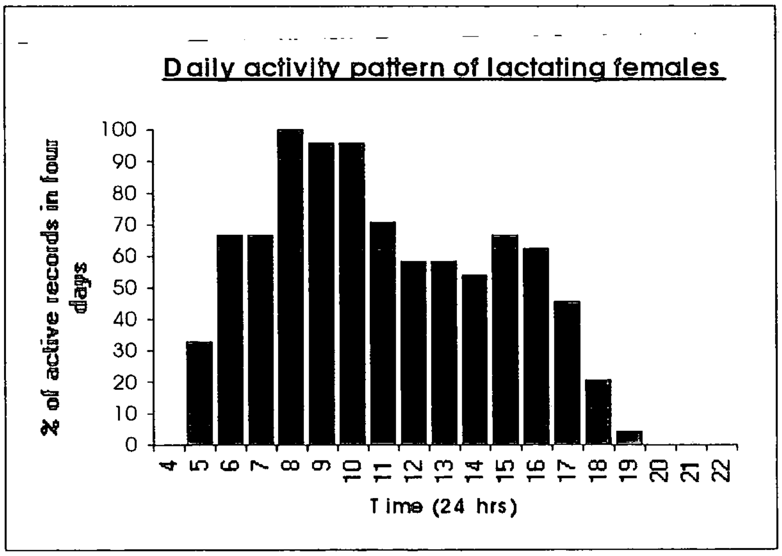


four days. However, it must be noted that such records do not represent successive activity hours during the same day as morning and afternoon records were taken in two different weeks (see section 2.2.2 ii).

The activity levels of non-lactating females were significantly higher in the morning period than in the afternoon period (Mann Whitney U test, P<0.02, *u*=1.5). These females concentrated their activity between 0500 hours and 1100 hours, only occasionally resuming activity in the afternoon. NL306 was the exception to this pattern. Her activity continued into the afternoon hours in a manner similar to that of the lactating females. On the fourth day she appeared to remain active between 0500 and 1500 hours. This long period of activity was not observed for any other non-lactating female.

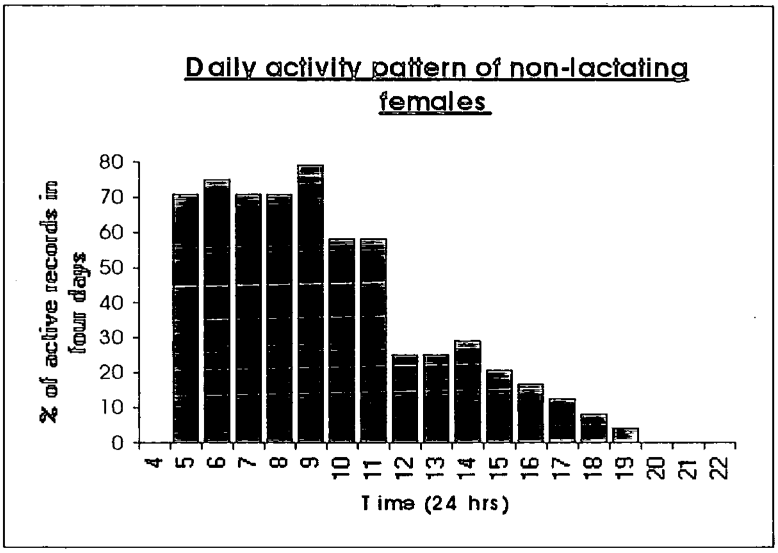
The difference between lactating and non-lactating female diurnal activity patterns is clear in and Figures 29 and 30 where female categories have been treated separately (Appendix IV). Activity is expressed as the percentage of total active and drey records for each hour of four days (*n*=24 per hour). For lactating females, the onset of activity was gradual with only 33% of records being active at 0500 hours. Activity rose in the early morning until a clear peak occurred between 0800 and 1000 hours with 100% of the records active at 0800 hours. A drop in activity occurred between 1200 and 1400 hours after which an afternoon peak rose to 66.7% at 1500 hours. Cessation of activity was more abrupt than that of the non-lactating females, falling from 62.5% (1600 hours) to zero (2000 hours) in four hours.

Fig.29



For non-lactating females morning activity commenced more abruptly with 75% of records active at 0500 hours. This remained relatively constant until 0900 hours, after which a drop in activity occurred. At 1200 a further, more considerable fall in activity reduced active records to 25%. Activity before 1200 hours was more than double that from 1200 hours onwards within the non-lactating females. A very gradual decline in active records occurred between 1400 (29.2%) and 1900 (4.2%) until cessation of activity at approximately 1930.

Fig.30



3.2.3 Habitat utilisation

An estimation of the area covered by each tree species within the study site was calculated using the digitised study site map on RANGES IV (Kenward 1990). Table 3.4 shows the coverage in hectares of each tree species within the study site and Figure 31 shows the percentage cover of each tree species.

Table 3.4. Area coverage in hectares and proportion of each tree species within the study site.

Species	**Coverage (ha)**	**Proportion**	**%**
Norway spruce (NS)	40.73	0.172	17.2
Lodgepole pine (LP)	110.50	0.468	46.8
Sitka Spruce (SS)	77.70	0.329	32.9
Serbian spruce (SerS)	7.40	0.031	3.1
Total	236.33	1.000	100.0

Table 3.5 shows the number and proportion of fixes used in compositional analysis for each squirrel recorded in each tree species during radio tracking. Note that proportions of zero were replaced by 0.001 so that log-ratios could be calculated in

order to render the proportions independent of each other for compositional analysis to be implemented (see section 2.3.4). Table 3.5 shows the number and proportion of fixes obtained in each tree species for each radio collared squirrel.

Fig.31

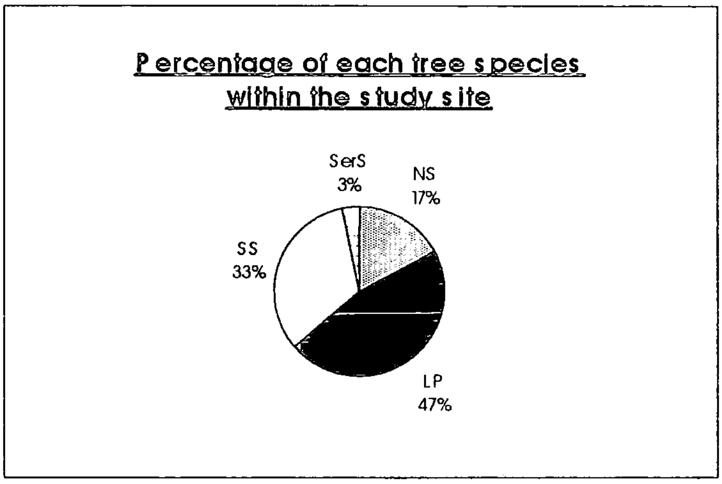


Table 3.5. The number of fixes from radio collared females in each tree species and the proportion of fixes in each species used in compositional analysis.

Tree species	**NS** Fixes	Prop.	**LP** Fixes	Prop.	**SS** Fixes	Prop.	**SerS** Fixes	Prop.	**Total** Fixes	Prop.
Female										
L268	5	0.167	16	0.533	9	0.300	0	0.001	30	1.0
L207	0	0.001	24	0.800	6	0.200	0	0.001	30	1.0
L218	1	0.034	19	0.655	9	0.310	0	0.001	29	1.0
L258	0	0.001	29	1.000	0	0.001	0	0.001	29	1.0
L236	0	0.001	17	0.567	7	0.233	6	0.200	30	1.0
L234	0	0.001	10	0.345	19	0.655	0	0.001	29	1.0
L8.6	0	0.001	24	0.857	4	0.143	0	0.001	28	1.0
NL212	16	0.533	8	0.267	6	0.200	0	0.001	30	1.0
NL296	0	0.001	26	0.900	4	0.100	0	0.001	30	1.0
NL244	3	0.100	14	0.467	9	0.300	4	0.133	30	1.0
NL303	12	0.400	5	0.167	12	0.400	1	0.033	30	1.0
NL286	5	0.179	16	0.571	7	0.250	0	0.001	28	1.0
Total	42		208		92		11		353	
% of total fixes	11.9		58.92		26.06		3.12		100	

The majority of fixes were obtained in lodgepole pine with Serbian spruce containing the fewest fixes. This correlates with total availability of these species within the study site (Table 3.4). Considerable tree-use variation between squirrels can be seen from the fix data. For example, all fixes obtained for L258 (*n*=29) occurred in lodgepole pine, whereas the majority of fixes for L234 were found in Sitka spruce (*n*=19).

NL303 and NL244 were the only two females to utilise all four species during radio tracking and L236 was the only other female with Serbian spruce-located fixes (*n*=6).

Fig.32

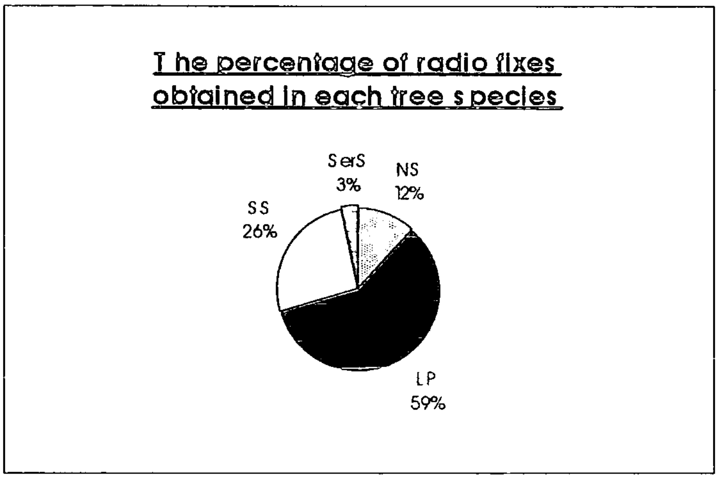


Table 3.6. The proportions of tree species used in compositional analysis within the total home range (MCP) of each radio collared squirrel.

	NS Prop.	LP Prop.	SS Prop.	SerS Prop.
Female				
L268	0.358	0.274	0.275	0.106
L207	0.001	0.888	0.115	0.001
L218	0.013	0.378	0.611	0.001
L258	0.001	1.000	0.001	0.001
L236	0.013	0.451	0.081	0.451
L234	0.001	0.708	0.296	0.001
L8.6	0.001	0.827	0.181	0.001
NL212	0.285	0.337	0.400	0.001
NL296	0.001	0.785	0.266	0.001
NL244	0.373	0.222	0.230	0.222
NL303	0.336	0.324	0.351	0.001
NL286	0.169	0.271	0.582	0.001

Clearly, the total home range proportions in Table 3.6 represent habitat use at a courser scale than the individual fixes in Table 3.5. Therefore, utilisation appeared to be more evenly distributed among each species. For example, the total range of L268 encompassed a proportion of Serbian spruce (0.106) which was not considered to be utilised when the fixes for this female were considered. However, many habitat types at this level remained unused, as they were when fixes were considered. For example, Norway spruce was not utilised at either scale by females L207, L258, L234, L8.6 or NL296.

Compositional analysis was used in order to compare utilised with available habitats for 12 radio collared females. Two levels were considered: Firstly, an overall comparison of the proportions of radio fixes in each tree species (habitat utilised) and the proportions of each tree species in the entire study site (habitat available). Secondly, a comparison of the proportions of each tree species within the total home range (habitat utilised) and the proportions of each tree species within the entire study site (habitat available).

Wilks'-lambda χ^2 results determined whether squirrels were utilising the habitat in a random manner or whether habitat preference was exhibited. Using total home range as the habitat utilised by each squirrel and the study site as available habitat did not yield a significant result (Wilks'-lambda $\chi^2 = 6.95$). That is, squirrels were not selecting habitat in a manner other than at random at this scale of analysis. However, using each individual fix from each squirrel as the utilised habitat and the study site as the available habitat provided a significant Wilks'-lambda χ^2 value of 19.46 ($P<0.001$, df=3). That is, squirrels were utilising habitat in a non-random manner and were thus showing significant preferences.

A *t*-test of the difference between the mean log-ratios (± 1 SE) was therefore used (Table 3.7) to determine the order in which tree species were selected. Habitats could then be ranked according to relative use and significant between-rank differences could be determined (Aebischer *et al.* 1993a, 1993b) (Table 3.8).

Table 3.7. Mean (±1 SE) log-ratio differences between utilised (squirrel radio locations) and available (total study site) habitat compositions for 12 squirrels.

	Habitat types (denominator)			
Habitat type (numerator)	NS	LP	SS	SerS
NS	---------------	2.715±0.905	1.855±0.768	0.296±0.934
LP	-2.792±0.932	--------------	-0.937±0.647	-2.498±0.69
SS	-1.855±0.768	0.860±0.577	--------------	-1.561±0.687
SerS	-0.296±0.934	2.420±0.676	1.561±0.687	---------------

Table 3.8. Simplified ranking matrix for squirrel habitat use showing preference and avoidance of each tree species. Positive signs indicate preference of species in columns over species in rows, negative signs indicate avoidance. Single signs are not significant, triple signs represent significant deviation from random use at $P<0.05$.

	Habitat types (denominator)			
Habitat type (numerator)	NS	LP	SS	SerS
NS	--------------	+ + +	+ + +	+
LP	- - -	--------------	-	- - -
SS	- - -	+	--------------	- - -
SerS	-	+ + +	+ + +	--------------

All species were selected in preference to Norway spruce although not significantly in the case of Serbian spruce (Table 3.8). Lodgepole pine was significantly selected over Norway spruce and Serbian spruce. Sitka spruce was significantly selected over Norway spruce and Serbian spruce and Serbian spruce was not selected to the extent of any other species.

Thus, there was a significant and equal preference for lodgepole pine and Sitka spruce and a significant and equal avoidance of Serbian spruce and Norway spruce. This provided a ranking order of squirrel selection for the four habitats of:

(lodgepole pine = Sitka spruce) > (Serbian spruce = Norway spruce).

Chi² goodness of fit analysis of habitat availability and utilisation provided data that could be compared with compositional analysis results. A comparison between the number of observed fixes and the number of expected fixes in each tree species, using the study site as habitat available (Table 3.4), showed that squirrels were not utilising habitats according to their availability (χ^2=21.871, 3df, $P<0.001$) (Table 3.9).

Table 3.9. Chi² goodness of fit table for habitat utilisation showing the number of observed fixes and the number of expected fixes for each tree species.

Habitat	**Observed no. fixes**	**Expected no. fixes**		χ^2	**P**
NS	42	0.172x353=	60.7160	5.76900	<0.025
LP	208	0.468x353=	165.204	11.0860	<0.001
SS	92	0.329x353=	138.376	5.01600	<0.05
SerS	11	0.031x353=	10.9430	0.00020	>0.05
Total	353		353.00	21.871	

Considering each habitat separately, Norway spruce was significantly avoided (χ^2=5.769, 1df, $P<0.025$), lodgepole pine was significantly preferred (χ^2=11.086, 1df, $P<0.001$), Sitka spruce was significantly avoided (χ^2=5.016, 1df, $P<0.05$) and Serbian spruce was utilised according to its availability (χ^2=0.0002, 1df, $P>0.995$).

The results correspond partially with those obtained from compositional analysis. Using Chi^2 analysis lodgepole pine was significantly preferred over the remaining species. However, Sitka spruce was avoided more significantly than Norway spruce which does not match the findings of compositional analysis.

An estimate of cone crops was obtained in order to compare habitat use with the food crop provided by each tree species (Table 3.10). Lodgepole pine provided relatively high cone crops in Autumn of 1993. Sitka spruce cone crops were found to be slightly lower and somewhat patchy in distribution. Norway spruce produced very few cones and, although Serbian spruce transects were not taken, virtually no cones were observed from this species.

Table 3.10. Cone crop density estimations of lodgepole pine, Sitka spruce and Norway spruce.

Species	**Density (per m^2)**
LP	1.24
SS	1.08
NS	0.01

Compositional analysis showed that lodgepole pine and Sitka spruce were significantly and equally preferred over Norway spruce and Serbian spruce. Chi^2 analysis suggested that lodgepole pine was preferred over all other species. The utilisation of trees by squirrels therefore appeared to be correlated with the cone crop levels and therefore seed availability of each conifer species.

4.0 DISCUSSION

4.1 Population density and biometrics

The density of red squirrels in Spadeadam Forest was estimated to be 0.10/ha and 0.09/ha which was particularly low when compared to data from other studies (Table 1.2). This was attributed to the low habitat quality of this plantation. Gurnell and Pepper (1988) noted that red squirrels occurred at similarly low densities in Thetford Forest, England (0.10/ha). Red squirrels in northern Spain also occurred at 0.10/ha (Purroy and Rey 1974) although the dominance of oak (*Quercus sessiliflora*) gave rise to this low deciduous population. In contrast, Pulliaianen (1982) reported a squirrel density of 10/ha in a mixed conifer/broadleaf forest in Finland noting that spruce cone yield was very high in the area of study.

As lodgepole pine provided the only abundant seed crop, limited resources meant that intraspecific competition was probably high. This appears to have restricted squirrel numbers (Wauters & Dhondt 1990) and influenced range size which was unusually high (section 4.2) in the present study. The data also support the fact that density is a major factor determining the size of squirrel ranges (Kenward 1985).

Significant seasonal and annual variations in tree squirrel populations have been related to seed supplies of important tree species (Wauters & Dhondt 1990, Andren & Limnell 1992). Kemp and Keith (1970) suggested that pine squirrel populations were affected by the abundance of flower buds in spring, which increased reproduction prior to rich cone crops in the autumn (see section 4.4.1). This meant that a high density of squirrels and good seed supplies occurred in the same year. Others have suggested that squirrel densities should increase in the year following a good cone crop due to winter survival and increased reproduction during years with large tree-seed supplies (Gurnell 1983, Obbard 1987). The very low density of squirrels in the present study seem to be related to low food availability and diversity. However, long term studies are required in order to correlate the density of squirrels found at Spadeadam Forest with the fluctuation of food availability.

Lactating females were not significantly heavier than non-lactating females in the present study (Table 3.1). Considerable weight variability among the lactating females may have been caused by a combination of individual differences (which also occurred within the non-lactating females) and by disparate lactation stages. Wauters and Dhondt (1989) found that females weighing less than 300 g did not come into oestrous. Considering this criteria, only one non-lactating female was below the required weight for reproduction in the present study. However, due to the poor habitat quality, it would appear that a higher weight criteria might determine whether females reach reproductive viability. Regular and long term capture data of female weight fluctuations before, during and after reproduction would be required to confirm this assumption.

4.2 Home range size and use

4.2.1 Total home ranges

Home range (MCP) sizes were very large compared with the findings from other studies (Table 3.2, Figs. 16 & 17). The mean home ranges were 8.68 ha for lactating females and 17.53 ha for non-lactating females. Wauters and Dhondt (1992) found the mean range size for females tracked in the same season as the present study (April-June) to be 2.94 ha. Poor habitat quality at Spadeadam appears to have limited population density and created the need for large home ranges. This seems to suggest that low density also permitted such extensive ranges (Kenward 1985).

To emphasise the unusually extensive ranges found at Spadeadam Forest, they should be compared with the home ranges of *male* squirrels which have consistently been shown to exhibit larger home ranges than females in other studies. Wauters and Dhondt (1992) found that the mean home range size for male red squirrels tracked in the same season as the present study (April-June) was 4.24 ha. Although this mean home range size was larger than that of the females' in their study, it was smaller than lactating and non-lactating female ranges at Spadeadam by 4.44 ha (104%) and 13.29 ha (313%) respectively. Hence, the Spadeadam ranges were massive in comparison. This is especially significant as male red squirrel movements are known to increase during this period when they are searching for receptive females (Holm 1989, Lurz, Pers. Comm.). Similarly, Kenward (1985) noted that male grey squirrel range size increased in spring in order to maximise their mating success, as did those of tassel-eared squirrels (Farentinos 1979).

Lactating females commonly show the smallest ranges within a squirrel population (Gurnell 1987, Kenward 1985). However, the smallest home range within the lactating females (L8.6, 6.16 ha) was still 1.92 ha, or 45% larger than the mean male range in Wauters and Dhondt's (1992) study. NL303 had the smallest range of all females (4.89 ha) which was also larger than the male mean by 0.65 ha (15%) in their study. Donohoe and Beal (1972) reported a fox squirrel population home range mean of 16.0 ha in Ohio which approaches the home range size of non-lactating females in the present study. However, no other sciurid studies show such extensive home range sizes.

Home range size has been directly related to habitat quality for many species of mammals (eg. McNab 1963) including red squirrels (Wauters & Dhondt 1992, Kenward 1985). This may explain the extensive movements of the those at Spadeadam Forest. Primary food sources are limited to four tree species. In any year, one or more of these species may fail to mast, thereby limiting food availability. The study site selected by Wauters and Dhondt (1992) comprised a greater variety of species, including oak (*Quercus robur*) and beech (*Fagus sylvatica*). The diversity of food, its availability and generally improved habitat quality may have reduced the need for large home ranges in their study.

Significant results were not obtained for the difference between the total range sizes of lactating and non-lactating females due to wide variation within the groups, although mean home range sizes appeared to differ considerably. Non-parametric assessment did not consider mean values but rank positions in order of range size. The range of NL303 was considerably smaller than the other females within the non-lactating category (Table 3.2, Fig.17) which influenced the outcome of the Mann-Whitney U test. A large standard deviation (±9.23) supports the fact that wide variation was evident within this group. NL303 may have been pregnant which would partly explain her reduced movements.

Kenward (1985) did find a correlation between the total range sizes of grey squirrels and sexual activity. Lactating females had significantly smaller ranges than either females that had failed to wean or non-breeding females. In contrast Kenagy *et al.* (1991) found that the home range size of golden-mantled ground squirrels peaked during the period of lactation.

Since radio tracking enabled the specific trees in which squirrels had settled to be identified, the accuracy of home range estimation was high. The sampling error that may have arisen when using triangulation techniques was therefore avoided (Springer 1979). The location of each fix on the site map was also considered to be accurate as carefully scaled measurements were taken. However, home range configuration using these data can only represent an *approximation* of squirrel range and movements due to the limitations of Minimum Convex Polygon (MCP) analysis detailed below.

The convex polygon method of determining home range can be criticized in two main ways. Firstly, it is very sensitive to movements on the periphery of the animal's home range, irrespective of the frequency with which that area may have been visited. The presence of extreme locations in the data may have a substantial effect on estimates of home range size (Anderson 1982, Samuel & Garton 1985). Secondly, there may be large areas of land that are never visited which are included within the polygon if an animal's range is an irregular shape (MacDonald *et al.* 1980). This was termed the 'empty area' effect by Voigt and Tinline (1980). This effect can be seen with L258, whose range covered a section of treeless bog (see Fig. 16). The absence of any radio fix from within this bog is clear in Figure 4, but the two most north-westerly fixes created one polygon edge that traversed the treeless section implying that it was utilised by the squirrel. This behaviour would be extremely unusual as red squirrels are normally confined to the tree canopy or forest ground. The range produced by the convex polygon was therefore highly misleading. The problem disappears when the core-area representation of L258 is plotted (Fig.20) which highlights the value of this application.

4.2.2 Core-areas

Delineating areas of *intense* use may be particularly important when studying the interactions of an animal with its environment and conspecifics (Samuel 1985). The margin of error evident when fix data are utilised in the construction of home ranges was highlighted in a study by Springer (1982) in which the home ranges and core areas of coyotes (*Canis latrans*) were plotted. The core-areas contained 83% of the radio locations but only 8.5% of the home range area. This indicates that peripheral locations represent only infrequent movements which deviate from the centre of activity. This central core may be defined as the portion of an animal's home range that exceeds an equal-use pattern and therefore provides a more useful representation of home range and habitat use than total (MCP) home range. However, core-areas must still be considered as approximations of spatial use.

Core-areas in the present study were based on 70% of the fixes obtained for each squirrel (Fig.19). This area contained 40% of the lactating females' and 38% of the non-lactating females' home range areas. This suggested that a slightly higher degree of fix clustering occurred within the central core of lactating females. Core-areas were found to be considerably smaller than home ranges (Figs.20 & 21) producing means of 3.46 ha and 6.67 ha for lactating and non-lactating females respectively (Table 3.2). A statistically significant difference in core-area size was evident between the categories, despite the large standard deviation for lactating females. Wauters and Dhondt (1992) also used 70% of fixes to determine core-areas in two populations of Belgian red squirrels. Core-areas were found to be 41% of the total range sizes for females in both coniferous and deciduous habitat in their study. Kenward (1985) used 60% of the fixes to obtain core-area estimations for grey squirrels in Monk's Wood.

Considering the core-areas as realistic representations of spatial use, the reasons for more limited movements by the lactating females may be attributed to reproductive status. Holm (1989) stated that food availability is the major influence upon the success of litters. Lack of food may lead to enforced cessation of lactation and resultant offspring mortality (Holm 1989). As such, squirrels have been found to consume over 80% more food during lactation (Havera 1979, M.C.Smith1968). This might suggest that range *expansion* must occur in order to obtain increased amounts of food. However, this was not the case in this study.

Given that massive energetic demands are placed on lactating females (Shillito Walser 1977) and that behavioural and ecological adjustments must be made to meet these demands, several hypotheses may be suggested to explain the reduction in core-area among lactating female red squirrels.

Wauters and Dhondt (1992) found the movements of lactating females to be concentrated around the maternal drey which would explain more limited core-area sizes. Females must visit the nest regularly in order to feed their young which depend exclusively upon her milk. Extensive forays by the female would therefore mean fewer visits to the young and higher energy expenditure, both of which would reduce the potential success of reproduction. Such extensive movements may therefore have been avoided by females in the present study. However, as maternal dreys were not identified it can not be suggested that particular dreys formed the centre of such activity.

The adoption of smaller core-areas during this period of lactation suggested that it enabled females to visit their young regularly whilst conserving energy that was required for the demands of milk production and suckling. Also, female red squirrels act aggressively in defence of their young (Holm 1989, Lurz, Pers Comm.), which suggests that offspring protection may be more effective when the female is close to the maternal drey site. Shillito Walser (1977) suggested that the limited movements of lactating tree shrews were an attempt to avoid the attention of predators. This may have also been true for the squirrels in the present study. That is, extensive forays by the females would have increased the risk of predation and would also have left offspring vulnerable to predators.

The smaller core-areas adopted by females during lactation in the present study may have reduced the availability of food resources. The implications of such reduced food intake and subsequent energy depletion may have therefore been compensated for by an increase in activity levels (see section 4.3). An alternative, or additional explanation for the way in which lactating females meet their metabolic requirements despite the adoption of smaller core-areas has been suggested by Wauters and Dhondt (1989). In their study, the dominant (heaviest) females were those that produced litters. As a result of this dominance they were able to settle in, and defend, the highest quality microhabitats with the most abundant food. This meant that range size could be reduced in order to meet the demands of caring for offspring detailed above. Lactating females in the present study were not significantly heavier than non-lactating females but may have still been able to defend core-areas more effectively during offspring protection.

Individual differences between female core-area sizes were clear (Table 3.2). For example, NL303 exhibited a core-area that was smaller than other non-lactating females (2.6 ha) which may have been due to improved habitat quality provided by the tree species that made up her range (see section 4.4). However, she was also highly active when compared to the other non-lactating females (Fig.25). Thus her behaviour resembled that of the lactating females.

Factors other than reproductive status may also affect home range and core-area size. Kenward (1985) suggested that density determined the average size of squirrel ranges in autumn through the use of exclusive core-areas. Doebel & McGinnes (1974) also implied that high grey squirrel densities caused small home ranges in their study. A similar effect was found in the ranges of pine squirrels (Price *et al.* 1986) where territoriality created exclusive ranges, the size of which were determined by population density. Home range size in tassel-eared squirrels (*S. aberti*) was found to increase in winter due to wide range foraging (Farentinos 1972, 1979). Bland (1977) and Thompson (1978) found an increase in range size for both sexes of grey squirrels during periods of limited food supply which caused a shift towards less suitable food items. Tonkin (1983) noted that seasonal variation in range size in British red squirrels was linked to changing foraging behaviour, from intensively searching small areas in summer to covering large distances for scatter hoarding tree seeds in Autumn. In contrast, Wauters (1986) and Wauters and Dhondt (1987) found that red squirrel ranges were smallest in autumn and winter when tree seeds were abundant and largest in the spring and summer when seed supplies became depleted making secondary food items progressively more important in the diet. Wauters and Dhondt (1992) found that seasonal variation in range size in their populations was caused by changes in the foraging behaviour of the squirrels which depended upon changes in the food supply. They listed breeding status as an additional factor involved in the determination of range size.

Thus, habitat quality particularly affects squirrel movement and subsequent spatial use. This can be related to reproductive status as those squirrels that are lactating represent dominant animals that select high quality habitat. It is important to note that 'individual home range area is a function of the way in which the local population of a species, not merely an individual, exploits its environment' (Damuth 1981).

It is therefore clear that several pressures might select for/against large range size (Kenward 1985) including habitat quality, female dominance, food abundance and population density. Data from the present study indicates that reproductive status also significantly affects range size.

4.2.3 Home range and core-area overlap

The 'empty area' problem (Voigt and Tinline 1980) of home range polygons described in section 4.2.2, may also occur with total home range overlaps between squirrels. It may appear that range overlap is evident due to the position of polygon edges when in fact such an interaction does not exist. Many of the range overlaps in the present study (Fig.23) disappear when core-areas are plotted (Fig.24). Ewer (1968) has argued that while home ranges often overlap, the core-areas do not. For this reason, core-area overlap will be concentrated upon.

Wauters *et al.* (1990) and Wauters and Dhondt (1992) stated that female red squirrels are promiscuous and defend intrasexual territories. Core-area overlap between lactating females did not occur in the present study and would therefore agree with this principle. However, core-area overlap did occur between lactating and non-lactating females (Fig.24, Table 3.3) which conflicts with the results of their studies. Two reasons may be offered in answer to this. Firstly, lactating females may have defended core-areas from other breeding females whilst allowing overlap with non-breeding females. The higher food requirements of lactating squirrels may have meant that core-areas were not large enough to meet the demands of more than one lactating female. That is, lactating females permitted the presence of non-lactating females with lower energetic requirements. Similarly, Wauters and Dhondt (1989) found that interactions were usually between a dominant (breeding) and a subordinate (non-breeding) female (Wauters & Dhondt 1989). The energetic benefits of defending a maternal core-area against non-lactating females would not have outweighed the costs.

However, the benefits of defence from other lactating females may have outweighed the potential costs of sharing food resources with other high-energy requirement squirrels. Secondly, considering that non-lactating females were less active than lactating females (Fig.25) and that afternoon activity among the former was much lower (Figs.29 & 30), perhaps temporal separation permitted range use overlap and the consequent utilisation of sections of mutual range.

The temporal separation of activity and thus, hypotheses regarding the temporal overlap of core-areas can be analysed for the interaction between L268 and NL303. Many of their fix locations were in the same area (Figs.4 & 14) and therefore core-areas of these females overlapped extensively (Fig.24, Table 3.3). L268 and NL303 were active for 52% and 48% of total records respectively (Fig.25). However, Figure 28 shows that the individual activity patterns for these females differed quite markedly. NL303 was almost continuously active for each of the four days between 0500 and 1100. She remained in her drey from 1200 onwards throughout each afternoon with the exception of the first day when she was active for two hours in the afternoon (1600 and 1700 hours). Of all the females, she was least active in the afternoon hours although her overall activity level was high with respect to other non-lactating females. In contrast, L268 was intensively active from approximately 0800 until 1300, after which activity decreased but clearly remained higher than that of NL303. The records for the first day show that she was active from 0700 until 1900 with a rest period of only two hours. Although the mean number of active hours per day differed little between NL303 and L268 (7.25 and 7.75 respectively), the *time* at which they were active did. As such, there was an apparent capacity for temporal separation of activity between mornings and afternoons between the two females. This would produce the spatial overlap seen in Figure 24 but mean that each female was present in the section of overlap at different times.

Kenward (1985) found that grey squirrel home ranges overlapped extensively and that squirrels were active from dawn through to dusk, which, he suggests, left little opportunity for the temporal separation found in chipmunks (*Tamias striatus*) (Getty 1981). However, he also found that core-areas were much smaller than total ranges and were generally exclusive. In the present study, overlap may be permitted as a result of unusually large home ranges and core-areas. The extensive movement of females may enable them to share sections of forest during different periods of the day. Extensive movements and therefore avoidance of other females may not be an option in higher density populations or where high habitat quality generates smaller ranges.

Core-area overlap did not occur between non-lactating females (Fig 24, Table 3.3). Perhaps these females were defending core-areas in preparation for breeding during the second breeding season. However, this would not explain the overlap that occurred with lactating females. Interestingly, Kenward (1985) noted that overlapping females tended to share dreys and in one case were mother and daughter. This tolerance of kin may explain some of the overlaps that occurred in the present study.

4.3 Activity

4.3.1 Total activity levels

The activity levels of tree squirrels have been shown to vary with season (Hicks 1949, Thompson 1977), daylight length, weather (Brown & Yeager 1945, Hicks 1949, Muul 1968, Doebel & McGinnes 1974, Pauls 1978, Kenward & Tonkin 1986), the diversity of food available and between different individuals (Holm 1989, Tittensor 1975). For example, Holm (1989) stated that there is a dramatic increase in the daily activity of red squirrels during spring which continues to increase throughout the summer. The majority of a squirrel's active time comprises foraging, feeding and caching behaviour (Gurnell 1987). Tonkin (1983) found that red squirrels spent 80% of their time engaged in these activities over the year. Similarly, Wauters and Dhondt (1987) found that 73% of activity during May was attributed to foraging. The activity levels of grey squirrels were found to be lowest in winter, highest in summer and at an intermediate level during the spring and autumn (Thompson 1977).

Tonkin (1983) found that red squirrels were active for a mean of 8.2 hours per day between March and May in an English mixed deciduous woodland. The present study showed comparable daily means in mid May of 8.75 hours and 6.25 hours for lactating and non-lactating females respectively with an overall mean of 7.5 hours per day. Wauters and Dhondt (1987) found that red squirrel activity levels were highest during May. When considering the number of hours of activity per day it must be noted that records in the present study were taken on each hour, between which periods of inactivity were possible (see section 2.3.3). Most studies have analysed the activity of squirrels irrespective of sex. As the present study focuses on females, inter-sexual disparity must be considered as an influential factor.

Few studies have described the differences in activity between breeding and non-breeding female squirrels. However, Smith (C.C., 1968) noted that a lactating pine squirrel utilised daylight hours for foraging to a greater extent than a male in the same habitat. He suggested that this was an attempt to meet the energetic requirements of lactation as the female's activity fell after weaning. Gurnell (1987) argued that activity during lactation may not always increase. He referred to grey squirrels that may restrict activity, when food supplies are high, in order to spend more time suckling young in the drey. In contrast, Thompson (1977) implied that increased energy requirements associated with reproduction in female grey squirrels resulted in increased activity during spring and summer.

The results in the present study agreed with the findings of Smith (C.C., 1968) and Thompson (1977). The lactating females were significantly more active than the non-lactating females (Fig.25). This suggests that the energetic demands of lactation *and* the need to spend periods of time in the maternal drey were high. That is, the lactating female must consume sufficient food to provide maintenance energy for herself and nourishment for her young (Hanwell & Peaker 1977, Oftedal 1984). In addition, she must be able to cease activity intermittently in order to feed her young without jeopardising her energetic balance. An increase in activity level must therefore occur before foraging can meet such demands. Pauls (1978) suggested that an optimal level of activity must be attained in order to maximise fitness (Pauls 1978).

Wauters and Dhondt (1987) found that the seed crop from coniferous trees depleted with the progression of spring. Squirrels therefore had to raise their level of activity in order to search for food items to increase the diversity of their diet. The shift in diet and activity pattern caused a decrease in the rate of energy intake which forced squirrels to spend more hours active per day. Although seasonal differences were not considered in the present study, comparisons can be made with their findings when analysing the total activity levels of females. The elevated activity levels associated with increased food intake required during lactation can be paralleled with the similar acceleration in activity required during periods of food shortage among non-lactating females. Activity may have been increased to meet the metabolic demands of lactation that were not satisfied with a reduced core-area (sections 4.2.2 and 4.2.3). An alternative suggestion is that lactating (dominant) females occupied the highest quality habitat which meant that smaller ranges were able to provide sufficient food resources (Wauters & Dhondt 1987). A combination of these two factors may have occurred.

By considering the active day in two parts, it was possible to analyse the differences between and within the female categories for morning and afternoon periods (Figs.29 & 30). This also considered the restriction of interpretation between the two periods, the data for which were taken in separate but consecutive weeks (section 2.2.2 ii).

It is clear that activity was concentrated before 1200 hours in both categories with more limited activity occurring in the afternoon, when lactating females were more active than non-lactating females. Considering that squirrel activity concentrates upon foraging and feeding (Gurnell 1987, Tonkin 1983), activity levels can be used as an indicator of food intake. The very low afternoon activity levels of lactating females suggested that concentrating foraging in the morning hours provided sufficient food intake for their requirements. This was not true of lactating females that were forced to forage intensively throughout the afternoon due to their commitment to offspring nourishment. It has been found that squirrels require periods of rest when the contents of the stomach reach capacity and to enable food digestion (Tonkin 1983, Gurnell 1987). The higher metabolic rate of lactating females suggested that the rate of digestion and energy expenditure was increased which therefore reduced the need for such extensive rest periods.

4.3.2 Diurnal activity patterns

The diurnal activity *patterns* of tree squirrels have also been shown to vary considerably with seasonal and climatic conditions (section 4.3.1). However, several common patterns emerge from research conducted during the same season as the present study.

Holm (1989) stated that a gradual change from a single morning peak in activity to a pattern of two phases occurs during spring, with a larger morning and smaller afternoon peak, separated by a period of rest in the drey. Aschoff (1957, 1966) found that the circadian activity pattern with two peaks was the most common form among mammals.

The results of the present study follow this bimodal pattern when all females are considered simultaneously (Fig.27) and when lactating females are considered separately (Fig.29). However, non-lactating females did not follow this pattern (Fig.30). The higher peaks of activity among lactating females during the morning and afternoon periods created an apparent lull in activity between 1200 and 1400 hours, although this reduction in activity was only slight in comparison with the decrease in activity after 1100 hours exhibited by the non-lactating females.

Commencement of activity differed between the categories. Non-lactating females became active shortly after dawn (0500 hours) and remained more or less continuously active until 1000 hours, after which activity dropped markedly. The onset of activity began more gradually within the lactating females but had peaked to 100% of records by 0800 hours. This suggested that lactating females may have been more reluctant to leave offspring in their maternal dreys until ambient temperatures had risen. Aschoff (1966) stated that the two peaks of activity found in many animals are often closely related to specific stimuli in the environment such as dawn and dusk. However, he also highlighted the fact that endogenous physiological rhythms are involved in determining activity patterns.

The length of morning suckling periods may have differed between lactating females due to variable litter sizes. This would have caused the more gradual onset of activity within this group (Fig.29). Non-lactating females were not influenced by the demands of offspring and appeared to become almost simultaneously active at first light (Fig.30). Lactating females became less active between 1200 and 1400 hours. Dreys may have been visited during this period in order for offspring to suckle or for food to be digested (Tonkin 1983, Gurnell 1987). However, the mid-day lull was not apparent for all lactating females. L8.6 and L272 were particularly inactive between 1200 and 1400 hours but L258 remained almost continuously active throughout this time (Fig.28). This may be attributed to individual behavioural differences.

Information on suckling bouts is sparse and could not be addressed in the present study. It is possible however, that suckling of young continued regularly throughout the day for periods of approximately 30 minutes. This would mean that the mid-day reduction of activity in many of the lactating squirrels could be attributed to rest and digestion of food consumed during the morning. The thermistor radio collars took between 5 and 10 minutes to register as active or non-active depending on the extremity of ambient and drey temperatures. Movements of less than 10 minutes from or to the drey may have therefore remained undetected. Lactating females appeared to fully utilise light availability before entering their dreys in the evening when ambient temperatures began to fall.

In contrast, non-lactating females reduced their activity by more than half from 1200 hours (Fig.30). They concentrated their feeding in the morning, after which only occasional movements were made from the drey. NL306 remained relatively active between 1300 and 1600 hours (Fig.28) showing a divergence from the other non-lactating females, as did her ranging behaviour (section 4.3.1). Weight data suggested that this female may have been pregnant which would explain this behaviour in part.

Cessation of activity among non-lactating females was far less abrupt than that of lactating females (Figs.29 & 30). The gradual decline between 1400 and 1900 hours seemed to suggest that activity was not governed by light and temperature as it was for the lactating females, but by satiation upto the mid-day period and a consequent need to rest and digest food in the afternoon. Thompson (1977) showed that grey squirrels were not pushed to the limit of time available for activity which equates with the behaviour of the non-lactating females in the present study.

In addition to the increased energetic demands imposed upon lactating females, temporal constraints may have interrupted feeding bouts. That is, in order to suckle their young, lactating females had to frequently interrupt their feeding pattern and return to the drey. Consequently, they had to feed for significantly longer periods throughout the day than the non-lactating females which were able to concentrate their activity upon intensive feeding throughout the morning and significantly reduce their activity in the afternoon.

Previous studies (Pulliainen 1973, Tittensor 1975, Thompson 1977, Tittensor 1977, Wauters 1984, Wauters & Dhondt 1987, Holm 1989) have shown that sciurids have a short unimodal pattern of activity in the winter which develops into a bimodal pattern with two peaks during the spring, the most accentuated peak occurring in the early morning with a lower peak in the afternoon. Aschoff (1957) termed this type of activity pattern as 'bigeminus'. The bimodality of this pattern becomes more pronounced with the progression of summer and extended light periods. The spring period therefore shows a pattern of activity between those of winter and summer. The results from the present study generally agreed with these conclusions. When all females were considered simultaneously, two peaks were evident with a noticeable lull in activity around the middle of the day, the extent of which may have increased during the summer. The red squirrel activity patterns found in May by Wauters and Dhondt (1987) and grey squirrel patterns reported by Thompson (1977) closely resembled the results in the present study, although the Spadeadam Forest females showed a less pronounced bimodal pattern and morning and afternoon activity peaks occurred slightly later.

4.4 Habitat quality and utilisation

4.4.1 Habitat availability and cone crops

As red squirrels are arboreal mammals, the number of habitat types at Spadeadam Forest was limited to those provided by four main coniferous species. As an artificial plantation of non-native species, the quality of these habitats was typically low. Ecological restrictions of limited food availability and diversity were therefore imposed upon the squirrels in the forest. In addition to the lack of ground vegetation and canopy heterogeneity within forest stands, the effect of mast crops upon the feeding regime of the squirrels severely reduced the suitability of the forest as prime habitat. In addition to conifer seeds, red squirrels feed extensively on fungi (Tittensor 1975, Gronwall 1982) and have been shown to cache fungi for winter feeding (C.C. Smith 1968). The availability of fungi may affect population dynamics on an annual basis but this food resource was not available during the period of the present study.

Although Sitka spruce cone crops were dense in some areas, lodgepole pine provided the only sizeable and exploitable cone crop in Autumn 1993 which meant that squirrels tracked during the study were generally restricted to feeding upon seeds remaining from this species. The value of Sitka spruce seeds in the diet of red squirrels is questionable due to the content of secondary compound polyphenols (tannins) (Lurz, Pers. Comm.). Norway spruce cone crops were very limited during the autumn and winter of 1993/1994 which meant that seed availability had been exhausted before the period of study (Lurz, Pers. Comm.). Serbian spruce trees were not abundant enough to influence squirrel habitat use patterns.

Limited seed availability meant that the value of the study site for red squirrel utilisation was poor. This was reflected in the low density (sections 3.1.1 and 4.1) and the large home range and core-area sizes of the squirrel population (section 3.2.1).

4.4.2 Habitat utilisation

Habitat utilisation by female squirrels was examined at two levels using compositional analysis (Aebischer & Robertson 1992, Aebischer *et al.* 1993a, Aebischer *et al.* 1993b): tree species selection within the overall study site and total home range (MCP) selection within the overall study site. Using the entire study site during habitat utilisation analyses was considered to provide a realistic representation of the habitat available to squirrels (Fig.3). Squirrel movement was not restricted which meant that selection of areas within the site indicated a preference.

Significant preferences were located when fixes were considered as habitat utilised and the study site was used as habitat available. It was assumed that the most accurate measurement of habitat use was obtained when individual fixes were considered (Figs.4-15) as this provided information as to the specific trees that were being selected. The value of radio locating squirrels to individual trees was highlighted in this respect. Total home range analysis was shown to produce highly arbitrary representations of spatial use as outlying fixes influenced the extremities of convex polygons (section 3.2.1). Therefore, it can be assumed that the use of total home range species composition as habitat utilised may produce similarly deceptive results in habitat utilisation analyses, providing a poor representation of tree species use. When the number of fixes in each tree species and the proportion of each tree species within the total home ranges were compared (Tables 3.5 and 3.6) a clear difference in tree selection was seen. That is, home range compositions suggested that more of the tree species were being utilised than actual fix locations showed.

Habitat utilisation was not tested by comparing fix locations with total home range composition due to the arbitrary nature of the total home ranges. Using the composition of tree species within the total home ranges would have lead to a poor representation of habitat availability and subsequently questionable accuracy of habitat preference and avoidance.

Squirrels showed a significant and equal preference for lodgepole pine and Sitka spruce and a significant and equal avoidance of Serbian spruce and Norway spruce (Tables 3.7 & 3.8). These results varied slightly from those obtained by Lurz and Garson (In press) in March 1993 when habitat utilisation was calculated for the same population of red squirrels. He found that lodgepole pine was preferred over Sitka spruce, Serbian spruce and Norway spruce which were significantly and equally avoided.

Chi^2 goodness of fit analysis of habitat utilisation also showed that squirrels were selecting tree species in a manner other than random (Table 3.9). Lodgepole pine was significantly preferred over the remaining species, as it was when compositional analysis was calculated. However, Chi^2 results showed that Sitka spruce was significantly avoided which differed from the results of compositional analysis in the present study but agreed with those found by Lurz and Garson (In press).

Aebischer *et al.* (1992) argued that compositional analysis considered several factors that were not addressed in other habitat utilisation analyses such as Chi^2 goodness of fit. Firstly, it places emphasis on the radio-collared animal as the sampling unit, avoiding problems such as statistical dependence upon numbers of fixes, non-independence among fixes, and separation of within-animal and between-animal variation. By pooling the fixes obtained for all squirrels Chi^2 analysis was prone to such non-independence problems. Secondly, all habitats are considered simultaneously taking into account that proportions describing habitat composition sum to 1. Thirdly, it enables relative, statistical ranking of habitat preference and fourthly, it utilises the wide array of ANOVA-like techniques such as comparison of group means, regression and co-variate adjustment which gives it applicability to the variety of problems involving habitat composition. Compositional analysis was therefore considered to provide a more accurate estimation of habitat use in the present study.

Cone crop data showed that lodgepole pine had produced the highest exploitable density of seeds during the 6 months before the present study. Habitat selection in the present study therefore appeared to be determined by cone crops and seed availability for each tree species as cone crop estimations for the year paralleled the relative use of each species by squirrels. Both Chi^2 and compositional analyses suggested that lodgepole pine was utilised more than the remaining species although the latter suggested that Sitka spruce was equally utilised. Spatial use by squirrels can therefore be discussed in relation to food availability.

Red squirrels have been shown to move to different types of habitat in response to fluctuations in food supply. Such responses may involve considerably large movements (Ognev 1940). In a comparison between deciduous and coniferous habitats, Wauters and Dhondt found that red squirrel range use varied more in the deciduous forest. This was related to the more extreme seasonal shifts in the squirrels' diet in the deciduous habitat. They also found that female range size in the coniferous forest decreased when pine seed abundance increased. Similarly, Andren and Lemnell (1992) found that red squirrels followed temporal and spatial variations in conifer seed supply in forests of Scots pine and Norway spruce in Sweden. Lewis (1980) found that grey squirrels concentrated foraging to patches yielding high rates of energy intake which influenced habitat use.

Lodgepole pine produces a cone crop each year which means that squirrels in the present study were relatively dependent upon this species for food. Squirrels are known to feed on the flower buds during spring and cache the seeds for winter feeding. The importance of this species at Spadeadam Forest is clear, especially when the low seed crops of the alternative species are considered. A similar reliance upon lodgepole pine has been shown by pine squirrels in North America (M.C. Smith 1968, Elliott 1988). Mast crops of Norway spruce appear only approximately every 8 years. The restricted value of Norway spruce is reflected by the significant avoidance of this species by squirrels, despite the fact that large sections were available for use within the study site (Fig.3).

Sitka spruce was significantly preferred and appeared to be utilised extensively for drey location. In contrast to the open canopy of lodgepole pine, the dense canopy of Sitka spruce provides ideal protection for dreys. Pulliainen (1973) also showed that red squirrels selected spruce trees rather than pines for drey construction. Pines were very rarely seen to be selected for drey construction in the present study. This suggests that pine may actually have been selected over Sitka spruce during foraging as many of the fixes recorded in Sitka spruce represented drey site locations.

Squirrels may not have fully exploited the seed crops provided by Sitka spruce as they contain secondary compound polyphenols (tannins) (Lurz, Pers. Comm.) that are toxic to mammals (Kenward 1992). The presence of tannins in acorns has also been shown to affect squirrel feeding preferences in North America (Smith & Follmer 1972, Smallwood & Peters 1986). Pulliainen (1973) found that the nutritive value of pine seeds was higher than that of Norway spruce which might partly explain the preference for this species. However, Formasov (1934) found that spruce seeds contained three times more protein than pine seeds in a study of the red squirrels of European Russia and suggested that they were preferred over pine. Seed availability is clearly the dominant factor affecting habitat use.

Studies have shown that the survival of potential breeding grey and pine squirrels and their breeding rate depend mainly on autumn mast crops (Smith & Barkalow 1967, Nixon & McClain 1969, 1975, Nixon *et al.* 1975). Brandl *et al.* (1991) found that red squirrel populations in Bavaria followed the delayed effects of masting on food availability. If this is the case with red squirrels in the present study it may explain why only a limited number of females reproduce each year. If lodgepole pine provides the only reliable annual mast crop then fewer females will reproduce in years when other species fail to mast.

Smith (1970) and Elliott (1974) found that certain trees were favoured by pine squirrels for feeding as a result of disparate cone crops from different trees. This may have been the case with the squirrels feeding on flower buds and green cones of lodgepole pines in the present study. Those females that had the smallest core-areas (L258, L8.6 and NL303) (Fig.22) also showed significant proportions of lodgepole pine within those core-areas (Figs.20 & 21). However, the core-areas of females L207 and NL296 also covered extensive areas of pine but were among the largest of core-areas which conflicts with this view. As the reproductive status of females significantly affected core-area size, comparisons of this sort must be treated carefully.

The equal preference of Sitka spruce (as determined by compositional analysis) may have also been related to the patchy distribution of cones provided by this species and their subsequent selection by squirrels. A number of individual Sitka spruce trees yielded high numbers of cones which may have been favoured by certain squirrels following the behaviour patterns mentioned above.

Many factors may have therefore contributed to the way in which habitat was selected by female squirrels. The major determinant was seed supply but dominance of particular females and the extent of range defence, availability of appropriate drey sites, variability of patch quality for foraging within tree species, population density and the extent of disturbance due to the proximity of roads must also be considered.

4.5 Concluding comments

Much ambiguity exists in determining the links between population density, range use, activity levels and patterns and food supply. In order to investigate relationships between such behaviour patterns and ecological variables, long term studies of all squirrels within an area are required (Kenward 1985). However, the present study has established that the demands of lactation during the first breeding period govern certain aspects of behaviour such as space use and activity. Habitat use is determined primarily by food availability but may be further affected by less obvious factors such as dominance hierarchies.

The restricted period of research and small sample sizes in the study limited conclusive interpretations to an extent. Further research is required in order to overcome these shortfalls and provide data that identifies long-term patterns.

REFERENCES

Aebischer, N.J., Marcström, V., Kenward, R.E., and Karlbom, M. (1993a) Survival and habitat utilization: a case for compositional analysis. *Marked Individuals in the Study of Bird Populations* (eds J.D. Lebreton & P.M. North), pp. 343-353. Birkhäuser Verlag Basel/Switzerland.

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993b) Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, 74(5), 1313-1325.

Aebischer, N.J. & Robertson, P.A. (1992) Practical aspects of compositional analysis as applied to pheasant habitat utilization. *Wildlife Telemetry: remote* monitoring and tracking of animals (eds I.G. Priede & S.M. Swift), pp. 285-293. Ellis Horwood Ltd., Chichester, UK.

Anderson, D.J. (1982) The home range: a new nonparametric estimation technique. *Ecology,* **63**, 103-112.

Anderson, E. (1965) Cone and seed studies in Norway spruce. *Studia Forestalia Suecica,* **23**.

Andrén, H. & Lemnell, P.A. (1992) Population fluctuations and habitat selection in the Eurasian red squirrel *Sciurus vulgaris. Ecography,* **15**, 303-307.

Aschoff, J. (1957) Aktivitatsmuster der Tagesperiodik. *Naturwissenschaften.*, **44**, 361-364.

Aschoff, J. (1966) Circadian activity pattern with two peaks. *Ecology,* **47**, 657-662.

Bahnak, B.R. and Kramm, K.R. (1977) The influence of environmental temperature and photoperiod on activity in the red squirrel (*Tamiasciurus hudsonicus*). *Int. J. Biometeorol.,* **21**, 164-180.

Bertram, B.C.R. & Moltu D.P. (1986) Reintroducing Red Squirrels into Regent's Park. *Mammal Rev.* **16**, No.2, 81-88.

Brandl, R., Bezzel, E., Reichholf, J. & Volkl, W. (1991) Population dynamics of the red squirrel in Bavaria. *Z. Saugetierkunde,* **56**, 10-18.

Brown, L.G. & Yeager, L.E. (1945) Fox squirrels and grey squirrels in Illinois. *Ill. Nat. Hist. Surv. Bull.,* **23**, 499-533.

Clapham, A.R., Tutin, T.G. & Moore, D.M. (1989) *Flora of the British Isles.* Cambridge University Press.

Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1989) Fitness costs of gestation and lactation in wild mammals. *Nature,* **337**, 260-262.

Corbet, C.B. & Southern, H.N. (1978) *The mammals of the Palearctic region.* British Museum (Natural History), Cornell University Press, London.

Currado, I., Scaramozzino, P.L. & Brussino, G. (1987) Note sulla presenza dello scoiattolo grigio (*Sciurus carolinensis* Gmelin, 1788) in Piemonte (*Rodentia: Sciuridae*). Ann. Fac. Sci. Agr. Univ. Torino, **14**, 307-331.

Damuth, J. (1981) Home range, home range overlap, and species energy use among herbivorous mammals. *Ecol. J. Linnean Soc.,* **15**, 185-193.

Deutch, R.S. (1978) *Seasonal activity of the red squirrel* (Tamiasciurus hudsonicus) *in a southern Ohio deciduous forest,* MS thesis, University of Dayton, Ohio.

Doebel, J.H. & McGinnes, B.S. (1974) Home range and activity of a grey squirrel population. *J. Wildl. Manage.*, **38**, 860-867.

Don, B.A.C. (1981) *Spatial dynamics and individual quality in a population of the grey squirrel (Sciurus carolinensis).* D. Phil. thesis, Oxford University.

Donohoe, R.W. & Beal, R.O. (1972) Squirrel behaviour determined by radio-telemetry. *Ohio Fish & Wildl. Report* **2**, 1-20.

Elliot, P.F. (1988) Foraging behaviour of a central-place forager: field tests of theoretical predictions. *The American Naturalist*, **131**, 159-174.

Ewer, R.F. (1968) *Ethology of mammals.* Legos Press, London.

Farentinos, R.C. (1972) Observations on the ecology of the tassel-eared squirrel. *J. Wildl. Manage.*, **36**, 1234-1239.

Farentinos, R.C. (1979) Seasonal changes in the home range size of tassel-eared squirrels. *SWest Nat.*, **24**, 49-62

Farjon, A. (1990) *Pinaceae.* Koeltz Scientific Books.

Flyger, V.F. (1960) Movements and home range of the grey squirrel, *Sciurus carolinensis,* in two Maryland woodlots. *Ecology*, **41**, 365-369.

Formasov, A.N. (1934) On the competition between species. Relationships between the squirrel (*Sciurus vulgaris* L.), crossbills (*Loxia curvirostra* L.) and great spotted woodpeckers (*Dryobates major* L.). *Doklady Akad. Nauk S.S.S.R.*, **3**, 197-199.

Getty, T. (1981) Territorial behaviour of eastern chipmunks (*Tamias striatus*): encounter avoidance and spacial time-sharing. *Ecology*, **62**, 915-921.

Grodzinski, W. & Sawicka-Kapusta, K. (1970) Energy values of tree-seeds eaten by small mammals, *Oikos*, **21**, 52-58.

Grönwall, O. (1982) *Aspects of the food ecology of the red squirrel (Sciurus vulgaris L.).* Ph.D. thesis, Univ. of Stokholm, Sweden.

Gurnell, J. (1983) Squirrel numbers and the abundance of tree seeds. *Mamm. Rev.*, **13**, 133-148.

Gurnell, J. (1987) *The Natural History of Squirrels.* Christopher Helm (Publishers) Ltd., Kent.

Gurnell, J. & Pepper, H. (1988) Perspectives on the management of red and grey squirrels. *Wildlife management in forests* (ed. D.C. Jardine), pp. 92-109. ICF Edinburgh.

Gurnell, J. (1991) Squirrels. *The Handbook of British Mammals* (eds C.B. Corbet & G.B. Harris), pp. 176-186. Blackwell Scientific Publications, Oxford, UK.

Hagner, S. (1965) Cone crop fluctuations in Scots pine and Norway spruce. *Studia Forestalia Suecica*, **33**, 1-20.

Hanwell, A. & Peaker, M. (1977) Physiological effects of lactation on the mother. *Symp. Zool. Soc. Lond. No.* **41**, 297-312.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woollard, T. & Wray, S. (1990) Home range analysis using radio tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mamm. Rev.*, **20**, 97-123.

Havera, S.P. (1977) Body composition and organ weights of fox squirrels. *Trans. Illinois State Acad. Sci.*, **70**, 286-300.

Havera, S.P. & Nixon, C.M. (1978) Interaction among adult female fox squirrels during the winter breeding season. *Trans. Illinois State Acad. Sci.*, **71**, 24-38.

Havera, S.P. (1979) Energy and nutrient cost of lactation in fox squirrels. *J. Wildl. Manage.*, **43**, 958-965.

Havera, S.P. & Smith, K.E. (1979) Anutritional comparison of selected fox squirrel foods. *J. Wildl. Manage.,* **43**, 691-704.

Hicks, E.A. (1949) Ecological factors affecting the activity of the western fox squirrel, *Sciurus niger rufiventer* (Geoffroy). *Ecological Monographs,* **19**, 288-302.

Holm, J. (1989) *The Red Squirrel.* Shire Natural History, Shire Publications Ltd., Bucks.

Ingles, L.G. (1947) Ecology and life history of the California Gray squirrel. *California Fish & Game* **33**, 139-158.

Jensen, T.S. (1990) The decline of the red squirrel in Denmark: a food hypothesis. *Flora og Fauna,* **96**, 31-34.

Jennrich, R.I. & Turner, F.B. (1969) Measurement of non-circular home range. *J. Theor. Biol.*, **22**, 227-237.

Kenagy, G.J., Masman, D., Sharbaugh, S.M. & Nagy, K.A. (1990) Energy expenditure during lactation in relation to litter size in free-living golden-mantled ground squirrels. *J. Anim. Ecol.*, **59**, 73-88.

Kenward, R.E. (1985) Ranging behaviour and population dynamics in grey squirrels. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (eds R.M. Sibley & R.H. Smith), pp. 319-330. Oxford: Blackwell Scientific Publications.

Kenward, R.E. (1990) RANGES IV. Software for Analysing Animal Location Data. Institute of Terrestrial Ecology, Natural Environment Research Council, Cambridge, UK.

Kenward, R.E. & Holm, J.L. (1989) What future for British red squirrels? *Biological Journal of the Linnaen Society* **38**, 83-89.

Kenward, R.E. & Tonkin, T.M. (1986) Red and grey squirrels, some behavioural and biometric differences. J. Zool., London **209**, 279-304.

Koppel, A., Troeng, E. & Linder, S. (1987) Respiration and photosynthesis in cones of Norway Spruce (*Picea abies* L. Karst.). J. Wildl. Manage.**33**, 234-240.

Lampio, T. (1967) Sex ratios and the factors contributing to them in the squirrel, *Sciurus vulgaris,* in Finland. *Finnish Game Res.*, **29**, 5-67.

Layne, J.N. (1954) The biology of the red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs), in central New York. *Ecological Monographs,* **24**, 227-267.

Lewis, A.R. (1980) Patch use by gray squirrels and optimal foraging. *Ecology,* **61**, 1371-1379.

Linzell, J.L. (1974) Mammary blood flow and methods and methods of identifying and measuring precursors of milk. *Lactation* **1**, 143-225 (eds B.L. Larson & V.R. Smith). New York and London:

Academic Press.

Lurz, P. (1992) *The Ecology of the Red Squirrel in the north of England.* PhD First Year Report, University of Newcastle.

Lurz, P.W.W. & Garson, P.J. (In press) Seasonal changes in ranging behaviour and habitat choice by red squirrels (*Sciurus vulgaris*) in conifer plantations in northern England. *Proc. Int. Coloq. on Ecol. Tree Squirrels.* Carnegy Museum, Pittsburgh.

MacDonald, D.W., Ball, F.G. & Hough, N.G. (1980) The evaluation of home range size and cofiguration using radio tracking data. *A handbook on biotelemetry and radio tracking* (eds. C.J. Amlaner Jr. & D.W. MacDonald), pp. 405-424).
Pergamon Press Ltd.

McNab, B.K. (1963) Bioenergetics and the determination of range size. *The American Naturalist,* No. **894**, 133-139.

Martin, R.D. (1966) Tree shrews: unique reproductive mechanism of systematic importance. *Science N.Y.*, **152**, 1402-1404.

Matthews, J.D. (1989) *Silvicultural Systems.* Oxford Science Publications.

Middleton, A.D. (1930) The ecology of the American grey squirrel (*Sciurus carolinensis*) in the British Isles. *Proceedings of the Zoological Society of London,* **1930**, 804-842.

Millar, J.S. (1975) Tactics of energy partitioning in breeding *Peromyscus. Can. J. Zool.,* **53**, 967-976.

Moller, H. (1983) Foods and foraging behaviour of red (*Sciurus vulgaris*) and grey (*Sciurus carolinensis*) squirrels. *Mammal Review,* **13**, 81-98.

Moller, H. (1986) Red squirrels (*Sciurus vulgaris*) feeding in a Scots pine plantation in Scotland. *J. Zool., Lond.,* **209**, 61-83.

Muul, I. (1968) *Behavioural and physiological differences on the distribution of the flying squirrel, Glaucomys volans.* Univ. Mich. Misc. Publ. Mus. Zool. No. 134.

Nixon, C.M. & McClain, M.W. (1969) Squirrel population decline following a late spring frost. *J. Wildl. Manage.,* **33**, 353-357.

Nixon, C.M. & McClain, M.W. (1975) Breeding seasons and fecundity of female gray squirrels in Ohio. *J. Wildl. Manage.*, **39**, 426-438.

Oftedal, O.T. (1984) Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symp. Zool. Soc., Lond.,* **51**, 33-85.

Ognev, S.I. (1940) *Animals of the USSR and adjacent countries. IV. Rodents.* Moscow, Leningrad. A USSR-Israel programme for Scientific Translations, 1966, Jerusalem.

Ostfeld, R.S., Pugh, S.R., Seamon, J.O. & Tamarin, R.H. (1988) Space use and reproductive success in a population of meadow voles. *J. Anim. Ecol.,* **57**, 385-394.

Pauls, R.W. (1978) Behavioural strategies relevant to the energy economy of the red squirrel (*Tamiasciurus hudsonicus*). *Can. J. Zool.*, **56**, 1519-1525.

Price, K., Broughton, K., Boutin, S. & Sinclair, A.R.E. (1986) Territory size and ownership in red squirrels: response to removals. *Can. J. Zool.,* **64**, 1144-1147.

Pulliainen, E. (1973) Winter ecology of the red squirrel (*Sciurus vulgaris* L.) in northeastern Finland. *Ann. Zool. Fennici,* **10**, 487-494.

Pulliainen, E. (1982) Some characteristics of an exceptionally dense population of the red squirrel, *Sciurus vulgaris* L., on the southern coast of Finland. *Aquilo Ser. Zool.*, **21**, 9-12.

Purroy, F.J. & Rey, J.M. (1974) Estudio ecologico y sistematico de la ardilla (*Sciurus vulgaris*) en Navarra. *Boletin de la Estacion Central de Ecologia*, **3**, 71-82.

Randolph, P.A., Randolph, J.C., Mattingly, K. & Mead Foster, M. (1977) Energy costs of reproduction in the cotton rat, *Sigmodon hispidus. Ecology*, **58**, 31-45.

Reynolds, J.C. (1981) *The interaction of red and grey squirrels.* PhD Thesis, University of East Anglia.

Samuel, M.D. & Garton, E.O. (1985) Home range: a weighted normal estimate and tests of underlying assumptions. *J. Wildl. Manage.*, **49**, 513-519.

Samuel, M.D., Pierce, D.J. & Garton, E.O. (1985) Identifying areas of concentrated use within the home range. *J. Anim. Ecol.*, **54**, 711-719.

Sarvas, R. (1962) Investigations on the flowering and seed crop of *Pinus sylvestris. Metsantutkimuslaitoksen Jull.,* **53**, 1-198.

Seber, G.A.F. (1982) *Estimation of animal abundance and related parameters.* Griffin, London. 506 pp.

Shillito Walser, E. (1977) Maternal behaviour in mammals. *Symp. Zool. Soc. Lond. No.* **41**, 313-331.

Shorten, M. (1954) *Squirrels.* Collins.

Shorten, M. (1962) Squirrels, their biology and control. *MAFF Bull.* **184**, 1-44.

Smallwood, P.D. & Peters, W.D. (1986) Grey squirrel food preferences: the effects of tannin and fat concentrations. *Ecology*, **67**, 168-175.

Smith, C.C. (1968) The adaptive nature of social organisation in the genus of tree squirrel *Tamiasciurus. Ecological Monographs*, **38**, 30-63.

Smith, C.C. & Follmer, D. (1972) Food preferences of squirrels. *Ecology*, **53**, 82-91.

Smith, M.C. (1968) Red squirrel responses to spruce cone failure in interior Alaska. *J. Wildl. Manage.*, **32**, 305-317.

Smith, N.B. & Barkalow, F.S. Jr. (1967) Precocious breeding in the gray squirrel. *J. Mammal.*, **48**, 328-330.

Springer, J.T. (1979) Some sources of bias and sampling error in radio triangulation. *J. Wildl. Manage.*, **43**, 926-935.

Springer, J.T. (1982) Movement patterns of coyotes in south central Washington. *J. Wildl. Manage.*, **46**, 191-200.

Swihart, R.K. & Slade, N.A. (1985) Testing for independence of observations in animals movements. *Ecology*, **66**, 1176-1184.

Thompson, D.C. (1977) Diurnal and seasonal activity of the grey squirrel (*Sciurus vulgaris*). *Can. J. Zool.*, **55**, 1185-1189.

Tittensor, A.M. (1975) *Red squirrel.* Forestry Record No. 101, HMSO.

Tittensor, A.M. (1977) Squirrels. *The handbook of British Mammals* (eds. G.B. Corbet & H.N. Southern), pp. 152-172. Blackwell Scientific Publications, Oxford.

Tonkin, J.M. (1983) Activity patterns of the red squirrel (*Sciurus vulgaris*). *Mammal Review 13, 99-111.*

Van Winkle, W. (1975) Comparison of several probablistic home range models. *J. Wildl. Manage.*, **39**, 118-123.

Voigt, D.R. & Tinline, R.R. (1980) Strategies for analyzing radio tracking data. *A handbook on biotelemetry and radio tracking* (eds. C.J. Amlaner Jr. & D.W. MacDonald), pp. 387-404). Pergamon Press Ltd.

Wauters, L.A. (1984) *Inleidende studie tot de populatie-ecologie van de Europese Rode eekhorn (Sciurus vulgaris).* Licentiaatsverhandeling. Universitaire Instelling Antwerpen.

Wauters, L. (1986) De eekhorn en het bos. *Bull. Soc. R. For. Belg.*, **93**, 269-278.

Wauters, L.A. & Dhondt, A.A. (1985) Population dynamics and social behaviour of red squirrel populations in different habitats. Brussels: *XVII Congress of the International Union of Game Biologists*, pp. 311-318.

Wauters, L.A. & Dhondt, A.A. (1987) Activity budget and foraging behaviour of the red squirrel (*Sciurus vulgaris*, Linnaeus, 1758) in a coniferous habitat. *Z. Saugetierk.*, **52**, 341-353.

Wauters, L.A. & Dhondt, A.A. (1989) Body weight, longevity, and reproductive success of the red squirrel (*Sciurus vulgaris*) in two different habitats. *J. Zool., Lond.*, **217**, 93-106.

Wauters, L.A. & Dhondt, A.A. (1992) Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitats and sexes. *Anim. Behav.* **43**, 297-311.

PLATES

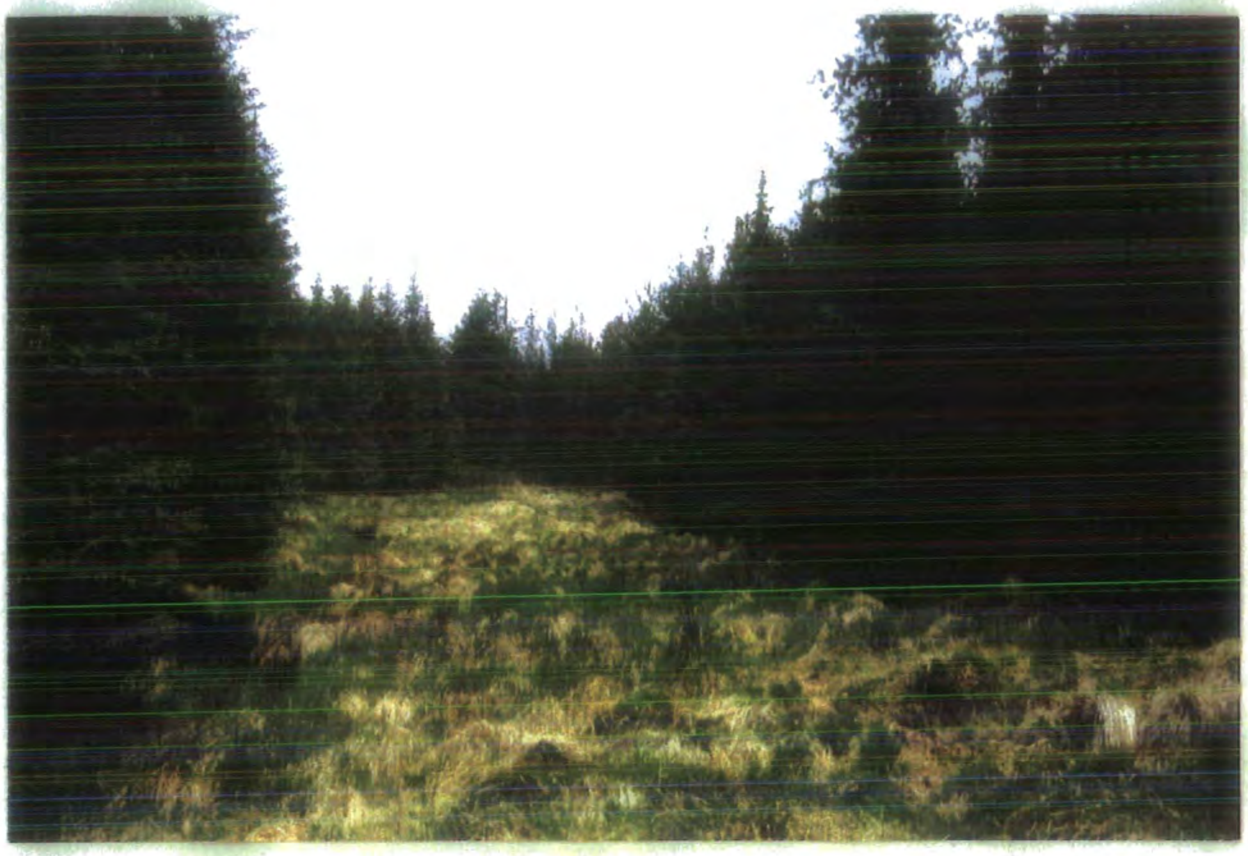


Plate 1. Norway spruce section at Spadeadam Forest.

Plate 2. The Fuller trap converted for squirrel capture.

Plate 3. Squirrel in handling cone being prepared for identification and weighing

Plate 4. Temperature sensitive thermistor radio collar.

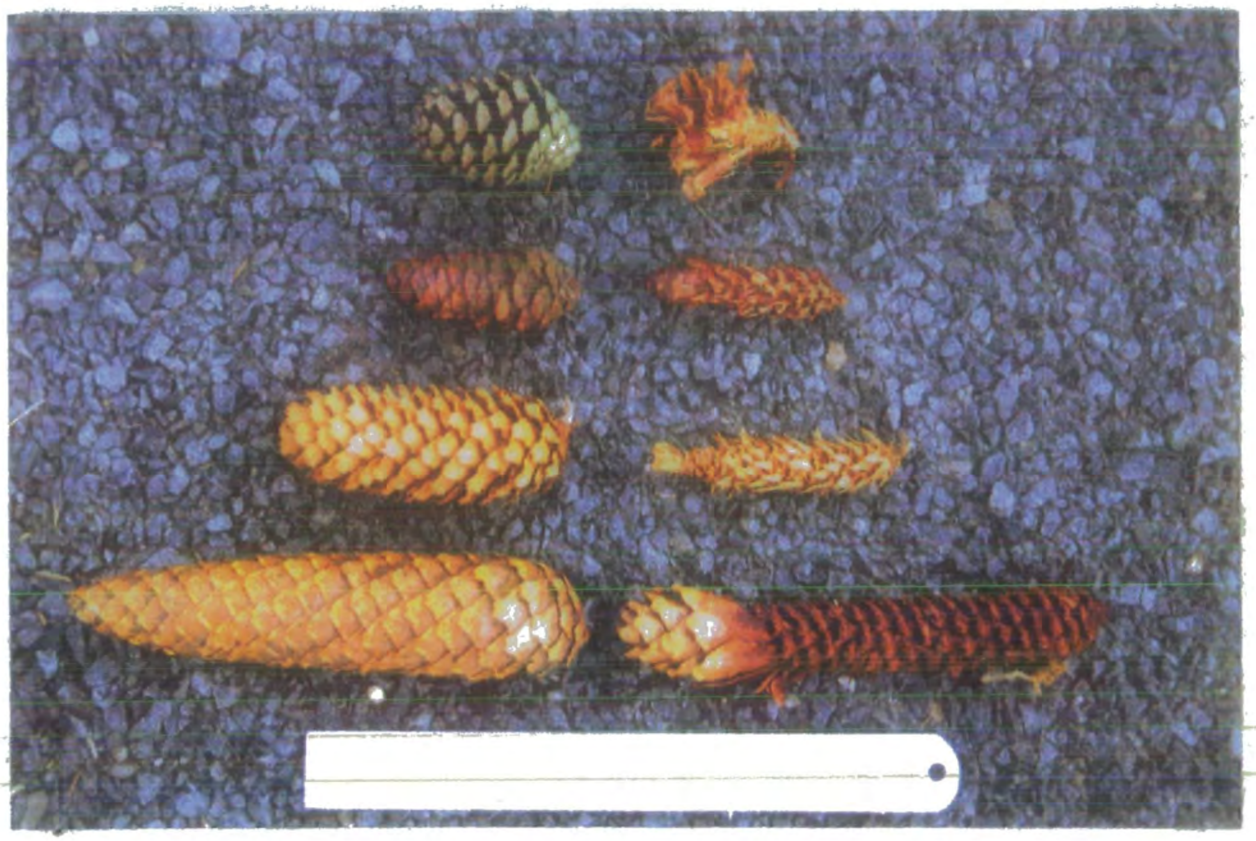


Plate 5. Complete and partially consumed seed cones. From top to bottom: lodgepole pine, Serbian spruce, Sitka spruce, Norway spruce (15cm rule).

APPENDICES

I. Capture data for squirrels trapped at Spadeadam Forest study site.

Day	**1**	**2**	**3**	**4**
Squirrel No.				
FC44	✓	✓		
M1	✓		✓	
M201	✓			
M310	✓			
F244	✓			
M8.6	✓			
M31	✓			
F218	✓			
F286	✓	✓		
MC38	✓			✓
F207	✓	✓	✓	
JuvA	✓			
F296	✓	✓		✓
JuvC	✓			
JuvB	✓			
F303		✓		
M348		✓		
FJuv		✓	✓	
JuvD		✓		
MC18		✓		
MC56			✓	
JuvE			✓	

II. Total activity levels of lactating and non-lactating females, expressed as a percentage of all active and drey records taken over a four day period (n=60).

Lactating females	% active records	**Non-lactating females**	% active records
L268	52	NL244	34
L207	60	NL303	48
L258	75	NL286	40
L234	72	NL278	33
L8.6	50	NL306	62
L272	52	NL236	33
Mean	60.17%		41.67%
Median	56%		37%

III. Active records for each hour of four days for combined lactating and non-lactating females expressed as a percentage of all active and drey records (*n*=48 per hour).

Time	**0500**	**0600**	**0700**	**0800**	**0900**	**1000**	**1100**	**1200**
%	52.1	70.8	68.8	85.4	87.5	77.1	64.6	42.6

Time	**1300**	**1400**	**1500**	**1600**	**1700**	**1800**	**1900**
%	39.6	41.7	43.8	39.6	29.2	14.6	4.2

IV. Active records for each hour of four days for lactating (L) and non-lactating (NL) females expressed as the number of active records and the percentage of total activity records for each female category (*n*=24 per hour).

Lactating females

Time	**0500**	**0600**	**0700**	**0800**	**0900**	**1000**	**1100**	**1200**
No.	8	16	16	24	23	23	17	14
%	33.0	66.7	66.7	100	95.8	95.8	70.8	58.3

Time	**1300**	**1400**	**1500**	**1600**	**1700**	**1800**	**1900**
No.	14	13	16	15	11	5	1
%	58.3	54.1	66.7	62.5	45.8	20.8	4.2

Non-lactating females

Time	**0500**	**0600**	**0700**	**0800**	**0900**	**1000**	**1100**	**1200**
No.	17	18	17	17	19	14	14	6
%	70.8	75.0	70.8	70.8	79.2	58.3	58.3	25

Time	**1300**	**1400**	**1500**	**1600**	**1700**	**1800**	**1900**
No.	6	7	5	4	3	2	1
%	25	29.2	20.8	16.7	12.5	8.3	4.2