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Conserving the red squirrel *Sciurus vulgaris* in Thetford Forest

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Conserving the red squirrel *Sciurus vulgaris* in Thetford Forest

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Summary

1. Studies on conserving the red squirrel (*Sciurus vulgaris*) in Thetford Forest began in 1992 in a 1700 ha area designated as the Red Squirrel Reserve. More than 90% of the Reserve is dominated by Scots (*Pinus sylvestris*) and Corsican (*P. nigra*) pine. The remaining trees in the Reserve are a variety of conifer species with some broadleaves, including oak (*Quercus robur*) and beech (*Fagus sylvatica*). The studies are currently sponsored by English Nature, Forest Enterprise and the People's Trust for Endangered Species. This report considers the effects of grey squirrel (*S.carolinensis*) removal and habitat structure on the numbers, distribution and health and welfare of red squirrels within the Reserve in the period from September 1992 to February 1996.

2. 1179 grey squirrels were removed between September 1992 and February 1996 using cage trapping methods, and humanely killed. Red squirrels were first seen within seven months of the start of grey squirrel control programme, and some were captured within nine months. These animals are believed to have been resident within the Reserve, rather than immigrants. Since that time, some 31 individual red squirrels have been handled. It is considered that the control of grey squirrels has benefitted the red squirrel population, but the control has not continued for long enough to demonstrate this unequivocally. It is recommended that the control of grey squirrels continue for at least two more years.

3. The control programme used was designed to maintain grey squirrel numbers at their lowest attainable level. The trapping effort was based on 72 man-days of labour a year with an estimated cost for labour and consumables at current rates of £2.61 ha^{-1} (this not include capital costs for equipment). It is not believed that this cost of control using trapping methods can be reduced. Estimates of the costs of control in broadleaf woodland, and fragmented woodlands using cage trapping or warfarin, are also given.

4. The grey squirrels were subjected to post-mortem examination. Annual cycles in numbers, reproduction and body condition closely resembled those seen in other types of woodlands. However, densities at the beginning of the control programme, 0.05 to 0.2 squirrels ha^{-1}, were considerably lower than those reported from broadleaf and mixed woodland. This was consistent with previous studies in Thetford Forest. The small patches of broadleaves were found to have an important effect on the trappability and demography of grey squirrels in the Reserve.

5. Red squirrels proved very difficult to trap. A minimum estimate of the probability of catching a red squirrel in a trap on any day that it was set was 0.016. Red squirrels were only found in the central and eastern parts of the Reserve and showed a clear preference for Corsican pine, Scots pine and mixed conifer (predominantly a mix of Corsican and Scots) between 21 and 35 years old. Red squirrels avoided Scots pine stands >55 years old that had been subjected to late or final thinning. Only 450 ha (26%) of the Reserve was considered suitable for red squirrels in terms of species and block size. It was estimated that an area of pine this size could carry on average of 250 red squirrels (range 50 to 500). It was not possible to estimate how many red squirrels there were in the Reserve because of the problems in catching the animals. Nevertheless, a best guess was that there were only 10 to 20 red squirrels in the Reserve in 1995, and no more than 40.

6. At least some red squirrels bred in each year of the study but it was not possible to estimate productivity. Fourteen adult squirrels are known to have died; 35% due to raptor predation or car collisions, and 57% due to disease, including parapoxvirus infection. There was no evidence of metabolic bone disease from blood biochemistry or radiographic tests. Further work on the epidemiology of parapoxvirus infection in both red and grey squirrels is recommended.

7. It is concluded that the current level of grey squirrel control should be maintained, and the small population of red squirrels is augmented by reintroducing animals from elsewhere in Britain. The results from the translocation studies and on habitat structure and management using GIS and habitat modelling will be presented in future reports.

Acknowledgements

We are very grateful for the ongoing support of English Nature, the Forest Enterprise, the Forestry Authority and the People's Trust for Endangered Species, and we are particularly indebted to Keith Bradbury, Sandy Greig, Valerie Keeble, Roger Mitchell, Tony Mitchell-Jones, Phil Ratcliffe, Brian Roebuck, and Rex Whitta MBE. We should also like to thank the many people who have helped and supported the work including: Charlotte Aybes, Elizabeth Barratt, Nicola Charlton, Michelle Dunn, Paul Fletcher, Samantha Greenwood, Antoinette Irvine, Peter Lurz, Sally Norris, Liz Olgivie, Stuart Orton, Tony Sainsbury, David Stapleford, and the Red Squirrel Survey Team.

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Finally, particular thanks are due to Harry Pepper for his advice, encouragement and support, and for reading a draft of this report.

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Contents

1. Background

During the 1980's, the future of the red squirrel (*Sciurus vulgaris*) in Thetford Forest seemed bleak. From the research carried out at that time it was concluded that red squirrels would probably disappear from the Forest within 20 years (Gurnell & Taylor, 1989; Gurnell 1996). This was also believed to be the case generally for most of England and Wales, and it was considered that there was also a risk to the Scottish populations (Gurnell & Pepper, 1991, 1993). The disappearance of red squirrels is linked to loss of habitat, habitat fragmentation, and the appearance of grey squirrels (*S. carolinensis*) (Gurnell, 1991a,b) although the detailed processes by which grey squirrels replace red squirrels are still not fully understood (Gurnell, 1987, 1996; Gurnell & Pepper, 1993). Grey squirrels, formerly introduced to many locations around the turn of the century (Shorten, 1954; Gurnell, 1987; Gurnell & Pepper 1993), continue to expand their range and exploit broadleaved and mixed woodland habitats (Gurnell & Pepper, 1991; 1993). Recently, it has been speculated that disease may be a contributing factor in the decline of the red squirrel (Sainsbury and Gurnell, 1995). Moreover, a change in planting policy in commercial forests (e.g. replacing Scots pine, *Pinus sylvestris*, and Norway spruce, *Picea abies*, with non-native species such as Corsican pine, *Pinus nigra var. maritima*, and Sitka spruce, *Picea sitchensis*, respectively) has probably lowered the red squirrel carrying capacity of some conifer forests (Gurnell & Pepper, 1988; Lurz *et al.*, 1995).

Grey squirrels started to colonise Thetford Forest in 1968 (Reynolds, 1981). During the 1980's, red squirrels were seldom seen although they were still present (Gurnell & Whitta, 1991; Whitta pers. comm.) with overall densities which were believed to be very low (<1 squirrel $10ha^{-1}$) (Gurnell, 1996; Gurnell & Pepper, 1988; Gurnell & Taylor, 1989). Their distribution appeared to be very patchy and local populations were vulnerable to extinction. Grey squirrels were, and still are, well established throughout the forest but they also have a heterogeneous distribution and densities are low ($<1ha^{-1}$) compared with broadleaved woodland ($2\text{-}8ha^{-1}$) (Gurnell, 1987, 1996; Gurnell & Pepper, 1991; Gurnell & Taylor, 1989; Lurz *et al.*, 1995).

Forest management prescriptions for conserving the red squirrels in conifer forests have been drawn up by Gurnell & Pepper (1988, 1991, 1993), and Gurnell (1996), and more recently Lurz *et al.* (1995) have considered red squirrels in spruce dominated plantations. In the longer term, the conservation of red squirrels must rely on developing appropriate forest structures which will favour red but discourage grey squirrels, and which can co-exist with normal forest management. One hypothesis which has gained some support (Gurnell, 1996) is that red squirrels have the advantage over grey squirrels in areas dominated by large tracts of coniferous forests.

Red and grey squirrels have coexisted within Thetford Forest for 25 years and therefore Thetford Forest has features which have enabled the red squirrel to persist in the presence of greys. Several studies have been carried out at Thetford (Gurnell 1991; 1996) and in the early 1980's the F.C. designated nearly 1000 ha of High Lodge Enclosure as a Red Squirrel Conservation Area. In 1991 English Nature introduced the Species Recovery Programme aimed at securing the long-term, self-sustained survival of species under threat. Accordingly, Thetford Forest was believed to be an ideal site for implementing and assessing management tactics for conserving the red squirrel and a joint project was initiated between English Nature, the Forestry Commission, and QMW College (JG). The project started in September 1992. In 1995, the People's Trust for Endangered Species became a co-sponsor.

2. Aims

The aims of the project were:

1. To assess habitat suitability for red squirrels within Thetford Forest and to prepare prescriptions for future forest management.

2. To study the effects of grey squirrel removal on the red squirrel population.

3. To examine the health and welfare of red squirrels involved in conservation programmes.

4. To study the effects of supplementary food on red squirrel ecology.

5. To develop protocols for the reintroduction of red squirrels to assist the recovery of small opulations, or to replace lost populations

6. To carry out experimental reintroductions of 20 or more red squirrels to the Reserve.

3. Scope of this report

Aim 4 above concerns the study on the effects of extra food on red squirrels with the food dispensed in red squirrel-only supplementary food hoppers. This was based on the hypothesis that exploitation competition for food is a primary cause of the replacement of the red by the grey squirrel, and that supplementing the food of red squirrels would give them a competitive advantage over grey squirrels. The hoppers initially used conformed to the design described by Pepper (1993) and Gurnell & Pepper (1993). Although it is believed that red squirrels used these hoppers occasionally (Gurnell, 1994), it was found that they did not work effectively and grey squirrels were gaining access to the food. In consequence the hoppers were counter-productive to the aims of the project (Gurnell & Venning, 1995). They were not used in 1995 and have now either been modified or replaced with a new design (see Smith 1994). These will be operational as from April 1996, when Forest Enterprise takes over their supervision. Further information concerning the hopper work can be found in Gurnell (1994, 1995). Consequently, Aim 4 will not be considered here.

Pilot reintroductions were carried out within the Reserve in 1993 (see Gurnell & Venning, in press) and 1994. This work will be followed by a full-scale experimental reintroduction of up to 20 squirrels in 1996. Therefore, Aims 5 and 6, and recommendations concerning protocols for the reintroduction of red squirrels, and have been considered in detail by Venning *et al.* (1997).

Following the above, this report will concentrate on Aims 1 to 3, i.e. the effects of habitat structure and management, and the removal of grey squirrels, on red squirrels in Thetford Forest, and the health and welfare of red squirrels.

4. Red Squirrel Reserve

In the summer of 1992, the Red Squirrel Conservation Area was enlarged to 1700 ha (Map 1) and was designated the Red Squirrel Reserve. It provides the focus for the conservation studies. Grey squirrels were known to be present throughout the Reserve and red squirrels had not been seen in the area for over 2 years. The Reserve was arbitrarily divided into 5 sectors, A to E (Map 1) to stratify the sampling effort.

Many subcompartments within the Forest contain a mix of two or more tree species and associated planting years. In order to assign each subcompartment with one species code and one age code for red squirrel suitability analysis, simple decision rules were used to classify these mixed compartments. The definitions adopted are presented in Table 1 (also see Gurnell, Clark and Feaver, 1995). Using these definitions, the tree species-age composition of the Reserve in 1995 is shown in Figure 1 and Appendix 5.

5. Red squirrel pre-release pen

A 1 ha pre-release pen was erected in the centre of the Reserve in 1993; the fence was built as described by Gurnell & Pepper (1993). A 4m wide strip of trees was cleared on each side of the fence. Nest boxes, food hoppers, and water stations were placed inside the pen. Two metre high bridges of pine tree trunks were erected across the fence, directly linking trees inside and outside the pen, when required. Although the pen was designed for the reintroduction studies and will be discussed in relation to this in a later report, both red and grey squirrels frequently climbed into the pen and remained inside until trapped or the bridges were erected. In 1995 an electric fence was added to the top of pen fence to deter grey squirrel entry. The pen has been the focal point of many of the observations made on Thetford red squirrels during the past three years.

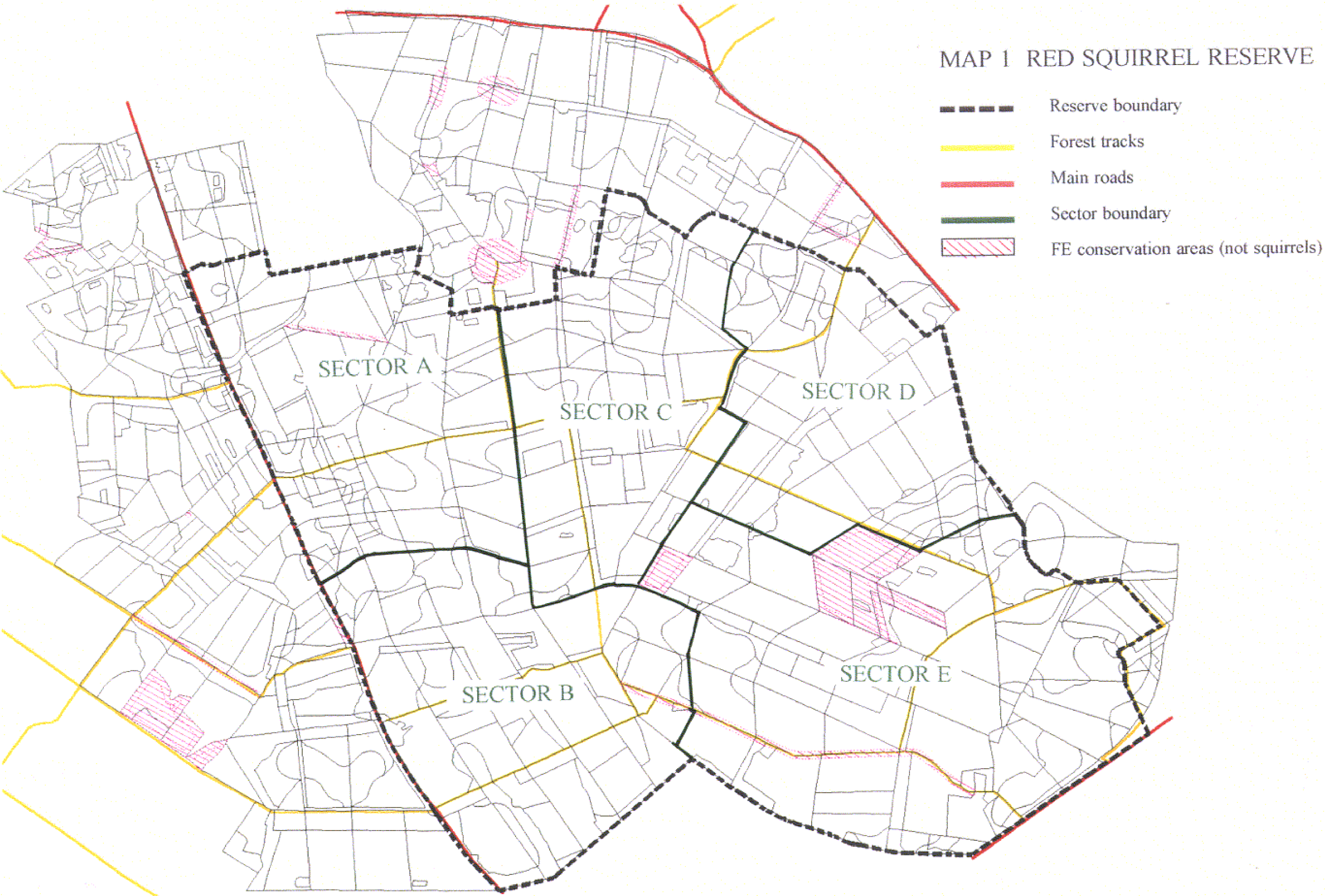
6. Methods

6.1. Grey squirrel removal and post-mortem examination

Starting in September 1992, between 8 and 10 multicapture cage traps (Rowe, 1980) at a density of one per 1-2 ha were used to capture grey squirrels in selected parts of the forest, especially towards the edge of the Reserve and, where possible, in places that contained broadleaf trees (Map 2). Traps were prebaited with whole maize for 1 week and set for 5 days. They were checked twice daily.

Captured grey squirrels were removed to the Forest Offices and humanely killed using CO_2. They were assessed for sex, weight and reproductive condition by external signs and post-mortem examination.

External signs of breeding in females were: swollen vulva (female in heat; Asdell, 1946), rominent teats with a lack of hair around them (i.e. lactating or suckling young), swollen abdomen and heavier than normal (pregnant). At post-mortem, the number of embryos or placental scars in the uterus were noted. The uterus was also recorded as thin and flaccid (female in anoestrus), or enlarged and firm. Females in heat typically have an enlarged, firm uterus resulting from an increased fluid content and vascularisation (Asdell, 1946).


MAP 1 RED SQUIRREL RESERVE
Reserve boundary
Forest tracks
Main roads
Sector boundary
FE conservation areas (not squirrels)
SECTOR A
SECTOR B
SECTOR C
SECTOR D
SECTOR E

Map 2

Red Squirrel Reserve and Research Study Sites

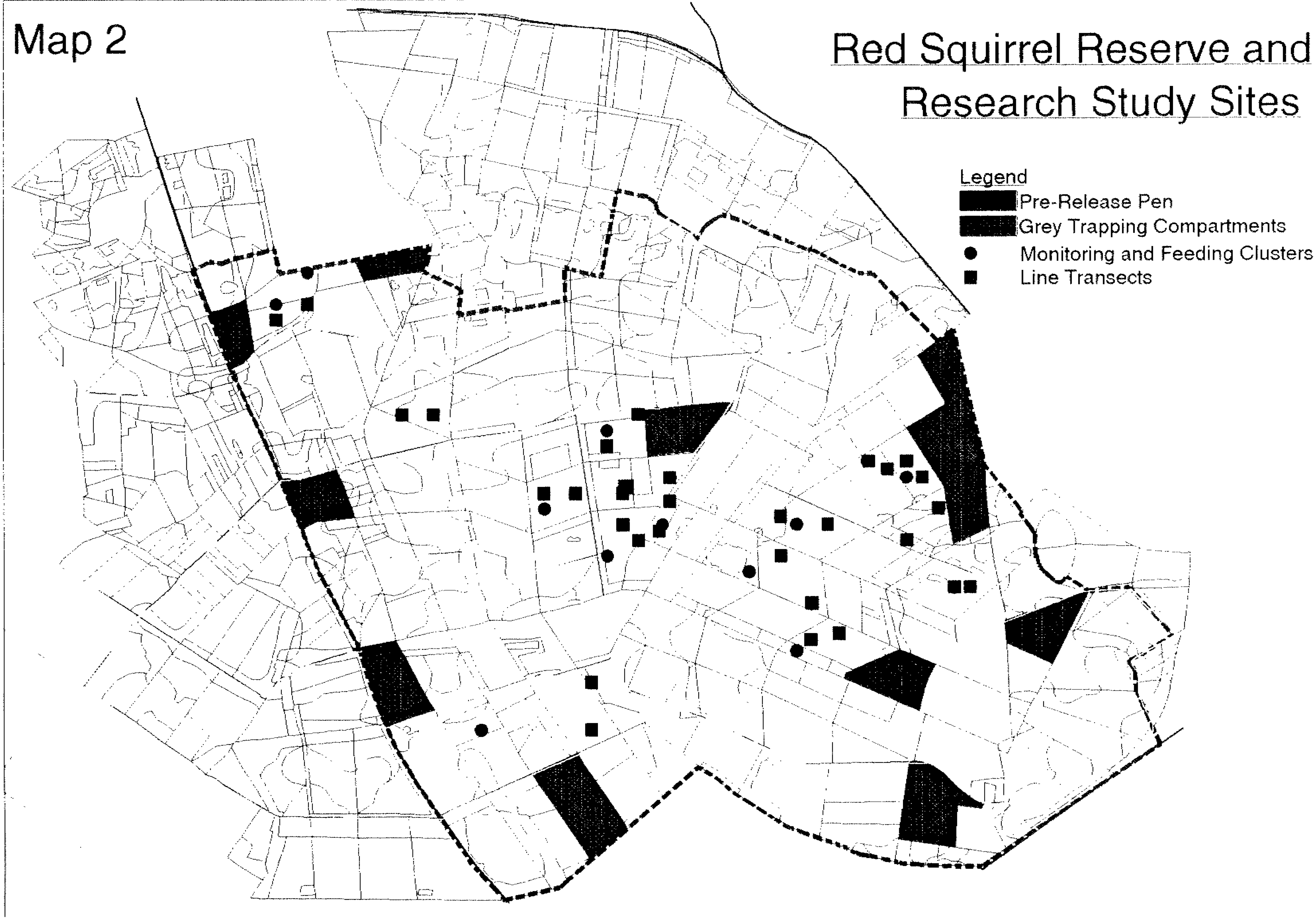


Table 1 Classification of tree species and age in subcompartments

(a) Tree species

Description	Code	Definition
Scots pine	SP	
Corsican pine	CP	
Lodgepole pine	LP	
Conifers dominant	CD	Mixture of broadleaves and conifers with conifers the largest area Plant year taken as for the dominant conifer species
Broadleaves dominant	BD	Mixture of broadleaves and conifers with broadleaves the largest area Plant year taken as for the dominant broadleaf species
Mixed conifers	MC	A mixture of conifer species. Plant year taken as dominant species
Mixed broadleaves	MB	A mixture of broadleaf species. Plant year taken as dominant species
Conifers and broadleaves e	CB	An approximately even mix of conifers and broadleaves. Earliest plant year taken
Broadleaves	BL	Broadleaves, mainly beech, but not a mixture

(b) Age

Age (years)	Code
1-10	1
11-20	2
21-35	3
36-55	4
>55	5

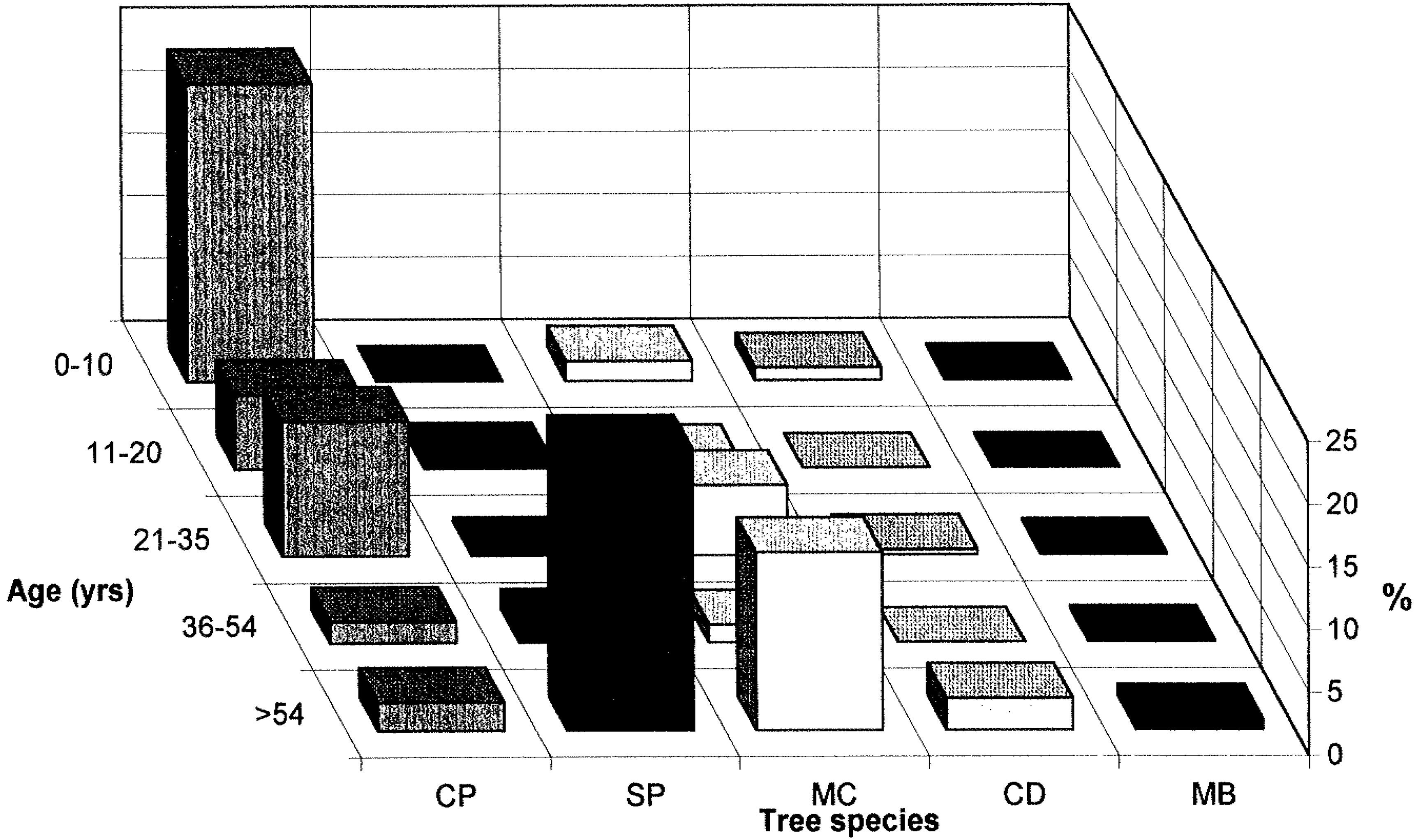


Figure 1 Tree species and age composition of the Reserve; see Table 1 for key

Breeding males had large, descended testes with blackened and course skin on the scrotum and staining of the periscrotal fur (Dubock 1976, 1979). The degree of staining was arbitrarily recorded on a scale from 0 (none) to 3 (abundant). At post-mortem, the maximum length and breadth of each testis was measured using vernier callipers, and an index of testes size for each animal obtained from the sum of the product of the length and breadth of each testis.

Also at post-mortem, the shin length of the left leg was measured with vernier callipers with knee and ankle joints fully flexed. This provided a linear measure of the size of the animal and an index of body condition was obtained by dividing body weight by shin length (see Don 1981). This measure has been termed the standardised body weight (g mm^{-1}). Two additional measures of body condition were taken; the relative amount of fat around the kidneys and the relative amount of general body fat in the abdominal cavity. Both these were subjectively scored on a scale from 0 (none) to 5 (abundant).

Eye lenses were removed and stored in 10% formal-saline to estimate age using eye lens weight according to the method and formula derived by Dubock (1979).

6.2 Red squirrel trapping

Within each sector, three clusters of hoppers and single-catch traps were established early in 1993. The distance between clusters was >300 m. Each cluster consisted of 3 hoppers, 20 m to 30 m apart and 5 monitoring traps. One trap was placed in the centre of the three hoppers and four were placed around the edge of the cluster with 50 m between traps. The traps were placed on boards fixed to trees 3 m to 4 m from the ground (Gurnell & Pepper, 1994). Slight changes in the distribution and number of clusters in each sector were made during the 3½ years of the study.

Traps were prebaited for 1 week with a mixture of peanuts, sunflower seeds, apple and maize (and with other foods such as cobnuts and hazelnuts as available) and set for 5 days. Traps were visited twice daily. Captured red squirrels were weighed, ear tagged (National Band and Tag. Co., USA, monel, black filled ear tags type 1005 size 1), and their breeding condition noted (from external signs - see above). Some were fitted with radiocollars (Biotrack, Wareham, Dorset). Red squirrel trapping started in March 1993.

6.3 Red squirrel radiotracking

Throughout the last 2½ years of the study, up to 4 red squirrels have carried working radiocollars at any one time. Initially, collars regularly came off the animals. Subsequently, collars with adjustable neck sizes have been used and these have proved to be more effective.

A detailed assessment of the home ranges of collared animals was made each summer and autumn with the help of students from QMW College. Fixes were made by homing in on an animal taking care not to disturb it. A distance and bearing was then taken to the nearest ride, and then a distance and bearing to one of many fixed points with known map coordinates established throughout the Reserve. Up to three fixes were taken on an animal during the day with two or more hours between each fix. The radiotracking data were analysed by RANGES4 and RANGES5 software (Biotrack and ITE, Furzebrook resp.). Fixes were also made every 1 or 2 weeks to determine the location of the animals and whether they were still alive.

6.4 Habitat assessments

6.4.1 Characteristics of compartments

During the summer of 1995, 20 compartments in sectors C and E were selected as representative of the age and tree species composition of the main types of habitat within the part of the Reserve most heavily used by red squirrels (see section 7.4). The following 10 measures were recorded for each compartment:

SPECIES	tree species
AGE	tree age (years) from P year
THINNING	none (1), late (2), final (3)
SD	stocking density (no ha^{-1}, based on number of trees in three 900 m^2 quadrats)
DBH	diameter at breast height (average from up to 30 trees)
NN	nearest neighbour distance between trees (average from up to 30 trees)
FC	% field cover (average from 15 1 m^2 quadrats)
DREY	a relative index of the number of dreys in the compartment obtained by counting all the dreys seen in two transect walks across the compartment
FEED	an index of squirrel feeding intensity (the mean number of cone cores in 15 1 m^2 ground quadrats)
CC	an estimate of % canopy cover (average from 10 measures using a sighting tube).
CONE	an index of the number of cones seen on edge trees using binoculars ranging from 0 (none) to 3 (many) (average from 10 estimates)

6.4.2 Tree seed crops and feeding remains

Two 1 m by 50 m transects were marked within 200 m of each hopper cluster. Cores of cones eaten by squirrels were collected at intervals of 6 weeks. Transect work was initiated in September 1992 with 13 lines (not all clusters had two lines at first) and was increased to 30 lines by November 1993. The transects were used to estimate feeding intensity and habitat utilisation.

During the first week in November each year, broadleaved seed crops were examined by making quadrat counts in several compartments containing broadleaved trees. Quadrats ranged in size from 1 m^2 to 100 m^2 (large quadrats were used when there were few seeds). Crops have been arbitrarily ranked on a four point scale: none, poor, moderate, abundant.

6.4.3 Red squirrel habitat selection

The age and species composition of habitats used by red squirrels (based on the results from radiotracking studies) from November 1994 to October 1995 were compared with all the habitats available within the Reserve, and with habitats selected from a set of random coordinates. Resource selection indices with confidence intervals and significance levels were calculated for these data to assess habitat preference and the suitability of the Reserve for red squirrels (Manly *et al.*, 1993).

6.5 Field work programme

From April 1993, a regular 6-week cycle of field work involving trapping squirrels, and assessing feeding remains, was established within the Reserve. Sectors A, B and C were worked during the first three weeks of the cycle, and sectors D and E during the second three weeks.

7. Results

7.1 Grey squirrel removal

To gain an understanding of the population ecology of grey squirrels in Thetford Forest, various analyses have been carried out on the removal data. The main findings from these analyses will be presented here. More detailed analyses on some aspects of the data will be reported elsewhere.

7.1.1 Numbers and distribution

In all, 1179 grey squirrels were captured between September 1992 and February 1996, a period of 3½ years. Detailed autopsies were stopped in September 1995 and, unless qualified, the following will refer to the 3 year period between September 1992 and August 1995. 385 squirrels were captured in the year 1, from September 1992 to August 1993; 420 in year 2, September 1993 and August 1994, but only 208 animals in year 3, from September 1994 to August 1995 (Figure 2). Thus approximately half the squirrels were captured in year 3 compared to the previous two years. Furthermore, distinct peaks in numbers trapped occurred in March/April in years 1 and 2, but this was not the case in year 3, although there was a small increase in the following bimonthly period (Figure 2). Most animals were captured in sectors A and E and fewest in sector B (Figure 3). Significant correlations ($p<0.05$) in numbers captured were found between sectors A and E, D and E, and A and B (Figure 4). Some sector pair-wise correlations may be lower than expected because sectors A, B and C were trapped 3 weeks before sectors C and D. Some animals were captured outside of the Reserve to the west of the Brandon Road (denoted Y in Figure 3) during the spring and summer each year suggesting that the annual cycles seen in the Reserve are a true reflection of numbers within the forest as a whole.

7.1.2 Population structure

7.1.2.1 Sex and age composition

The age composition of the grey squirrel population was assessed from the external characteristics and body weight at the time of capture, and an estimate of age derived from eye lens weight using the procedures and equation derived by Dubock (1979). Three age classes have been used: juvenile <6 months of age, yearling 6-14 months, and adult >14 months.

After the first three months of trapping, we have assumed that numbers captured resulted from immigration into the Reserve. However, there is no obvious difference in the pattern of the structure of the population between the first three months and the rest of the study. For example, it might be that the animals moving into the Reserve should consist mainly of young animals dispersing into the vacant area. In the contrary, there was an increase in the proportion of adults after the first few months, and there was a consistent annual cycle with adults forming the bulk of the late winter to spring peaks in numbers (Figures 5a, 5b). Both yearlings and juveniles were captured in every bimonthly period and there was a relative peak in the autumn which is consistent with a normal autumn dispersal period, although established populations would also contain a large number of young animals at the end of the breeding season (Figure 5b; see section 7.1.3.).

The overall male:female sex ratio for adults and yearlings was 1.35:1; this is significantly different from 1:1 ($X^2 = 16.7$, $p<0.001$). Consistently more males than females were trapped, except in the autumn of each year which coincided with a cessation in breeding (Figure 6). For juveniles the sex ratio, 0.73:1, was significantly biased towards females at ($X^2 = 5.8$, $p<0.025$).

7.1.2.2 Body size, weight and condition

There were significant associations between body weight (w) and shin length (s) in males ($r = 0.71$, $n=566$, $p<0.01$) and females ($r = 0.80$, $n=500$, $p<0.01$). The correlation coefficients were only slightly lower when age in weeks (a) was held constant (males $r_{ws.a} = 0.68$, females $r_{ws.a} = 0.78$) and they were not substantially altered when the data were log transformed. The relationships between body weight and age and shin length and age are shown in Appendices 1 and 2.

Overall, adult female squirrels were significantly heavier than males but there was no significant difference between their shin lengths (Tables 2 and 3). Breeding male adults had slightly longer shin lengths than non-breeding male adults (Tables 2 and 3). Standardised body weights were significantly larger in females than males, and in breeding than non-breeding individuals (Tables 2 to 4). This indicates that breeding animals were in slightly better condition than non-breeding animals, especially females.

To assess body condition over the duration of the study, the medians rather than the means of the standardised body weights for each bimonthly period have been used. A comparison of these measures over three years shows that both breeding males and females tended to be in poorer condition during the 1993 breeding season and at the beginning of 1994 (Figure 7, Table 4); thereafter, body condition was similar to or above the long-term median value.

The correlation between kidney fat and general body fat indices was high ($r = 0.87$, $n = 1059$, $p<0.001$). In 48% of pairwise comparisons, body fat was equal to kidney fat, and in 44% of comparisons, the body fat index was one score larger than the kidney fat index (Figure 8). This indicates that body fat accumulates at the same time or slightly before kidney fat and it may be a more sensitive index of body condition. Only body fat will be considered below.

Distinct yearly cycles in body fat can be seen in 1993 and 1994 with troughs in the summer or early autumn respectively (Figure 9, Table 5). This pattern was not so obvious in 1995, when fewer animals were trapped. In general, the higher the body fat index, the higher the mean body weight of the animal. There was no general relationship between fat index and shin length, but mean standardised body weight also increased with fat index (Table 6). However, there was a large amount of variation around the mean values in these relationships making it difficult to interpret whether it is better to use standardised body length or general body fat as a measure of body condition. An advantage of using standardised body weight is that it does not require carrying out an autopsy. Further analyses of body condition will be carried out elsewhere.

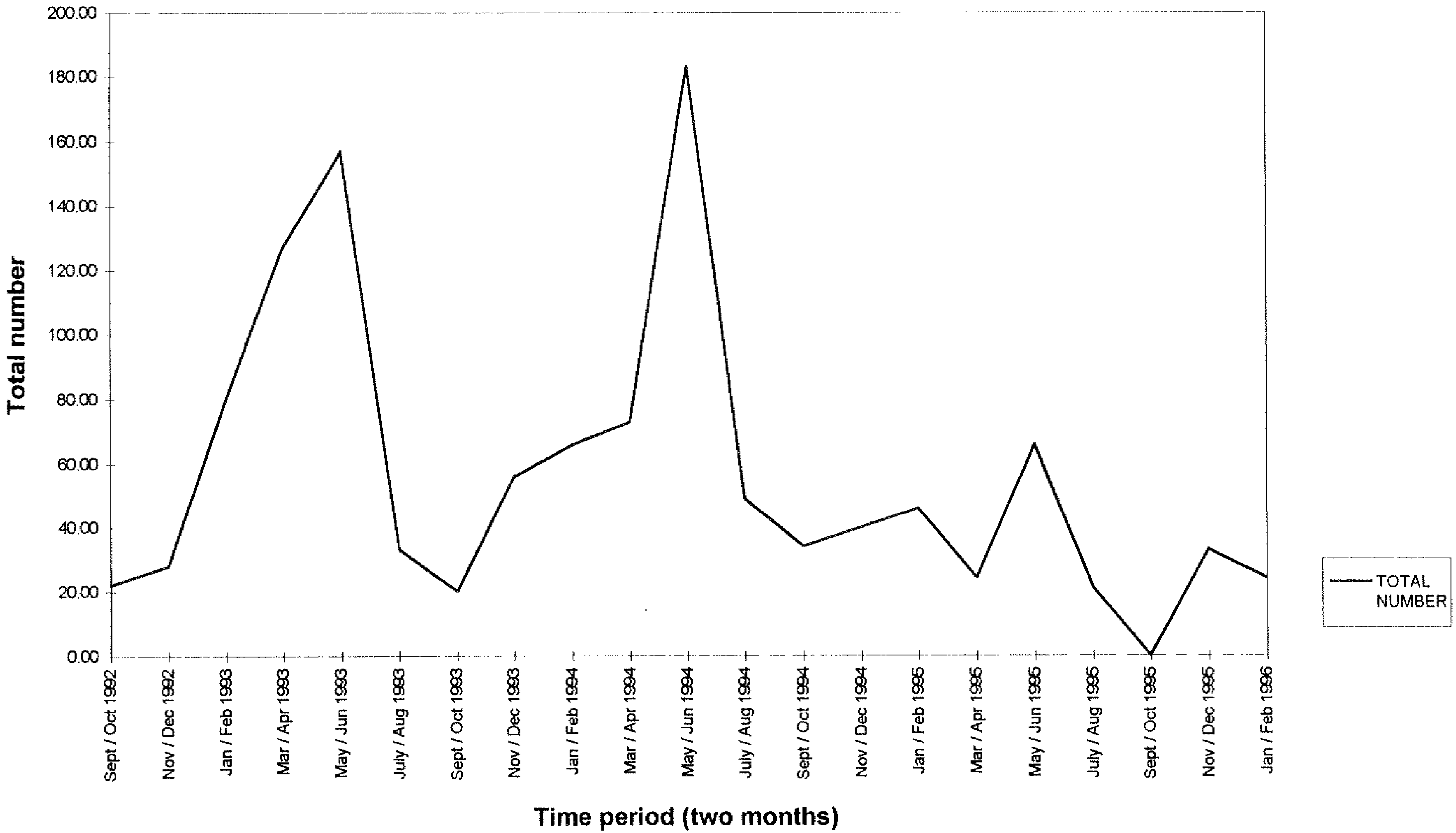


Figure 2 Total number of grey squirrels captured during each bimonthly period.

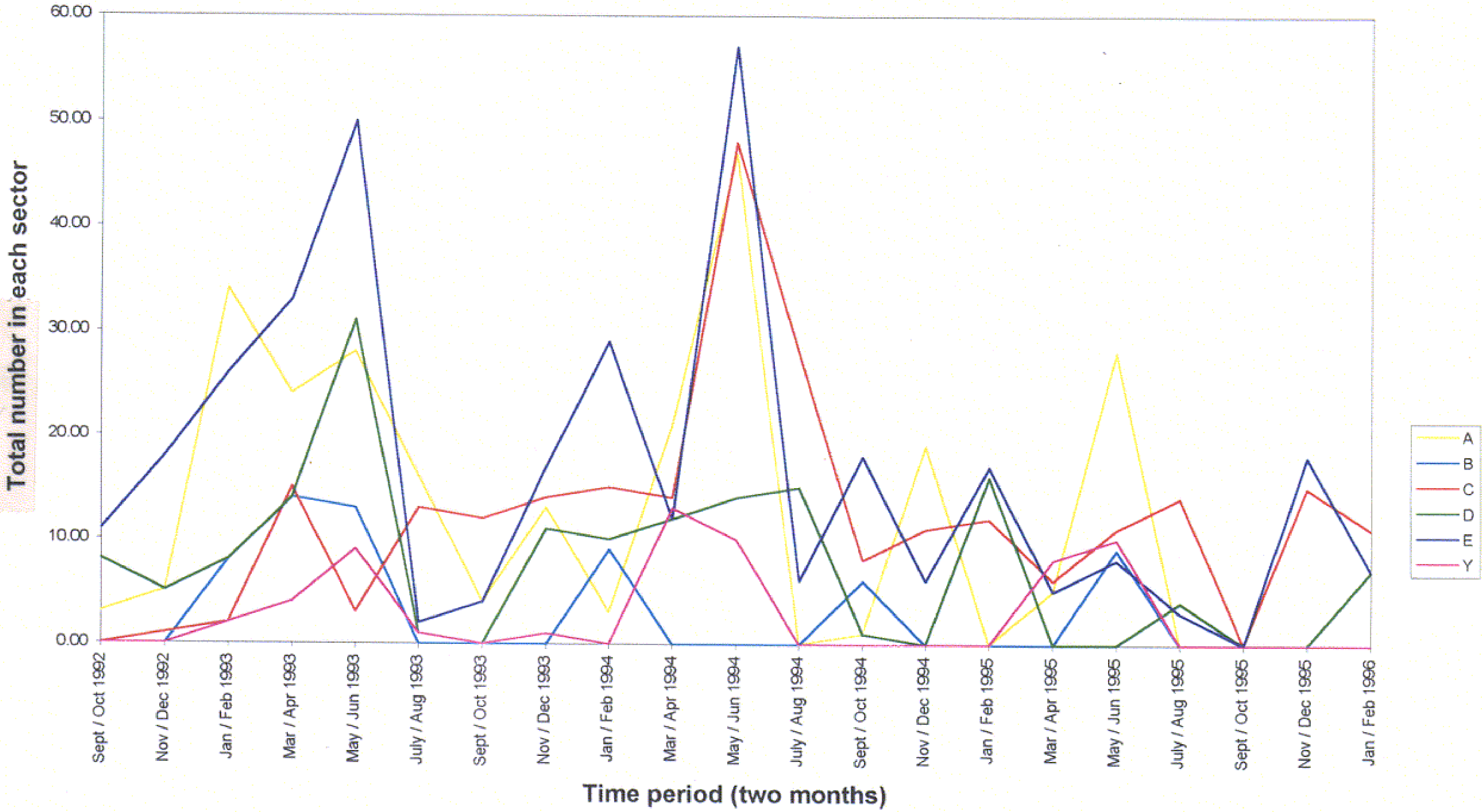


Figure 3 Total number of grey squirrels captured in each sector in each bimonthly period.

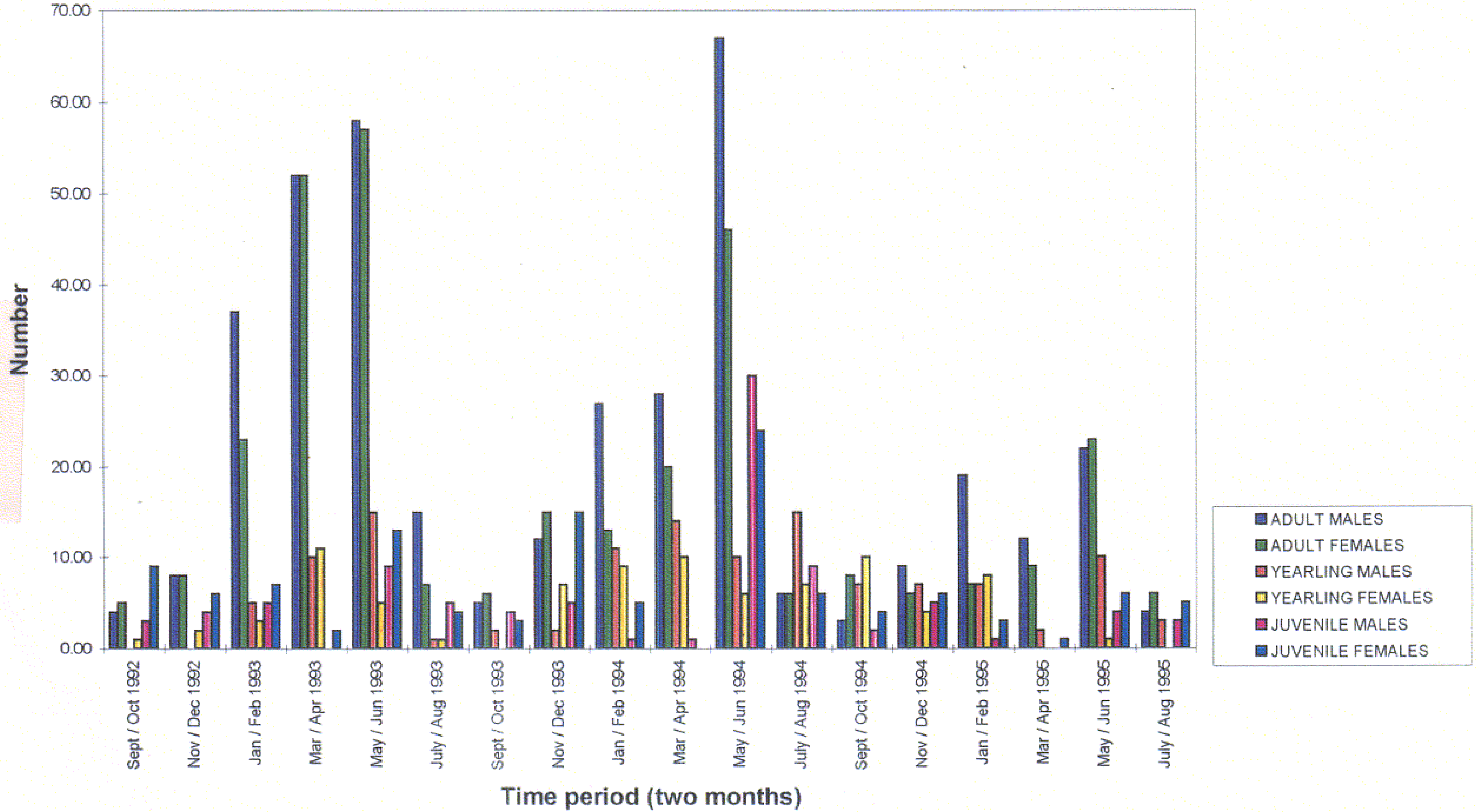
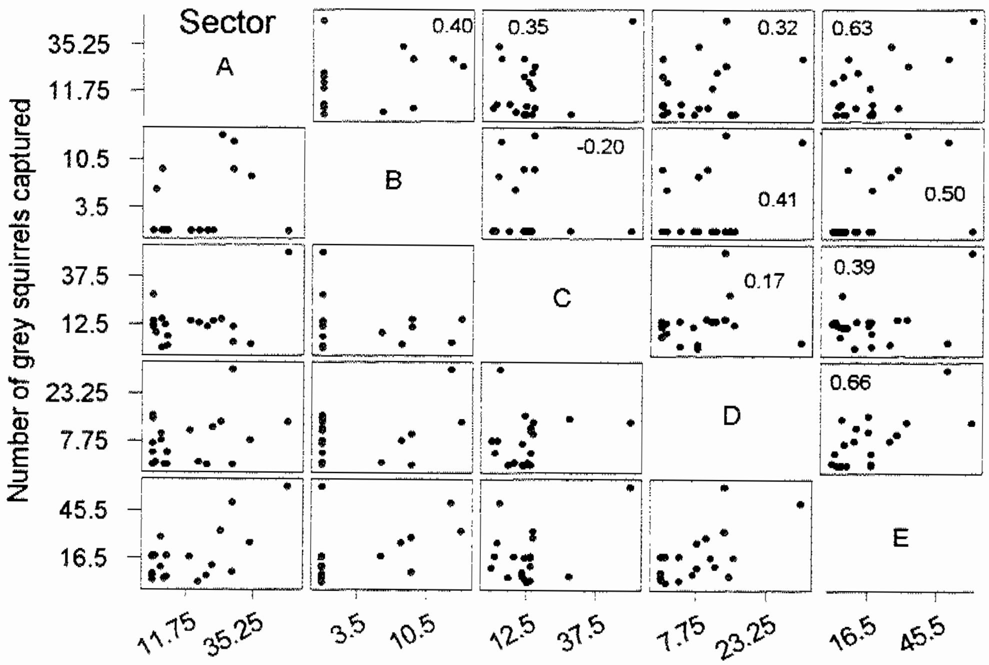


Figure 5 Sex and age composition of grey squirrels captured in each bimonthly period.

Figure 4 Matrix plot for numbers of grey squirrels captured in each sector for bimonthly periods from Sept/Oct 1992 to July/Aug. 1995.



Figures in the upper diagonal boxes are correlation coefficients. They are significant at $p<0.05$ if greater than 0.47 (two sided).

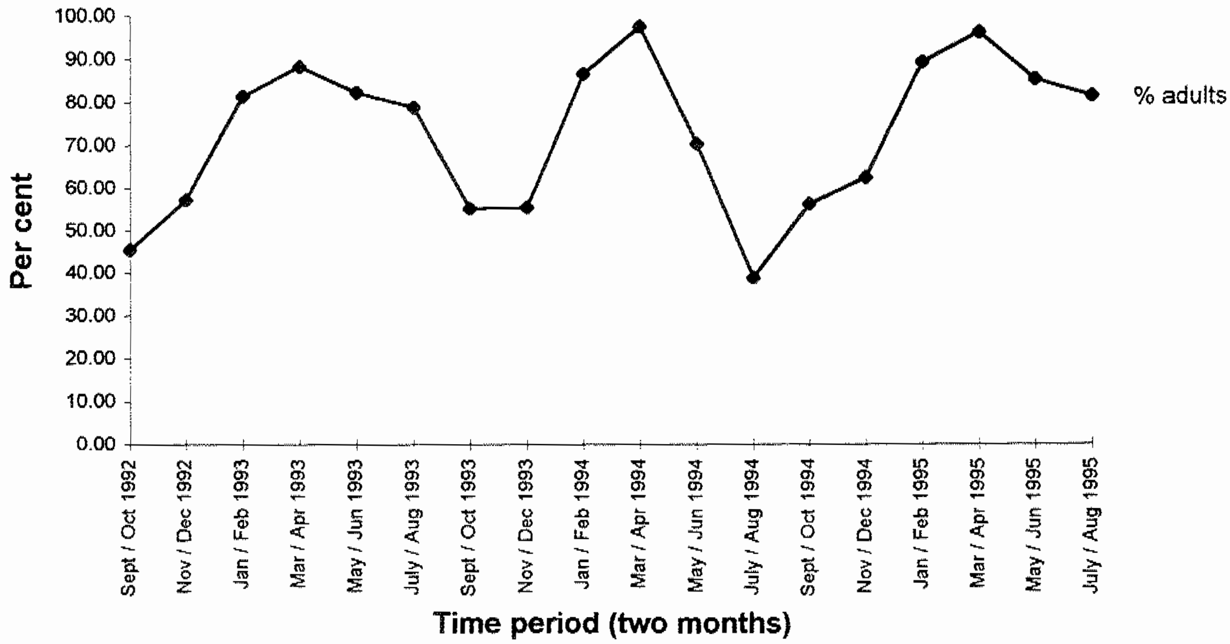


Figure 5b Per cent adults captured in each bimonthly period

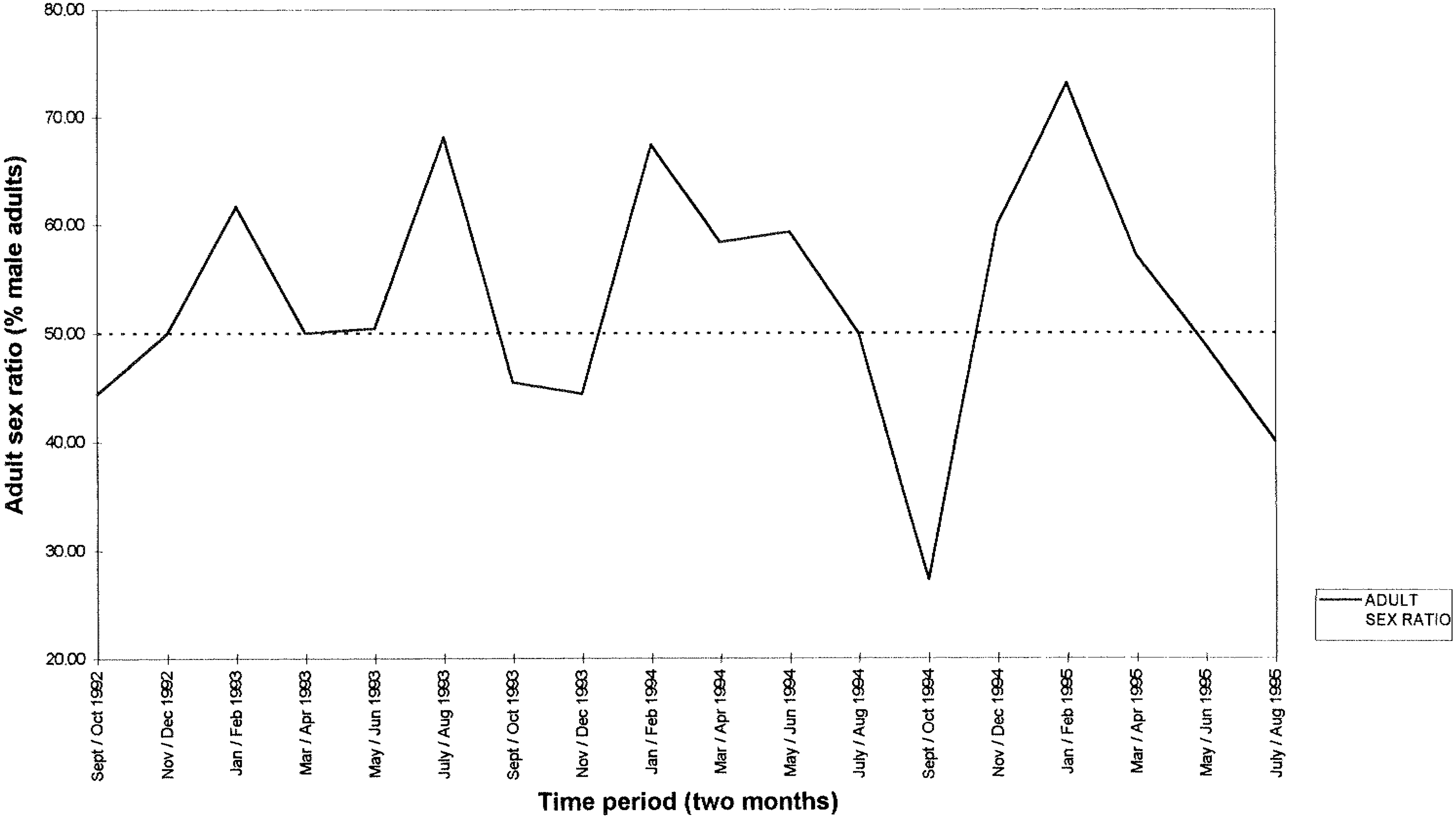
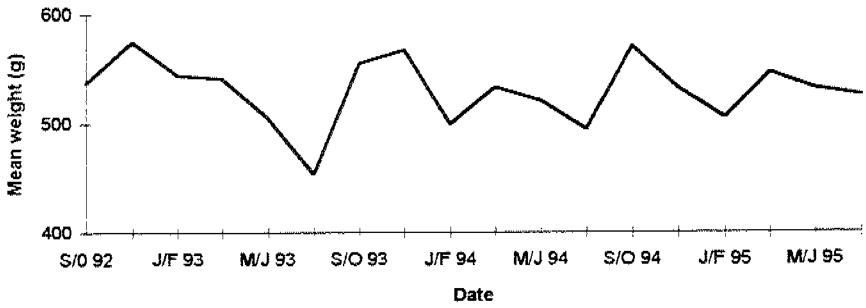
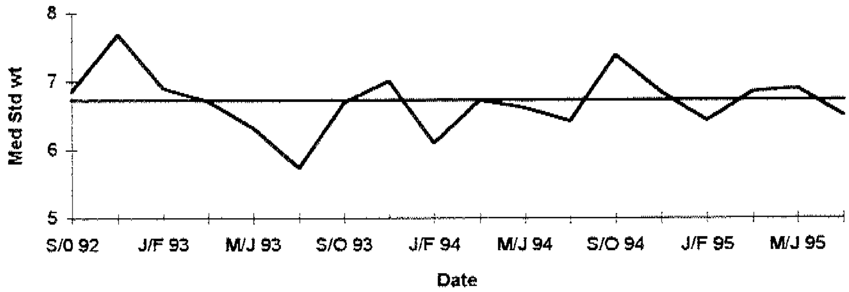


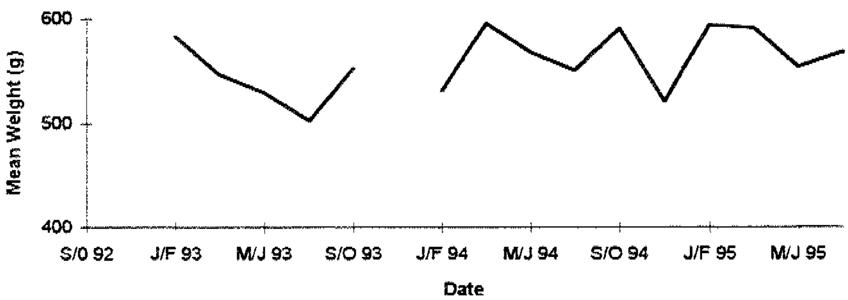
Figure 6 Adult grey squirrel sex ratios (% males) in each bimonthly period.

(a) Breeding males





(b) Breeding females



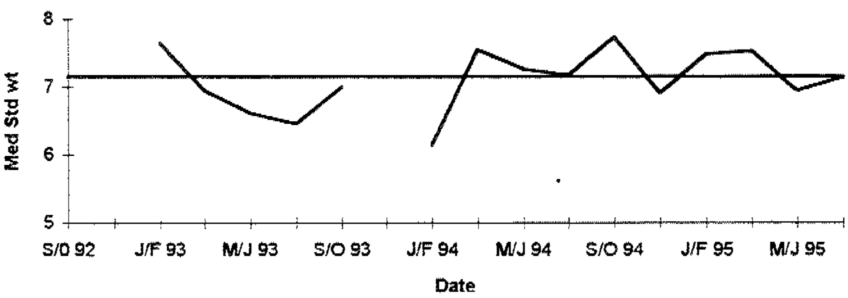


Figure 7 Mean body weight and median standardised body weight of adult breeding males (a) and females (b) for each bimonthly time period. The horizontal lines on the median standardised body weight graphs are the overall median values across all time periods.

(i) Weight (g) and (ii) Shin length (mm)

(a) Non-breeding

	(i) Weight (g) Adult	Juvenile	(ii) Shin length (mm) Adult	Juvenile
Male				
n	95	125	89	106
mean	510	358	78.3	71.9
std	34.1	94.4	3.12	5.51
Female				
n	229	152	207	143
mean	529	363	78.7	71.4
std	46.3	96.6	3.41	5.81
(b) Breeding				
Male				
n	339	0	370	0
mean	520	-	79.2	-
std	50.0	-	3.04	-
Female				
n	552	0	147	0
mean	529	-	79.0	-
std	53.0	-	2.74	-

(III) Standardised weight (weight/shin length; g/mm)

(a) Non-breeding

	Adult	Juvenile
Male		
n	87	106
mean	6.5	4.94
std	0.45	1.12
Female		
n	203	143
mean	6.7	5.1
std	0.57	1.07
(b) Breeding		
Male		
n	365	0
mean	6.6	-
std	0.63	-
Female		
n	146	0
mean	7.0	-
std	0.64	-

Table 2 Mean weight, shin length and standardised body weight for different age and breeding groups

(i) Anova table for body weight

Source	df	Mean Square	F	p
Sex	1	115452	49.65	0.000
Br	1	49628	21.34	0.000
Sex*Br	1	7996	3.44	0.064
Error	872	2325		
Total	875			

(ii) Anova table for shin length

Source	df	Mean Square	F	p
Sex	1	1.824	0.19	0.663
Br	1	52.156	5.44	0.020
Sex*Br	1	10.42	1.09	0.298
Error	809	9.595		
Total	812			

(iii) Anova table for standardised body weight

Source	df	Mean Square	F	p
Sex	1	37.8	37.8	0.000
Br	1	5.8	16.1	0.000
Sex*Br	1	1.1	3	0.086
Error	797	289.7		
Total	800			

Table 3 Analyses of variance for adult body weight, shin length and standardised body weight according to sex and breeding condition.

(a) Breeding adults

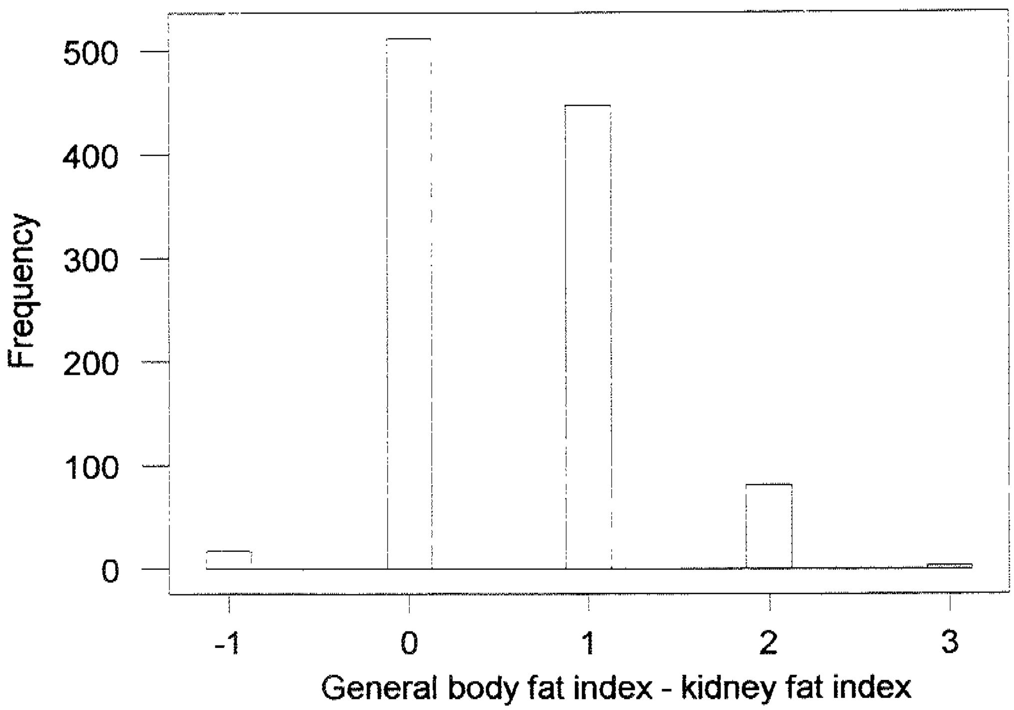
Date	Weight (g)						Standardised weight (g/mm)					
	Male			Female			Male			Female		
	Mean	n	CV (%)	Mean	n	CV(%)	Mean	n	CV(%)	Mean	n	CV(%)
S/0 92	538	4	6	590	1	0	7	3	63	7.8	1	
N/D 92	553	6	15	--	0		7	3	58		0	
J/F 93	544	30	8	583	8	8	7	29	51	7.4	8	8.3
M/A 93	541	50	9	546	38	10	7	49	35	6.9	38	9.2
M/J 93	503	62	9	534	26	7	6	56	43	6.7	25	6.5
J/A 93	454	14	9	502	6	8	6	14	31	6.4	6	5.3
S/O 93	555	3	11	552	3	11	7	3	23	6.9	3	8.3
N/D 93	570	10	6	--	0		4	9	40		0	
J/F 94	499	25	6	530	6	10	6	23	47	6.4	6	9.9
M/A 94	534	33	7	593	12	8	7	31	39	7.4	10	7.7
M/J 94	509	69	9	573	19	9	7	45	48	7.3	16	8.7
J/A 94	494	8	7	550	4	6	7	7	48	7.1	4	7.1
S/O 94	570	2	0	590	1	0	7	2	30	7.7	1	
N/D 94	532	13	7	520	1	0	7	13	38	6.9	1	
J/F 95	505	24	7	593	3	8	6	24	42	7.5	3	6.5
M/A 95	546	13	8	588	8	13	7	13	44	7.5	7	12.5
M/J 95	529	26	8	553	7	8	7	26	51	7.1	7	6.6
J/A 95	534	7	27	567	3	7	7	7	66	7.3	3	6.8

(b) Non-breeding adults

Date	Weight (g)						Standardised weight (g/mm)					
	Male			Female			Male			Female		
	Mean	n	CV (%)	Mean	n	CV(%)	Mean	n	CV(%)	Mean	n	CV(%)
S/0 92		0		549	5	5		0		7.0	5	4.6
N/D 92	525	2	7	565	5	7	7	1		7.2	3	10.3
J/F 93	510	11	6	541	16	8	6	11	5	6.9	15	8.4
M/A 93	508	8	4	509	16	6	6	8	5	6.5	14	6.9
M/J 93	493	6	10	529	35	8	6	5	9	6.6	28	7.2
J/A 93	497	4	1	455	2	14	6	3	3	5.6	2	15.3
S/O 93	500	3	5	420	2	10	7	3	9	5.2	2	10.0
N/D 93	545	2	1	550	18	7	7	1		7.0	16	6.1
J/F 94	484	11	4	512	15	10	6	11	5	6.4	15	10.2
M/A 94	496	7	7	522	17	8	6	7	5	6.6	16	7.2
M/J 94	523	6	7	537	34	7	7	3	4	6.9	22	6.1
J/A 94	510	4	5	527	3	4	7	4	5	7.0	3	1.7
S/O 94	514	5	5	531	11	5	6	5	4	7.0	11	4.4
N/D 94	513	3	6	543	6	4	7	3	8	7.0	6	1.5
J/F 95	480	1		494	12	8	6	1		6.3	12	7.6
M/A 95	450	1		490	1		6	1		--	0	
M/J 95	508	6	4	539	17	8	7	6	4	6.8	17	7.9
J/A 95	480	1		477	6	12	6	1		6.3	6	6.9

Table 4 Bimonthly mean body weights and standardised body weights for breeding and non-breeding animals. CV = Coefficient of variation, n = sample size.

Figure 8 Histogram of the difference between kidney and body fat indices



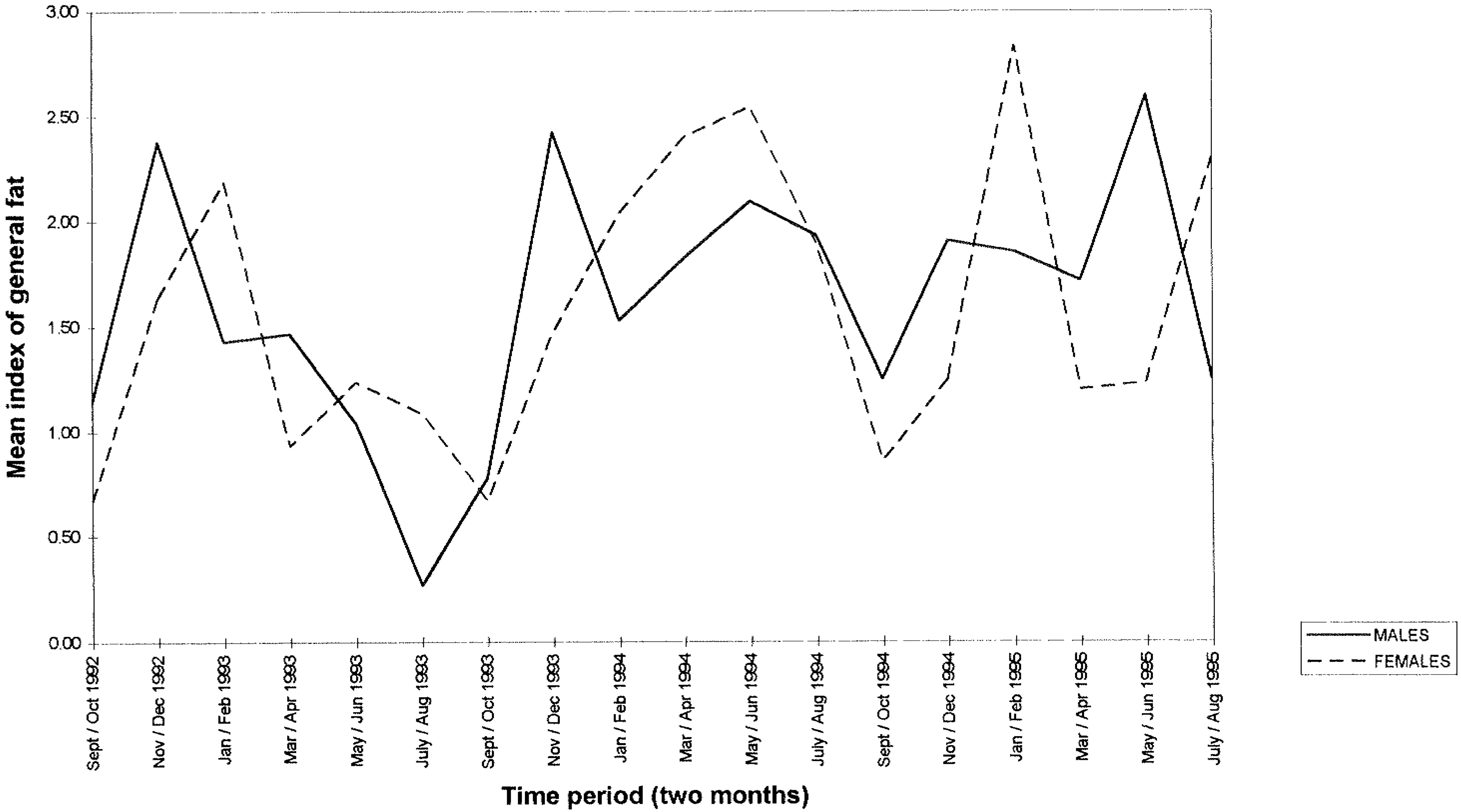


Figure 9 Mean male and female indices of general body fat for each bimonthly period

	Male			Female		
Date	Mean	n	CV (%)	Mean	n	CV(%)
S/0 92	1.14	7	60	0.67	15	122
N/D 92	2.38	8	31	1.64	11	41
J/F 93	1.43	47	69	2.19	32	41
M/A 93	1.47	58	70	0.93	60	100
M/J 93	1.04	75	103	1.24	63	97
J/A 93	0.27	19	171	1.09	11	96
S/O 93	0.78	9	140	0.67	9	106
N/D 93	2.42	19	29	1.47	32	85
J/F 94	1.53	36	79	2.04	27	54
M/A 94	1.83	40	61	2.40	30	54
M/J 94	2.09	107	63	2.54	74	51
J/A 94	1.93	29	79	1.89	18	79
S/O 94	1.25	12	84	0.86	21	92
N/D 94	1.91	21	52	1.25	16	90
J/F 95	1.85	27	63	2.83	18	35
M/A 95	1.71	14	77	1.20	10	110
M/J 95	2.60	36	53	1.23	30	110
J/A 95	1.25	8	83	2.30	10	77

Table 5 Mean indices of general body fat for each bimonthly period. CV = coefficient of variation (%), n = sample size.