ENGLISH NATURE

Grey squirrel control for red squirrel conservation

A Study in Thetford Forest

No. 453 - English Nature Research Reports

Forestry Commission

working today
for nature tomorrow

English Nature Research Reports

Number 453

Grey Squirrel Control for Red Squirrel Conservation
A Study in Thetford Forest

John Gurnell[1] & Janie Steele[2]
[1]School of Biological Sciences, Queen Mary, University of London E1 4NS
[2]Forest Enterprise, Thetford Forest, Suffolk IP27 0TJ[1]

Report prepared for English Nature
and the Forestry Commission

February 2002

ISSN 0967-876X

Summary

1. A three year study on controlling grey squirrels for red squirrel conservation was carried out in Thetford Forest, East Anglia between 1998 and 2001. The control area was 4600ha in size and centred on the 1700 ha red squirrel reserve which had been the focus of red and grey squirrels studies in Thetford Forest since 1992.

2. The control area was divided into nine control zones. Each zone was 500 ha, except for Zone 1 in the centre of the control area which was 600 ha. The zones were divided into three bands (Inner = Zone 1, Middle = Zones 2 to 5, Outer = Zones 6 to 9) according to their distance from the centre of the control area. The control year ran from mid-November in year x to mid September in year x+1. Each zone was trapped with eight clusters of three traps every 9-10 weeks. In Year 1 trapping was carried out by a Control Operator (CO) for four days with two trap rounds per day; this was equivalent to 0.5 person-years (≡ 1.09E-04 person-years ha^{-1}). In addition, private woodland to the south-east was trapped by keepers from the Elveden Estate, and the Research Ranger (JS) working in the reserve also trapped grey squirrels in tree mounted, single capture traps in Zone 1. In Year 2 the number of trap rounds per trap week was increased to 10 (≡ 0.58 person-years or 1.26E-04 person-years ha^{-1}). To increase the control effort per unit area further, only the Inner and Middle Bands were trapped in Year 3 (≡ 2.23E-04 person-years ha^{-}).

3. To provide context for the interpretation of the results, the following terms have been defined:

   3.1. control effort: the number of squirrel traps set multiplied by the number of trap rounds that the traps were operated during a specific time period (eg trap week) within a specific area (eg zone or band), eg the number of trap-rounds $week^{-1}$ $year^{-1}$;
   3.2. trapping efficiency: the number of squirrels captured per trap-round, eg a high trapping efficiency is a high catch per unit effort or a large number of squirrels captured $trap\text{-}round^{-1}$;
   3.3. control efficiency: a high control efficiency will be reflected in a low catch per unit effort, and *vice versa*.

4. To aid interpretation of the findings, we present comparisons with the results obtained from controlling grey squirrels within the reserve between 1992 and 1998. We also present the findings from two short studies carried out in the summers of 2000 and 2001 that investigated the effectiveness of control.

5. The number of grey squirrels captured each year increased from 688 in Year 1, to 716 in Year 2 and to 805 in Year 3. As expected, the number of animals captured declined during each trap week, but squirrels were still being trapped at the end of the week in Years 1 and 3. This was not so evident in Year 2 but it is possible that some traps were not set for the full trap week in this year.

6. There were no differences in the number of squirrels captured $trap\text{-}round^{-1}$ $band^{-1}$ in any control year. Moreover, there were no consistent trends in the numbers of squirrels captured $trap\text{-}round^{-1}$ $band^{-1}$ $period^{-1}$ within each year.

7. More squirrels than expected were trapped in the eastern part of the control area, fewer in the northern part.

8. Slightly more adult males than females were captured each year. Information on the breeding condition of the females and the age structure of the trapped 'population' showed that the squirrels bred between January and August with peaks in the spring and summer. Studies on cone feeding transects in the eastern part of the control area indicate that food availability in terms of pine cones was moderate to good throughout the study and was particularly good in 2000. These results support the idea that Scots and Corsican pine forests are good habitats for grey squirrels.

9. The number of squirrels captured each year in the red squirrel reserve between 1992 and 1996 was lower than during the control studies in 1998-2001. However, the trapping efficiency was much higher in the early period, and this was attributable to a lower control effort during these years.

10. The summer studies in 2000 and 2001 involved hair tubes, feeding transects, live trapping and radiotracking selected squirrels before, during and after control was carried out in Zone 3. There was no difference in the proportion of hair tubes visited before during and after in either year. There was a decline in cone feeding from before to after control, and in the number of squirrels captured trap-round^{-1}, in 2000 but not in 2001. None of the six radio-collared squirrels were captured during the control week in 2000, and only one of seven in 2001. These results demonstrate that many grey squirrels were present in the vicinity of the control compartments but were trapped during the control operations;

11. It is concluded the control effort was too low at all stages of the study to reduce grey squirrel numbers significantly, or indeed to maintain them at low numbers, in the centre of the control area. Thus, the control efficiency was poor and this results from the presence of a large number of untrapped animals.

12. Further studies are recommended:

    12.1. to carry out control studies in conifer forests of different tree species composition;
    12.2. to compare the effectiveness of ground placed and tree mounted traps on numbers captured;
    12.3. to investigate the effects of increasing the length of the prebait period and the type of bait used on squirrel trappability;
    12.4. to assess different levels of control effort (number of trap-rounds area^{-1} time period^{-1}) taking into account the required costs of control in terms of the number of person-years or the number of person-years ha^{-1}.

Acknowledgements

We would like to thank Brian Ball for carrying out the control work in years 1 and 2, and Dave Hooton in year 3. We are grateful to the keepers of the Elveden Estate for their assistance with the control programme. We are also grateful to Christine Neilson and Sarah Barnes for help with field work in the summer of 2000, to the staff at the Thetford Forest District Office for their cooperation and assistance, and to Harry Pepper for discussion and guidance. The work was carried out as part of a larger project on conserving the red squirrel in Thetford Forest sponsored by English Nature, the Forestry Commission and the People's Trust for Endangered Species.

Contents

List of tables

List of figures

1. Introduction

The aim of this study is to assess the success and efficiency of controlling grey squirrels (*Sciurus carolinensis*) for red squirrel (*S. vulgaris*) conservation using live trapping methods in Thetford Forest, East Anglia. Thetford Forest was originally planted with Scots pine (*Pinus sylvatica*) between 1925 and 1940, and over the past 30 years, this has gradually been replaced by a second rotation crop of Corsican pine (*P. nigra*). The forest also contains about 10% broadleaves as well as <5% of other conifers and unplanted land (Simpson and Henderson-Howat, 1985). The three year project started in November 1998. The study area was centred on the red squirrel reserve which has been the focus of red and grey squirrel studies since 1992. The reserve was 1700 ha in size and situated in the part of the forest called High Lodge. Since the 1980s, the central part of the reserve had been managed for red squirrels, and many of the broadleaf trees had been removed (see Gurnell *et al.* 2002). To aid interpretation of the results from the control study, we present comparisons with the results obtained with grey squirrel control data collected within the reserve between 1992 and 1998. We also present the findings from two short studies looking at the effectiveness of control carried out in the summers of 2000 and 2001.

2. Terminology

We define the following terms that are used throughout the report; some of them will be described further in the Section C: Methods.

Control Area - 4600 ha in Years 1 and 2 centred on the Red Squirrel Reserve (see Gurnell *et al.* 1997 and Figure 1). This was reduced to 2600 ha in Year 3.

Control Year - From mid-November in calendar year x to mid-September in calendar year x+1

Control Period - In Years 1 and 2, a period of 9 to 10 weeks within which each zone (see below) was trapped once. In Year 3 each Zone was trapped once every 5 to 6 weeks. There were four control periods per year in Years 1 and 2, and seven in Year 3.

Control Bands - Control areas or annuli defined by inner and outer circumferences according to their distance from the centre of the reserve (Figure 2). Inner Band: the central part with radius of 1.38 km, 600 ha in area. Middle Band: 1.5 km wide with outer radii 2.88 km from the centre of the Reserve, 2000 ha in area. Outer Band: 0.95 km wide with outer radii 3.83km from the centre of the Reserve, 2000 ha in area. Trapping was not carried out in the Outer Band in Year 3.

Control Zones - The Middle Band comprised Zones 2 to 5, each 500 ha in area (Figure 2). The Outer Band comprised Zones 6 to 9, each 500 ha in area. The Inner Band was equivalent to Zone 1.

Trap week - Traps set and inspected for a number of rounds (see below) within one week.

Trap round - A visit to all the traps that have been set in a time of 2 to 3 hours. Each day, the traps were visited once in the morning and once in the evening. There were 8 trap rounds in each trap week in Year 1, and 10 in Years 2 and 3.

One trap-round - this was one trap set for one round.

Three additional terms will be used within this report to provide a context for interpreting the results; these are control effort, trapping efficiency, and control efficiency.

Control effort - This was based on the number of squirrel traps set multiplied by the number of trap rounds that the traps were operated during a specific time period (eg trap week) in each zone or band, ie the number of trap-rounds. The annual control effort in Zones 2 to 9 in Years 1 and 2 was the same, with each zone being trapped four times, and each zone having the same area (500 ha). No control was carried out in the Outer Band in Year 3, ie in Zones 6 to 9. The control effort was thus higher in each zone in Year 3 compared with Years 1 and 2, with each zone being trapped seven times during the year. Zone 1 (= Inner Band) was trapped in each period in each year. The control effort was different in this zone for two reasons: the area of Zone 1 was 600 ha, and additional trapping was carried out in this zone by the Research Ranger.

Trapping efficiency - This was the number of squirrels captured per trap-round (ie catch per unit effort). A high number of squirrels captured per trap-round indicates that the trapping was efficient and *vice versa*.

Control efficiency - A high trapping efficiency may be achieved with a low control effort, and it does not necessarily mean that the number of grey squirrels in the Control Area is being reduced. Thus, in contrast to trapping efficiency, the aim of the control programme was to achieve a low number of captures per trap-round, ie a high control efficiency, which would be reflected in a low catch per unit effort. This in turn would depend on the level of control effort. If the level of control effort was too low, then a high control efficiency may not have been achieved.

3. Methods

3.1 The study area

Grey squirrels were removed from throughout the red squirrel reserve (1700ha) plus a surrounding area of 2900ha (Figure 1); this was termed the control area. Superimposed on the control area were control zones (numbered 1 to 9, see Figure 2), and these zones were grouped into three bands according to their distance from the centre of the reserve: the Outer Band - Zones 6-9, the Middle Band - Zones 2-5, and the Inner Band - Zone 1.

3.2 Live trapping methods

Live trapping was carried out from November to September in 1998-1999, called Control Year 1 (abbreviated to Year 1 below), 1999-2000, Control Year 2, and 2000-2001, Control Year 3. Slight changes were made to the live trapping protocol each year in response to the results obtained. These essentially concerned increasing the control effort each year and details are included below.

Live trapping was carried out using ground placed, multi-capture live traps (Fuller or Longmeadow traps) in clusters of three within a compartment at a density of 1 trap per 0.5 to 1 ha.

In Year 1, the field protocol was based on one person, the Control Operator (CO), taking 6.5 days to operate 16 clusters of three traps in two zones (8 clusters in each zone) for eight trap rounds, termed one trap week. In all, there were 130 person-days in Year 1 which was costed as the equivalent of a 0.5 person-year. In Years 2 and 3, the trap week was extended to 10 rounds, ie 7.5 days, equivalent to a 0.58 person-year, each year.

In Years 1 and 2 each zone was trapped four times during the control year, representing four trap periods. In Year 3 each zone was trapped seven times during the control year. The trapping timetable for each year is shown in Table 1.

Year 1 - live trapping was carried out concurrently in two concentrically adjacent zones: Zones 2+6, Zones 3+7, Zones 4+8, Zones 5+9, except for Zone 1 which was trapped on its own.
Year 2 - live trapping was carried out concurrently in two concentrically opposite zones (one inner zone and one outer zone): Zones 3+9, Zones 4+6, Zones 5+7, Zones 2+8, except for Zone 1 which was trapped on its own.

Year 3 - the Outer Band (Zones 6-9) was not trapped, and Zones 2+4 and 3+5 were trapped together with Zone 1 trapped on its own.

A standard procedure for operating the traps was adopted:

Control compartments, and the positioning of the traps within the compartments, were subjectively selected on the basis that they would be likely to catch grey squirrels, eg compartments containing mature trees and with the traps positioned at the base of large trees with little or no field vegetation in the vicinity (this allowed the squirrels to see the bait from the canopy). When in position, the traps were covered in waterproof, polythene sheets (bin liners) and twigs and leaf litter to ensure that captured animals remained dry and unstressed. Each trap week involved the following routine of work:

a. Traps were placed at pre-selected locations on a Monday and prebaited with whole maize.

b. The traps were checked and the bait replenished on Friday.

c. The traps were set as late as possible in the evening of the following Monday.

d. The first visit to the traps (ie trap round) was not be made before 10.00 and the second visit was carried out as late in the afternoon as possible.

e. In Year 1, the traps were checked for the last time at 10.00 on Friday and the traps picked up, and checked before storage or moving to the next area. In Years 2 and 3 the traps were checked for the last time at 10.00 on Saturday.

f. All grey squirrels trapped were humanely killed, weighed, sexed and breeding condition assessed from external signs (see Gurnell 1996a).

There were some variations to the above protocols. In some trap weeks, the traps were first set in the evening with the first trap round on the following morning; in some weeks the traps were first set in the morning with the first trap round on the evening of that day. Some clusters were not trapped during Period 1 in Year 1 when the study was being established. In addition, only one trap round per day was carried out in some compartments between November and January at the beginning of Year 3. These have been taken into account in the analysis of catch per trap-round below. It is also believed that occasionally some clusters of traps may not have been trapped in all periods in Years 1 and 2, and that some trap weeks may have been terminated early. However, there are no accurate records, and no account of this has been taken in the analyses to follow.

In addition to the control in Zone 1 carried out by the CO, live trapping was carried out by the Research Ranger (JS) as part of the ongoing red squirrel studies carried out within the Reserve. Grey squirrels captured by the Research Ranger were given a more detailed post-mortem analysis (see Gurnell *et al.*, 1997). Furthermore, trapping in the private woodlands to the south of the control area in Zone 8, was carried out by keepers from the Elveden Estate.

Table 1 Trapping Dates

The date refers to the beginning of the trapping week

Year 1

PERIOD	Zone 1	Zones 2+6	Zones 5+9	Zones 4+8	Zones 3+7
P1	16 Nov 98	30 Nov 98	14 Dec 98	4 Jan 99	18 Jan 99
P2	8 Feb 99	22 Feb 99	8 Mar 99	22 Mar 99	5 Apr 99
P3	19 Apr 99	3 May 99	31 May 99	14 Jun 99	28 Jun 99
P4	12 Jul 99	26 Jul 99	7–11 Aug 99	23 Aug 99	6 Sep 99

Year 2

PERIOD	Zone 1	Zone 3+9	Zones 4+6	Zones 5+7	Zones 2+8
P1	29 Nov 99	13 Dec 99	10 Jan 00	24 Jan 00	14 Feb 00
P2	28 Feb 00	13 Mar 00	26 Mar 00	10 Apr 00	24 Apr 00
P3	8 May 00	22 May 00	5 Jun 00	19 Jun 00	3 Jul 00
P4	17 Jul 00	31 Jul 00	14 Aug 00	29 Aug 00	11 Sept 00

Year 3

PERIOD	Zone 1	Zones 2+4	Zones 3+5
P3-1	27 Nov 00	10 Dec 00	2 Jan 01
P3-2	15 Jan 01	29 Jan 01	12 Feb 01
P3-3	26 Feb 01	12 Mar 01	26 Mar 01
P3-4	9 Apr 01	24 Apr 01	8 May 01
P3-5	21 May 01	4 Jun 01	18 Jun 01
P3-6	2 Jul 01	16 Jul 01	30 Jul 01
P3-7	13 Aug 01	27 Aug 01	10 Sept 01

3.3 Summer studies on the effectiveness of controlling grey squirrels

To provide information on how effective the control trapping was, a series of additional studies were carried out in the summers of 2000 and 2001 in the central and eastern parts of the Control Area (see Appendix Map 1). These involved live trapping using tree mounted

traps, radiotracking studies on selected grey squirrels, and hair tube and feeding transect surveys in the vicinity of eight control compartments in Zone 3 before, during and after the control was carried out. Standard methods were used (see Gurnell & Pepper 1994; Gurnell *et al.*, 1997, Gurnell *et al.*, 2001a and Gurnell *et al.*, 2001b); details of the timetable of activities are given in Appendix Table A1.

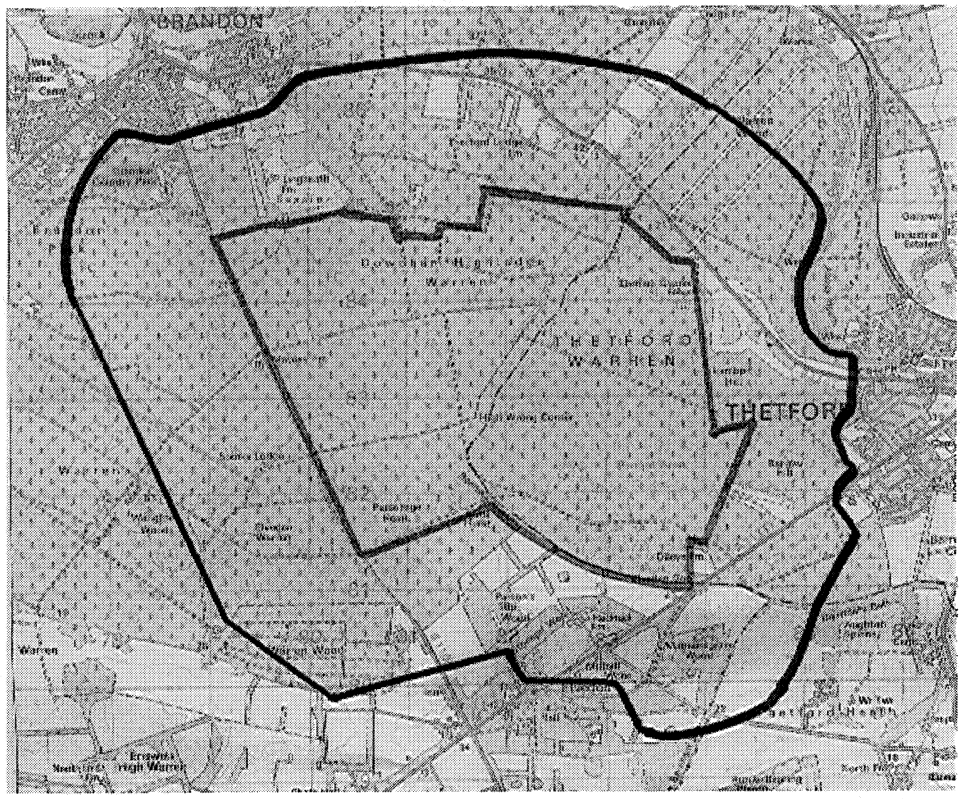


Figure 1 The control area

consisting of the Red Squirrel Reserve (red line) plus a 1.5km buffer zone (blue line)

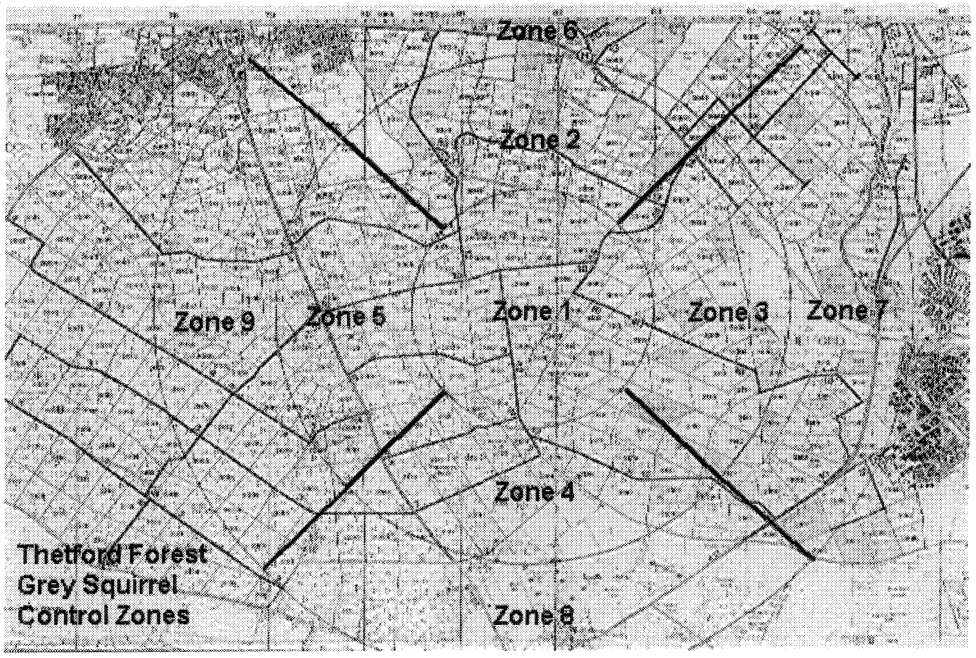


Figure 2 Thetford Control Zones

3.4 Data analysis

Data sets were tested for normality. If the data were normal, or could be normalised by transformation, parametric statistical tests have been used, otherwise non-parametric tests have been used. Statistical tests were carried out using the software packages *Minitab 13*, or *Xlstat*.

4. Results for 1998-01

4.1 Numbers removed

The total number of squirrels removed in each zone in each period and year is shown in Table 2; this includes grey squirrels trapped by both the CO and the RR. Slightly more squirrels were captured in Year 2 than Year 1 and substantially more in Year 3. Most squirrels were captured in Period 3 in Years 1 and 2 (April/May to June/July) and most in Period P3-1 (November to January) and P3-5 (May to June) in Year 3.

Relatively high and increasing numbers of squirrels were captured in the Inner Band (Zone 1) in each year (Table 2; Year 1 - 15% of total, Year 2 - 20%, Year 3 - 25%). Numbers captured in Zones 2-9 in each year (Zones 2-5 in Year 3) differed significantly from an expected uniform distribution (Table 3). Zones to the north (Zones 2 and 6) consistently captured fewer animals than expected whereas zones to the east (Zones 3 and 7) generally captured more. There was no clear pattern in capture success to the south (Zones 4 and 8) and west (Zones 6 and 9).

Considering the bands irrespective of zone, there was an association between numbers trapped in Inner and Middle Bands, and year (Table 4). Numbers trapped in Year 1 were similar to expected, but more squirrels were caught in the Inner Band in Year 2 and fewer in Year 3. The distribution of captures will be considered in more detail below.

4.2 Trapping Efficiency

4.2.1 Number of grey squirrels captured in each trap round

The effectiveness of the removal trapping programme within a trap week will be reflected by the number of squirrels trapped during each trap round. If trapping is efficient, it will be expected that few, or no squirrels will be captured towards the end of the week. Some grey squirrels were still being captured at the end of the trapping week in Years 1 and 3; this was less clear cut in Year 2, and may have been because not all traps were set for the full week (Figure 3). This was consistent across bands. The zigzag appearance to the plots of numbers trapped against trap round (Figure 3) relates to whether odd numbered rounds were carried out in the morning or evening (see Section C). More squirrels are trapped in the morning than the evening rounds, and the latter is dependent on the time the traps were checked in the morning.

Table 2 Numbers of grey squirrels removed in each zone and each period

a. Numbers of grey squirrels removed in each zone and each period in Years 1 and 2
Period 1 = November to January/February, Period 2 = February to April, Period 3 = April to June (Year 1) or May to July (Year 2), Period 4 = July to September.

			Period				
Year 1	**Band**	**Zone**	**1**	**2**	**3**	**4**	**Total**
1	1	1	41	26	33	5	105
	2	2	5	14	16	4	39
		3	34	18	38	0	90
		4	25	27	49	1	102
		5	22	6	20	0	48
	3	6	29	21	12	3	65
		7	23	19	27	2	71
		8	4	31	49	4	88
		9	7	21	52	0	80
		Total	190	183	296	19	688
2	1	1	28	16	37	62	143
	2	2	11	9	17	2	39
		3	18	14	33	20	85
		4	3	3	11	12	29
		5	10	3	22	2	37
	3	6	17	17	32	3	69
		7	20	10	51	1	82
		8	8	43	32	3	86
		9	16	58	57	15	146
		Total	131	173	292	120	716

b. Numbers of grey squirrels removed in each zone and each period in Year 3
Period 3-1 = November to January, Period 3-2 = January to February, Period 3-3 = February to March, Period 3-4 = April-May, Period 3-5 = May to June, Period 3-6 = July, Period 6-7 = August to September.

		Period							
Band	**Zone**	**P3-1**	**P3-2**	**P3-3**	**P3-4**	**P3-5**	**P3-6**	**P3-7**	**Total**
1	1	46	27	18	14	85	25	10	225
2	2	24	7	22	17	12	2	7	91
	3	45	28	60	49	28	30	41	281
	4	41	10	25	17	30	5	5	133
	5	21	4	11	8	21	5	5	75
	Total	177	76	136	105	176	67	68	805

Table 3 Distribution of captures according to Zone

X^2 statistics test whether the distribution of captures was different from a uniform distribution. (a) individual Zones, (b) concentric Zones pooled together (Years 1 and 2). Negative numbers indicate captures lower and positive numbers, higher than expected. Yellow nos. on a red background = P <0.001 for X^2 cell values, red nos. on a yellow background P<0.01, bold nos. P<0.05.

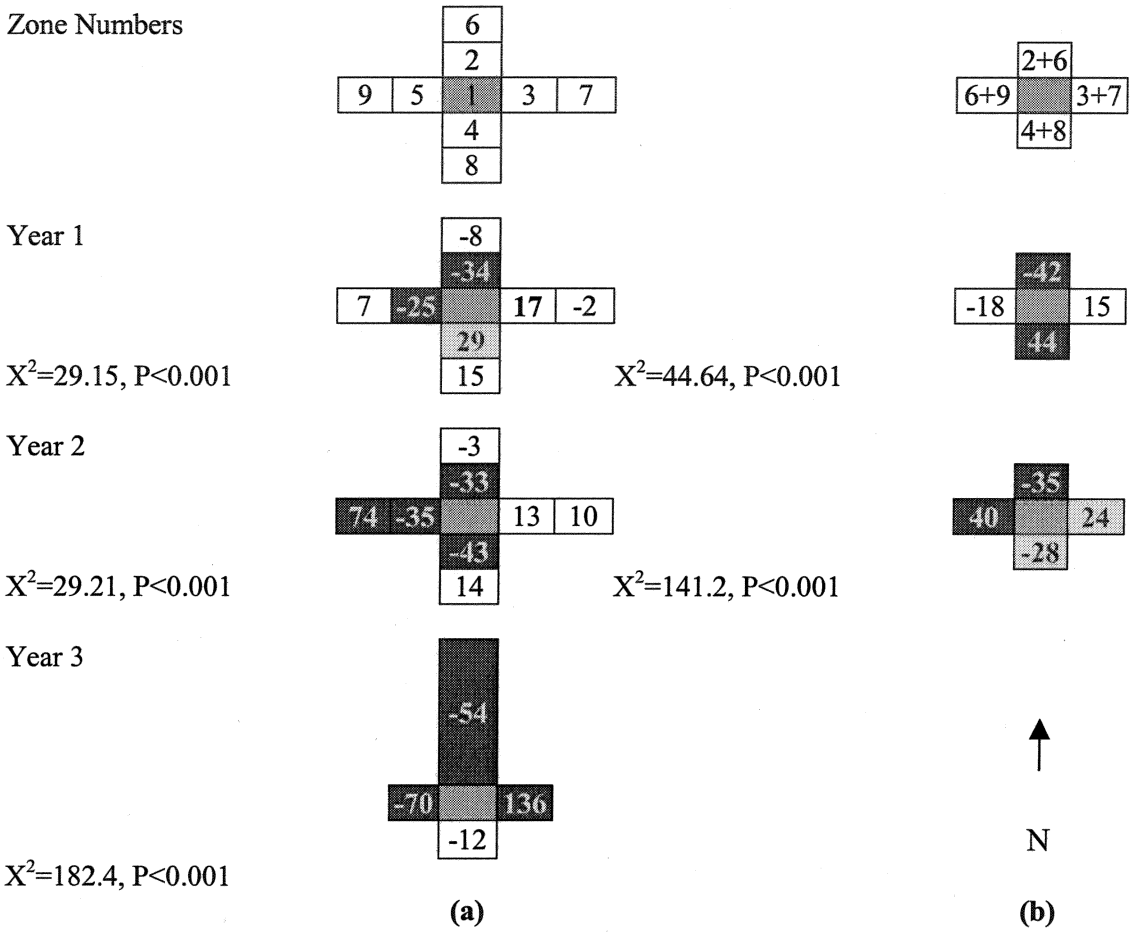


Table 4 Observed and Expected (in brackets) numbers of grey squirrels captured in Bands 1 and 2 in each Year

X^2_2 for independence of Band and Year = 28.06, P<0.001.** = significant difference between observed and expected for that cell, P<0.01.

	Inner Band	Middle Band
Year 1	105 (119)	279 (264)
Year 2	143 (103) **	190 (230) **
Year 3	225 (250) **	580 (554) **

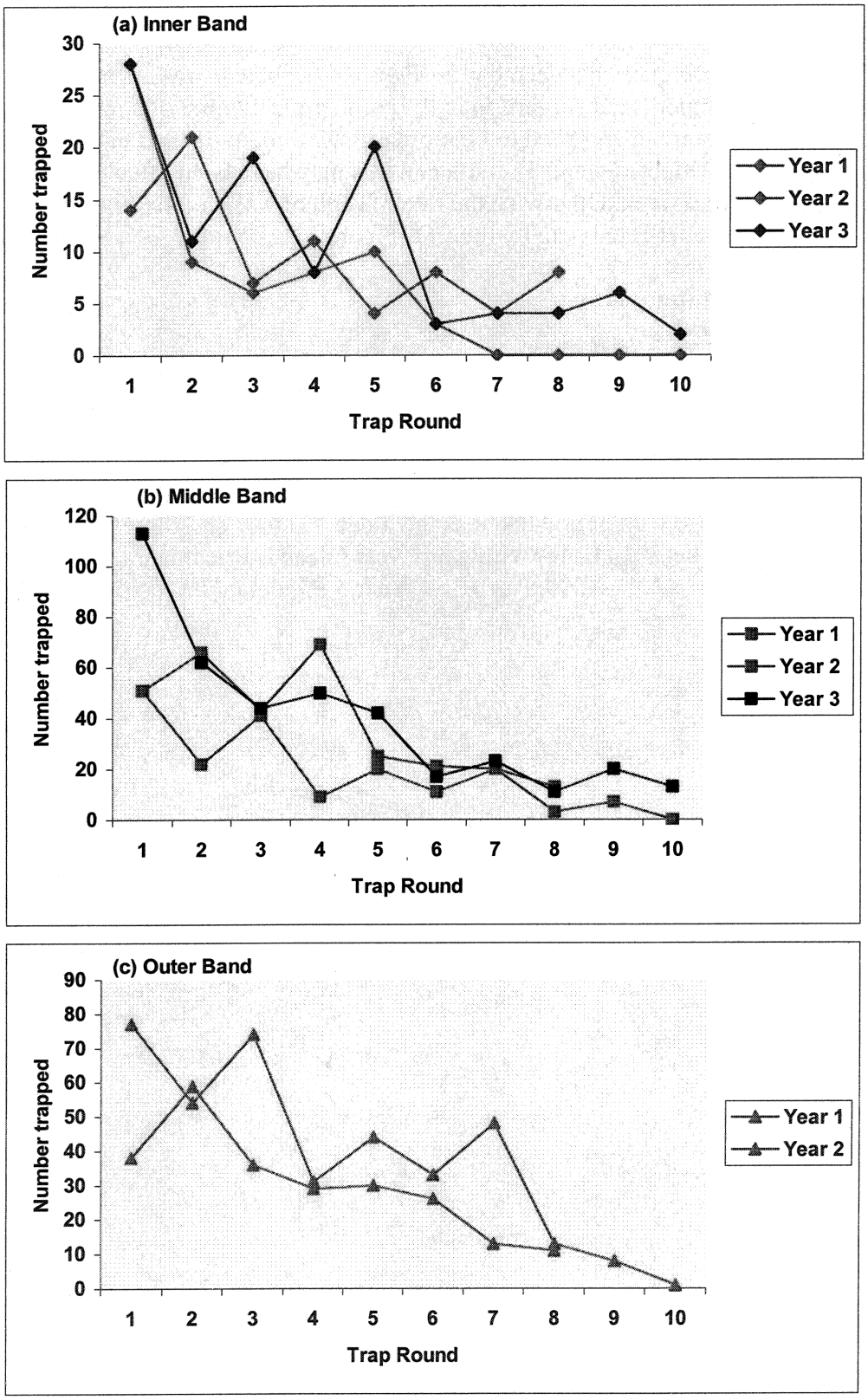


Figure 3 **The number of squirrels trapped in each round in each Band in each Year**

4.2.2 Cumulative number of squirrels captured in each trap round

There are few clear differences between bands (Figure 4) or between years and who carried out the control in the Inner Band (Figure 5) in the cumulative number of squirrels captured during a trap week. Trapping appeared to be more efficient in the Inner Band in Year 2 as carried out by the CO (Figures 4 and 5), but again this may have been affected by not trapping for the full trap week. Otherwise the rate of capture was slightly higher as carried out by the RR, in the Inner Band than by the CO (Figure 5).

4.3 Control Efficiency

To standardise for slight variations in trapping effort between periods and years, and because of the increased control effort in the Inner Band (Zone 1), the number of captures trap-round^{-1} band^{-1} has been examined (Table5, Figure 6). To test whether there was a significant difference in return on control effort between each band within each year, the mean numbers of captures trap-round^{-1} band^{-1} have been analysed using Friedman's non-parametric randomised block anova, with period taken as the block (Figure 7). There were no significant differences between bands within any year (Year 1, Friedman's $X^2_2 = 1.5$, P = 0.472, Year 2 Friedman's $X^2_2 = 2.00$, P = 0.368, Year 3 Friedman's $X^2_1 = 1.29$, P = 0.257).

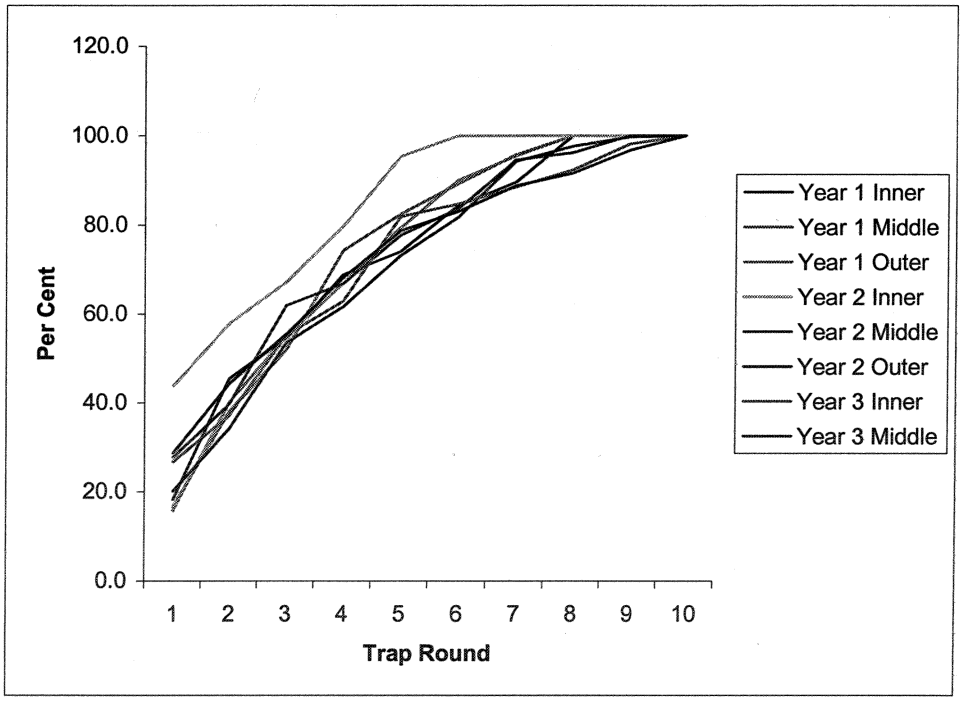


Figure 4 Cumulative per cent of total captures of grey squirrels captured by the Control Officer (CO) during the trap week each year in the Inner, Middle and Outer Band

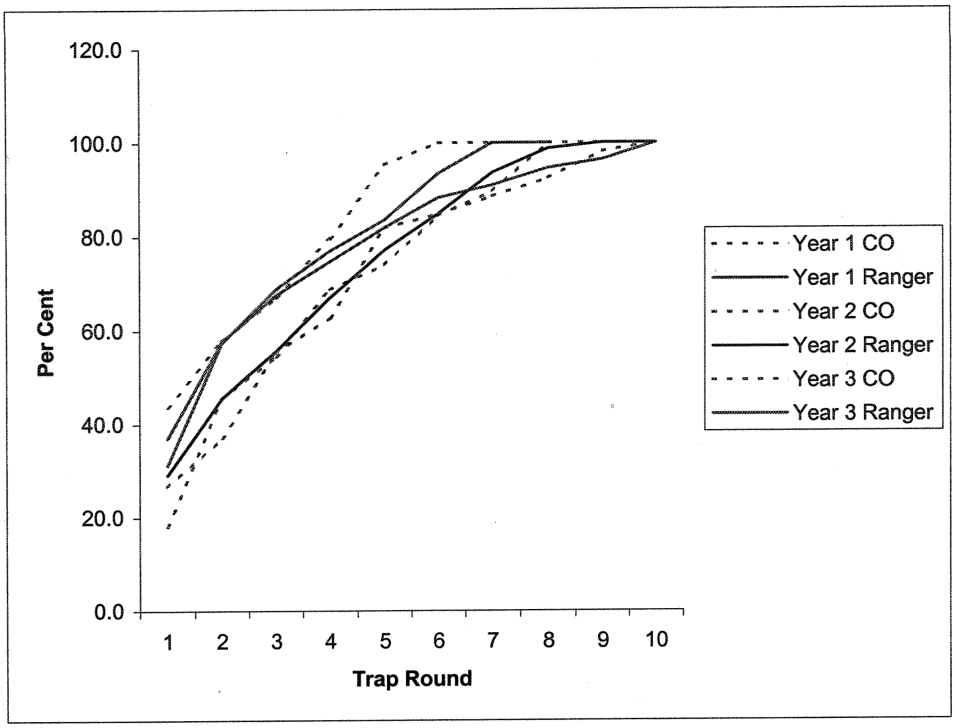


Figure 5 **Cumulative per cent of total captures of grey squirrels captured during the trap week each year in the Inner Band by the Control Officer (CO) and the Ranger**

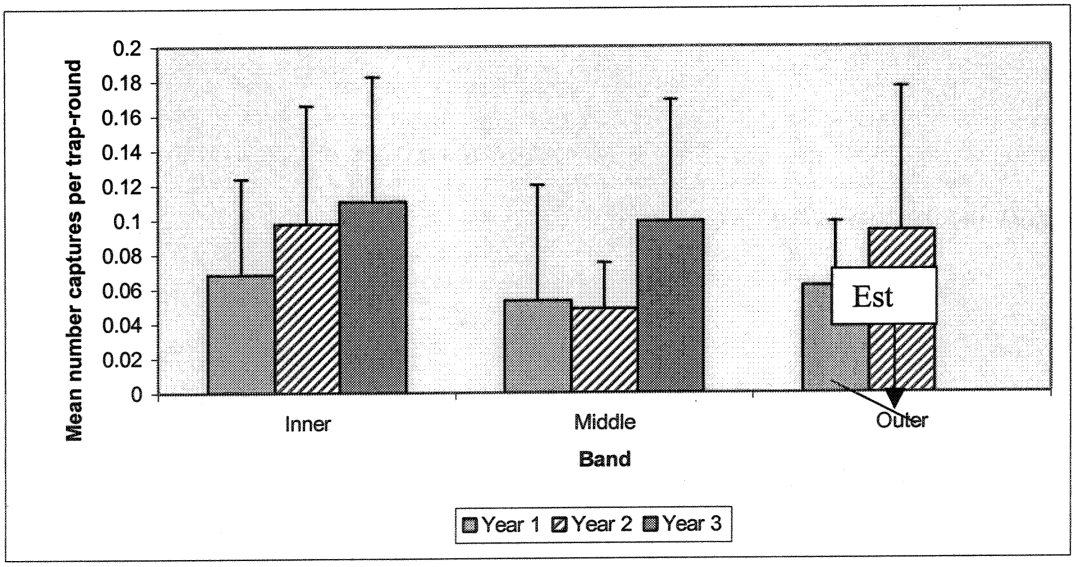
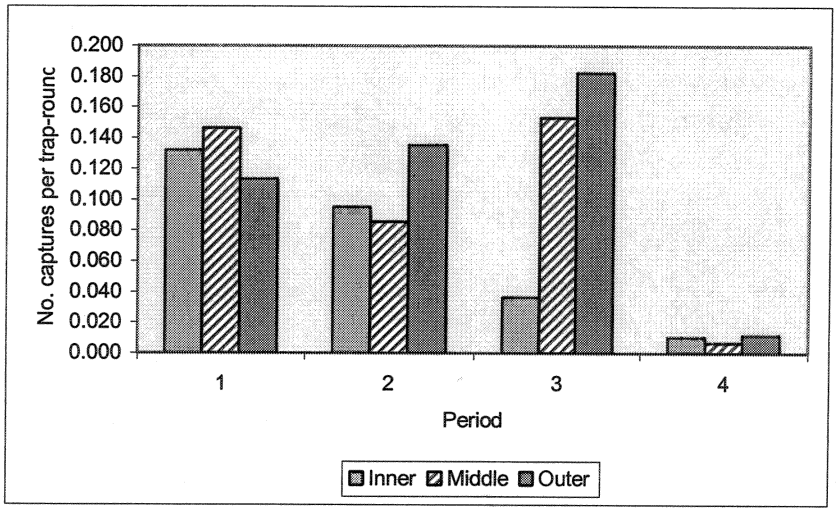
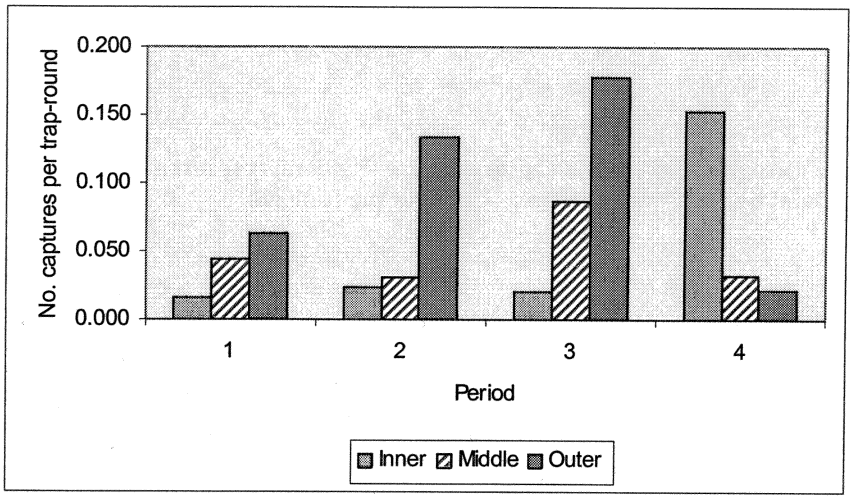


Figure 6 **Mean number of animals captured per trap-round by the CO according to Year and Band (+ 1 stdev.)**

(a) Year 1



(b) Year 2



(c) Year 3

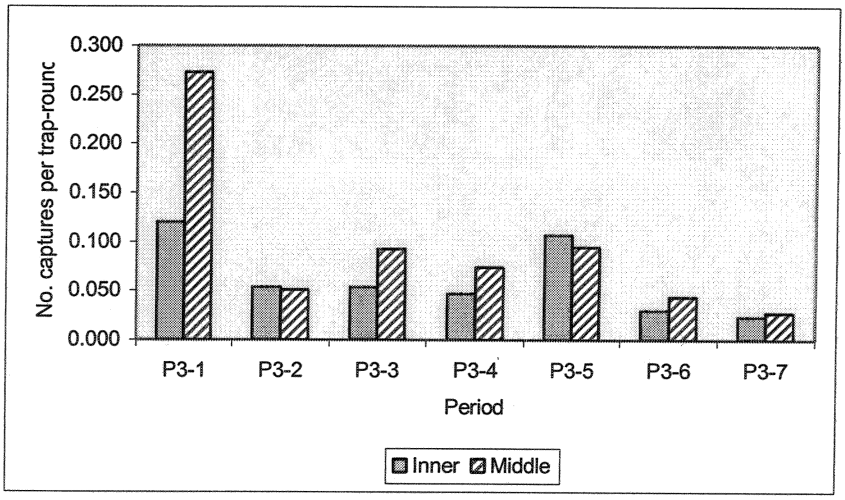


Figure 7 Number captured per trap-round by the Control Operator (CO) in each Band for each Period in each Year

However, if the data are examined according to period, some differences become evident. The return from the Inner Band in Year 1 declined from Period 1 to Period 3 (Figure 7; few animals were captured in Period 4). This was expected if the control was having an effect. However, the return from the Inner Band in Year 2 was consistently low during the first three periods compared with the other bands and increased markedly in Period 4. In contrast, the return increased in the Outer Band during the first three periods, then dropped in Period 4. In Year 3 where the year was divided into seven periods, no particular trend was apparent, although the return was lowest in the last two periods. No trend is apparent in the return from the Middle Band in any year. These data have been examined in one further way by calculating the ratio between the return in the Inner and the Middle Bands in each period in each Year (Figure 8). If the control was being efficient, this ratio should decline with time. There was a slight decline between Periods 2 and 3 in Years 1 and 2, but thereafter there was an increase to Period 4. No trend is apparent across the seven periods in Year 3.

4.4 Numbers of captures according to tree species and age in control compartments

Although the control compartments were selected to maximise the return on effort, there was some variation in numbers captured according to compartment tree species and age (Table 6). Mixed conifer and Corsican pine sub-compartments were general good with the exception of one CP compartment 61-70 years old. In contrast, SP compartments were generally less successful. Some of these compartments were very open with a lot of field vegetation (particularly bracken), and probably accounts for this. These findings are difficult to disentangle from the effects of the geographical position of each compartment within the control area in relation to the nature of surrounding compartments and immigration routes.

Table 5 Number of squirrels captured per trap-round in each band and zone for each period in each year

Period 1 = November to January/February, Period 2 = February to April, Period 3 = April to June (Year 1) or May to July (Year 2), Period 4 = July to September. Period 3-1 = November to January, Period 3-2 = January to February, Period 3-3 = February to March, Period 3-4 = April-May, Period 3-5 = May to June, Period 3-6 = July, Period 6-7 = August to September

(a) Year 1

		Period			
Band	**Zone**	**1**	**2**	**3**	**4**
1	1	0.132	0.095	0.036	0.010
2	2	0.042	0.083	0.083	0.021
	3	0.283	0.107	0.198	0
	4	0.130	0.116	0.227	0.005
	5	0.131	0.036	0.104	0
3	6	0.201	0.146	0.063	0.016
	7	0.137	0.099	0.141	0.010
	8	0.056	0.172	0.255	0.021
	9	0.058	0.125	0.271	0

(b) Year 2

		Period			
Band	**Zone**	**1**	**2**	**3**	**4**
1	1	0.017	0.023	0.02	0.153
2	2	0.046	0.038	0.071	0.008
	3	0.075	0.058	0.138	0.063
	4	0.013	0.013	0.046	0.050
	5	0.042	0.013	0.096	0.008
3	6	0.071	0.071	0.133	0.013
	7	0.083	0.042	0.208	0.004
	8	0.033	0.179	0.133	0.013
	9	0.067	0.242	0.238	0.058

(c) Year 3

		Period						
Band	**Zone**	**P3-1**	**P3-2**	**P3-3**	**P3-4**	**P3-5**	**P3-6**	**P3-7**
1	1	0.120	0.053	0.053	0.047	0.107	0.03	0.023
2	2	0.200	0.029	0.092	0.071	0.050	0.008	0.029
	3	0.375	0.117	0.129	0.121	0.117	0.125	0.038
	4	0.342	0.042	0.104	0.071	0.125	0.021	0.021
	5	0.175	0.017	0.046	0.033	0.088	0.021	0.021

Table 6 The number of sub-compartments trapped according to tree species and age

with the mean catch per control year underneath. BE = beech, DF = Douglas fir, OK = oak, SP = Scots pine, CD = conifers dominant, CP = Corsican pine, MB = mixed broadleaves, MC = mixed conifers.

				Age (years)				Tree Species
Tree Species Code	**<=20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**>70**	**Average**
BE/DF/OK/SP						1		
						17.5		17.5
CD							1.0	
							11.5	11.5
CP	3	8	13	3	1	1	3	
	6.9	11.9	11.5	14.5	12.5	1.0	11.5	11.1
CP/SP						2		
						4.0		4.0
MB					2		1	
					7.7		6.0	7.1
MC		3	9	1	2		18	
		4.9	12.9	16.0	7.5		13.3	12.2
SP			1		1	1	11	
			8.5		2.0	4.0	3.0	3.4
SP/DF		1						
		7.5						7.5

4.5 Food supplies within the control area 1998-2001

As part of the ongoing studies on squirrel ecology within Thetford, cone feeding transects lines in Zones 1 and 3 were monitored throughout the control study; the methods have been described elsewhere (Gurnell *et al.*, 1997; Gurnell *et al.*, 2001). Feeding was moderate from

1998 through to the autumn of 1999. Thereafter feeding was very high during 2000 and still high during 2001 suggesting food supplies were good in these years (Figure 9). Although there were few broadleaf trees within the control area, only a small number of squirrels was trapped in Period 4 Year 1, this may have been partly attributable to a good broadleaf seed crop in the autumn of 1999 (but see Discussion).

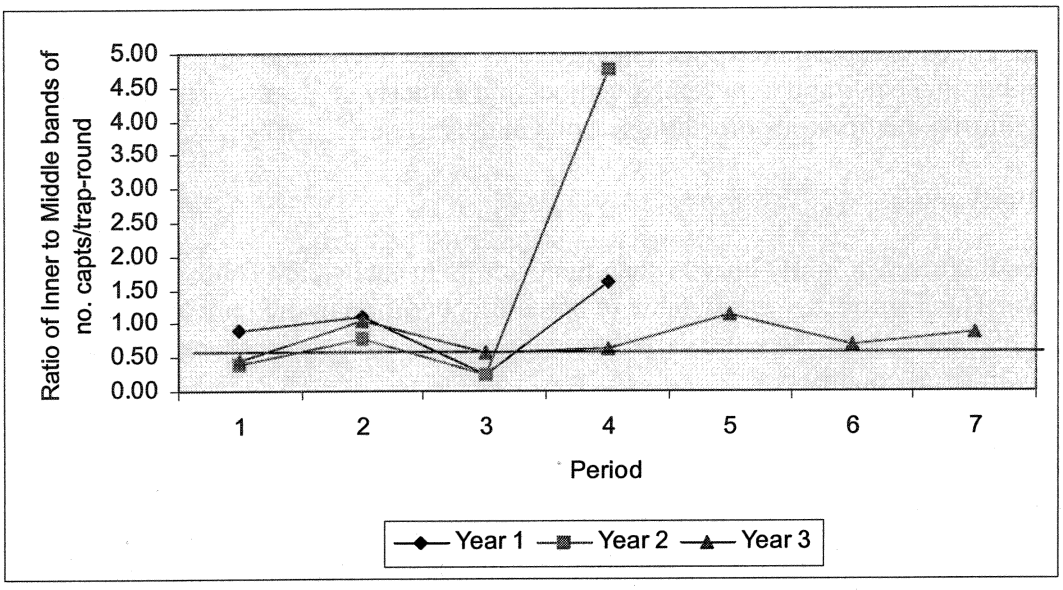


Figure 8 Ratio of mean number of squirrels captured per trap-round by the CO in Inner and Middle Bands according to Year

For Years 1 and 2, Period 1 = November to January/February, Period 2 = February to April, Period 3 = April to June (Year 1) or May to July (Year 2), Period 4 = July to September. Periods 1 to 7 in Year 3 = Periods P3-1 to P3-7 respectively. Period 3-1 = November to January, Period 3-2 = January to February, Period 3-3 = February to March, Period 3-4 = April-May, Period 3-5 = May to June, Period 3-6 = July, Period 6-7 = August to September.

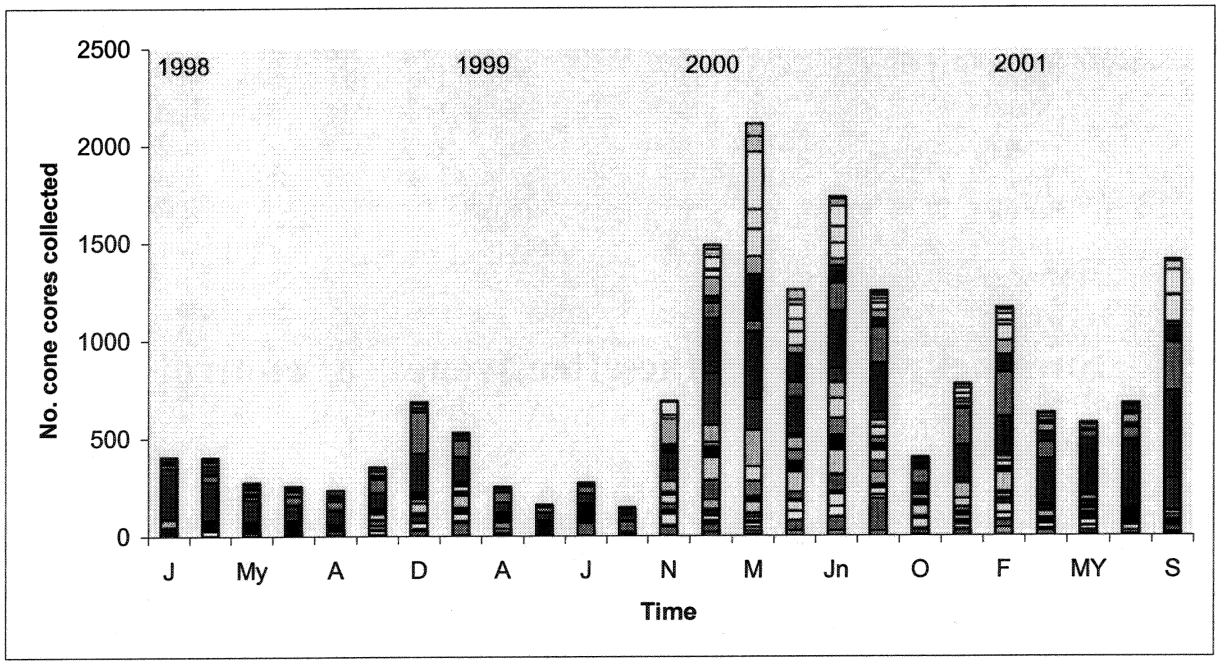


Figure 9 The numbers of cone cores removed from feeding transects between 1998 and 2001

The colours refer to different feeding transects (n=22). The transects were in Zones 1 (n=10) and 3 (n=12).

4.6 Population demography

4.6.1 Sex ratio and population structure

Slightly more adult males than adult females were captured in all three years (Year 1 55% males, $X^2_1 = 6.32$ P = 0.0120, Year 2 59% males $X^2_1 = 14.30$ P = 0.0002, Year 3 54% males $X^2_1 = 3.34$ P = 0.0678. The structure of the populations in each year is shown in Figure 10. Juveniles tended to be captured between April and September, although some were captured in December in Year 1 and between November and January in Year 3. This suggests late breeding during the previous breeding seasons in these years.

4.6.2 Body mass

Females adults were slightly heavier than male adults in each year (Table 7; $F_{5,1415} = 21.09$, $P<0.001$). This is probably attributable to breeding condition in the females; females were heaviest in Year 1. However, the variation in body mass was not large and the squirrels were generally in good condition.

4.6.3 Breeding

The proportion of adult males and females breeding in each period is shown in Figure 11. Males averaged 67% per period with medium or large testes throughout the study. However, large testes do not indicate that the males are fecund, and a better definition of breeding is given by the incidence of pregnant and/or lactating females. On average, 24% of adult females were breeding in every period and there were peaks in spring in Years 1 and 3 and in summer in Year 2.

Table 7 Mean adult body weights for each sex and each band in each year

Year	Sex	Band 1			Band 2			Band 3				
		n	mean	stdev	n	mean	stdev	n	mean	stdev	F	P
1	Female	41	566	56.7	110	567	51.6	106	556	53.6	1.12	0.327
	Male	39	527	44.0	125	521	55.0	148	518	50.1	0.53	0.591
2	Female	25	531	47.0	50	548	50.3	100	544	52.6	0.89	0.414
	Male	47	504	31.6	61	503	47.9	129	521	46.1	4.99	0.008
3	Female	79	527	46.0	202	541	45.1				5.39	0.021
	Male	92	512	41.6	234	534	43.0				17.13	<0.001

5. Summer studies on the effectiveness of control

5.1 Trapping

Trapping success was better before the control period than during or after in the summer 2000 study (Table 8). None of the squirrels captured during the removal were tagged or radio-collared. In the trap period after the control, six were tagged and three were radio-collared. In summer 2001, trapping success increased slightly during the study (Table 8). Only two tagged and one radio-collared squirrel were captured during the control period, but eight tagged and five radio-collared squirrels were captured after the control period. Clearly the control trapping each summer was only catching a relatively small proportion of the squirrels living in the area at that time.

Table 8 Trapping success before, during and after control in Zone 3 during the summers of 2000 and 2001

The 'During Control' was carried out in the standard way by the CO. Squirrels were tagged and released in the Before trapping studies; they were removed in the After trapping studies.

Time	Individuals Captured	Before	During Control	After
Summer 2000	No. squirrels caught	27	14	14
	No. caught per trap-round	0.1222	0.0583	0.0519
Summer 2001	No. squirrels caught	25	26	32
	No. caught per trap-round	0.089	0.108	0.119

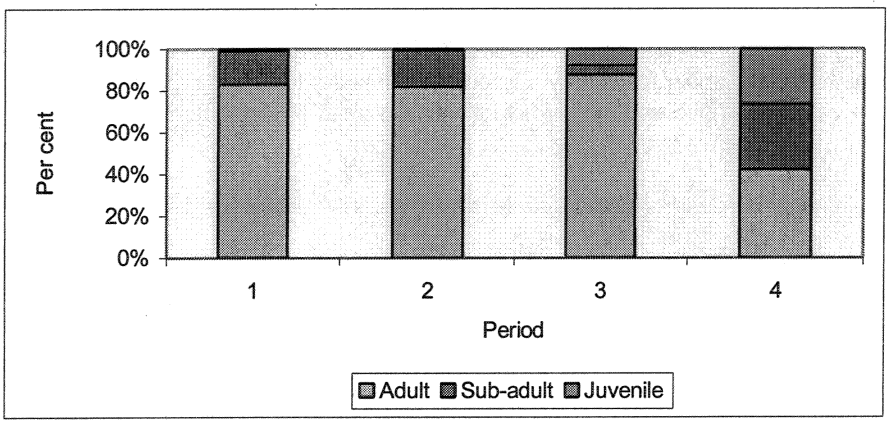
5.2 Hair Tubes

The proportion of tubes visited in each grid by grey squirrels was high in all periods in both years (mean number visited = 82%, n = 24, stdev. = 17.6%) (Figures, 12 and 13). There was no significant difference among Before, During and After in 2000 ($F_{2,15}$= 0.30, P = 0.772), and, although only two grids of tubes were used in 2001, there was no obvious difference between them.

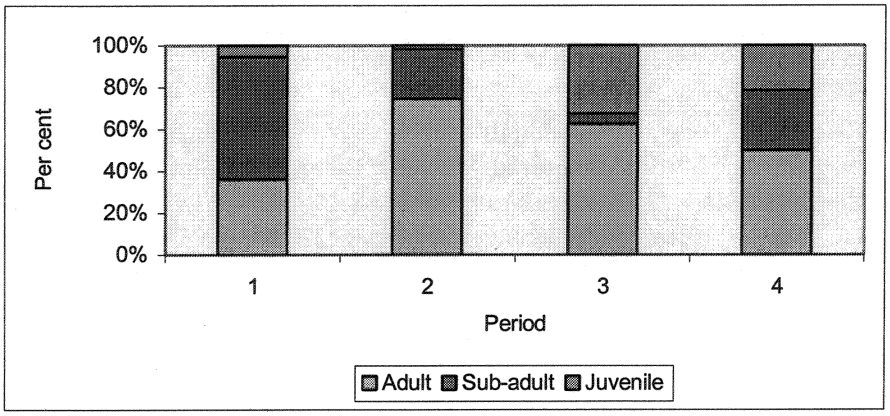
5.3 Cone feeding

There was a large amount of variation in the number of cones eaten among transect lines (in 2000, mean = 16 cones line^{-1}, Coefficient of Variation = 202%, n = 30; in 2001, mean = 18 cones line^{-1}, CV = 192%, n = 30). Nevertheless there was a significant reduction in the mean number of cones eaten in 2000 (Figure 14; randomised block anova on log transformed data, with line = block, $F_{2,18}$ = 9.1, P = 0.002), but not in 2001 (Figure 15; randomised block anova on log (x+1) transformed data, with line = block, $F_{2,18}$= 1.5, P = 0.24). Thus, there is some evidence from the feeding studies that grey squirrels were reduced in number by the control in 2000, but not 2001.

(a) Year 1



(b) Year 2



(c) Year 3

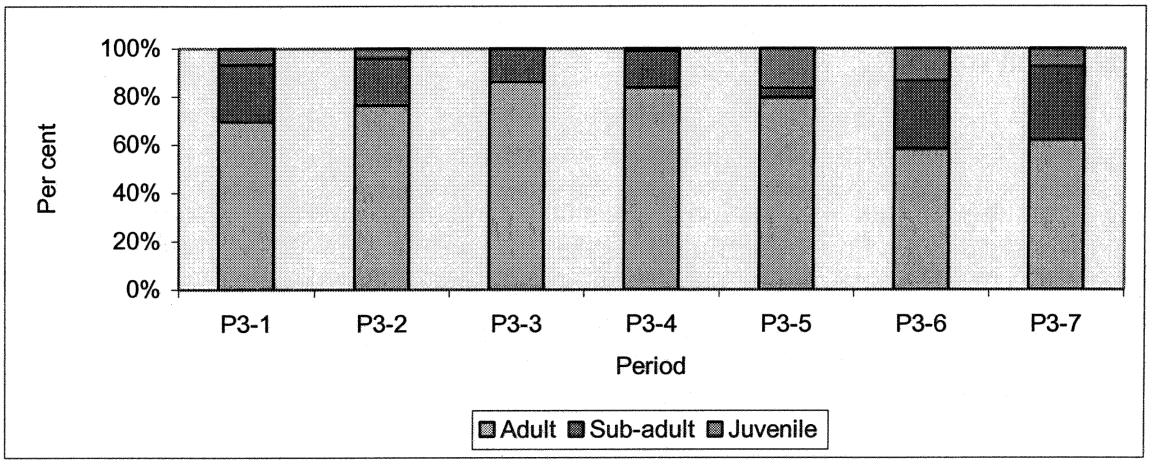
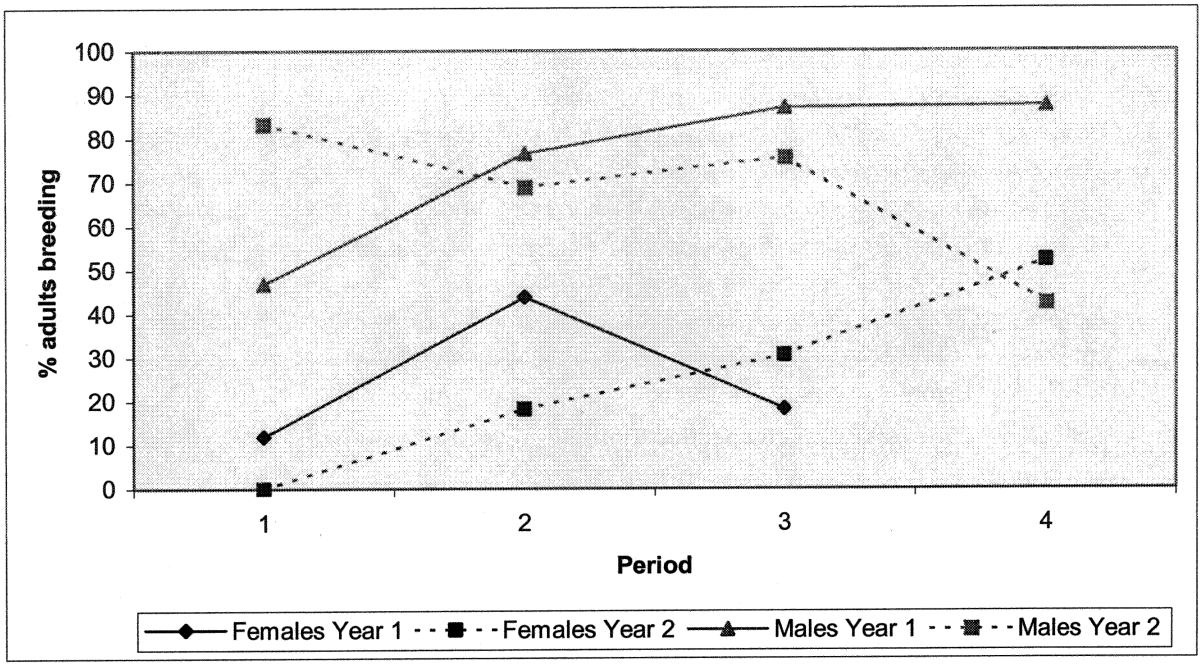


Figure 10 Number of adults, subadults and juveniles captured each Period in each Year

The % figures above the bars refer to the per cent SA of the Total. Period 1 = November to January/February, Period 2 = February to April, Period 3 = April to June (Year 1) or May to July (Year 2), Period 4 = July to September. Period 3-1 = November to January, Period 3-2 = January to February, Period 3-3 = February to March, Period 3-4 = April-May, Period 3-5 = May to June, Period 3-6 = July, Period 6-7 = August to September.

(a) Years 1 and 2



(b) Year 3

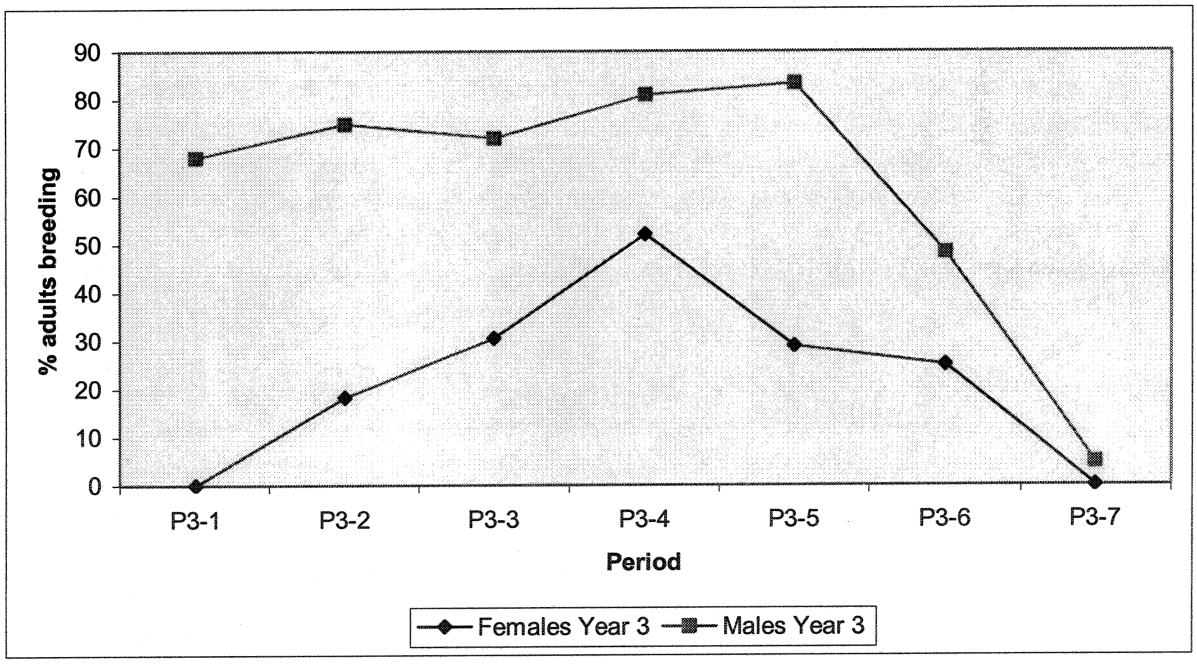


Figure 11 Percent of adult males (medium or large testes) and females breeding (pregnant or lactating) according to Year and Period

No females were captured in Period 4 Year 1. Period 1 = November to January/February, Period 2 = February to April, Period 3 = April to June (Year 1) or May to July (Year 2), Period 4 = July to September. Period 3-1 = November to January, Period 3-2 = January to February, Period 3-3 = February to March, Period 3-4 = April-May, Period 3-5 = May to June, Period 3-6 = July, Period 6-7 = August to September.

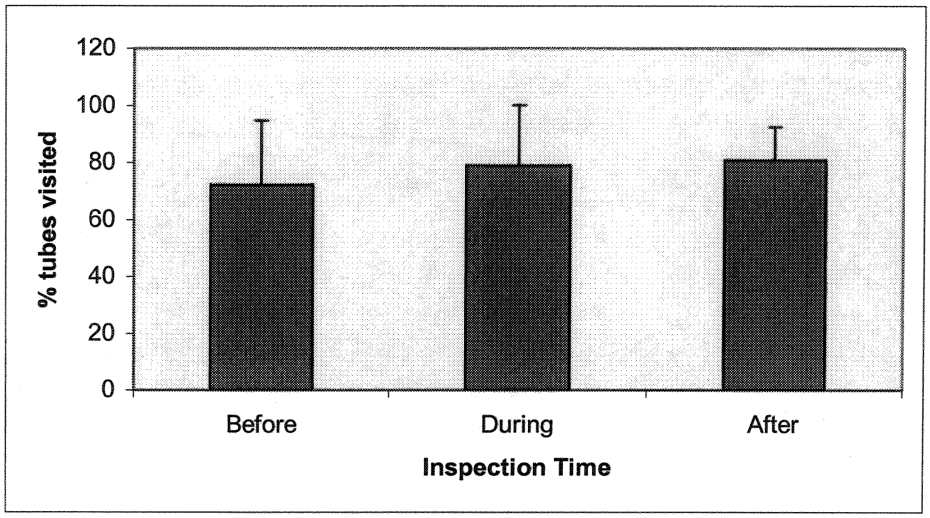


Figure 12 Mean per cent of hair tubes visited before, during and after the control carried out in Summer 2000 (+ 1 stdev)

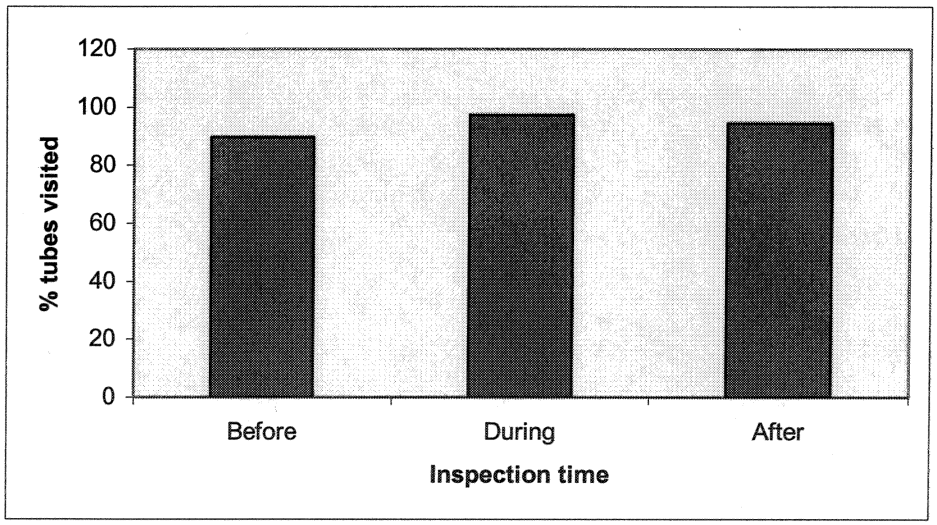


Figure 13 Mean per cent of hair tubes visited before, during and after the control carried out in Summer 2000

(Only two grids of tubes used.)

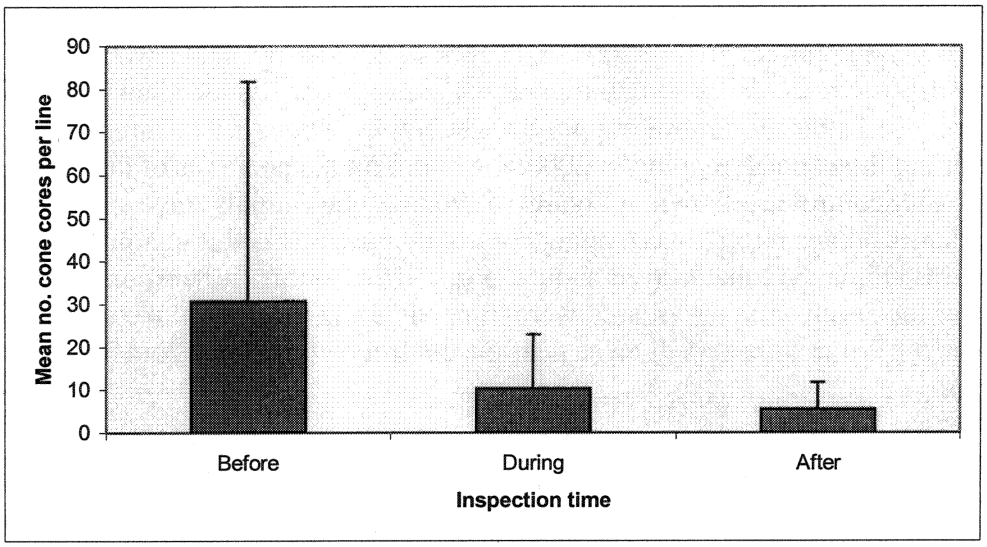


Figure 14 Mean number of cone cores collected per line before, during and after the control carried out in Summer 2000 (+ 1 stdev)

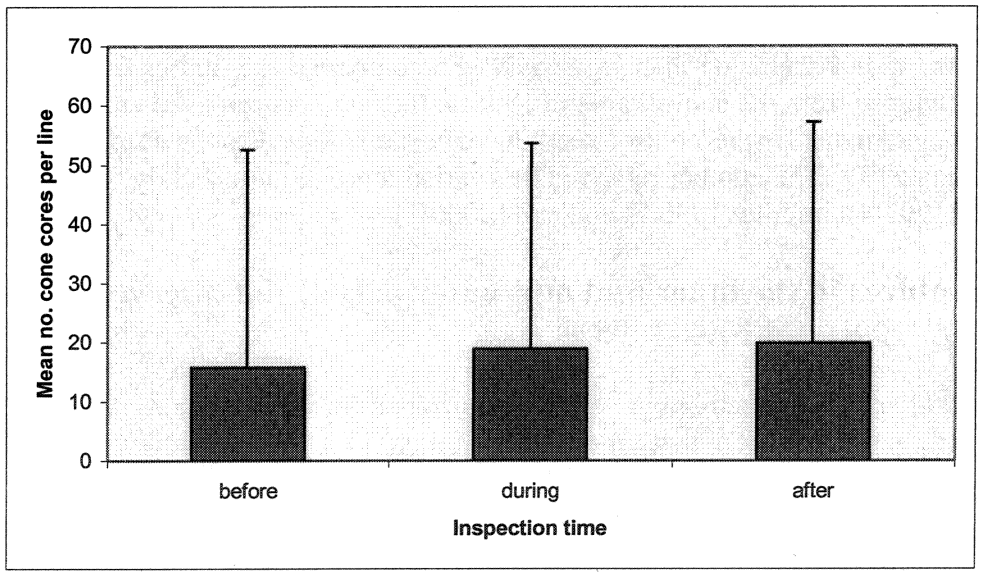


Figure 15 Mean number of cone cores collected per line before, during and after the control carried out in Summer 2001 (+ 1 stdev)

5.4 Radiotracking studies

Six squirrels were radio-collared in 2000 and seven in 2001. The studies were not designed to accurately measure home range size, but to reveal the approximate locations of the animals before, during and after the control trapping week. None of the radio-collared squirrels were captured during the control trapping in 2000; the approximate positions of the animals before, during and after control are shown in Figure 16. Most of the animals stayed within a small area with ranges adjacent to or overlapping control compartments throughout the study. The exception was animal 862 that moved about 1.5 km to the south after the control week. In 2001, one of the seven animals collared were trapped during the control week; as before the others remained within quite small areas near the control compartments but avoided capture (Figure 17).

6. A comparison of the 1998-01 results with grey squirrel removal between 1992 and 1998

6.1 Yearly trends 1993-2001

Before the Control programme began in November 1998, grey squirrels had been controlled within the Reserve (ie approximately in the area of the Inner and Outer Bands) since September 1992. In the period proceeding this control study, numbers removed each year varied between 213 (1995) to 473 (1993) (Figure 18). Numbers removed were considerably higher between 1999 and 2001 than previously. To compare these figures from the Reserve directly with those from the control area in 1998-9, the numbers removed each year between November and August (ie the 'control year') have been expressed as the number removed per hectare (Figure 19). The number removed ha^{-1} varied throughout the study, with peaks at the beginning (1992/4), middle (1996/7) and end (2000/1).

6.2 Captures in the inner and mid-outer part of the reserve between 1992-1996 and 1997-1998

Between 1992 and 1996, the removal of grey squirrels from within the reserve was carried out by the Research Ranger at that time, Tim Venning. In 1997, and until the control study began in November 1998, the responsibility for grey squirrel control was taken over by the other FE Rangers whose beat included part of the Reserve. The RR continued to trap grey squirrels in the central part of the reserve. Here we look at the number of grey squirrels removed between 1992 and 1996, and between 1997 and 1998.

During both these periods, control was carried out in five sectors (A to F), with sector C being in the centre of the reserve (see Gurnell *et al.* 1997). Sector C falls entirely within Control Zone 1 and, although slightly smaller than Zone 1, it is interesting to look at how many squirrels were removed in Sector C (called the Inner Band) and the surrounding Sectors A, B, D and E, here called the Mid-outer Band to distinguish it from the Middle and Outer Band of the control area. The number of grey squirrels removed and the number caught trap-$round^{-1}$ in 1992-96 are shown in Figures 20 and 21 respectively. Two patterns are evident, numbers caught in Periods 2 and 3 were greater than in Periods 1 and 4, and the number caught trap-$round^{-1}$ were similar in the two zones.

The number of grey squirrels removed and the number caught trap-round^{-1} in 1997-8 are shown in Figures 22 and 23 respectively. In this analysis, the annual pattern of removal seen between 1992 and 1996 was not evident with periods 2 and 4 having the highest figures in the mid-outer band and periods 1 and 3 in the inner band (Figure 22). It is known that control was not carried out consistently across the reserve and throughout the year in 1997-98, with the western half of the reserve particularly being neglected. Moreover, because of the trapping carried out by the RR, the number of trap-rounds carried out in the inner band (1426) throughout the year was not much less that the control effort carried out in the rest of the reserve, ie the mid-outer zone (1632). The result of this is that the number of grey squirrels captured trap-round^{-1} was considerably lower in the Inner Band than the Mid-outer Band (Figure 23).

Since grey squirrel removal was not carried out efficiently in 1997-98, it is not a good year to use as a benchmark for the control carried out in the control area between 1998 and 2001. However, when we compare the three periods 1992-96 (reserve), 1997-98 (reserve) and 1998-99, 1999-2000, and 2000-2001 (control area) we find that the return for effort was much higher for 1992-1996 than the other two years, which were similar (using periods and bands as replicates, $F_{4,49} = 76.74$, $P < 0.001$) (Figure 24). This suggests that trapping was less efficient in all years after 1992-96, despite it being generally evident that control efficiency was poor in all years.

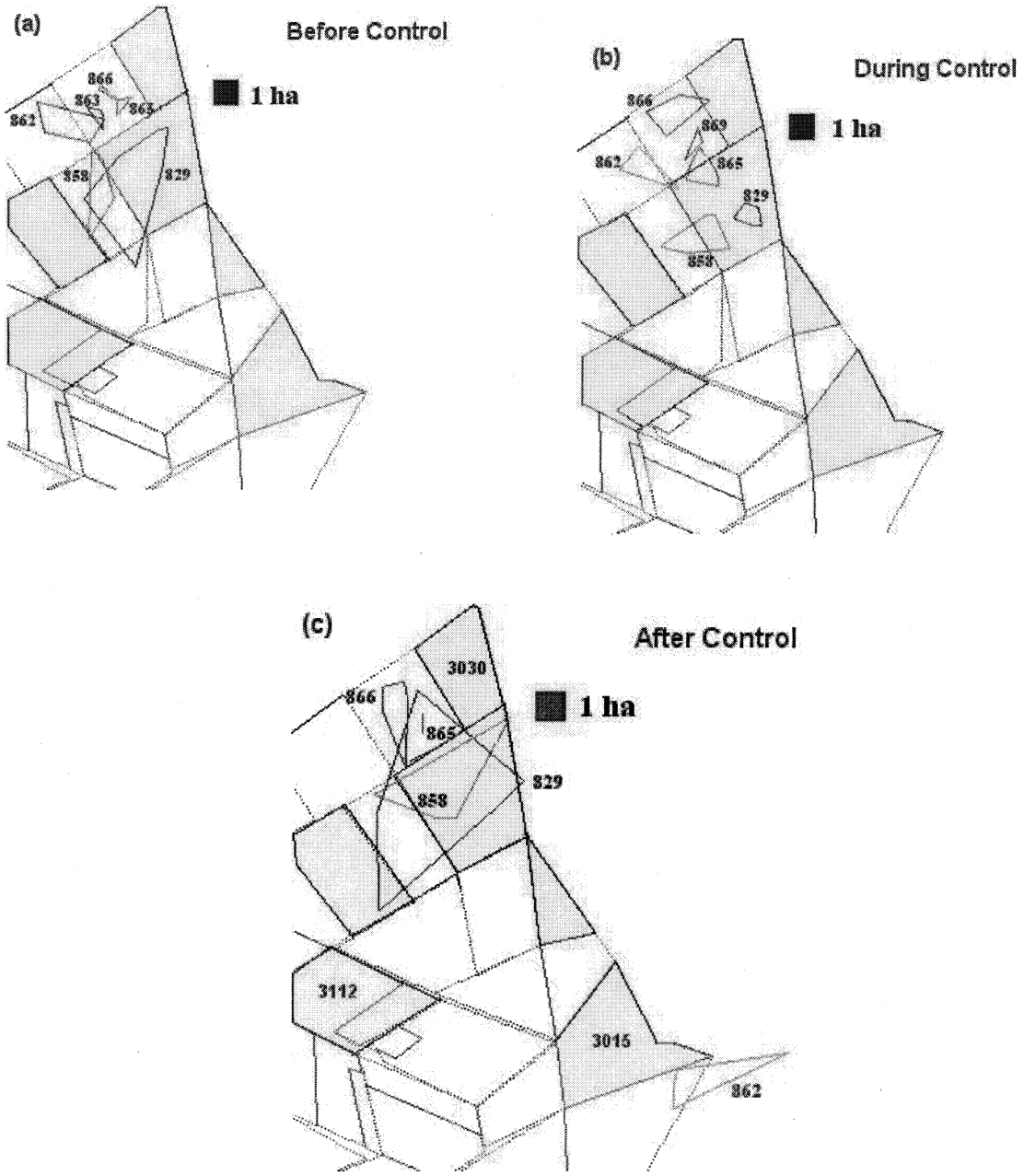


Figure 16 Minimum Convex Polygon areas for radio-collared grey squirrels before, during and after the control in 2000.

The yellow compartments are the control compartments. Three compartment numbers are given for reference in (c).

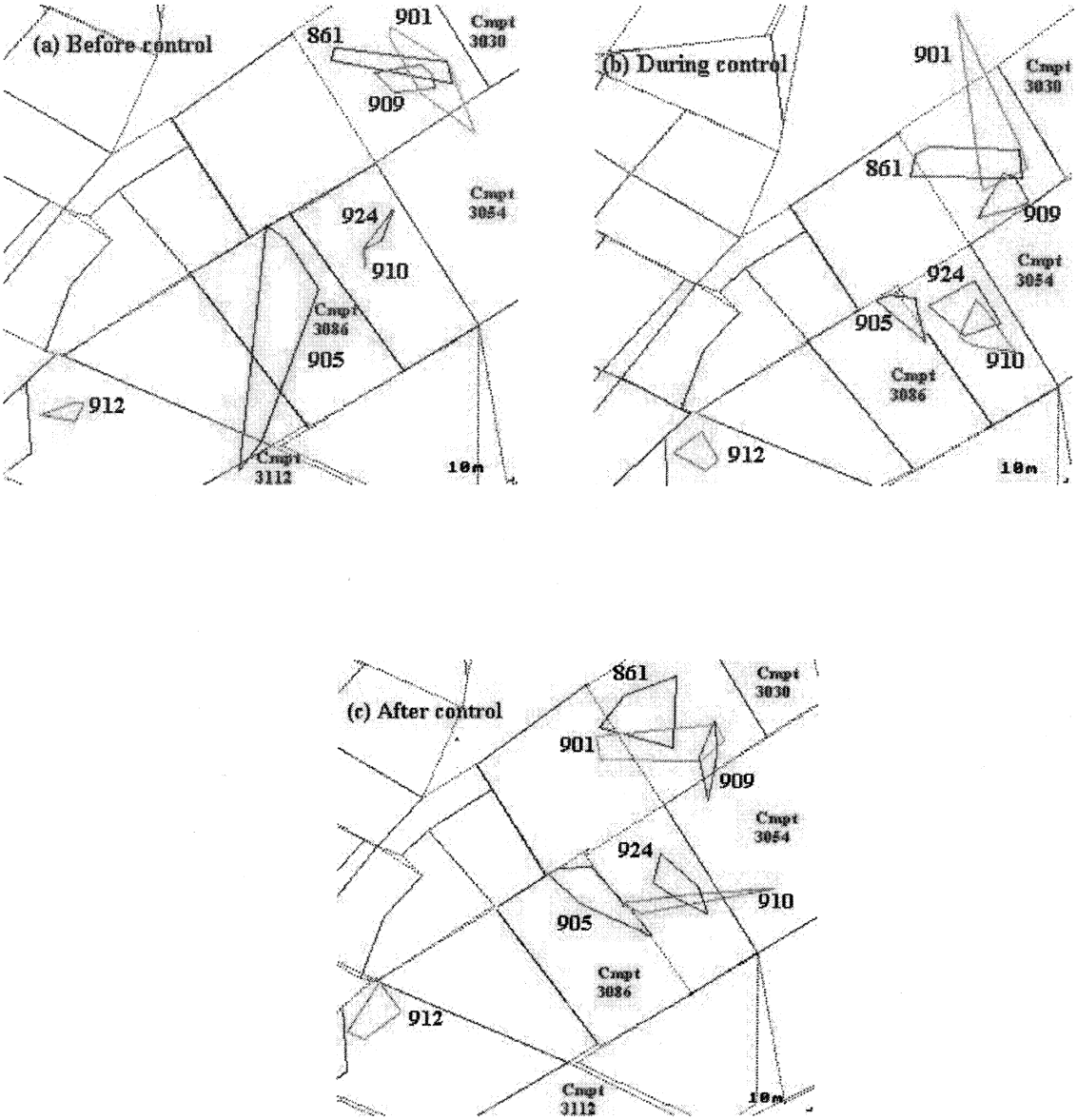


Figure 17 Minimum Convex Polygon areas for radio-collared grey squirrels before, during and after the control in 2001

Red numbered compartments are the control compartments. Animal 901 was captured twice in compartment 3054 during the control week, but was released each time rather than removed.

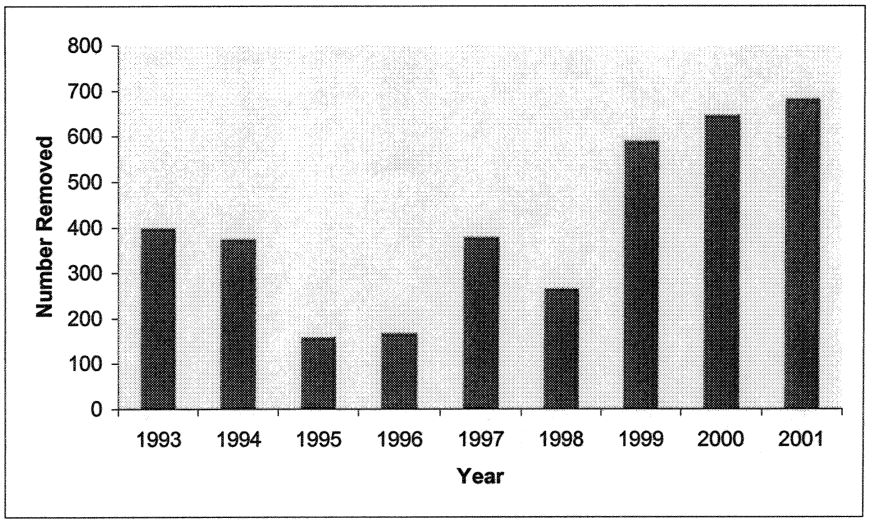


Figure 18 The number of grey squirrels removed each calendar year from the Red Squirrel reserve from 1993 to 2001

Since removal was stopped in October 1998, the 1998 figure has been adjusted by adding the mean number captured in November and December from 1993 to 1997.

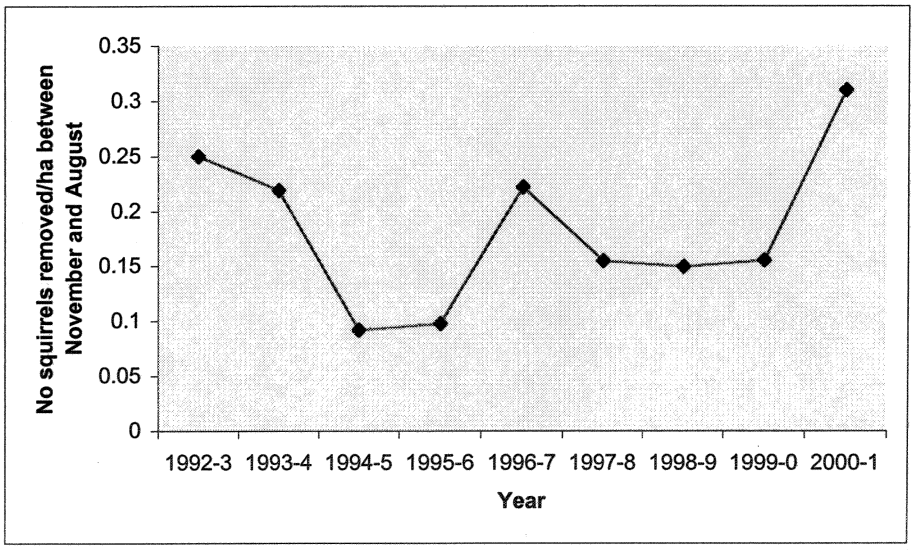


Figure 19 The number of grey squirrels removed ha-1 between November and August from 1992 to 2001

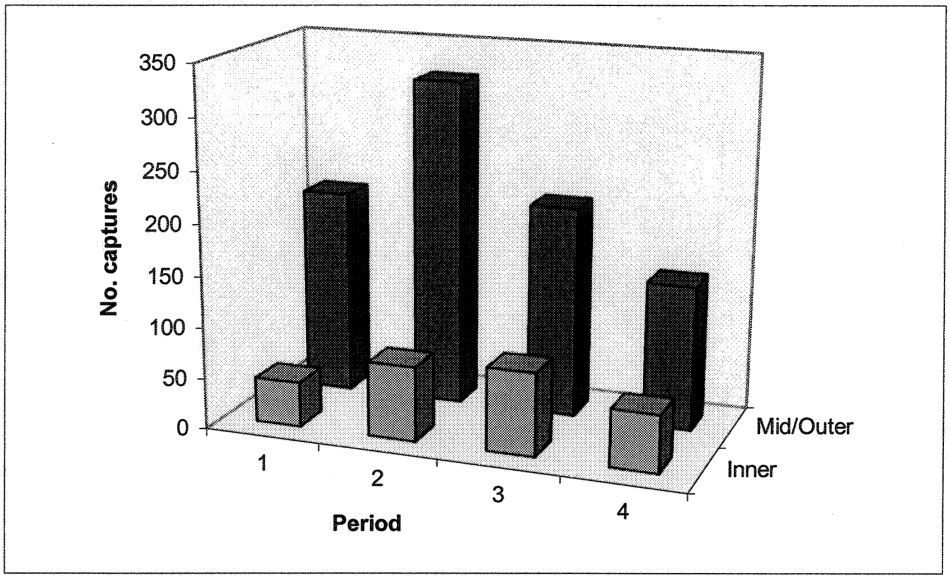


Figure 20 The number of grey squirrels removed from the Inner and Mid-outer Bands of the reserve between 1992 and 1996

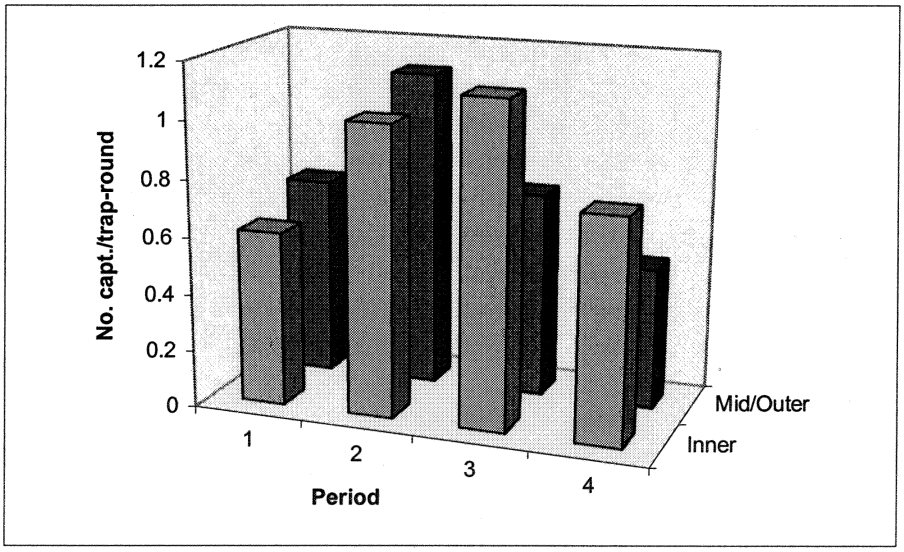


Figure 21 The number of grey squirrels caught trap-round-1 in the Inner and Mid-outer Bands of the reserve between 1992 and 1996

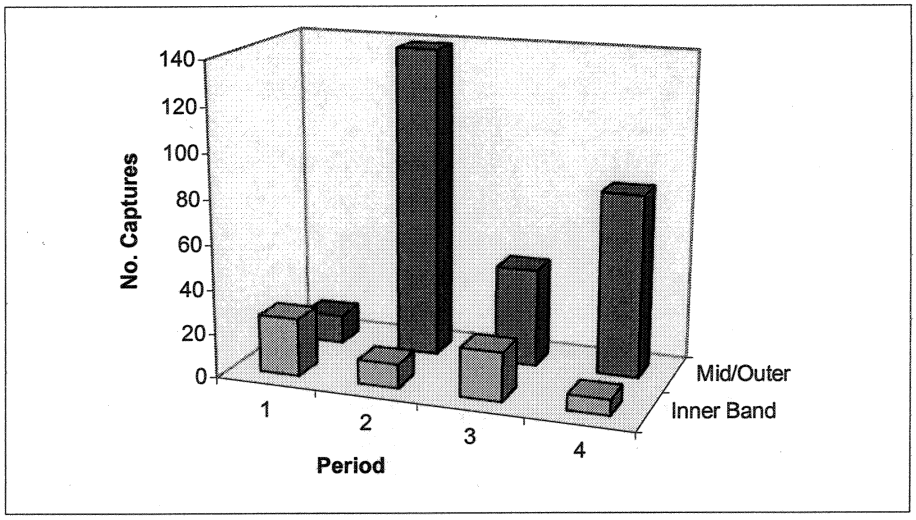


Figure 22 The number of grey squirrels removed from the Inner and Mid-outer Bands of the reserve in 1997-98

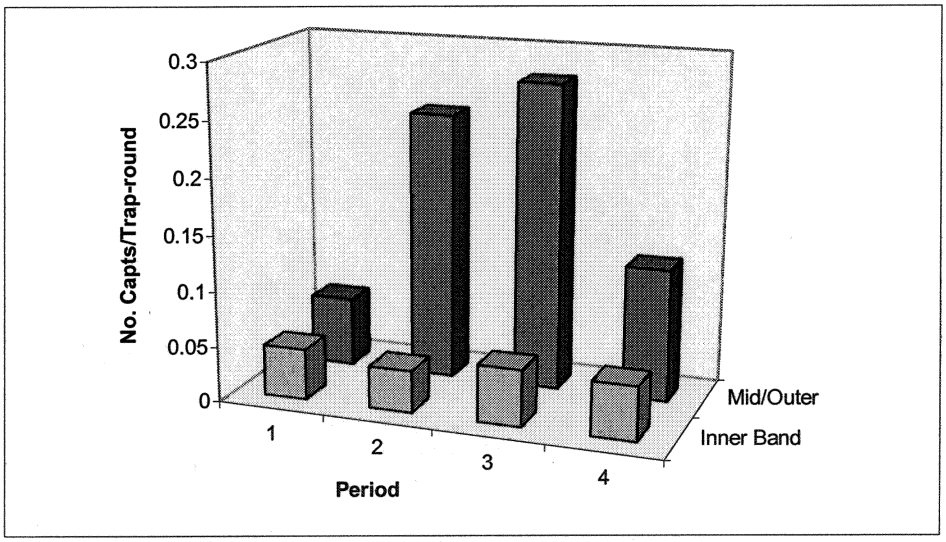


Figure 23 The number of grey squirrels caught trap-round-1 in the Inner and Mid-outer Bands of the reserve in 199798

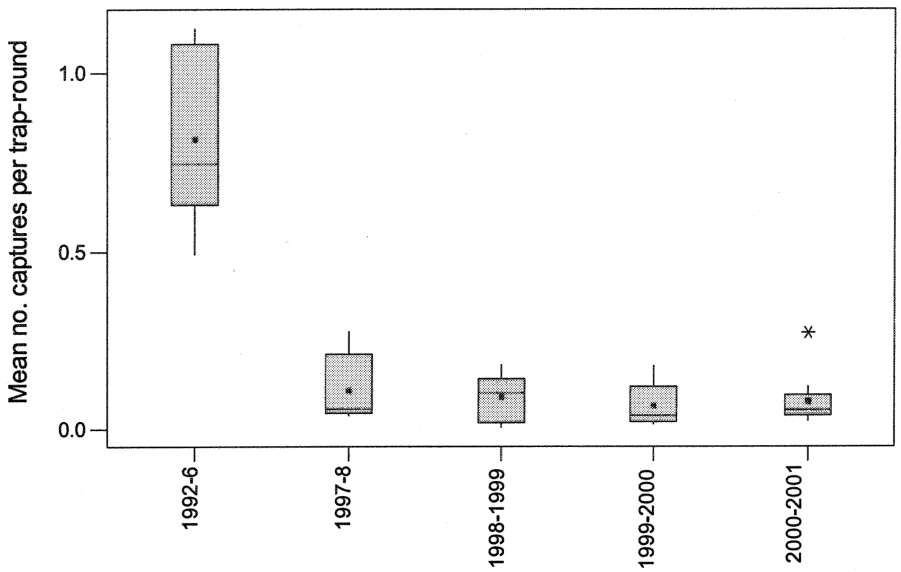


Figure 24 Boxplot of the number of grey squirrels caught trap-round-1 for 1992-96 (Reserve only), 1997-98 (Reserve only) and 1998-99, 1999-2000, and 2000-2001 (Control Area)

(Means are indicated by solid circles.)

7. Discussion

7.1 Control Efficiency

The number of squirrels captured in any time period is affected by several factors, including weather (Perry *et al.*, 1977), the annual cycle in numbers and the trappability (= the probability of catching an animal in a set trap) of the animals. In turn trappability is affected by natural food availability (Gurnell 1996a). For example, between April and June, natural food supplies for squirrels in conifer forests can be scarce (ie between the time of tree flower and bud availability in the spring and the new cone crop in the summer - see Gurnell 1987, Moller 1983) if the cone crop of the previous year has been utilised. This may be one reason why captures were high in these time periods in this study. However, the feeding transects showed that cones were being eaten at all times during the study and it is not thought that food supplies were ever poor. It was also noticeable that very few squirrels were captured in Period 4 (July to September) in Year 1. This may have been related to squirrels feeding on the new crop of broadleaf seeds at this time (12th July to 6th September), although July and the first half of August are normally too early for developing broadleaf tree seeds to greatly influence trappability. One problem here is that the control periods cover about two months, which makes an examination of the timing of events difficult. Low catches between July and September were not seen in the other two years. In general, grey squirrels are particularly difficult to catch during the autumn in forests that contain broadleaf trees (Gurnell 1996a), and even small numbers of broadleaf trees within conifer forests are known to affect trappability (Gurnell *et al.* 1997). Although there is only a small amount of evidence (see Gurnell *et al.* 1997), it appears that grey squirrels were more trappable than red squirrels in Thetford. This is thought to be due to red squirrels finding plenty of food in the canopy of the trees and not coming to the ground very often. In general, red squirrels are more arboreal than grey squirrels (eg Kenward & Tonkin 1986, Wauters *et al.* 2000). It is also noticeable that, although large numbers of grey squirrels were captured, the evidence suggests that many grey squirrels were not trapped; we will return to this below.

With respect to the annual cycle of numbers, peak numbers of squirrels would be expected to be present after breeding. The duration of breeding this depends on, for example, whether both early (spring) and late (summer) litters are produced (Gurnell 1987, 1996a); the former may be skipped when food supplies are very poor. In fact most squirrels were trapped between February and July in Years 1 and 2 but not Year 3. However, some breeding did take place throughout most of each control year (see Section D.5.3) and most juveniles were captured between April and September, although some juveniles were captured between November and January in Year 3. The evidence from the population demographic and body mass data show that the pine forests at Thetford were good habitats for grey squirrels; the animals were of good body size, and bred throughout the breeding season with spring and summer peaks as found in broadleaf habitats (Gurnell, 1987, 1996a). The studies were not designed to estimate grey squirrel densities, but the cone feeding studies indicate that densities varied between 0.7 ha^{-1} in 1998/9 to >3 ha^{-1} in 2000 in that part of the control area (unpubl.); these are good to very high densities for grey squirrels in conifer plantation forest (Gurnell 1987).

Trapping efficiency was much higher between 1992 and 1996 than 1998-2001, but this results from the lower trapping effort carried out in the former years. In fact, between 1992 and 1996, there was no evidence that grey squirrels were being removed in sufficient numbers to effectively reduce the number of grey squirrels in the central part of the reserve.

Similarly, between 1998 and 2001, and despite the higher control effort, there is no consistent evidence that grey squirrels were being significantly reduced in the Inner Band, neither was there a gradation from low to high trapping efficiency from the Inner to the Outer Band. Therefore, the control efficiency was consistently poor. In simple terms, the primary ecological requirement of red squirrels is an absence of grey squirrels (Gurnell & Pepper 1993). Thus, the objective of a grey squirrel control programme for red squirrel conservation would be to remove grey squirrels from the target area, here the Inner Band or Zone 1 and thereafter keep them at very low numbers in order that resident red squirrels would not be subjected to the effects of interspecific competition (see Wauters & Gurnell 1999; Wauters *et al.* 2000, 2001, 2002). This was not being achieved with the level of control effort used in this study, ie in terms of person-years ha^{-1}, 1.09E-04 person-years ha^{-1} in Year 1, 1.26E-04 person-years ha^{-1} in Year 2 and 2.23E-04 person-years ha^{-1} in Year 3.

Apart from a reduction in trap success and cone feeding from before to after control 2000, the two summer studies indicate little effect of control on the numbers and activity of grey squirrels in an around the control compartments in Zone 3. This was particularly elegantly demonstrated by the radio-tracking studies. Although not designed to measure home range size as such, the studies clearly suggest that the squirrels were either not entering control compartments, even though nearby, or they were active in them but not being trapped. Thus, the squirrels were not being attracted to the traps. Control effort was increased slightly between Years 1 and 2 and substantially in Year 3. One simple conclusion is that the control effort was still not high enough in Year 3. However, it may not be as simple as this and further studies are required on the efficiency of trapping grey squirrels in pine and other types of conifer forest; these are discussed below.

7.2 Grey squirrel control for red squirrel conservation

7.2.1 Methods of control

Standard methods of grey squirrel control include shooting, cage live trapping (see Pepper and Currie 1998) and kill trapping (eg with approved spring traps, The Spring Trap Approval Order 1995) and the use of 0.02% warfarin poison on a wheat bait dispensed from approved hoppers between 15th March and 15th August (Control of Pesticides Regulations 1986, also The Grey squirrels [Warfarin] Order 1973 in England and Wales, the Wildlife and Countryside Act 1981 in Britain, and the Protection of Animals Act 1912 in Scotland; Pepper & Curry 1998). Shooting and kill trapping are generally less efficient than live trapping (Gurnell 1999). The use of warfarin poison is the most common method of controlling grey squirrels for tree damage prevention. However, it is not permissible to use warfarin where red squirrels are at risk, and at present live trapping offers the only method of controlling grey squirrels for red squirrel conservation even though it is labour intensive and costly (Gurnell 1999). An important difference between cage trapping and using poison is that cage trapping is a pulsed removed method whereas poisoning is continuous. Grey squirrels have a high vagility (Gurnell 1987) and a high population resilience (*sensu* Sullivan 1986); woodland cleared of resident squirrels can be recolonised in as little as a month (Pepper, 1985; Hodge & Pepper, 1998). There is no evidence that grey squirrels were cleared from any part of the study area for any length of time using the control effort applied in this study.

7.2.2 Further research

On the basis of the results obtained here, there are three considerations for further study with respect to the efficiency of controlling grey squirrels for red squirrel conservation:

Forest type and area

The accumulating evidence suggests that Scots and Corsican pine forest are favourable conifer habitats for grey squirrels, especially when food supplies, in terms of the cone crops, are good (this study, also see Gurnell 1996b, Gurnell *et al.*1997, Kenward *et al.*, 1998, Smith 1999, Wauters *et al.*, 2000). The food supplies were moderate to very good throughout this study, and large numbers of grey squirrels were present in the control area at all times. In addition, there was a ready supply of animals on the outside of the control area to enter and quickly replace those animals removed. Immigration occurred all around the control area, with a slight bias towards the east. In forest types that are believed to be less favourable to grey squirrels, eg forests that are predominantly Sitka spruce (*Picea sitchensis*), then the levels of control effort applied here might be more effective. The target area for control, the buffer zone and the surrounding landscape also need to be considered (Gurnell & Pepper, 1991, 1993, Pepper & Patterson, 1998). In this study, the buffer zone for the central part of the study area (Zone 1) was 2.45 km wide in Years 1 and 2, and 1.5 km in Year 3. However, in neither time period did these effectively act as buffers; grey squirrels were trapped at all times throughout the control and 'buffer' areas.

Type of trap and trap placement

Multi-capture live traps were used on the ground in this study because it was believed that the chances of catching a red squirrel in a trap at Thetford were very remote. However, where red squirrels are at risk of being captured, it is advisable to only use single capture live traps, preferably with a nest box attached (see Gurnell & Pepper 1994), to avoid catching greys and reds in the same trap; this could result in injury or death to the red squirrel(s) (Bruemmer 1996). In addition to the type of trap used, there is an increasing amount of evidence that grey squirrels are more easily trapped in conifer forests in traps placed 2m to 3m up the side of trees than those placed on the ground (this study, Gurnell *et al.* 1997, Smith 1999, Matthews 2000). A detailed study looking at Tree versus Ground, and Single versus Multicapture traps at Thetford would provide valuable information on this.

Trapping method

The summer studies on the effectiveness of control clearly showed that many squirrels were active in or around the control compartments but were not trapped. Thus, it seems, that squirrels were not being attracted to the traps. There are two ways that might improve this situation: (i) by increasing the length of the pre-bait period to encourage more animals to locate and feed at the traps, and (ii) change the type of bait used. Anecdotal evidence suggests that changing the bait from whole maize to a mix of peanuts, sunflower seeds, wheat and hazelnuts; see Gurnell & Pepper 1994) could improve captures. Thus studies on the length of the prebait period and type of bait would be rewarding.

Control effort

The results from the summer study suggest that the control efficiency could be improved by having a higher density of control compartments and/or trapping each compartment more frequently. This could only be achieved by increasing the Year 3 control effort further, for example, almost doubling it to 1.0 person-years. Although this would be an interesting exercise, the costs would be becoming prohibitively high, and it would be unlikely that this level of investment would be used to control grey squirrels for red squirrel conservation elsewhere in the country.

8. References

BRUEMMER, C., 1996. The trappability and welfare of red squirrels (*Sciurus vulgaris*) and grey squirrels (*Sciurus carolinensis*) in different designs of live trap. MRes., The University of Edinburgh.

GURNELL, J., 1983. Squirrel numbers and the abundance of tree seeds. *Mammal Review,* **13**: 133-148.

GURNELL, J., 1987. *The natural history of squirrels*. London: Christopher Helm. 201pp.

GURNELL, J., 1989. Demographic implications for the control of grey squirrels. *In*: R. Putman, ed. *Mammals as Pests*, pp. 131-143. London: Croom Helm.

GURNELL, J., 1996a. The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. *Journal of Applied Ecology,* **33**: 325-338.

GURNELL, J. & PEPPER, H., 1994. *Red squirrel conservation: field study methods*. Forestry Authority Research Information Note No. 255. Edinburgh: Forestry Commission.

GURNELL, J., 1996b. Conserving the red squirrel. *In:* P. Ratcliffe & J. Claridge, eds. *Thetford Forest Park: the ecology of a pine forest*. pp. 132-140. Edinburgh: Forestry Commission.

GURNELL, J., 1999. Grey squirrels in woodlands: managing grey squirrels to prevent woodland damage. *Enact,* **7**: 10-14.

GURNELL, J., LURZ, P.P.W. & PEPPER, H., 2001a. *Practical techniques for surveying and monitoring squirrels*. Forestry Commission Practice Note 11. Edinburgh: Forestry Commission. 12pp.

GURNELL, J., WAUTERS, L.A., PREATONI, D. & TOSI, G., 2001b. Spacing behaviour, kinship and dynamics of the grey squirrel in a newly colonised deciduous woodland in north Italy. *Canadian Journal of Zoology,* **79**: 1533-1543.

GURNELL, J. & PEPPER, H., 1991. *Conserving the red squirrel*. Research Information Note No. 205. Edinburgh: Forestry Commission.

GURNELL, J. & PEPPER, H., 1993 A critical look at conserving the British red squirrel *Sciurus vulgaris*. *Mammal Review,* **23**: 125-136.

GURNELL, J., SAINSBURY, T. AND VENNING, T., 1997. *Conserving the red squirrel in Thetford Forest*. Published Report for English Nature, Forestry Commission and the People's Trust for Endangered Species,113 pages. Peterborough: English Nature,

GURNELL, J., CLARK, M.J., LURZ, P.W.W., SHIRLEY, M.D.F. & RUSHTON, S.P., 2002. Conserving red squirrels (*Sciurus vulgaris*): mapping and forecasting habitat suitability using a Geographic Information Systems Approach. *Biological Conservation*, **105**: 53-64.

HODGE, S. & PEPPER, H.W., 1998. *The prevention of mammal damage to trees in woodland.* Forestry Practise Advice Note 3. Edinburgh: Forestry Commission.

KENWARD, R.E. & TONKIN, J.M., 1986. Red and grey squirrels: some behavioural and biometric differences. *Journal of Zoology, London,* **209**: 279-281.

KENWARD R.E., HODDER K.H., ROSE R.J., WALLS C.A., PARISH T., HOLM J.L., MORRIS P.A., WALLS S.S., DOYLE, F.I., 1998. Comparative demography of red squirrels (*Sciurus vulgaris*) and grey squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. *Journal of Zoology,* **224**: 7-21.

KREBS, C.J., 1999. *Ecological Methodology* 2nd Edit. U.S.A: Addison Welsey Educational Publications Ltd.

MATTHEWS, J.E., 2000. Red squirrels (*Sciurus vulgaris*) on the island of Anglesey, North Wales: past, present and future. MPhil thesis, Queen Mary, University of London.

PATTERSON, G. & PEPPER, H., 1998. *Red squirrel conservation*. Forestry Commission Practice Note 5, 4pp. Edinburgh: Forestry Commission.

PEPPER, H.W., 1985. The protection of broadleaved woodlands against bark-stripping damage by grey squirrels. The Game Conservancy review of 1985, pp. 106-111. Fordingbridge: The Game Conservancy.

PEPPER, H. & CURRIE, F., 1998. *Controlling grey squirrel damage to woodlands*. Forestry Commission Practice Note 4, 4pp. Edinburgh: Forestry Commission.

PEPPER, H. & PATTERSON, G., 1998. *Red squirrel conservation*. Forestry Commission Practice Note 5, 4pp. Edinburgh: Forestry Commission.

PERRY, H.R., PARDUE, G.B., BARKALOW, F.S & MONROE, R.J., 1977. Factors affecting trap response of the gray squirrel. *Journal of Wildlife Management,* **41**: 135-143.

SIMPSON, L.M. & HENDERSON-HOWAT, D.B., 1985. *Thetford Forest Management Plan*. Forest Record 130. Edinburgh: Forestry Commission.

SMITH, D.F.E., 1999. Grey squirrel, *Sciurus carolinensis*, and feeding biology in a conifer forest. PhD thesis, Queen Mary, University of London.

SULLIVAN, T.P., 1986. Understanding the resiliency of small mammals to population reduction: poison or population dynamics. *In:* C.G.E. Richards & T.Y.Ku, eds. *Control of Mammal Pests*, pp. 69-82. London: Taylor & Francis.

WAUTERS, L.A. & GURNELL, J., 1999. The mechanism of replacement of red squirrels by grey squirrels: a test of the interference competition hypothesis. *Ethology,* **105**: 1053-1071.

WAUTERS, L.A., LURZ, P.W.W. & GURNELL, J., 2000. The effects of interspecific competition by grey squirrels (*Sciurus carolinensis*) on the space use and population dynamics of red squirrels (*S. vulgaris*) in conifer plantations. *Ecological Research,* **15**: 271-284.

WAUTERS, L.A., GURNELL, J., MARTINOLI, A. & TOSI, G., 2001. Does interspecific competition with grey squirrels affect the foraging behaviour and food choice of red squirrels. *Animal Behaviour,* **61**: 1079-1091.

WAUTERS, L.A., TOSI, G. & GURNELL, J., 2002. Interspecific competition of grey on reds: do grey squirrels deplete tree seeds cached by red squirrels. *Behavioral Ecology and Sociobiology.*

Appendix

	Compartment No.								Control Period	
									Before	(During)	After
A. Summer 2000											
Control Cmpts	3030	3054	3091	3115	3112	3138	3086	3159		31st Jul	
Live trapping: 5 clusters of 5 traps 100m to 200m apart	3043	3086	3111	3113	3135	3138	3053		26th Jun		7th Aug
Hair Tubes: 6 grids of 20 tubes 100 m between tubes	3043 /3054	3086 /3053	3111 /3135	3137 /3112	3143 /3144	3175 /3155			31st Jul	7th Aug	14th Aug
Feeding Transects: 20 x 50 m Lines, 2 lines /cmpt	3111	3086	3053	3035	3138				31st Jul	7th Aug	14th Aug
B. Summer 2001											
Control Cmpts	3030	3054	3091	3115	3112	3138	3086	3144		30th Jul	
Live trapping: 4 clusters of 5 traps 100m to 200m apart	3053	3111	3135	3138	3086	3043			18th Jul		20th Aug
Hair Tubes: 2 grids of 20 tubes 100 m between tubes		3086 /3053	3111 /3135						30th Jul	6th Aug	13th Aug
Feeding Transects: 10 x 50 m Lines, 2 lines /cmpt	3086	3053	3135	3138	3113	3111			30th Jul	6th Aug	13th Aug

Table A 1 Times table for the summer studies on the effectiveness of grey squirrel control