

Monitoring red squirrels *Sciurus vulgaris* and grey squirrels *Sciurus carolinensis* in Britain

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ABSTRACT

1. In Britain, five indirect methods have been used to survey for the presence of red *Sciurus vulgaris* and grey squirrels *S. carolinensis* and to monitor population trends through time. These are: visual counts along line transects, the use of hair tubes, counts of dreys, cone line feeding transects in conifer forests and feeding signs on whole maize bait at feeding stations.
2. Drey counts and cone feeding transects cannot differentiate between red and grey squirrels and are not suitable for areas where both species may be present. Hair tubes require expertise and facilities to identify hairs to species, and the relationship between tube visits and animal density in different habitats is only known for red squirrels in Sitka spruce *Picea sitchensis* dominated plantations. Visual counts along line transects are the simplest method to do and require little equipment. However, in general, few squirrels are seen in a single count which leads to difficulties in estimating densities.
3. In this paper we present data from several studies carried out in Britain to illustrate the type of data that may be collected, and to evaluate their accuracy and precision with which they could detect population change. Hair tube lines and drey counts required the fewest number of samples to detect population change. When effort was also considered, visual transects and drey counts were more economical. However, none of the monitoring methods discussed is very precise and it may be best to monitor squirrels only in terms of relative changes in numbers or indices of numbers through time.
4. Our results for red and grey squirrels also illustrated that the number of samples required to detect population change is likely to differ according to the size of the survey area. Monitoring programmes should therefore be carefully planned in relation to spatial scale in order to be able to detect real population changes. Species-specific, quantitative thresholds to determine the significance of detected declines may need to be established for threatened UK mammals and assessed in relation to what would constitute a significant decline and whether it requires management intervention.

Keywords: census techniques, drey counts, feeding transects, hair tube surveys, monitoring, power analysis, tree squirrels, visual surveys

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INTRODUCTION

The successful implementation of wildlife management and conservation plans relies on accurate information regarding species abundance, distribution, habitat use, and population trends (e.g. Broome, 2001; Ferrand & Gossman, 2001; Ripple *et al.*, 2001), and monitoring forms a crucial component of biodiversity action plans in the UK (Anonymous, 1995). Moreover, monitoring population trends is vital for forecasting how threatened populations respond to conservation management or changes in the environment (Macdonald, Mace & Rushton, 1998). This applies particularly to situations where native mammals are threatened by the spread of alien species, e.g. water voles *Arvicola terrestris* and American mink *Mustela vison* (Barreto *et al.*, 1998), red squirrels *Sciurus vulgaris* and grey squirrels *Sciurus carolinensis* (Shorten, 1954; Lloyd, 1983; Ó Teangana *et al.*, 2000), or where species damage crops or property, e.g. grey squirrels in relation to damage to commercial timber crops (Kenward, 1983; Gurnell, 1987, 1999; Gurnell & Pepper, 1988, 1993). The impacts of grey squirrels are also being seen in other countries where grey squirrels have been released, such as in north Italy (Gurnell, 1996a; Wauters *et al.*, 1997; Lurz *et al.*, 2001) and Vancouver Island, Canada (Bruemmer *et al.*, 2000).

A number of methods are available to survey for the presence of red and grey squirrels, and to monitor changes in numbers and distribution through time. Live trapping and marking squirrels is the most direct way of obtaining data about population numbers, although this method can be complicated by variations in the probability of catching individuals within and between trapping periods (e.g. Gurnell, 1983, 1996b; Lurz, Garson & Rushton, 1995). Live trapping and handling squirrels also require expertise, and, in the case of red squirrels in the UK, a licence from a Country Agency under the Wildlife and Countryside Act (1981). There are five commonly used indirect (i.e. they do not involve trapping and handling squirrels) tree squirrel survey and monitoring methods: the use of whole maize bait at feeding stations, drey counts, cone feeding transects, hair tube surveys and visual surveys. Some census methods have been used more often than others. For example, there have been very few studies that have used drey counts or feeding transects, whereas several studies have used visual counts and hair tubes. Ideally, these indirect methods should be validated against the results from independent live trapping studies (e.g. Jennelle, Runge & MacKenzie, 2002), but this has only rarely been carried out.

In this paper, we review the application of current squirrel census methods in Britain (Gurnell, Lurz & Pepper, 2001) based on data collected from several studies. In addition, we evaluate their relative accuracy and the amount of effort required to achieve a specified precision in detecting population change, and make recommendations on their applications and future research needs.

METHODS

Squirrel monitoring

There are five indirect methods of monitoring squirrels that have been used in Britain (Table 1). Precise details on how to carry out the different methods are given by Gurnell *et al.* (2001); also see Gurnell & Pepper (1994). Individual field workers tend to tailor the methods to their own requirements and so here, for illustrative purposes, we briefly describe a typical way that each method may be used:

- 1. Drey counts.** Dreys are semi-permanent structures in woodland and individual squirrels usually use several at a time. The number of dreys in an area of woodland is systematically counted and an estimate of squirrel density is derived from a published relationship of the number of dreys used by individual squirrels. Relationships are published for red squirrels in

Table 1. Indirect squirrel census methods (from Gurnell *et al.*, 2001)

Method	Can it detect squirrel presence	Can it distinguish red squirrels from grey	How good is it for estimating densities	What type of woodland
1. Drey counts	Not always	No	Poor-moderate	All*
2. Feeding transects	Yes	No	Moderate	Conifer
3. Hair tube surveys	Yes	Yes	Poor-moderate	All
4. Visual surveys	Yes	Yes	Moderate	All
5. Whole maize bait	Yes	No	No	All

*But difficult in dense plantations.

conifer, mixed and broadleaf woods in Belgium (Wauters & Dhondt, 1988) and for grey squirrels in predominately broadleaf woods in southern England (Don, 1985). We do not have published information on the density of grey squirrel dreys in conifer forests.

2. Feeding transects. Feeding transects are marked out as 50 m × 1 m lines in conifer forest at a density of about one transect every four hectares. At regular intervals (e.g. 4–8 weeks or at a minimum of once a year), all the uneaten cones and eaten cone cores (stripped cones) are collected. The lengths of the cone cores that result from squirrel feeding are measured and the amount of seed energy present in a cone of that size estimated from previously derived relationships between cone size and energy content for the conifer trees in that area. From the information collected from all the transects in a particular forest, estimates of the amount of energy consumed per day per unit area are obtained. These are converted into squirrel densities based on standard estimates of squirrel energy consumption in the literature.

3. Hair tube surveys. Hair tube surveys employ a set number (e.g. 20) of baited PVC tubes, *c.* 30 cm long by 6.5 cm diameter, spaced out within a wood in the form of a line or a grid, with 100 m between adjacent tubes. Each tube is fixed to a tree at a height of *c.* 2 m and has small plastic or wooden blocks covered with sticky tape fixed on the roof at each end of the tube. As a squirrel enters the tube to get bait left inside, it leave some of its hairs on the tapes. These are removed and examined later using a microscope. The species of squirrel, or other mammal, that entered the tube can be identified by the characteristics of the cuticle scale pattern, medulla and cross-section of the hairs (Teerink, 1991; Dagnall, Duckett & Gurnell, 1995). The proportion of tubes visited within a set time period (e.g. 2 weeks) provides a relative measure of squirrel numbers.

4. Visual surveys. They are based on standardized time-area counts of squirrels. Within a wood, pre-determined survey lines of a set length (e.g. 1000 m) are walked just after dawn. All squirrels seen are recorded, and their perpendicular distances to the survey line estimated. The visual 'belt' width of the survey line is estimated, using either graphical methods or by calculating a detection function by fitting a curve to the frequency distribution of detection distances using standard distance sampling equations. From this information, the density of squirrels is estimated.

5. Whole maize bait. The presence of squirrels can be simply determined from the remains of yellow whole maize put out as feed or, for example, in hair tubes. Squirrels are the only species to remove the germ from the maize grain and discard the rest intact, leaving a characteristic 'squirrelled' grain of maize. This method has not been used to estimate squirrel numbers or density and will not be considered further here.

Only visual counts and hair tubes can be used to distinguish red and grey squirrels, and squirrel feeding transects are only useful in conifer forests (Table 1). Brief details of the studies used to illustrate the application of each method are provided in the Appendix.

Estimates of power

For visual survey, hair tube survey and feeding transect methods, we adopt the term 'sample' to refer to a visual count transect, a grid or line of hair tubes, or a feeding transect. We carried out estimates of power on the number of samples needed for the different methods to detect population change confidently. Most data available were based on studies working in large forests or on a number of separate woodlands on an island, and were not carried out for the purpose of this analysis. Therefore, some data sets are more suitable for power analysis than others and the results presented should be viewed as a first, rather than a definitive, estimate. Where available, we have used data from more than one field study for red and grey squirrels in different habitat types and from these data we have estimated population densities (see Gurnell *et al.*, 2001). In doing so, we assume that the different methods were used to obtain samples of squirrel densities in order to detect population change through time, even if this was not always the objective. A data set was taken to be a single year of sampling at one woodland site (irrespective of area), and each density estimate derived from a sample was considered to be a sample from the true population of densities. Bootstrapping (Manly, 1998) was used to obtain an estimate of the population variance from each set of density estimates.

Calculations of power require an effect size (the amount by which the population has changed from one year to the next), a sample size (the number of samples used) and a level of significance (the probability of accepting the null hypothesis when it is false). The ability of hair tubes, cone feeding transects and visual counts to detect changes in population size was determined as follows: each density estimate was increased or decreased by the desired effect size (-25% to $+25\%$ in steps of 5%), and bootstrapping was again applied to generate variance estimates for the new population densities. Monte Carlo simulation was then used to generate 10 000 sets of samples drawn randomly from normal distributions using the sample means and estimated population variances. The number of replicates within each sample was varied. The resulting two samples (using the mean from the field data and the changed mean) were compared using *t*-tests (assuming unequal variances at $\alpha=0.10$). Knowing the null hypothesis to be false, the number of true negatives (i.e. the avoidance rates of type II errors) was calculated from the 10 000 simulations. The proportion of true negatives is, by definition, the statistical power of the *t*-tests to detect an effect size equal to the amount of population change. For all the census methods analysed here, there existed replicate data collected over subsequent years or in different sites. The power analysis was performed on each data set separately, and a mean power was calculated for each effect size and sample size.

Due to the paucity of replicated drey counts available to us, the estimation of the power of this census method is different from the other three methods. The sample is the woodland surveyed to obtain the density estimate rather than, for example, a transect. We calculated squirrel density estimates from drey densities using the published regression relationships (Don, 1985; Wauters & Dhondt, 1988). From these we generated random Poisson deviates with the estimate as the mean. We then estimated power based on these derived samples.

Estimates of effort

Gerrodette (1987) suggests that, as the generally accepted level of avoidance of type I errors (α) is 0.05, for symmetry's sake the avoidance level of type II errors (β) should be the same (corresponding to an acceptance level for power of 0.95). However, Cohen (1988) suggests an acceptance level of power of 0.80, and many authors (e.g. Hayes & Steidl, 1997; Reed & Blaustein, 1997) have treated this as a goal for retrospective power analysis. This level of power cannot be achieved in the analysis presented here because, rather than being repeated samples from the same population, each of our density estimates is pooled from

many different studies, resulting in an unrealistically high variance in the data. Thus, to compare the effort required to carry out each of the four census methods, we estimate the number of person-days required to achieve a power of 0.60. By choosing this acceptance level, we have decided that we want to avoid type II errors more often than accept them; but recognize that further studies, with the sample sizes that we suggest, are likely to achieve levels of power greater than we have estimated due to the smaller variance expected from a comprehensive monitoring scheme. The estimates do not involve travel time to and from the sites, and they will clearly vary according to how fast individuals work in the field and local field conditions. Thus, they should be treated as approximate guidelines.

Drey counts: here we estimate that it will take 0.5 person-days to count the number of dreys in a woodland of about 10 ha in area.

Feeding transects: each sample unit of one feeding transect line requires 0.25 person-days to collect all of the stripped cones, to identify the species responsible, and to measure the length of the cones. Each line will also require about 0.25 person-days to establish (mark out, rake clear of litter) in the first place. Therefore, we estimate 0.5 person-days per sample here.

Hair tube surveys: each density estimate is based on a sample of at least 20 individual hair tubes, which require 0.5 person-days to bait and 0.5 person-days to collect the hair blocks 2 weeks later. We also estimate it will take 0.5 days to examine the tapes on the blocks and identify hairs, although this will clearly depend on experience. In addition, each line or grid of tubes requires about 1.0 person-days to establish in the first place. We therefore estimate 2.5 person-days per sample for using this method.

Visual surveys: we assume that it will take about 0.2 person-days to walk one 1 km transect. In some instances, set up time, e.g. to mark out the transect line, might be involved.

RESULTS

Application of monitoring methods

Drey counts

The presence or absence of dreys has been used to indicate the presence or absence of squirrels. This is a useful method in certain types of study, especially those concerned with the distribution of squirrels within the landscape in relation to woodland patch size and connectivity. For example, Fitzgibbon (1993) looked at the distribution of dreys in farm woodland in eastern England, and several studies have looked at the distribution of red squirrel dreys in relation to habitat fragmentation (e.g. Verboom & van Apeldoorn, 1990; Celada *et al.*, 1994). However, very little work has been done on using dreys to estimate squirrel density since the original studies of Don (1985) and Wauters & Dhondt (1988). In fact, we only have data from Thetford Forest in eastern England. One set of data, from 1974, illustrates the patchy distribution of dreys across a large area (723 ha) of fairly even-aged forest, and suggests that drey counts from small woodland areas are likely to be difficult to generalize to a larger scale (Table 2). At that time, the forest still consisted mainly of the first rotation crop of Scots pine *Pinus sylvestris*, although some compartments (stands of trees defined by Forestry Commission boundaries) had been replanted with the second generation crop of Corsican pine *P. nigra*. Only red squirrels were present in the forest then, and, although they were not trapped, they were very numerous (Rex Whitta, personal observation). It can be seen that the density of dreys in each forest compartment varied considerably between 0 and 5.5 per hectare with a mean of just over 1.0 per hectare (Table 2 and Fig. 1).

In 1998, drey counts were carried out at two sites, A and B, in Thetford Forest; by this time, grey squirrels had replaced red squirrels in this part of the forest. Drey densities were 1.7 and 2.0 per hectare, respectively (Table 3). Regression relationships to convert drey density

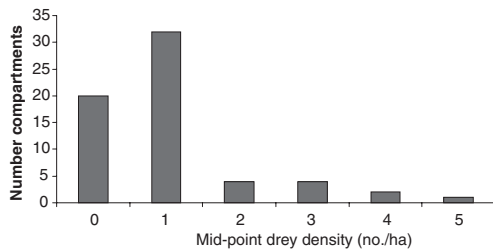


Fig. 1. Frequency histogram for forest compartments according to red squirrel drey densities in part of Thetford Forest in 1974 (see Table 2).

Table 2. Maximum, minimum and mean densities of red squirrel dreys in 63 compartments containing conifer trees of 40–47 years in Thetford Forest in 1974 (data from Rex Whitta, unpublished)

Tree species	Cmpt. (<i>n</i>)*	Total area (ha)	Drey density (no./ha)			
			Minimum	Maximum	Mean	CV (%)
Corsican pine	1	12	–	–	1.0	–
Corsican/Scots pine	4	49	1.1	3.6	1.9	63
European larch/Scots pine	2	29	0.1	0.6	0.4	93
Scots pine	56	633	0.0	5.5	1.0	103
Total	63	723	0.0	5.5	1.1	100

CV, coefficient of variation.

*Cmpt., forest compartment. In the 1970s and 1980s, annual surveys for the presence of red squirrel dreys, as well as sightings of red squirrels, were carried out across a large part of Thetford Forest in eastern England using volunteer assistance (Rex Whitta personal communication). A further 17 compartments (total area 198 ha) consisting of Corsican pine <12-year-old were censused but contained no dreys.

Table 3. Drey counts at two sites A and B in Thetford Forest in 1998

Site	Cmpt. no.	Area searched (ha)	Dreys no.	Density dreys (no./ha)	Density 1 squirrels* (no./ha)	Density 2 squirrels* (no./ha)	
A	3	5.6	8	1.4	0.37	1.04	
	4	5.1	11	2.2	0.56	1.63	
	9	3.0	4	1.3	0.35	0.96	
	8	6.0	10	1.7	0.43	1.26	
	10	5.4	11	2.0	0.53	1.48	
	Mean				1.7	0.45	1.27
	CV (%)				21	21	21
B	60	6.3	7	1.1	0.29	0.81	
	74	7.7	17	2.2	0.57	1.63	
	75	7.5	15	2.0	0.52	1.48	
	90	5.4	14	2.6	0.67	1.92	
	Mean				2.0	0.51	1.46
	CV (%)				32	32	32

Cmpt., forest compartment; CV, coefficient of variation.

*Density 1 used the equation for red squirrels of Wauters & Dhondt (1988) to estimate squirrel density from drey density, and density 2 used Don's (1985) equation for grey squirrels.

to squirrel density are not available for grey squirrels in conifer forest (see Table 3); however, grey squirrel densities are similar to red squirrel densities in pine plantation forest (Gurnell, 1987, 1996c; Lurz *et al.*, 1995) and the red squirrel conversion of dreys to squirrel densities is believed to be more realistic.

Squirrel feeding transects

The numbers of fallen whole and eaten cones collected on transects are a function of the tree species present, governing the timing of seed ripening and dispersal (e.g. Gurnell & Anderson, 1996), and the number of years between good seed years or mast crops (Silvertown, 1980). Studies in Clocaenog Forest North Wales by Cartmel (2000) illustrate these points. The number of cones eaten by red squirrels and whole, uneaten cones were monitored under four different conifer species over a 6-year period between 1993 and 1998 (Figs 2 and 3, respectively). There was a high correlation between the number of eaten and whole cones for Norway spruce *Picea abies* ($r_s = 0.80$, $n = 23$ seasons, $P < 0.0001$), Scots pine ($r_s = 0.81$, $n = 23$, $P < 0.0001$) and Japanese larch *Larix kaempferi* ($r_s = 0.86$, $n = 23$, $P < 0.0001$), but a poorer correlation with Sitka spruce *Picea sitchensis* ($r_s = 0.49$, $n = 23$, $P = 0.009$). Most transect lines were sited under Norway spruce, but cones were only produced by this species in 1996. Scots pine had good seed years in 1993–94 and 1996–7, and Japanese larch in 1996. Sitka spruce produced cones in most years, but not many were eaten. This is unusual since Sitka spruce are said only to produce a good crop every 3–5 years (e.g. Matthews, 1955, 1989; Gordon & Faulkner, 1992). Norway spruce tends to have long time intervals between mast years, varying between 3 and 10 years, but Scots pine produce good cone crops every 2 or 3 years, and larch every 3–5 years. Sitka spruce tend to disperse their seed in the autumn, as do larch, although

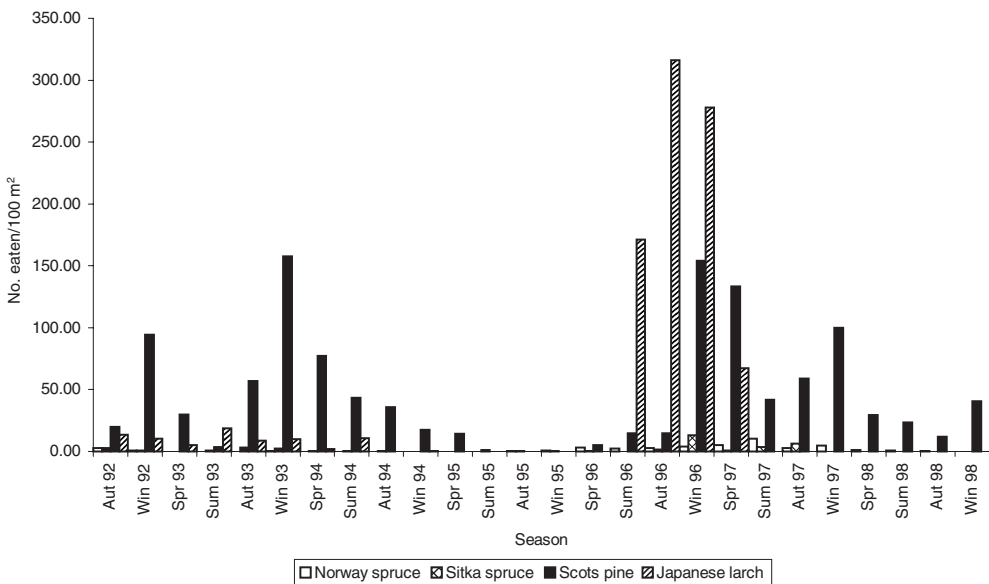


Fig. 2. Cones eaten by red and grey squirrels collected on 50 m by 1 m feeding transect lines under four types of conifer in Clocaenog Forest, North Wales, 1992–98, expressed as number of cones eaten every 100 m²/season (Cartmel, 2000). Winter, December–February; spring, March–May; summer, June–August; autumn, September–November. The seasonal results have been pooled from monthly inspections ($n = 65$). The number of feeding transects examined under Norway spruce varied between 2 and 35 (average 17.7), under Sitka spruce 1–9 (average 5.2), under Scots pine 1–4 (average 3.4), and under Japanese larch 1–4 (average 2.7).

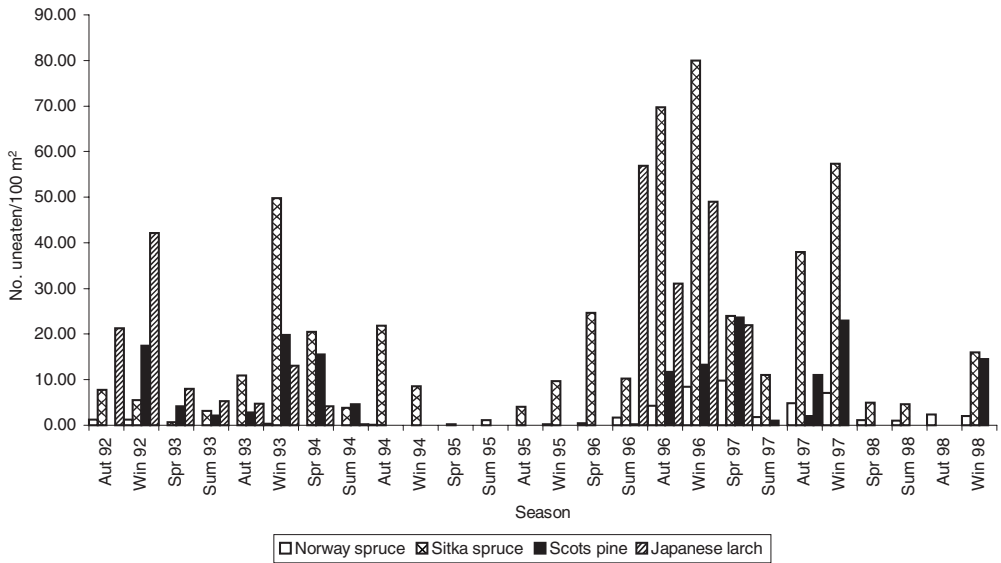


Fig. 3. Whole (uneaten) cones collected on feeding transect lines under four types of conifer in Clocaenog Forest, North Wales, 1992–98 (Cartmel, 2000), expressed as number of cones per 100 m². Further information as Fig. 2.

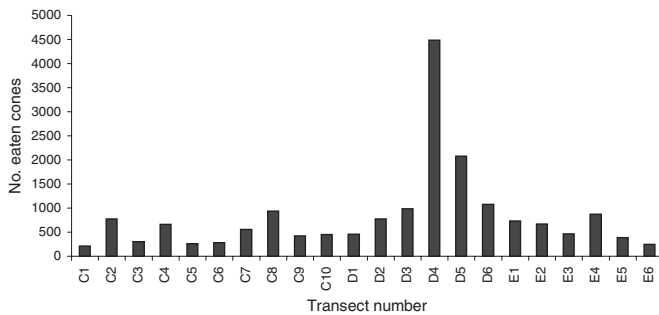


Fig. 4. Total number of pine cones eaten by grey squirrels collected from each of 22, 50 m × 1 m transects in Thetford Forest between 1998 and 2001 (unpublished data). C, D and E transect numbers refer to three different parts (sectors) of the forest (see Gurnell, Sainsbury & Venning 1997).

they may retain some cones on the trees over winter or for longer periods. Both Norway spruce and Scots pine shed their seed in the spring. Cartmel’s study illustrates how feeding transects can be used to monitor seed crop abundance and relative habitat utilization. To convert the number of cones eaten to estimates of squirrel densities requires information on cone morphometrics and energy content (see Gurnell *et al.*, 2001). This information was not available for Clocaenog Forest, but two other studies, one in Thetford Forest in eastern England and one in Spadeadam Forest in northern England, illustrate how density estimates may be achieved.

The studies in Thetford Forest involved investigating 22 transect lines, 50 m × 1 m, sited in three parts or sectors of the Forest every 2 months for 4 years. The tree species were Corsican pine (20 lines) and Scots pine (two lines); the squirrels feeding in the pines were grey squirrels. There was a high degree of variability in the data, both in space (Fig. 4) and time (Fig. 5). Using information on cone morphometrics and energy values for the seeds taken from cones removed from felled trees, the energy consumption in terms of kJ/ha/day were calculated for each part of the forest, and these converted to animal’s densities assuming that an average

Fig. 5. Total number of eaten cones collected every 6 weeks from 22 transect lines in Thetford Forest (see Fig. 4).

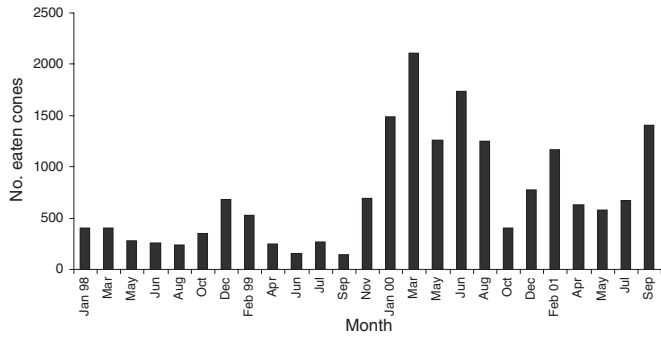


Fig. 6. Estimates of grey squirrel densities from eaten cones collected on feeding transects for each part or sector of Thetford Forest. C, D and E transect numbers refer to three different parts (sectors) of the forest (see Figs 4 and 5).

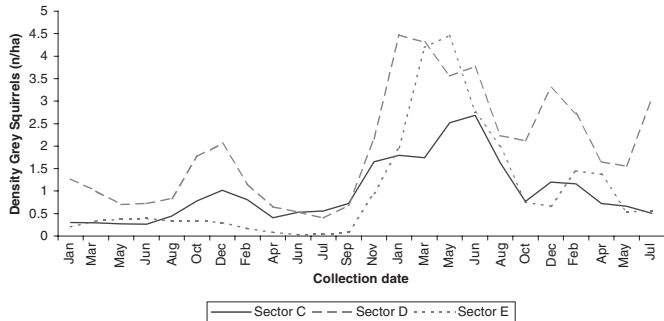
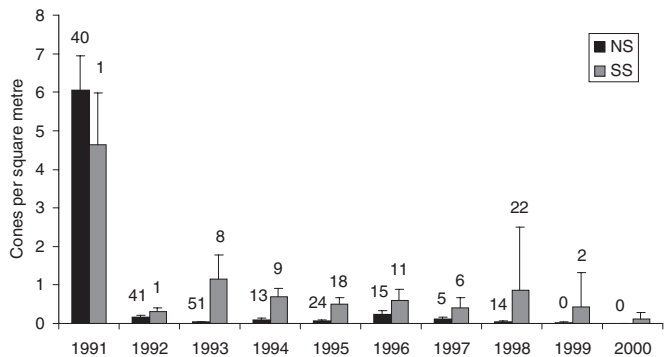


Fig. 7. Mean cone densities (+ 1 S.E.) for Norway spruce (NS) and Sitka spruce (SS) at Spadeadam Forest 1991–2000 based on cone feeding transects (Lurz, 1995). Numbers above the bars indicate the proportion (%) of cones stripped by red squirrels.



adult grey squirrel consumed 1000 kJ/day (Gurnell *et al.*, 2001). Trends in squirrel densities are shown in Fig. 6. There was a high degree of concordance for the estimates from the three parts of the forest (Kendall's coefficient of concordance, $W = 0.85$, $n = 24$, $P = 0.0001$). Density estimates fluctuated annually and densities were especially high in 1999–2000 resulting from the high cone crops in that year. The increase in numbers in that year resulted partly from reproduction but also from squirrels moving into the forest in response to high levels of food availability and grey squirrel control.

The study at Spadeadam Forest formed part of an intensive 3-year study on red squirrel ecology in Sitka spruce-dominated plantations as well as a longer-term monitoring programme for red squirrels in the Forest District (1991–2001). Cone feeding transects were used both to estimate annual changes in cone crop and to determine red squirrel feeding behaviour and densities. Figure 7 illustrates annual cone crops in Sitka spruce and Norway spruce and

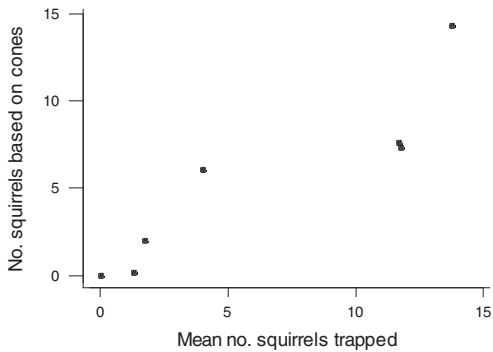


Fig. 8. Relationship between the mean number of red squirrels trapped ($r = 0.91$, $n = 7$, $P < 0.005$) at Spadeadam Forest (Lurz, 1995) over the course of 1 year and the number of squirrels estimated based on the density of cone cores on feeding transects and cone energy values of 2.48 kJ/cone for Lodgepole pine, 5.25 kJ/cone for Sitka spruce, 9.6 kJ/cone for Norway spruce and an energy requirements for red squirrels of 700 kJ/day.

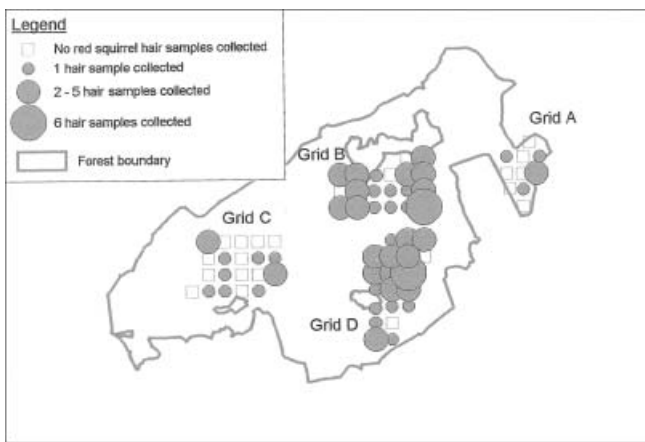


Fig. 9. Frequency of presence of red squirrel hairs at different stations on grids of hair tubes in Pentraeth Forest, on the Island of Anglesey, Wales, between June 1998 and March 1999 (see Matthews, 2000 for more details).

the proportion of stripped cones in these species. Figure 8 shows the relationship between the mean number of red squirrels trapped over the course of 1 year at different sites at Spadeadam Forest (Lurz, 1995) and the mean number of red squirrels estimated from the densities of cone cores collected on transects under the different conifer species. Red squirrels adjusted their space and habitat use each year according to the size of the cone crops and this was reflected in the amount and locations of stripped cones for the different conifer species. The good relationship between the mean estimated number of squirrels, based on feeding signs, and the mean annual numbers of squirrels trapped at a site suggests that cone transects may be used to monitor population trends over time (Fig. 8).

Hair tubes

In contrast to feeding signs and dreys, which look similar for both squirrel species, hair tubes can distinguish between red and grey squirrels (Table 1). They can be used to determine the presence of either or both species, as for example at Clackmannanshire, Scotland (Garson & Lurz, unpublished; Table 4) and in Pentraeth Forest, Anglesey (Fig. 9), and to estimate population size. The latter requires a calibration with trapping which has been carried out for red squirrels only at Wauchope Forest and Spadeadam Forest (Garson & Lurz, 1998). In these forests, population estimates were obtained by live trapping and by hair tubes surveys in 11 sites (Table 5). The relationship between the number of tubes used in each site and the

Table 4. Distribution of red and grey squirrels in Clackmannan District in 1996. Data are based on combined hair tube transects (20 tubes per site, checked after 2 weeks) and records of sightings by local residents collected during January–February 1996

Site	Location	Type*	% Hair tubes used		Species of squirrel sighted by residents†
			R	G	
Birkhill	NS 9393	C	25	5	R, G
Gartlove	NS 9392	C	5	15	R
Dollarbeg	NS 9796	M	5	35	R, G
Dollar Glen	NS 9699	M	0	20	G
Arndean	NS 9898	B	0	35	G
Burnbrae Wood	NS 9691	C	5	25	R, G
Gartmorn	NS 9094	C	5	5	–
Lawmuir Wood	NS 9496	C	10	25	R, G
Alva Park	NS 8997	B	0	10	–
Blackmuir	NS 8795	B	0	10	–

*The forest type is indicated by C, conifer; B, broadleaf; M, mixed. †Data referring to red squirrels are indicated by 'R' and grey squirrels by 'G'.

Table 5. Results of hair tube calibration project in 1996 and 1997 (Wauchope and Spadeadam Forest) indicating site composition, the number of tubes with red squirrel hairs and the number of individual squirrels trapped

Year	Site	Tree species	Area (ha)	Trap sequence*	Tubes per site (<i>n</i>)	Tubes used (<i>n</i>)	Squirrels (<i>n</i>)
1996	1	SS NS LP	28	1	20	12	11
1996	2	SS LP	30	1	20	6	5
1996	3	SS LP	34	2	20	18	16
1996	4	SS	32	2	20	5	1
1996	5	SS NS LP	30	1	20	6	8
1997	6	SS	18	1	20	16	6
1997	7	SS NS LP	26	1	20	8	6
1997	8	SS	28	2	20	17	9
1997	9	SS JL	24	2	20	9	5
1997	10	SS LP	35	2	29	25	14
1997	11	SS LP	16	2	11	1	0

SS, Sitka spruce; NS, Norway spruce; LP, Lodgepole pine; JL, Japanese larch.

*1, trapping carried out before hair tube survey; 2, trapping carried out after hair tube survey.

number of individual squirrels trapped (Fig. 10) was investigated using generalized linear modelling (McCullagh & Nelder, 1983). To estimate density requires a definition of the area of forest from which the animals were being sampled. This was difficult to define within these large conifer plantation forests, and introduces an error on the estimate. This is not the case when the numbers rather than densities are considered. Therefore, the number of squirrels trapped at each site was related to the number of tubes used at each site using a model with a Poisson error structure (Table 6). Sixty-six per cent of the variation was explained by the model and thus the relationship may be used to estimate squirrel abundance with moderate accuracy. However, it may be better to use hair tubes to monitor relative trends in population indices over time rather than estimate numbers.

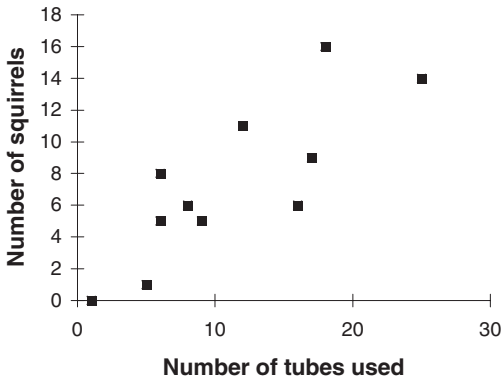


Fig. 10. The relationship between the number of red squirrels present (trapped) and the number of hair tubes used from a hair tube calibration study at Spadeadam and Wauchope Forests ($r_s = 0.85$, $n = 11$, $P < 0.001$) (Garson & Lurz, 1998).

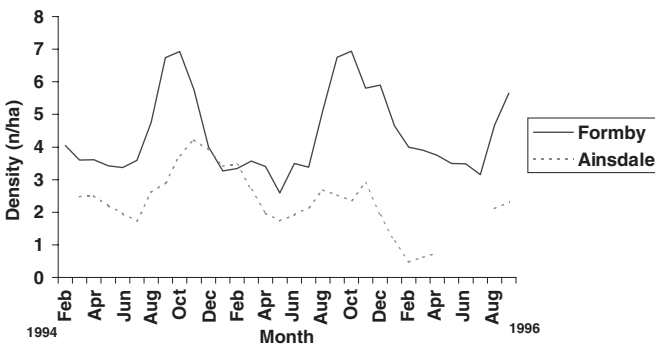


Fig. 11. Estimates of densities using visual counts from coastal pine plantations at Formby Red Squirrel Reserve and Ainsdale NNR, Merseyside, England (from Shuttleworth, 1997). The squirrels at Formby have been provided with supplementary food by visitors to the reserve over a number of years.

Table 6. Results of a generalized linear modelling analysis to predict the number of individual squirrels in the different sites from the number of hair tubes used by red squirrels and the type of tree species mixture [three types were identified: (i) Sitka spruce, (ii) Sitka spruce/Japanese larch or Sitka spruce/Lodgepole pine, (iii) Sitka spruce/Norway spruce/Lodgepole pine]

Regression parameters	Slope coefficient	S.E.	d.f.	Parameter estimate/S.E. (-t)	% Cumulative deviance reduction
Number of tubes used	0.07593	0.01547		$P < 0.005$	
Species mix	-0.3070	0.1404		$P < 0.05$	
Constant	1.656	0.3469		$P < 0.005$	
			8		66

Visual surveys

Two studies have used visual counts successfully to produce estimates of red squirrel densities; Shuttleworth (1997) monitored squirrels in two coastal pine plantations at Formby and Ainsdale in north-west England (Fig. 11), while Bryce *et al.* (1997) studied squirrels in a coastal pine plantation at Fife in east Scotland. The mean monthly density for Formby was 4.4 squirrels per hectare [$n = 32$, coefficient of variation (CV) = 29%], for Ainsdale, 2.3 squirrels per hectare ($n = 28$, CV = 40%) and the mean density from 10 surveys for Fife was 4.0 squirrels per hectare (CV = 70%). A characteristic of these study sites is that red squirrel numbers were high compared with those found in other studies, which generally range from

Table 7. Visual counts of red squirrels made along 1 km transects in different habitat types in Clocaenog Forest, North Wales, in 1992–93; only two grey squirrels were seen during these surveys (Cartmel, 2000)

Habitat type	Age (years)	Surveys (<i>n</i>)	Total number seen	Mean number of squirrels		One sighting per <i>x</i> metres
				per survey	CV (%)	
Norway spruce	> 50	23	5	0.22	194	4600
	< 50	23	5	0.22	238	4600
Sitka spruce	> 50	21	4	0.19	269	5250
	< 50	21	3	0.14	335	7000
Scots pine and Japanese larch	> 50	23	40	1.74	123	575
	< 50	21	7	0.35	168	3000
Total		132	64	0.49	235	2063

CV, coefficient of variation.

Table 8. Visual counts of red and grey squirrels made along 1–1.2 km transects in broadleaf and conifer habitats in Cumbria (Sarah Bentley & Corrie Bruemmer, unpublished)

	Grey squirrels		Red squirrels		Both species	
	Broadleaf	Conifer	Broadleaf	Conifer	Broadleaf	Conifer
Number of woods surveyed	9	7	9	7	9	7
Total number of surveys	45	48	45	48	45	48
Total number of squirrel seen	2	1	25	77	27	78
Average number of squirrel seen per survey	0.04	0.02	0.56	1.6	0.6	1.63
Coefficient of variation (%) of squirrels seen per survey	550	700	163	120	160	117
Average number seen per kilometre	0.04	0.02	0.48	1.36	0.52	1.38
One sighting per <i>x</i> metres	25 800	56 700	2064	736	1911	727

>0.1 to 1.4 squirrels per hectare (e.g. Gurnell, 1987; Lurz *et al.*, 1995). Consequently, the number of squirrels seen during visual counts was also high. For example, at Fife the number of squirrels seen on each survey along a 2-km transect averaged 15 squirrels (CV = 38%). Adequate sample sizes enable the visual belt either side of the transect line to be estimated, and hence the density of animals calculated (cf. Buckland *et al.*, 2001; Gurnell *et al.*, 2001). A problem with most other visual count studies of red squirrels (all types of woodland) or grey squirrels (conifer forests only), in Britain, is that very few animals are sighted on the transects in any one survey. This makes density estimation difficult, if not impossible. This is illustrated by studies carried out in North Wales (Table 7) and Cumbria (Table 8). These low counts are partly a function of low detection probabilities in some habitats, especially dense conifer (see Table 7), and partly because squirrel densities are actually relatively low in some habitats. Unless independent live trapping is carried out, it is not possible to disentangle these two effects.

When the number of sightings is low, the results for transect lines can be pooled in space and/or time, or the variation among transects used in the analysis. There are two studies where this has been carried out. The first was on Jersey in the Channel Islands, where live trapping was also carried out. The visual counts were carried out on two or three line transects in each of three different study areas monthly between 1995 and 1997 (Table 9; see Magris, 1998). The mean number of squirrels seen per survey were better than those seen in

Table 9. Visual counts of red squirrels made along transects lines in three mixed broadleaf study areas on the Island of Jersey, Channel Islands (Magris, 1998)

Study area/transect line	Length (m)	Surveys (<i>n</i>)	Squirrels seen (<i>n</i>)	Average number seen per survey	CV (%)	One sighting per <i>x</i> metres
St Peters – lower	370	32	21	0.66	200	564
St Peters – middle	210	32	12	0.38	148	560
St Peters – upper	400	32	14	0.44	164	914
Railway walk – lower	450	32	35	1.09	144	411
Railway walk – middle	420	32	32	1	127	420
Waterworks – lower	520	32	12	0.61	162	1387
Waterworks – middle	450	32	24	1.16	155	600

CV, coefficient of variation.

Table 10. Visual counts of grey squirrels made along 1 km transects lines repeated on three consecutive days in pine forest at Thetford, East Anglia (Janie Steele, Amanda Lloyd & John Gurnell, unpublished)

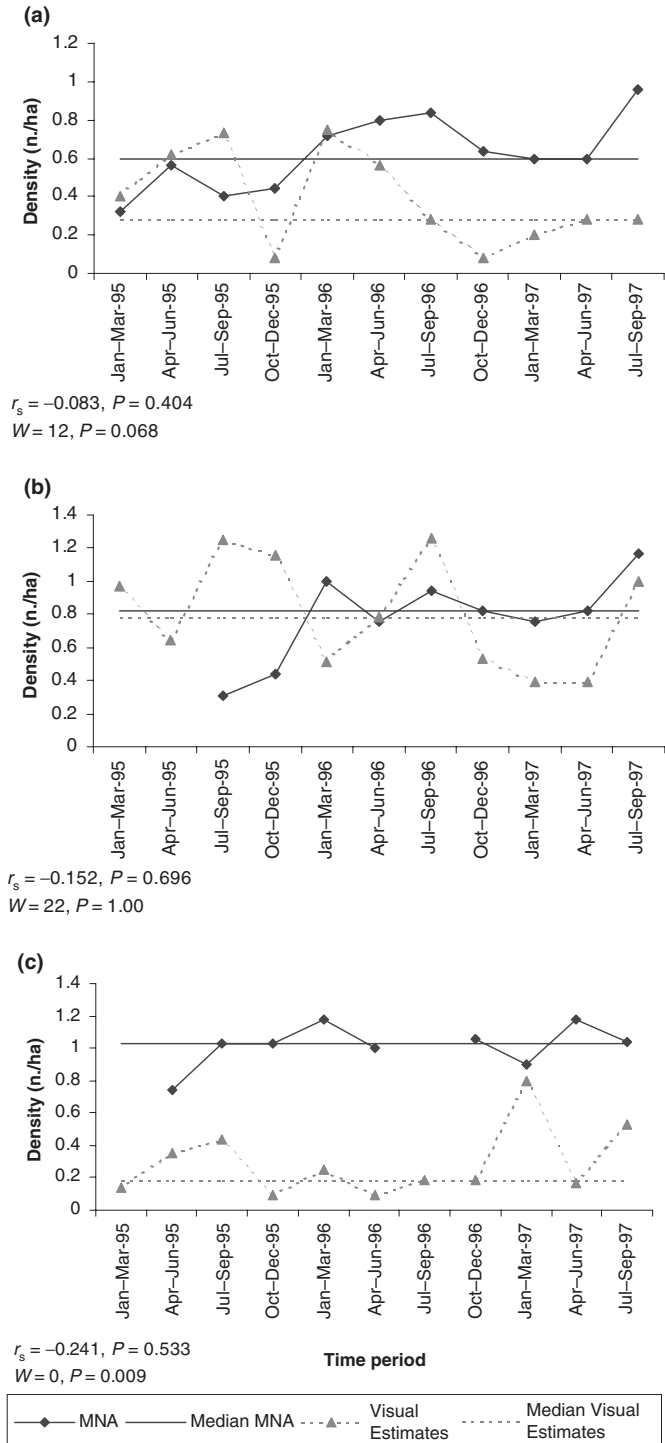
Area	Month	Transect line	Surveys (<i>n</i>)	Squirrels seen (<i>n</i>)	Average number seen per survey	CV (%)	One sighting per <i>x</i> metres	Density for each area (no./ha)
A	July	A1	3	12	4.0	100	250	0.54
		A2	3	15	5.0	53	200	
	August	A1	3	44	14.7	31	68	1.88
		A2	3	54	18.0	15	56	
B	July	B1	3	1	0.3	173	3000	0.22*
		B2	3	4	1.3	87	750	
	August	B1	3	11	3.7	57	273	0.63
		B2	3	7	2.3	25	429	

*Too few animals seen to reliably estimate density.

the Welsh and Cumbrian studies, but was still small (mean number seen per survey = 0.61, CV = 176%, $n = 224$), although survey lines were short because of the configuration of the woodlands. Live trapping was also carried out in the study areas for 7–10 days (i.e. until >90% of captured animals were recaptures) in January, April, July and October each year. This enabled comparisons to be made between estimates of density derived from the live trapping and visual counts (Fig. 12). The correlation between the two density estimates was poor in all three study areas and there was a significant difference in the long-term median density estimates in two of the three study areas.

The second study was carried out on grey squirrels in two study areas (area A 47 ha and area B 52 ha; the areas were 2 km apart) in Corsican and Scots pine compartments in Thetford Forest, East Anglia (see Gurnell, 1996c). The visual counts were carried out on three 1200 m lines in each study area on three consecutive days in July and in August 1997. Numbers seen varied considerably from day to day, between periods and between study areas (Fig. 13). Day-to-day variation may result from differences in weather conditions affecting activity patterns, and differences in patch utilization for food. In general, numbers seen were considerably higher 1 month later in August than they were in July. There were no significant differences among the four transect lines in July (Friedman's $\chi^2 = 5.68$, d.f. = 3, $P = 0.09$, using day counts as blocks), but there were in August (Friedman's $\chi^2 = 7.93$, d.f. = 3, $P = 0.0035$). *Post hoc* pairwise comparisons showed that there was no differences between the two lines within the study areas, but there were differences among the lines from the two study areas (Table 10).

Fig. 12. Minimum number alive (MNA) estimates of densities based on live trapping and density estimates from visual surveys derived using the graphical method (see Gurnell *et al.*, 2001) of red squirrels for three study sites on the Island of Jersey, Channel Islands, 1995–97. (a) St Peters Valley, (b) Railway Walk, (c) Waterworks Valley. r_s , Spearman's correlation coefficient between MNA and visual count estimates; W , Mann–Whitney statistic for comparing median live trapping and visual count estimates. Horizontal bars are long-term median values. Live trapping was carried out in January, April, July and October. Visual counts were based on pooled monthly surveys for each of the study areas for periods of 3 months starting in January, April, July and October.



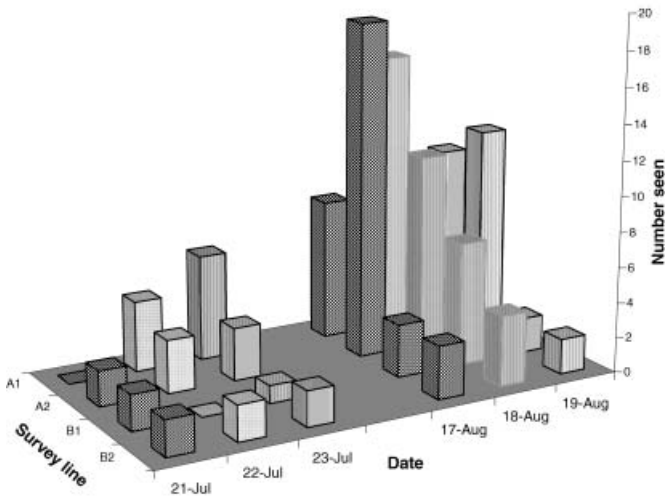


Fig. 13. The number of grey squirrels seen on each of three transect lines on three consecutive days in two pine plantation study areas in Thetford Forest, East Anglia, in 1997 (Janie Steele, Amanda Lloyd & John Gurnell, unpublished).

Many of the findings reported here undermine confidence in the use of visual surveys to estimate squirrel densities, especially when the numbers of sightings per survey are low. The Thetford results indicate the benefit of replicating transect lines in time and space. Grey squirrels usually occur at densities of 2 to >8 per hectare in broadleaf woodland but visual surveys have not been carried out in Britain. Healy & Welsh (1992) concluded from their studies on grey squirrels in USA that visual time-area counts are suitable for estimating grey squirrel abundance, especially when sighting rates are >1 per kilometre, although they had no independent estimates of numbers derived from live trapping.

Estimates of power efficiency

The results from the power analysis (Fig. 14a–f) indicate that all cases, particularly the largest population changes ($\pm 25\%$), achieve sufficient statistical power to be confident of a true population change. The graphs illustrate the numbers of samples that are needed and this increases with a decrease in population change. It should be noted that in all cases power was calculated to be greater for decreases in population density than increases. This is an artefact of the method used; by artificially decreasing population densities for the power calculation, the variance in the density estimates is also decreased, and therefore power is increased. Of the monitoring methods analysed, hair tube lines and drey counts needed the fewest number of samples to detect population change confidently.

Figure 15 compares the different methods based on the number of samples needed to achieve a power of 60% (i.e. there is a 40% chance of accepting a false hypothesis of no change). The large number of samples needed are a reflection of the variability in the data in the example studies. For example, seed/cone density (and therefore squirrel abundance) is highly patchy in conifer plantation forest (Lurz, 1995), and therefore results collected on replicate lines have high variation within years. The larger the monitoring area and the spatial variation in the indices of population density (i.e. feeding remains, dreys, tube hits and sightings), the more difficult it is to reliably detect population change and larger the number of samples are needed.

We have therefore also looked at the number of samples needed to monitor at the level of the individual study site (40–60 ha) and used available hair tube data over 4 years (1995–98).

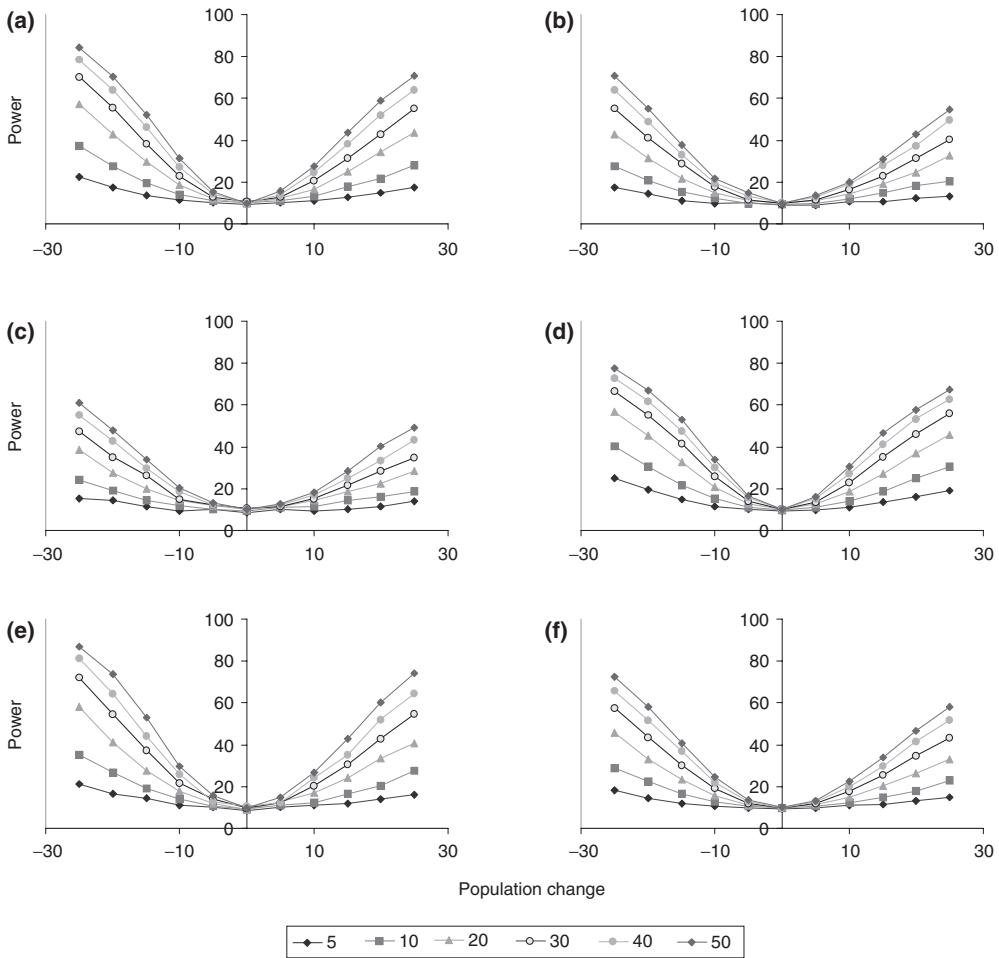


Fig. 14. The average power to correctly reject a null hypothesis of no population change for different sample sizes (number of transects in a monitoring study). (a) Drey counts for red squirrels in Belgium, (b) visual counts for red squirrels in Jersey, (c) feeding transects for red squirrels in Spadeadam Forest, (d) drey counts for grey squirrels in the UK, (e) hair tubes for red squirrels in Wauchope Forest, (f) feeding transects for grey squirrels in Thetford Forest.

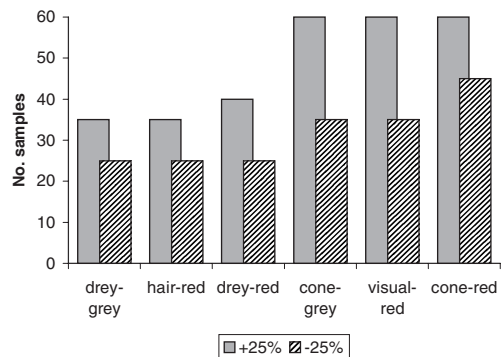


Fig. 15. A comparison of the minimum number of samples required to achieve a power of 60% for the different monitoring methods. Only the largest population changes are considered. Drey-grey, drey counts for grey squirrels; hair-red, hair tubes for red squirrels; drey-red, drey counts for red squirrels; cone-grey, cone counts on feeding transects for grey squirrels; visual-red, visual counts for red squirrels; cone-red, cone counts on feeding transects for red squirrels.

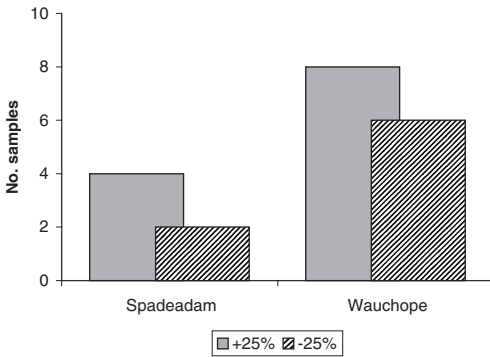


Fig. 16. Number of hair tube samples (transects) needed to detect population change (at 60% power) in specific plantations between 1995 and 1998 at Spadeadam and Wauchope Forests.

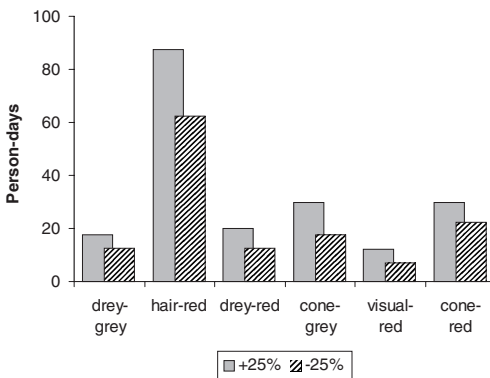


Fig. 17. Comparison of the effort per transect line required to achieve a level of 60% power for drey counts (0.5 person-days), visual transects (0.2 person-days), cone transects (0.5 person-days) and hair tube lines (2.5 person-days). Drey-grey, drey counts for grey squirrels; hair-red, hair tubes for red squirrels; drey-red, drey counts for red squirrels; cone-grey, cone counts on feeding transects for grey squirrels; visual-red, visual counts for red squirrels; cone-red, cone counts on feeding transects for red squirrels.

Figure 16 contrasts a site at Spadeadam Forest (stable annual numbers) with a site at Wauchope Forest (fluctuations in annual numbers). The results illustrate that very few samples (range 2–8) are required to detect population change for monitoring known local populations. There were not enough suitable data to carry out this type of analysis for the other three monitoring methods and more field data are needed at both the site and the landscape (e.g. forest) scale.

Effort

Based on our estimates of person-days, we compared the four monitoring methods to determine the relative effort required to detect population change with the number of samples needed to achieve the 60% level (see Figs 15 and 17). Visual transects, followed by drey counts, would be more economical in terms of person power for monitoring squirrel populations than cone transects or hair tubes with the latter requiring the most effort (Fig. 17).

DISCUSSION

To estimate the population size of squirrels directly requires the use of mark-recapture live trapping techniques that are both time consuming and depend on expertise in handling live animals efficiently and humanely. This provides data on relative population size as well as information on breeding activity and condition of the animals. However, for many types of monitoring work, limited time, money and the required experience in trapping and handling means that this is not an option. Thus, there is a need to develop practical ways to monitor changes in indices of squirrel numbers through time. Only one of the four indirect methods considered here, visual counts, involves monitoring individual animals. The other three

methods monitor signs of the presence of squirrels, i.e. hairs left in tubes, cones that have been eaten or dreys in trees. However, if the methods are used in a standard way, then relative changes in indices (sightings, hair tube visits, cone cores or dreys) can be useful without the need to convert the indices to squirrel numbers or densities. Nevertheless, estimates of numbers or densities are often required. For feeding signs, hair tubes and dreys, indices have to be changed into numbers of squirrels, and then, for all methods, numbers have to be changed into densities. Errors will occur at both these stages. Trying to comprehend the area of woodland in which the squirrels live is a particularly thorny problem, especially for feeding signs and hair tubes. Ideally, the results from applying each method in each study site should be calibrated against independent estimates of squirrel densities derived from live trapping. However, for the reason stated above, this cannot be justified in most cases, and so the findings have to be interpreted using the results from studies carried out elsewhere. This again introduces error, and a problem that we have encountered in reviewing these methods is that too few studies have attempted to calibrate the indirect methods, and no studies have attempted to evaluate the precision of the calibration or the reported changes in population size. This is despite the fact that statistical power analysis has been advocated as a tool to improve study design and assess the biological significance of results in animal studies (Thomas & Juanes, 1996; Steidl, Hyes & Schaubert, 1997; also see Gerrodette, 1987, for an example concerning monitoring Californian sea otter *Enhydra lutris* populations).

One particular application of squirrel-monitoring methods concerns the numbers and distribution of red and grey squirrels in areas of overlap. Only two methods, visual surveys and hair tube surveys, are suitable in these situations and there are potential complications in the use of both methods. In the case of visual surveys, a clear sighting is necessary to identify the squirrel as being red or grey, and, especially at a distance in the canopy, it is not always easy to distinguish the two species. A decision has to be made on whether to record the squirrel as red, grey or 'uncertain'. More than one or two 'uncertains' on a transect walk will make it virtually impossible to estimate the numbers of red and grey squirrels separately. The possible complication with hair tubes in areas of overlap between the two species is that red squirrels may be deterred from entering tubes after grey squirrels have visited them. Red and grey squirrels are known to have used the same hair tubes (Jean Matthews, personal communication; Sandro Bertolino, personal communication), as they have dreys (e.g. Reynolds, 1981, based on hairs left in dreys and so the order of occupancy was not known, Kenward & Hodder, 1998), nest boxes (e.g. Gurnell & Taylor, 1989, based on hairs and so the order of occupancy was not known) and traps (e.g. there was no trap avoidance by red squirrels after greys had entered traps in the extensive studies of red and grey squirrel competition in the north of England and Italy, see Wauters & Gurnell, 1999; Wauters, Lurz & Gurnell, 2000; Wauters *et al.*, 2001a,b; Wauters, Tosi & Gurnell, 2002; also see Kenward & Hodder, 1998). The balance of evidence suggests that there is no deterrent effect by greys on reds at hoppers, feeding stations or traps, but further, specific studies would be of interest.

Errors in the population status can affect management decisions and ultimately the survival of the species concerned (Reed & Blaustein, 1997). Our results for red and grey squirrels illustrate that the number of samples required to detect population change is likely to differ according to the method used and the spatial scale of the monitoring programme. We have not dictated any particular area of woodland in our power analysis, although guidelines on the density of samples have been given by Gurnell *et al.* (2001). For example, it has been suggested that one feeding transect should be used in every 4 ha of woodland. The power analysis suggests that up to 60 transect lines may be necessary which would be equivalent to about 240 ha of woodland. Clearly, this is a large task, and one would not

Table 11. Some of the practical problems associated with using squirrel monitoring methods

Method	Practical problems
Visual surveys	The probability of detecting a squirrel is often very low The probability of detection varies greatly among habitats Needs a good sighting to distinguish red from grey squirrels Squirrels may react to the presence of the observer and hide For density – estimating the perpendicular distance of the squirrel to the transect line can be difficult
Hair tube surveys	May be more effective when squirrels are moulting Requires the use of microscopes for examining hairs, and removing hairs from the tapes can damage or tear them Calibration has only been done for red squirrels in Sitka spruce-dominated plantations
Drey counts	Do not distinguish species Dreys can be difficult to see in the canopy and may be confused with bird nests Dreys often hidden among epiphytes In old woods, squirrels may nest in dens (holes) in trees rather than dreys There are no data available on drey use by grey squirrels in conifer
Feeding transects	Do not distinguish species Only in conifer Estimating density is complex and involves estimating how much food energy is in the cones that the squirrels eat

want to pack such a large number of units into a small area – it rather defeats the idea of an easy-to-use method.

The findings presented are a first attempt in assessing the precision of available methods in detecting population change based on published data. All the methods have their advantages and disadvantages (see Table 11 and Gurnell *et al.*, 2001) and all can be used to monitor relative changes in numbers or habitat utilization. However, none of the methods gives estimates of population density that provide a high degree of confidence. As a result of the inherent variability in each of the methods, they all have a low precision, requiring between 25 and 60 samples to achieve a power of 60%. On this basis, we find it difficult to advise that such a large number of samples must be used. Hair tube surveys and drey counts required the fewest number of samples to detect population change, however, visual transects and drey counts were more economical. Nevertheless, it does not seem sensible to suggest one method is better than another, and the one to use will depend on the biological questions asked and the local circumstances in terms of available resources, habitat composition and individual preference. Other possible monitoring methods, such as road casualties (Brandl *et al.*, 1991), snow tracking (e.g. Pulliainen & Jussila, 1995), the use of nest boxes (e.g. Shuttleworth, 1999) and focal feeding points, give information on squirrel presence and to some extent abundance, but there is a need to compare their relative effectiveness and cost in combined studies.

CONCLUSIONS

Our main conclusions are that none of the monitoring methods discussed here appear to be very precise. It is unlikely that the large number of samples required to be confident about detecting real population change would be used in most surveys as this would need a considerable commitment in terms of time and money. Thus it may be best to monitor squirrels only in terms of relative changes in numbers or indices of numbers through time. However, our initial assessment is based on data collected from different sources for different purposes, and there is a need to carry out a comprehensive assessment of all the methods for

both species, with independent validation and combined with a power analysis. Monitoring programmes also need to be carefully planned in relation to the scale of the survey in order to be able to detect real population changes (e.g. Stalmans *et al.*, 2001). Species-specific, quantitative thresholds to determine the significance of detected declines may need to be established for threatened UK mammals (see Reed & Blaustein, 1997). Squirrel population sizes fluctuate widely in relation to changes in seed crop patterns (Gurnell, 1987) and observed population declines in red squirrels, for example, may need to be assessed in relation to what would constitute a significant decline and whether they require management intervention.

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APPENDIX

Studies used as source of monitoring data in the paper

Study area	Forest type	Species	Monitoring method				Reference
			Drey	Feed	Visual	Hair	
Thetford Forest, Norfolk	Conifer (predominately Corsican and Scots pine)	Red*	X				Rex Whitta, unpublished
		Grey	X				Steel, Lloyd & Gurnell, unpublished
		Grey		X			Gurnell & Steele, unpublished
Spadeadam Forest, Cumbria	Conifer (predominately Sitka spruce)	Red		X		X	Garson & Lurz (1998); Lurz (1995)
Formby and Ainsdale, Merseyside	Conifer (predominately Scots and Corsican pine)	Red			X		Shuttleworth (1997)
Tentsmuir, Fife Cumbria	Conifer (predominately Scots pine) Conifer/broadleaf	Red Red/grey			X		Bryce <i>et al.</i> (1997) Bentley & Bruemmer, unpublished
Wauchope Forest, Scotland	Conifer (predominately Sitka spruce)	Red/grey				X	Garson & Lurz (1998)
Clackmannan District, Scotland	Mixed conifer/ broadleaf	Red/grey				X	Garson & Lurz (unpublished)
Clocaenog Forest, North Wales	Conifer (predominately Sitka spruce)	Predominately red/some grey			X		Cartmel (2000)
Pentraeth Forest, Anglesey	Mixed conifer	Red/grey				X	Matthews (2000)
The Island of Jersey, Channel Islands	Mixed broadleaves	Red			X		Magris (1998)

Drey, drey counts; feed, feeding transects; visual, visual surveys; hair, hair tubes.

*Only red squirrels were present in this part of Thetford Forest at the time of these drey counts (1974); now grey squirrels are found throughout Thetford and red squirrels are rare or absent altogether (Gurnell, unpublished).