

The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England

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Summary

1. The population ecology of grey squirrels *Sciurus carolinensis* living in a 9-ha oak *Quercus robur* wood in southern England was studied between 1976 and 1987 using live-trapping techniques. Trapping was carried out in winter, spring and summer. The availability of tree seeds during the autumn of each year, and the severity of cold weather over each winter were also measured to examine their effects on squirrel population dynamics.

2. Capture probabilities of squirrels in winter, and to a lesser extent in spring, were inversely related to food availability and data from these two seasons were not considered dependable. The analyses concentrated on the summer populations.

3. The long-term average summer density of squirrels was high at 8.8 ha^{-1} (SE 3.41 ha^{-1}) demonstrating that the oak wood was high quality habitat for grey squirrels. Over 10 of the 12 years, summer densities were remarkably similar, ranging between 7 ha^{-1} and 10 ha^{-1} (mean 8.5 ha^{-1} , SE 0.95 ha^{-1}). However, numbers were driven upwards in 1977 to a density approaching 18 ha^{-1} and downwards in 1982 to a density of about 3 ha^{-1} : a 6-fold difference.

4. In good seed years, breeding starts in December, in poor seed years the start of breeding is deferred until the spring. There was no or very little spring breeding in 5 years when food supplies were poor. Female reproductive success was positively associated with food availability. Partial correlation analysis showed that the level of association was not improved when the effects of winter weather were taken into account. The number of new adult females in the summer population was positively associated with food availability but there was no association between new males and food. This suggests that food availability is more important to breeding females than breeding males.

5. Persistence from summer to winter was positively associated with food availability, but persistence from summer to spring and to the following summer were not. Partial correlation analyses showed that the severity of winter weather tended to mask the effects of food availability on persistence and the partial correlation coefficients were higher when the effects of weather were held constant. Adult females had the highest persistence between summers (52%, $n = 11$, SE 6%), followed by juvenile females (38%, $n = 7$, SE 8%), adult males (36%, $n = 11$, SE 4%), and juvenile males (21%, $n = 7$, SE 7%). The persistence of adult males but not females was inversely related to the initial number of males present.

6. In males, there was no significant difference in winter body mass between years and winter body mass was not associated with food availability, although there were very few data for winters when the food supply was good. In 7 years when the food supply was poor to moderate, there was an increase in mean body mass between summer and winter in 4 years, and a decrease in 3 years.

7. The data were explored using ordination techniques; first a standardized principal component analysis and then the canonical form of principal component analysis or redundancy analysis. The analysis was carried out on years derived from MNA of males and females and various combinations of the environmental variables: food

availability (FOOD) and the severity of winter weather (TEMP). The ordination biplots clearly showed the high correlation between MNA males and MNA females and that FOOD was the most important environmental variable. TEMP on its own had no effect but FOOD \times TEMP was important.

8. Following on the exploratory data analysis and for predictive purposes, a general linear model between the numbers of squirrels in the summer populations and sex, FOOD and FOOD \times TEMP as explanatory variables accounted for 77% the variance in squirrel numbers among years.

9. This study shows that tree seed availability is the most important factor limiting grey squirrel densities, but this factor both positively and negatively interacts with the severity of winter weather to affect grey squirrel population dynamics.

Key-words: *Sciurus carolinensis*, demography, population dynamics, food supply, weather.

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Introduction

Although opportunists and generalists, the primary food source for tree squirrels is tree seeds and it is not surprising that their population ecology is closely associated with the availability of seeds (Gurnell 1983, 1987). The size of tree seed crops varies considerably among tree species, sites and years (Silvertown 1980; Fenner 1991; Gurnell 1993) and is largely unpredictable (Gurnell 1983). Consequently, the amplitude of the annual cycle of numbers in squirrel populations, and their distribution among different forest habitats, varies among years (Gurnell 1983; Gorman & Roth 1989). Grey squirrels, *Sciurus carolinensis* Gmelin, were introduced into Britain from eastern North America several times between 1879 and 1920 (Shorten 1954) and are now found throughout much of England, Wales and parts of Scotland. Their range continues to expand with the consequent loss of the native red squirrel, *S. vulgaris* L. (Gurnell & Pepper 1993). Grey squirrels also cause a considerable amount of economic damage to forests by removing bark from trees (Kenward 1983, 1989; Gurnell & Pepper 1988) and they may hinder the establishment of new woodland (Gill *et al.*, 1995). The main tree damage period in Britain is between April and July when cambial activity is high, the bark is easy to peel and natural foods, such as tree seeds, leaf buds and flowers, and fungi are scarce (Gill 1992; Gurnell & Pepper 1988). Although squirrels eat the phloem tissue, bark stripping is not caused by a shortage of food because damage still occurs close to food sources such as poison hoppers. However, damage has been positively linked to squirrel numbers during the damage period, especially the number of juveniles (Rowe 1983; Kenward & Parish 1986), and it is believed that it may be influenced by antagonistic interactions among members of the population at this time (Kenward 1983; Gill *et al.*, 1995). Accordingly, the number of juvenile squirrels present and the overall population size dur-

ing the damage period, and consequently the amount of damage caused, are related to the size of the tree seed crop the previous autumn (Gurnell 1983, 1989).

The use of warfarin poison is the only cost-effective method of controlling grey squirrels currently available (Pepper 1990), and a priority of management is to minimize its wide-scale use as much as possible (Gurnell & Pepper 1988). The intention of this paper is to provide a firm baseline to how much control should be applied in situations where grey squirrels are a pest. The paper examines the predictive relationship between two important but easily quantified environmental variables, tree seed availability and winter weather, and the population dynamics of grey squirrels over a 13-year period in a high-quality habitat and in the absence of control.

Methods

The study was conducted in a 9 ha, 170-year-old oak (*Quercus robur* L.) wood in Alice Holt Forest on the borders of the counties of Hampshire and Surrey in southern England (Grid Ref. SU 801 435). In addition to oak, which dominated the tree canopy, there were several large beech (*Fagus sylvatica* L.) and sweet chestnut (*Castanea sativa* Mill.) trees (see Gurnell 1993). The understorey consisted of hazel (*Corylus avellana* L.) with occasional holly (*Ilex aquifolium* L.) and hawthorn (*Crataegus monogyna* Jacq.). Where there were gaps in the canopy resulting from tree fall the ground vegetation was well developed, notably bracken (*Pteridium aquilinum* L.) and bramble (*Rubus* spp.), as well as forbs and grasses. Further details of the study area are presented by Ludolf (1986).

The study area was bounded on the northern side by a railway line, which acted as an effective barrier to squirrel movement, and 0.5 ha of woodland adjacent to the railway was clear-felled in 1978 (Fig. 1). There was a mixture of woodland on the other three sides of the study area which did not act as a barrier to

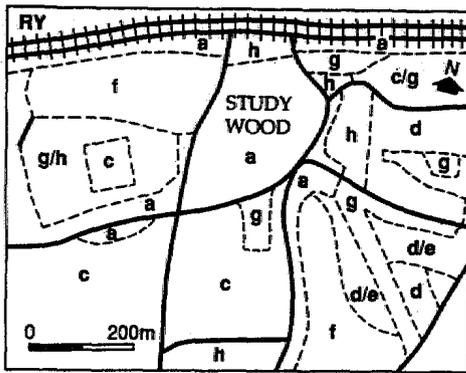


Fig. 1. Map showing the study wood and surrounding habitats. Solid lines = roads and tracks, dotted lines = habitat boundaries, RY = Railway, a = mature oak, c = immature hardwoods, d = mature Corsican pine, e = mature Scots pine, f = immature conifer, g = other mature conifers, h = rough grassland.

squirrel movement. To the west was a young Norway spruce (*Picea abies* L.) plantation planted in 1966, and an open grass and picnic area. To the south there was a forest track and a young oak plantation, planted in 1956, and to the east was a road and then a Corsican pine (*P. nigra* Arnold) plantation and an area of clear-fell.

Grey squirrels numbers were not controlled in Alice Holt Forest over the period of the study.

SQUIRREL TRAPPING

Between 1976 and 1988, grey squirrels were studied by standard capture-mark-recapture methods during the winter (January), spring (April, but not in 1976 and 1977) and summer (June–July), using Legg multi-capture traps (Rowe 1980). Ten traps were evenly placed throughout the wood. Dubock (1979) had used similar methods to study the same squirrel population between 1973 and the winter of 1975.

The traps contained maize as bait and were covered with waterproof sheeting and leaf and woody debris in such a way that the insides of the traps were kept dry and dark. The traps were prebaited with whole maize for 7 days before being set. Two rounds of the traps were made each day, between 3 and 5 h after sunrise and as late in the evening as possible before dark. Trapping was carried out for between 7 and 17 rounds depending on the number of new animals being trapped and the weather. Trapping was discontinued after 7 rounds when a total of only one or two new individuals were captured on rounds 5, 6 and 7, or when the weather was very cold and/or very wet. An exception to this was in the summer of 1977. Very large numbers of individuals were captured at this time and 17 trap rounds in June were followed by a further 13 trap rounds 3 weeks later in July. Over the entire study period, 700 individuals were captured a

total of 2350 times; no trap mortalities occurred during this time (see Gurnell 1987).

Each individual captured was uniquely marked by toe-clipping, weighed to the nearest 5 g using a spring balance, and its sex and breeding condition noted. The reproductive condition of males was based on the size and position of the testes. Breeding males had large scrotal testes; non-breeding animals had small testes. Females were recorded as non-breeding, lactating or had recently finished lactating. Grey squirrels were handled in a wire mesh handling cone and it was not always easy to decide if a female was pregnant. Females were only classified as being pregnant if it was clear from their body mass and size of abdomen. Consequently, the number of females pregnant is likely to be underestimated. In addition, the recording of female breeding condition was considered unreliable in the first summer (1976), and data for this year are omitted. Juvenile animals less than 6 months old were identified in the summer samples on the basis of body mass, condition of the pelage and by the lack of breeding condition.

Squirrels may breed twice in a year. They may enter breeding condition in mid-winter (e.g. December–January) with litters produced in the spring (e.g. March–April), followed by a second breeding pulse with litters produced in the summer (e.g. July–August) (Gurnell 1983, 1987). The time from conception to weaning is about 16 weeks and so juveniles captured during the summer sample result from matings which occurred in March or earlier. Thus, the summer samples do not include juveniles which may be recruited from matings after this time. An index of reproductive success has been taken as the number of juveniles captured in the summer per adult female.

Grey squirrels are not attracted to traps when tree seeds are available (Gurnell 1983, 1987; Perry *et al.* 1977). For this reason capture probabilities, here defined as the number of individuals captured of those known to be alive, are invariably very low during the autumn and no attempt was made to systematically sample the population at this time of the year. Also, capture probabilities are often poor during the winter, and sometimes through to the following spring, depending upon the size of the previous autumn's seed crop. Information from Dubock's study was used to calculate capture probabilities for 1976. The trapping results for the last year of the study, 1988, from winter through to autumn, were consistently very poor. This was a result of a large seed crop in the autumn of 1987 and food availability must have been good throughout the year. Consequently, population data for the winter, spring or summer 1988 have not been presented.

MONITORING SEED AVAILABILITY

The fall of oak, sweet chestnut, beech and hazel seeds between 1975 and 1987 was monitored using 75 coni-

cal seed traps (catching area 0.17 m²) placed at the intersections of a 30 m × 30 m grid within the wood. A canvas seed bag was tied around the hole at the bottom of each trap during periods of seed collection which lasted from August until seed fall had stopped; this was in October or November in most years. The seeds were removed from the bags every 2–3 weeks except in 1976 when they were removed every week. The counts of seeds available were converted to a quantity of seed energy available per hectare using the mean dry weights and the calorific values of the seeds. Full details are presented by Gurnell (1993). This index of seed availability has been denoted FOOD.

WINTER WEATHER

Daily weather records were obtained from the Alice Holt Meteorological Station situated some 400 m from the study area. A similar index of the severity of winter to that developed by Gosling (1981) in his work on coypu (*Myocastor coypus* Molina) was adopted. This cold weather index, called TEMP, for a particular winter (taken from the previous November to March of the year in question) is calculated from the sum of the squares of the runs of days with minimum temperatures $< 0^{\circ}\text{C}$ and maximum temperatures $< 5^{\circ}\text{C}$. Thus, the higher the index, the more severe the weather during this time.

DATA ANALYSIS

Population analyses

Because of wide variations in trap success in winter and spring, the summer population data are considered the most reliable and the analyses have concentrated on this season. However, the complete data set has been used to estimate summer male and female population sizes using a modified Jolly–Seber model with bootstrap standard errors and confidence intervals after Buckland (1980). The minimum number of animals known to be alive (MNA) was only slightly lower than the Jolly–Seber estimates and fell within the Jolly–Seber lower 95% confidence interval. Survivorship curves for adults and juveniles have been estimated by a mark–recapture survival analysis using the modified Jolly–Seber model (Buckland 1982). The time base used for estimating the survivorship curves was half-years from winter and summer data. Because MNA estimates were similar to Jolly–Seber estimates of population size, and in order not to lose information from the beginning and end years of the study, other demographic analyses have been based on MNA.

Statistical analysis

To search for patterns among the TEMP and FOOD environmental indices and various demographic vari-

ables from the summer populations, exploratory analyses using correlation and partial correlation techniques have been used. Sample sizes are small with only 12 years of data. Moreover, the FOOD and TEMP variables are not normally distributed and the use of transformations of these variables to normalize them, and of non-parametric rank correlation analyses were explored. However, with a sample of only 12 years, the selection of a transformation to normalize satisfactorily the information proved to be difficult and, further, the use of rank correlations yielded low correlation estimates as a result of generalization of the sample information. Thus, I decided to estimate Pearson's correlation coefficients as descriptors of the level of association between variables without inferring statistical significance.

The data have been explored using standardized Principal Component Analysis (PCA) on years based on male and female numbers, and the canonical form of PCA, redundancy analysis, which incorporates environmental variables, using CANOCO software. General linear models have been used to develop a model for estimating population size from combinations of the environmental variables TEMP and FOOD, using SAS software. Means and standard errors (SE) or coefficients of variation (CV) have been used as the measures of variation where appropriate.

Results

TRAPPING SUCCESS

Male capture probabilities were significantly negatively associated with FOOD in all seasons; in contrast a significant negative correlation in females was only obtained for winter data (Table 1). However, the summer correlation coefficient between male capture probabilities and FOOD is deceptive in that capture probabilities were consistently high at this time (mean 0.90, range 0.82–0.97; Table 1).

Probabilities of capture were slightly higher in males than females in the summer ($F_{1,20} = 5.62$, $P = < 0.05$). A possible explanation for this is that females are less trappable when nursing young. Overall, however, a two-way analysis of variance of capture probabilities among sexes and seasons did not reveal any sex-season interaction ($F_{2,60} = 0.30$, $P > 0.05$), or a significant difference between the sexes ($F_{1,60} = 0.92$, $P > 0.05$), but there was a significant difference among seasons ($F_{2,60} = 9.56$, $P < 0.001$). Capture probabilities were lowest in winter but there was a lot of variation among years because of differences in food availability. Capture probabilities were intermediate in spring with less variability, and highest in summer with least variability (Table 1).

The relationship between FOOD and winter capture probabilities (Table 1) were particularly influenced by the result for 1979 (Fig. 2). The seed index was not high over this winter but seed fall was late in

Table 1. Probability of capture, expressed as the proportion captured of the numbers known to be alive. r = correlation coefficient between the probability of capture and FOOD, an index of the size of the previous autumn's seed crop

Year	Winter		Spring		Summer	
	Male	Female	Male	Female	Male	Female
75						
76	0.63	0.43			0.85	0.68
77	0.05	0.00			0.82	0.91
78	0.76	0.80	0.31	0.24	0.97	0.85
79	0.08	0.09	0.43	0.43	0.84	0.48
80	0.67	0.74	0.71	0.79	0.95	0.71
81	0.77	0.70	0.78	0.63	0.92	0.93
81	0.83	0.88	0.88	0.89	0.93	0.60
83	0.50	0.43	0.91	0.85	0.82	0.88
84	0.34	0.37	0.78	0.67	0.97	0.87
85	0.77	0.59	0.88	0.78	0.96	0.97
86	0.11	0.10	0.06	0.32	0.83	0.60
87	0.88	0.79	0.90	0.92		
<i>n</i>	12	12	10	10	11	11
Mean	0.53	0.49	0.66	0.65	0.90	0.77
CV(%)	58	62	45	37	7	21
<i>r</i>	-0.75	-0.76	-0.71	-0.53	-0.66	-0.03

1978, which may have resulted in an underestimate of seed availability earlier in the autumn, and seeds continued to be available on the forest floor through to March 1979 (Gurnell 1993). When the data for 1979 are left out, the correlation coefficient between FOOD and winter capture probabilities increases to -0.86 for males and -0.85 for females (no statistical significance for correlation coefficients is inferred: see Methods).

POPULATION NUMBERS

Jolly-Seber estimates for summer population size with 95% confidence intervals, and MNA for males and

females are shown in Fig. 3. MNA values were only slightly lower than the Jolly-Seber estimates and fell well within the lower confidence interval. The MNA for spring, and winter as well as summer are shown in Table 2. Numbers were highest in summer in all years, with the exception of 1982 when there was a decline from the winter numbers. Winter numbers were similar to or lower than spring in all years except 1978. The mean MNA in summer was 79 ($n = 12$, CV 38%), with a high peak in 1977 (161 individuals) and marked low in 1982 (25 individuals, Table 2). Using the absolute area of the wood, 9 ha, this gives a mean density of squirrels 8.8 ha^{-1} (CV 40%). This represents a foraging density of animals and is considered to be an over-

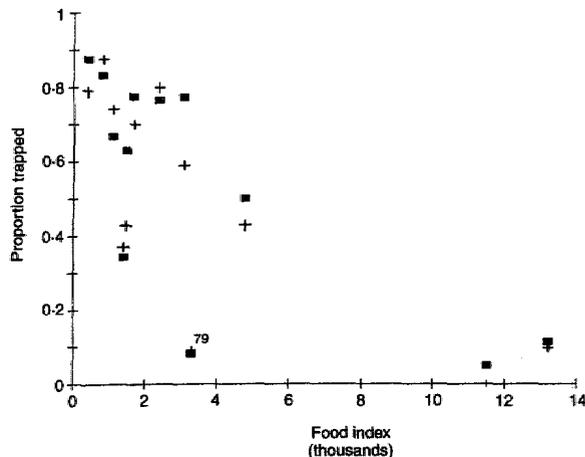


Fig. 2. Capture probabilities plotted against the index of food availability (FOOD). Results from 1979 noted. ■ males; +, females.

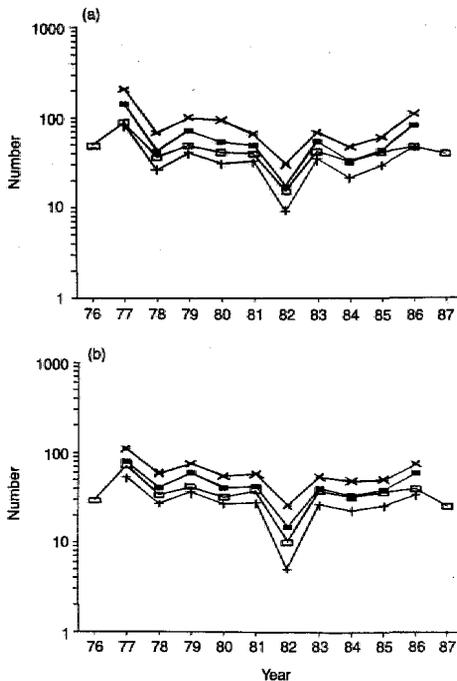


Fig. 3. Jolly-Seber estimates of summer population size with 95% upper and lower confidence intervals, and the minimum number known to be alive, MNA, for males and females. ■, Jolly-Seber estimates; ×, upper confidence intervals; +, lower confidence intervals; □, the MNA.

estimate of the density of the population resident in the wood. Without the extreme years, 1977 and 1982, population densities varied between 7 ha^{-1} and 10 ha^{-1} ($n = 10$, mean = 8.5 ha^{-1} , CV 12%). The equivalent mean Jolly-Seber estimate of population density with-

out 1977 and 1982 is 11 ha^{-1} ($n = 8$, CV 26%) but this excludes the first and last years in the data set, 1976 and 1987. The data set only spans 12 years and to make full use of it, i.e. to include the years 1976 and 1987, MNA have been used in the following analysis.

Adult sex ratios (m/f) varied between 1.46 and 0.74, and was less than unity in four years: 1977, 1979, 1981 and 1985 (Table 2). The overall sex ratio was 1.1 (CV 23.5%) which was not significantly different to 1.0 ($\chi^2 = 9.5$, 11 d.f., $P > 0.05$).

RECRUITMENT

No juveniles were recruited to the summer populations in 1978, 1980 and 1982 and few were captured in 1984 and 1987 (Table 2). This suggested no or poor spring breeding in these years. The index of breeding recruitment, the number of juveniles per adult females, was highest in 1979 (2.09) and was greater than 1.0 in three other years: 1977, 1983 and 1986 (Table 2).

In those summers when juveniles were captured (Table 2), the mean number of male juveniles was 12 (CV 111%) and females, 8 (CV 115%). Excluding 1976 when 8 male and 1 female juveniles were captured, the juvenile sex ratio was 1.5 (cf. Table 2) which was not significantly different from 1.0 ($\chi^2 = 8.4$, 6 d.f., $P > 0.05$). However, many more juvenile males were captured in 1977, 1979 and 1985.

The pattern of breeding condition in male squirrels, as subjectively determined by the size of the testes, did not conform to Dubock's (1979) synchronized seasonal cycle with sexual development maximal in December and May and minimal in August. Note that Dubock's study was carried out between 1972 and 1975 in the same oak wood in Alice Holt Forest as

Table 2 MNA of squirrels in winter, spring and summer, and recruitment (new adults, juveniles), and sex ratios in the summer populations

Year	MNA			No. new adults		No. Juvs	Juvs per Ad. Fem.	Sex ratio (m/f)	
	Winter	Spring	Summer	Male	Female			Adult	Juv.
76	48	*	78	—	—	9	0.32	1.46	8.00
77	43	*	161	24	24	70	1.52	0.98	1.69
78	83	55	70	18	13	0	0.00	1.06	—
79	35	37	91	8	3	48	2.09	0.79	1.67
80	52	57	73	28	8	0	0.00	1.28	—
81	61	54	78	14	11	24	0.83	0.86	1.67
82	34	26	25	4	4	0	0.00	1.50	—
83	17	42	80	19	15	28	1.17	1.17	1.00
84	49	63	65	6	6	3	0.10	1.00	0.50
85	56	70	78	13	11	23	0.74	0.77	2.83
86	39	40	88	11	5	34	1.36	1.16	1.13
87	51	53	66	26	7	2	0.08	1.46	†
<i>n</i>	12	10	12	11	11	12	12	12	8
Mean	47.3	36.9	79.4	15.5	9.7	20.1	0.7	1.1	2.3
CV(%)	34.4	61.7	38.6	57.7	66.3	111.4	104.6	23.1	96.3

* No sampling.

† Both males.

the work described here. Male squirrels were not considered to be in breeding condition in the winters of 1978, 1980, 1982, 1984 and 1987 (winters when capture probabilities were good and little seed food was available). Moreover, the proportion of males in breeding condition in June/July varied significantly among years ($\chi^2 = 124.5$, 10 d.f., $P < 0.005$), ranging from 0% in 1979 to 100% in 1987 (Table 3). Dubock showed that testes can regress or increase in size over short periods of 1–2 months; the exact timing of this must have affected the proportions of animals with large or small testes in this study and suggests that the period of minimal sexual development may be as early as June in some years.

Few females were classified as pregnant or lactating in the summer populations (Table 3). The number of pregnant females may be under-represented because of difficulties in determining pregnancy, and the number of females lactating may be under-represented because they were not captured at this time. No real patterns emerge from examining these data. However, only in 1983 and 1985, and possibly 1978, were there more than 10 females pregnant or lactating in summer populations which would indicate a substantial recruitment of young animals in late summer or early autumn. Low numbers of breeding females in summer populations in years following good seed crops may be attributable to the fact that few females produce two litters in one breeding season, and not more than a third of all females in very good seed years (Nixon & McClain 1975; Nixon *et al.* 1975; Gurnell 1983).

In most years, especially 1980 and 1987, more new or unmarked males entered the population between summers than new females (Table 2). The sex ratio of new adults was 1.84 (CV 56%) which was significantly different to 1.0 ($\chi^2 = 28.38$, 10 d.f., $P > 0.05$). There was no significant association between the number of juveniles captured and new males ($r = 0.04$, $n = 11$, $P > 0.05$) or new females ($r = 0.50$, $n = 11$, $P > 0.05$).

PERSISTENCE

The proportions of summer adults persisting to winter, spring and summer the following year are

shown in Table 4. On average, most adults and juveniles disappeared from the population between summer and winter. Thereafter, persistence was good until the summer. Adults persisted better than juveniles and females better than males. Hierarchical log-linear analysis (program ILOG, Bakeman & Robinson 1994) using three factors – persistence, sex and year – from summer to winter showed that the simplest model to fit the adult data was the saturated model (Table 4). The same was found on analysing adult persistence from summer to summer. Thus, all factors and interactions of all factors are important. Significant differences between males and females according to year are shown in Table 4. Significantly more females persisted from summer to winter in 6 years, and from summer to summer in 5 years. The only year when males persisted better than females was 1981. Numbers of juveniles were only large enough to analyse for persistence in 1977, 1979, 1981, 1983, 1985 and 1986. The simplest log-linear model to fit the juvenile data showed no interactions among factors, but that differences in persistence differed among years and sexes (Table 4). Persistence of juveniles was better in 1979 and 1984 than in the other years, and female juveniles persisted better than juvenile males.

The survival of adult males to the following summer was negatively correlated with the initial MNA of adult males in the population ($r = -0.69$, $n = 11$, $P < 0.05$). There were no other significant associations between initial numbers and survival estimates of adults or juveniles.

SURVIVORSHIP CURVES

Survivorship curves combined by years from marking for adults and juveniles, males and females are shown in Fig. 4. Adult females survived best through to 1 year with 50% surviving. Figures for the other sex/age categories were similar: 34% adult males, 34% juvenile males and 29% juvenile females. The maximum survival time recorded was 6.5 years in adult females

Table 3. Breeding condition of squirrels in the summer populations. Only animals included with clear assignment of condition except in the case of pregnant animals whose incidence may be misrepresented. Non-Br = not breeding, Br = breeding, Preg = pregnant, Lact = lactating, F-Lact = recently finished lactating. Breeding condition for animals in 1976 not included. In 1978 one female was clearly pregnant; 11 others were possibly pregnant

Year	77	78	79	80	81	82	83	84	85	86	87
No. males	27*	38	16	37	21	14	24	32	39	42	27
Non-Br (%)	11	32	100	43	81	64	96	9	49	74	0
Br (%)	89	68	0	57	19	36	4	91	51	26	100
No. females	31	25	10	20	27	6	22	29	34	33	12
Non-Br (%)	29	48	20	85	41	33	36	24	26	70	100
Preg (%)	0	4(48?)	0	5	0	0	0	0	29	3	0
Lact (%)	3	0	40	0	11	0	50	0	0	3	0
F-Lact (%)	68	0	40	10	48	67	14	76	44	24	0

*June sample only.

Table 4.

(a) Proportion of adults and juveniles known to be alive in one summer persisting to the following winter, spring and summer. * on female numbers indicates a significant difference between male and female persistence for that year (at 5% level, $G^2 > 3.841$). (b) Three-factor ($S = \text{sex}$, $P = \text{persistence}$, $Y = \text{year}$) log-linear models, using the short-hand, square bracket notation of Bakeman & Robinson (1994). Other combinations of second and third factor terms were explored but were rejected. The simplest model to fit the data is denoted #

(a)

Year	Age	Males surviving to:			Females surviving to:		
		Winter	Spring	Summer	Winter	Spring	Summer
76	Adult	0.44	—	0.44	0.75*	—	0.75*
	Juv	0.38	—	0.38	1.00	—	1.00
77	Adult	0.58	0.38	0.31	0.63	0.33	0.30
	Juv	0.20	0.11	0.07	0.31	0.19	0.19
78	Adult	0.33	0.33	0.31	0.68**	0.65	0.62*
	Juv	—	—	—	—	—	—
79	Adult	0.58	0.53	0.21	0.87*	0.74	0.65*
	Juv	0.27	0.27	0.27	0.44	0.44	0.44
80	Adult	0.39	0.34	0.27	0.74**	0.65	0.58*
	Juv	—	—	—	—	—	—
81	Adult	0.64	0.60	0.44	0.31*	0.21	0.17
	Juv	0.00	0.00	0.00	0.11	0.11	0.11
82	Adult	0.53	0.47	0.40	0.70	0.70	0.60
	Juv	—	—	—	—	—	—
83	Adult	0.79	0.79	0.64	0.79	0.79	0.79
	Juv	0.64	0.64	0.50	0.50	0.50	0.50
84	Adult	0.39	0.39	0.32	0.81**	0.71	0.61*
	Juv	0.00	0.00	0.00	0.50	0.50	0.50
85	Adult	0.54	0.54	0.58	0.61	0.61	0.58
	Juv	0.29	0.29	0.24	0.17	0.17	0.17
86	Adult	0.69	0.45	0.38	0.88	0.80	0.64
	Juv	0.11	0.06	0.06	0.19	0.13	0.13
<i>n</i>	Adult	11	10	11	11	10	11
Mean		0.54	0.48	0.38	0.71	0.62	0.57
CV (%)		26	29	31	22	32	32
<i>n</i>	Juv	8	7	8	8	7	8
Mean		0.24	0.20	0.19	0.40	0.29	0.38
CV (%)		90	117	99	71	62	79

(b)

Persistence	Log-linear models	G^2 value	d.f.	<i>P</i>
I. Adult				
Summer to winter	[SPY] #	0.00	0	
	[SP] [SY] [PY]	28.7	10	< 0.005
Summer to summer	[SPY] #	0.0	0	
	[SP] [SY] [PY]	22.4	10	< 0.025
II. Juvenile				
Summer to winter	[SPY]	0.0	0	
	[SP] [SY] [PY]	7.3	5	0.5 > <i>P</i> > 0.1
	[SY] [PY]	8.7	6	0.5 > <i>P</i> > 0.1
	[PY] [S]	18.9	11	0.1 > <i>P</i> > 0.05
	[S] [P] [Y] #	39.3	16	< 0.005
Summer to summer	[SPY]	0.0	0	0.5 > <i>P</i> > 0.1
	[SP] [SY] [PY]	5.9	5	0.5 > <i>P</i> > 0.1
	[SY] [PY]	9.4	6	0.5 > <i>P</i> > 0.1
	[PY] [S]	19.6	11	0.05
	[S] [P] [Y] #	46.2	16	< 0.005

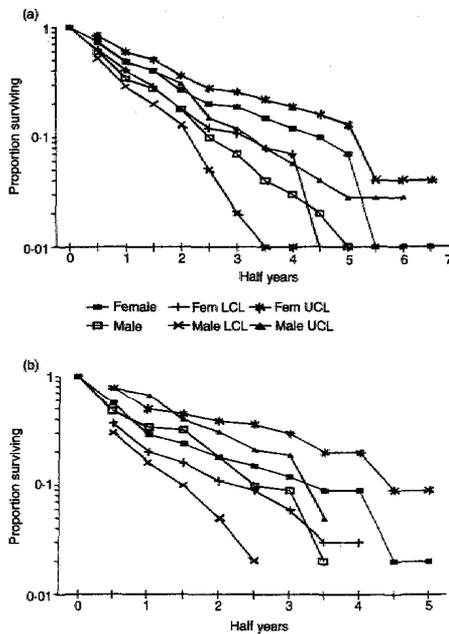


Fig. 4. Survivorship curves with 95% confidence intervals. (a) Adults (b) Juveniles.

followed by 6 in years adult males, 5 years in juvenile females and 3.5 years in juvenile males.

NET POPULATION REPRODUCTIVE RATE

The net population reproductive rate ($R_0 = MNA_{t+1}/MNA_t$) varied from 0.3 to 3.2 (Table 5) demonstrating that the population can quickly increase by a factor of 3, or quickly decrease by a factor of 3 between summers. There is a negative density relationship between R_0 to the following summer and the number initially present in the population ($r = -0.69$, $n = 11$, $P < 0.05$), demonstrating that the higher the summer population, the lower R_0 to the following year and the lower the summer population the higher R_0 to the following year. However, this

Table 5. Cold weather index (TEMP), food availability index (FOOD) and the net reproductive rate (R_0)

Year	TEMP	FOOD	R_0
75	215	1500	—
76	136	11500	2.06
77	193	2400	0.43
78	343	3300	1.29
79	171	1100	0.8
80	104	1700	1.08
81	305	800	0.32
82	100	4800	3.2
83	24	1400	0.81
84	504	3100	1.2
85	916	13200	1.12
86	237	400	0.75

relationship is largely influenced by the results for 1982, when very low numbers were followed by a high net reproductive rate, and 1977, when high numbers were followed by a low net reproductive rate (Table 5) and it is better to interpret this result by saying that the population can quickly return to average levels when driven to exceptionally high or low numbers.

EFFECTS OF FOOD AND WEATHER ON POPULATION DYNAMICS

The important findings are shown in Table 6. Most correlation coefficients involving TEMP were negative and most involving FOOD were positive. In the majority of cases the partial correlation coefficients were larger than the correlation coefficients. This indicates that the variables FOOD and TEMP were interdependent and antithetical, thus masking underlying relationships between FOOD or TEMP and the other variables. For example, the effects of severe winter weather were moderated when the food supply was good, and intensified when food supply was poor.

Correlation coefficients between survival to spring and summer are low and have not been included in Table 6. Survival to winter was positively associated with FOOD. The partial correlation of new females with FOOD was also positive, but there was no association between new males and FOOD. Correlation coefficients involving Net Reproductive Rate were all low, but there was a good correlation between the number of juveniles per female and FOOD which was not improved when TEMP was held constant. This demonstrates that food availability positively influenced female reproduction in the spring but the severity of the winter weather had no effect.

The correlation and partial correlations of the number of the MNA for adults and juveniles were all positively associated with FOOD (Table 6). In addition, there were negative partial correlations of MNA with TEMP.

EXPLORATORY DATA ANALYSIS USING ORDINATION TECHNIQUES

The data have been explored using ordination techniques (using the program CANOCO). First, a standardized principal component analysis (PCA) was carried out on years derived from the numbers of males and females (MNA). This shows that the first axis represents numbers from low to high (note data points for 1982 and 1977, low and high number years, respectively), and the second axis the ratio of males to females from high to low (Fig. 5a). The eigenvalue for the first PC axis is 0.965, for the second 0.035. The data were then explored using the canonical form of PCA, redundancy analysis (Jongman *et al.* 1987), by considering linear combinations of the environmental variables, FOOD and TEMP. Thus, in the redundancy analysis, the PCA axes have been constrained

Table 6. Correlation coefficients and partial coefficients between FOOD and TEMP indices and populations statistics. Partial correlations between statistic and FOOD or TEMP have been calculated with TEMP or FOOD held constant respectively. Coefficients here have been used to simply describe the levels of association and no statistical inferences as to their significance have been made

Statistic	Age	Sex	Corr. TEMP	Part. Corr. TEMP	Corr. FOOD	Part. Corr. FOOD
Numbers surviving from summer to winter	Adult	Male	0.01	-0.64	0.70	0.83
		Female	-0.03	-0.37	0.45	0.56
	Juvenile	Male	-0.09	-0.32	0.30	0.42
		Female	-0.10	-0.46	0.44	0.60
Reproduction (No. juv per fem)			0.33	-0.05	0.65	0.59
New animals	Adults	Male	-0.26	-0.29	-0.02	0.13
		Female	-0.36	0.50	0.37	0.68
Net rep. rate			-0.15	-0.44	0.41	0.57
MNA	Adult	Male	-0.28	-0.46	0.18	0.41
		Female	-0.25	-0.35	0.37	0.63
	Juvenile	Male	0.17	-0.59	0.69	0.73
		Female	0.22	-0.44	0.80	0.83
	Total	Male	-0.02	-0.60	0.66	0.80
		Female	-0.01	-0.70	0.72	0.87
	Total	All	-0.02	-0.67	0.70	0.84

to linear combinations of the environmental variables and the relative positions of the year-points have moved (Fig. 5b). The eigenvalue for the first axis is 0.765, and for the second 0.003 and, together, the environmental variables account for 77% of the variation in numbers among years. Apart from 1977, years tend to be clustered around the centre of axis 1, including the year 1982. The environmental arrows in Fig. 5b approximate the covariances between years and environmental variables. Further, the MNA of males and females have also been represented by arrows and the angle between pairs of arrows reflects the correlation coefficient between them. Thus, the MNA of males and females are highly and positively correlated and FOOD is the most important environmental variable, having a slightly higher positive correlation with numbers of males than numbers of females. The FOOD \times TEMP variable is less highly correlated with numbers. TEMP on its own can be seen to have no effect on numbers.

POPULATION MODEL

Following directly from the above, general linear models were estimated to predict summer population sizes from the environmental variables. As seen above, the factor TEMP on its own had no effect but the interaction between FOOD and TEMP was significant and important. Therefore, FOOD and FOOD \times TEMP were used as the environmental variables. 77% of the variation in summer numbers was explained by

the model (Table 7). There was a small but significant sex effect with male numbers estimated as *c.* 7 animals larger than female numbers, although the standardized residuals for the very low population year, 1982, were larger than 2 and a further model leaving out the 1982 data increased R^2 to 85%. However, the above exploratory analysis, and the fact that the data set is too small to identify outliers, suggest that it would be inappropriate to omit the 1982 data. Other models were explored and rejected, for example, by using a logarithmic transformation of the population counts, R^2 was reduced to 42%.

BODY MASS

Adult body mass data for summer and winter were analysed to see whether there were differences among

Table 7. Coefficients and their significance for a general linear model with MNA summer population sizes as the dependent variable and FOOD, FOOD \times TEMP and SEX as the explanatory variables. Other combinations of variables were tried and rejected

Term	Coefficient	d.f.	<i>t</i> -value	R^2 (%)
CONSTANT	30.55	1	10.57***	77
FOOD	0.005056	1	7.69***	
FOOD \times TEMP	-4E-06	1	4.92***	
SEX				
Female	-7.417	1	-2.24*	
Male	0			

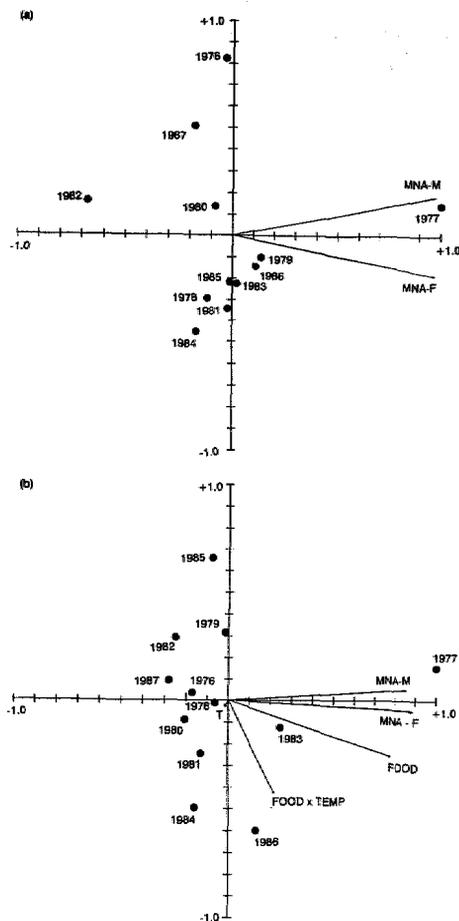


Fig. 5. (a) A biplot of years and squirrel numbers (MNA) from a standardized principal component analysis. MNA-M, MNA for males; MNA-F, MNA for females. (b) A RDA ordination diagram of the squirrel data with environmental variables represented by arrows. The length of the arrows reflects their importance; the cosine of the angle between pairs of arrows approximates the correlation between them. FOOD = FOOD variable, T = TEMP variable, FOOD \times TEMP = FOOD \times TEMP variable.

years and whether FOOD influenced the changes in body mass from summer to winter. Since female body mass may be influenced by reproductive condition, especially in summer, only the data for males have been used. Unfortunately, few animals were captured in winters with a good food supply (Table 8). There was no significant difference among years for mean winter body mass and there was no association between winter body mass and FOOD for samples > 1 ($r_s = -0.04$, $n = 9$, $P > 0.05$). There was a significant difference among means for the summer body mass data (Table 8). There was also a tendency for summer mean body mass to be positively related to FOOD ($r_s = 0.51$, $n = 13$, $0.05 < P < 0.1$). Although not included in Table 8, there was no association between mean spring body mass and FOOD for years

when spring body mass data were available ($r_s = 0.25$, $n = 9$, $P > 0.05$).

In years with little food there was an increase in average body mass from summer to winter in four years, three of which were significant, and a decrease in three years (Table 8). Percentage changes, either increases or decreases, were generally small and less than 7% on these occasions. Kenward & Tonkin (1986) reported marked increases in mean body mass between summer and winter of the order of 20%. This level of increase may have occurred in years with good autumn food supplies but the data were too few to corroborate this.

Discussion

LIMITATIONS OF THE DATA SET

Two factors have been of particular influence in this study. The first is the inverse relationship between capture probabilities and tree seed availability. This has affected the quality of the squirrel demographic data collected. Trapping in the summer was the least affected and summer population data are considered to be reasonable and the most reliable. Inevitably there are, however, some gaps in the data, such as juvenile recruitment in the autumn. Capture probabilities are not a simple function of seed production in the autumn. It is dependent on the rate of depletion of seed numbers on the forest floor through the autumn and winter and into the spring (Gurnell 1993). This in turn is a function of the numbers of seed eaters, including squirrels, other small mammals and birds (e.g. Nilsson 1985), and seed caching. Populations of mice and voles were also monitored in this study and results for these animals will be considered in a separate paper.

The second factor of influence is that the oak wood can be considered to be a macro-patch situated in a mosaic of other forest habitats or patches, each patch differing in food availability (also see Don 1981; Gorman & Roth 1989; Riege 1991). Home range size varies considerably in squirrels but can be as large as 10 ha or more, i.e. larger in size than the study area (Don 1983; Kenward 1985). Moreover, squirrels may commute distances of up to a kilometre during the day to feed (Don 1981; Ludolf 1986). The habitats around the oak wood mainly consisted of conifers or young hardwood plantations, except for some remnant 6-m wide border strips of 170-year-old oak along the sides of the roads and the railway (Fig. 1). These border strips act as corridors and are important components of squirrel habitats (Fischer & Holler 1991). In fact, the oak wood and the border oak were the most favoured habitat for squirrels offering prime habitat (Ludolf 1986). However, food supplies in surrounding habitats would affect the timing and extent of the numerical response (including dispersal) of squirrels to seed numbers in the oak wood. In 1980

Table 8. Male body weights for summer and winter populations. From the top the rows are in order of increasing food availability in the autumn between the summer and winter populations. The analysis of variance was carried out among summer or winter populations (excluding sample sizes of 1). The *t*-tests were carried out between summer and winter populations in years where winter sample sizes were >4

	Summer				Winter			
	<i>n</i>	wt (g)	<i>s</i>	Year	<i>n</i>	wt (g)	<i>s</i>	<i>t</i>
1986	24	540	28.9	1987	28	574	52.0	2.92**
1981	23	580	50.4	1982	14	566	55.0	0.76
1979	16	570	39.0	1980	12	561	63.0	0.40
1983	23	567	34.5	1984	10	574	37.0	0.48
1975		ND		1976	16	572	47.0	—
1980	39	533	50.0	1981	21	529	50.2	0.38
1977	36	552	43.4	1978	27	568	58.8	4.00**
1984	30	509	24.4	1985	10	546	40.8	2.71*
1978	35	527	51.0	1979	1	620	—	—
1982	14	510	28.0	1983	5	576	78.3	1.84
1976	26	523	18.7	1977	1	480	—	—
1987	38	534	43.7	1988	0	—	—	—
1985	23	520	27.0	1986	1	510	—	—
1988	12	548	22.1	1989		ND		
ANOVA	$F = 7.61^{**}$				$F = 1.65$			

* $P < 0.05$; ** $P < 0.01$.

ND, no sample taken.

and 1981, live trapping was carried out in 143 ha of forest centred on the oak wood (Ludolf 1986). It was found that more than 30% of the squirrels captured in the oak wood commuted to and from other habitats.

There are some peculiarities in the data which are believed to result, at least in part, from the interaction of the above two factors. One of the most striking oddities is the difference among the summer trapping results for 1977, 1986 and 1988 following the very large and essentially similar seed crops in the autumns of the previous years. In the summer of 1977, very high numbers of squirrels were captured and it was necessary to trap for a second time. It can be suggested that food and weather conditions favoured a very early and successful period of breeding in 1977 resulting in the very high population numbers that summer. However, female squirrels showed few signs of reproductive activity in the summer, and this may have been related to high population densities and a shortage of food at that time (Gurnell 1981). Late spring, early summer is often a critical period of food availability for tree squirrels (Gurnell 1987; Koprowski 1991). Furthermore, the high trap success in 1977 can also be attributed to high population densities at a time of food shortage. Squirrels might be expected to disperse, especially the young, under these conditions but sampling may have taken place before this occurred.

Throughout 1988 it was difficult to catch squirrels at any time and it has not been possible to present any results for this year. Clearly food conditions were good throughout 1988, which resulted in poor trap success. In 1986 trapping was reasonably successful, although population numbers were not greatly differ-

ent to several other summers that followed autumns with smaller seed crops. However, the 1985/1986 winter was the coldest during the 13-year study (Table 5) and this may have delayed spring breeding in some animals and resulted in a lower summer population size than might have been expected.

POPULATION DYNAMICS

Despite the shortcomings in the data set outlined above, there are several notable results which emerge from the analysis. The first has been alluded to above in that the oak wood can be considered to be a particularly good habitat for grey squirrels. This is reflected in the long-term average summer numbers of 43 males ($n = 12$, CV 39%) and 36 females ($n = 12$, CV 39%) and approximates to a density of 8.8 squirrels ha^{-1} , which is high in comparison with most grey squirrels studies (see Gurnell 1983). One reason for this is that it probably more accurately represents the density of foraging rather than resident squirrels. Even so, it has only been exceeded by densities in oak/hickory forests in North America (Mosby 1969; Montgomery *et al.* 1975). Excluding the results for 1977 and 1982, the population size in the summer had ranged from 7.2 ha^{-1} to 10 ha^{-1} . However, in 1982 the density was 2.8 ha^{-1} and in 1977 17.9 ha^{-1} ; these two exceptional years showed that the population can fluctuate by a factor of six and shows the value of long-term descriptive studies. Although this result is not a simple function of food availability, it is interesting to note that food supplementation experiments

in mammals usually only produce density increases of 1.5–2.5 times (critically reviewed by Boutin 1990).

In general, more adult females persisted from one summer to the next than the other age/sex categories. Possible explanations for these differences between the sexes in adults is the importance of site fidelity and good food resources to female reproductive success (Wauters & Dhondt 1989, 1993) and that males tend to move over larger areas than females, especially during the breeding season when they are searching for mates (Kenward 1985). The number of new females entering the population in the summer was affected by food availability; this was not the case for new males. This suggests that the density of breeding females rather than breeding males is affected by local food conditions.

It is unclear why more juvenile females persisted than juvenile males. It suggests a female-biased natal philopatry which is common in mammals (Greenwood 1980). A problem with the results from this study is that it is believed that many spring-born young disperse around June (e.g. Don 1981) and the timing of summer trapping may have missed some of these dispersing animals. It is generally believed that many dispersing summer-born animals move to suboptimal habitats and, if they survive, move back into favourable habitats during the following spring and summer (Don 1981). Although spring-born young may be under-represented in the summer population, the index of spring breeding success (i.e. the number of juveniles per adult female) was positively related to food availability and unaffected by the severity of winter weather.

Persistence of squirrels is lowest from summer to autumn; thereafter it improves considerably and losses of adults from winter to the following summer are relatively small. Based on MNA, food availability was positively associated with the persistence individuals from summer to winter, especially in adult males, but not from summer to spring or to the following summer. The severity of winter weather was negatively associated with persistence from summer to winter and to some extent masked the effects of food availability. Late summer and autumn dispersal is important in grey squirrels (Don 1981) and Thompson (1978b) has speculated that dispersal at this time is the ultimate factor regulating grey squirrel populations. During late summer and autumn, competition among individuals results in animals spacing themselves out in relation to patch food availability. Dominant squirrels remain in the most favourable habitats whereas subordinates, which include young, emigrate (also see Pasitschniak-Arts & Bendell 1988; Wauters & Dhondt 1992). Thus, the annual input of the tree seed crop has a marked effect on the numbers and social organization of grey squirrels at the time of the establishment of the breeding populations in mid-winter or spring.

The finding that tree squirrel populations are lim-

ited by food availability is well substantiated (see Gurnell 1983) and has been demonstrated experimentally (e.g. Sullivan 1990; and see Boutin 1990). The results here are in agreement with this but they also show the importance of a modifying factor, the severity of winter weather. Very cold weather increases the energy required for body maintenance and reduces the activity and hence foraging time of squirrels (see Gurnell 1987). The weather index used here positively weights the length of the periods of very cold weather; the longer the period then the more difficult it is for squirrels to obtain sufficient energy to maintain body mass and condition. This effect is exacerbated when food availability is low, requiring an increased foraging effort.

The availability of tree seeds has been shown to be particularly critical but, by inference, so is the availability of alternative foods. This is especially true when the seed crop fails or during the late spring and early summer when seeds, buds and caterpillars are not plentiful. Although the diet of squirrels is reasonably well known (Moller 1983; Gurnell 1987), little is understood about the interaction between nutritional requirements of squirrel populations and the abundance of alternative foods. It is interesting to note that average body mass of male animals in winter was good (> 560 g overall) irrespective of the prevailing food conditions. Maintaining body mass in years of poor seed availability will be important not only to over-winter survival but also to reproductive success when breeding starts later in the spring (see Thompson 1978a,b; Wauters & Dhondt 1989).

The population models showed a good level of prediction of population numbers during the summer. The study clearly demonstrates the links between the positive relationship between summer population size and food availability, and the negative relationship between food availability and capture probabilities. Gurnell (1989) has suggested that a simple measure of winter trapping success could be used as a management tool to predict the size of squirrel populations during the summer and, consequently, likely tree damage levels and the population control effort required. Studies on the usefulness of this approach are currently being carried on a large scale in forests in southern England (Gurnell, unpublished).

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