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Gerald A. Kemp; Lloyd B. Keith

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DYNAMICS AND REGULATION OF RED SQUIRREL (*TAMIASCIURUS HUDSONICUS*) POPULATIONS¹

GERALD A. KEMP AND LLOYD B. KEITH

Department of Wildlife Ecology, University of Wisconsin, Madison 53706

Abstract. This paper describes red squirrel population dynamics on two intensive study areas (Camp and Main) in mixed-forest types near Rochester, Alberta. It also examines local and regional population fluctuations, and their relationship to cone crops and weather factors.

Adult red squirrel numbers on our study areas varied little from 1967 to 1968. Yearly differences in reproductive output were caused principally by changing ovulation and pregnancy rates. Mean litter size increased significantly from 3.4 in 1967 to 4.3 in 1968; while the per cent adult females breeding increased significantly from 67 to 88. A life-table analysis of age-ratio data estimated mean annual mortality among juveniles (postweaning) at 67%; and an adult mortality rate of 34% for yearlings and 61% for older cohorts. A time-specific estimate of adult mortality on the Camp study area during the year starting summer 1967 was 21%.

Red squirrel territories appeared to be of two distinct types: (1) defended winter food caches which were subsequently abandoned during the summer, and (2) "prime" territories in which a specific area was defended year round. During the summers of 1967 and 1968, 31% and 26% of study-area adult populations occupied prime territories. The distribution of prime territories chiefly reflected the presence of mature seed-producing conifers, and hence a potential year-round food supply. Deciduous areas were particularly important in overwintering the juvenile cohort.

Fur returns were used as population indices in determining synchrony and periodicity of red squirrel fluctuations. Fluctuations tend to occur synchronously over much of the Prairie Provinces. Furthermore, mean intervals between peak years in Alberta (2.6) and Saskatchewan (2.8) were significantly shorter than in random series of comparable length, while the 2.9-year mean interval in Manitoba approached significance.

A statistically significant correlation was found between white spruce cone crops and red squirrel populations in Alberta as indexed by annual fur harvests. The negative correlation between cone crops in late summer and rainfall during summer of the preceding year was almost significant. This supported the widely held view that weather factors influence bud differentiation and hence determine the size of the following year's cone crop. Our contention that cone production may in this way provide a vehicle through which weather affects squirrel populations was supported by a number of statistically significant negative correlations between Alberta and Saskatchewan fur returns and the preceding year's summer rainfall. Such a mechanism would explain the observed widespread synchrony of population fluctuations, since extensive regional weather patterns could be involved.

Between one and three million red squirrels (*Tamiasciurus hudsonicus*) are commonly harvested each winter in Canada. The Province of Alberta is the largest single producer. The economic value of this fur harvest usually exceeds 1 million dollars, placing the red squirrel among the country's top three furbearers. Because of high quality pelts and relatively stable prices, many Alberta trappers consider the squirrel as the mainstay of the fur industry.

The natural regulation of red squirrel population is still poorly understood, but recent work has implicated both territoriality and food supply as important limiting factors (Brink and Dean 1966, M. Smith 1968, Smith 1968). Previous study-area locations have ranged from the hardwoods of New York (Hamilton 1939, Layne 1954), to the coniferous forests of south-central British Columbia (Smith 1968), northeastern Alberta (Wood 1967) and central Alaska (M. Smith 1968). The

present paper describes the dynamics of red squirrel populations in mixed forests near Rochester, central Alberta; it also documents and evaluates certain regional population phenomena noted in extensive fur returns.

STUDY AREAS AND METHODS

The Rochester area, 100 km north of Edmonton, lies within the aspen- (*Populus tremuloides*) dominated southern edge of the Boreal Forest. Except for the Tawatinaw River valley and several lateral coulees, the country is flat to gently undulating.

Red squirrel population estimates were obtained on two intensive study areas (Fig. 1). The 110-ha Camp study area was situated 2.4 km south of Rochester on the northwest-facing slope of the Tawatinaw valley. Here, aspen and balsam poplar (*Populus balsamifera*) were the main deciduous forest cover, with scattered white spruce (*Picea glauca*) and one 1.6-ha black spruce (*Picea*

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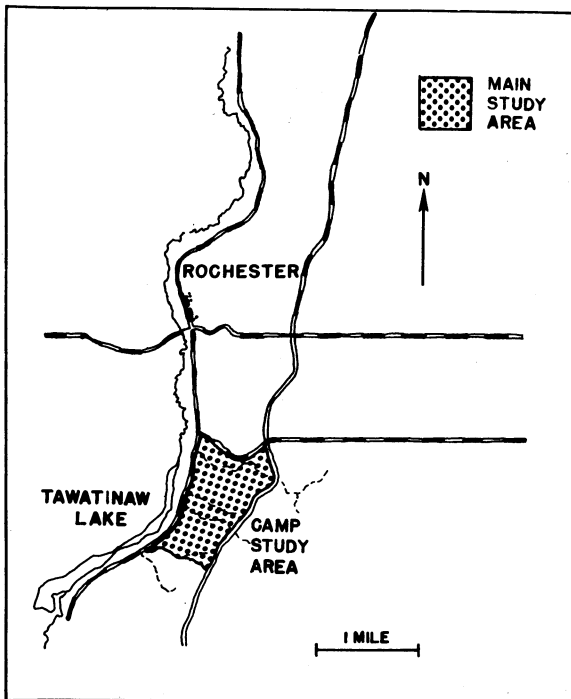


FIG. 1. Map showing study area locations near Rochester.

mariana) stand on a lowland site. Line-intercept sampling of the shrub vegetation indicated that 40% of this area is covered by a hazel (*Corylus cornuta*) understory.

The 65-ha Main study area, 4 km northeast of Rochester, was characterized by a central aspen-dominated ridge flanked by two parallel bogs. The principal conifer, black spruce, was located on the wet bog-upland edges, with some scattered white spruce on more mesic sites. Jack pine (*Pinus banksiana*) was widely distributed over much of the upland area; here alder (*Alnus crispa*) was the dominant understory species. This study area was devastated by fire in late May 1968, when over 90% of the seed-producing conifers were destroyed.

Trapping and marking

Intensive trapping and marking of red squirrels was conducted throughout the summers of 1967 and 1968 (June–August), and during a 10-day period in April 1968. Additional data were obtained for 1965 and 1966 from animals accidentally taken in snowshoe hare (*Lepus americana*) traps (Meslow and Keith 1968). Squirrel trapping data were supplemented with specimens collected near study areas by shooting. From these specimens we determined ovulation and implantation rates through counts of corpora lutea and placental scars respectively; and estimated population age ratios using eye-lens weights as aging criteria.

Red squirrels were captured in unbaited National Livetraps, size 15 by 15 by 48 cm, placed on runways; trap density was roughly proportional to numbers of active runways. This technique resulted in 264 captures during 1967 and 1968. A numbered toe-clipping system (Melchior and Iwen 1965) provided permanent identification of livetrapped squirrels, while colored ear wires (Halvorsen pers. comm.) allowed individual field recognition. Of the 12 animals marked during the summer of 1967 on the Camp study area and recovered in the summer of 1968, 8 had retained both ear wires in good condition, 3 had lost 1 wire and 1 animal had lost both. Differential application of Nyanzol D dye (Melchior and Iwen 1965) permitted visual separation of juveniles and adults during the summer months.

Census techniques

All female red squirrels taken on study areas in spring were implanted subcutaneously with a gelatin capsule of radioactive calcium, Ca^{45} (Rongstad 1965). When later the toes of trapped juveniles were clipped in marking, these were utilized to obtain the ratio of radioactive to non-radioactive young in the population as a basis for a Lincoln-index estimate of adult numbers. Because sex ratios were not significantly different from 1:1 and the proportion of nonbreeding adult females was determined each year, an estimate of total adult females and hence total adults could be derived from the radioactive-nonradioactive ratio among juveniles.

Three independent Lincoln-index estimates of the adult cohort on the two study areas were secured by: 1) retrapping of marked animals, 2) re-observation of color-marked animals, and 3) trapping of juveniles born to Ca^{45} -implanted females. Tests for homogeneity of trap response (Table 1) indicated that the distribution of total captures did not differ significantly from a Poisson, i.e. they tended to occur at random. We thus feel justified in using retrapping to obtain marked-unmarked ratios for Lincoln-index calculations. Completion of the 0-capture category of each truncated distribution (Table 1), and their subsequent summation, yielded additional estimates of population size.

The distribution of squirrel observations also followed a Poisson, but they were, as shown later, principally limited to a particular cohort of the population (the prime territory holders) and did not represent a random sample of the total adult population.

Juvenile population estimates for 1968 were obtained from retrapping marked individuals.

TABLE 1. Distribution of total captures of adult squirrels in National Livetraps near Rochester, Alberta, summers 1967 and 1968

No. of captures for individual squirrels	Camp study area				Main study area	
	1967		1968		1967	
	No. of squirrels	Poisson $m=0.700$	No. of squirrels	Poisson $m=0.350$	No. of squirrels	Poisson $m=0.368$
0.....	?	27.8	?	23.8	?	18.0
1.....	18	19.5	27	25.0	20	18.0
2.....	9	6.8	9	13.1	6	9.0
3.....	1	1.9	6	4.6	3	3.8
4.....	0		2	1.2	2	
5.....	0		0		0	
Totals.....	28+?	56.0	44+?	67.7	31+?	48.8
Chi-square ^a		1.25 $P=0.27$		3.33 $P=0.18$		1.59 $P=0.20$

^aThe truncated frequency distribution (0-capture data missing) of squirrel captures were tested against appropriate truncated Poisson distributions for which the 0-capture category had been estimated using a "maximum likelihood" technique described by Hartley (1958). We followed Cochran's (1954) recommendation that minimum expected values in Chi-square tests of unimodal distributions be not less than 1, $df=n-2$.

TABLE 2. Adult red squirrel population estimates for 1967 and 1968 from Camp and Main study areas

Camp study area			Main study area		
Mean date	Numbers estimated	Basis ^a	Mean date	Numbers estimated	Basis
July 10, 1967	36 (24-68) ^b	A	July 8, 1967	36 (28-56)	A
	28 (24-34)	B		36 (28-56)	B
	48 (29-131)	C		47 (31-94)	C
	56	D		49	D
	17	E		23	E
	Mean=37		Mean=38		
April 14, 1968	28 (22-34)	B	April 14, 1968	35 (27-42)	B
	42 (18-86)	C			
	Mean=35				
June 15, 1968	34 (21-63)	A			
	30 (28-32)	B			
	49 (46-53)	C			
	68	D			
	35	E			
	Mean=43				

^aNumbers estimated based on:
 A. Lincoln index; trapping of radioactive young from Ca ⁴⁵-implanted females.
 B. Lincoln index; reobservation of color-marked individuals.
 C. Lincoln index; retrapping of marked individuals.
 D. Completion of 0-capture category using a "maximum likelihood" technique.
 E. Completion of 0-observation category using a "maximum likelihood" technique.
^bConfidence limits are at the 95% level, as interpolated from "confidence belts for proportions" in Steel and Torrie (1960:458).

Age and sex criteria

Pelage condition and weight provided the most reliable criteria for distinguishing young of the year from adults up to the time trapping ceased in late August. The open-furred appearance of the juvenile tail combined with the light grey belly-fur were in contrast to the dense tail-fur and darker belly-fur of the adults. In late summer, adult weights were rarely below 180 g while juveniles seldom exceeded 165 g.

Off-study-area adults collected for information obtainable only through post-mortem examination were aged by eye-lens weights. Lenses from 97 known-age animals (Rusch 1970), provided an

excellent basis for aging adults. Eye lenses were dried for 5 days at 80°C in a gravity-convection oven.

Sex was determined externally by perineum lengths of livetrapped study-area individuals. Perineum lengths were ≤0.5 cm in adult females and ≥3.0 cm in adult males. Perineum lengths of juvenile males were always >2.3 cm.

SQUIRREL POPULATION

Lincoln-index population estimates by three independent methods indicated no significant change in breeding populations on the two study areas from 1967 to 1968 (Table 2). Due to the fire, no

estimates were made for the Main study area in June 1968.

Population estimates from reobservation are probably biased low, as mentioned earlier, but they too at least remained relatively constant throughout the period covered. Since the standard error on the adult population estimate for June 1968 (from retrapping marked animals) is smaller than from the Ca^{45} -implantation method, we feel it affords the best single assessment of population size. The overall densities of about 13.5 adult squirrels per 100 acres (5.5/100 ha) on the Camp study area and 23.7 (9.6/100 ha) on the Main study area are comparable to those reported for other largely deciduous areas in New York (Layne 1954).

Reproduction

The reproductive performance of the red squirrel population was principally affected by changing ovulation rates and the per cent of the adult females breeding. A female was considered nonbreeding if it showed a complete absence of placental scars. No uteri were encountered which showed corpora lutea and no placental scars. The percentage of adult females breeding increased significantly from 67% ($n = 43$) in 1967 to 88% ($n = 39$) in 1968. An even greater difference was noted by Smith (1968) between 1962 and 1963, when 83% and 32% of the adult females bred.

Wood (1967) reported that 84% of his adult females 2 years and older, and 73% of his yearlings, had bred in 1966. Our data too suggest a higher incidence of nonbreeding among young females. In 1967, 8 of 12 nonbreeding females were yearlings; while in 1968, all 3 nonbreeders were yearlings.

Mean litter size as determined by placental-scar counts increased significantly from 3.4 to 4.3 between 1967 and 1968 (Table 3), a situation similar to the increase from 2.9 to 3.8 between 1963 and 1964 reported by Smith (1968). Although in the 2 years 40% and 39% of our females had litters of 4, the number of litters of 5 and 6 rose markedly in 1968 (Table 3). There was no difference (t -test) between yearling and older females in numbers of implantation sites.

Layne (1954), summarizing information on litter sizes from several authors, also reported a range from 2 to 8; his mean of 4.9 is higher than our 3.9, Wood's (1967) 4.0, and Smith's (1968) 3.3.

Differences between counts of corpora lutea (325) and implantation sites (297) indicated an average preimplantation loss of about 9%. This did not vary significantly from 1967 to 1968.

TABLE 3. The distribution of litter sizes for red squirrels as determined by placental scar counts, 1967 and 1968

Year	Litter size								Mean litter size
	1	2	3	4	5	6	7	8	
1967									
Number.....	1	7	14	17	4	0	0	0	3.4(3.1-3.7)*
Per cent.....	2	16	33	40	9	0	0	0	
1968									
Number.....	0	1	8	15	10	3	1	1	4.3(3.9-4.7)
Per cent.....	0	3	21	39	26	8	3	3	

*95% confidence interval.

Layne (1954) reported that two litters per season were common on his study area in central New York. In the 4 years for which we have specimens and trapping data (1965-68), no evidence of a second litter was detected. During 1967 and 1968, none of our marked females exhibited exceptionally early or late pregnancies which might have indicated multiple littering.

As our intensive trapping activities did not commence until early June, we had little opportunity to observe the onset of breeding activity. However, one instance of copulation was observed on April 15, 1968. If we consider the time each year at which significant numbers of juveniles become available for trapping as a function of the earliness or lateness of breeding, then captures of red squirrels in hare traps during summer 1965-68 give some indication of variability in breeding peaks. Dates at which total juvenile captures first exceeded adult captures were: July 15, 1965, August 10, 1966 and 1967, and August 1, 1968. Thus mean dates of breeding probably differed by up to a month between years.

Age composition

The age composition of fall populations (Table 4) was estimated from eye-lens weights of adults collected during summer, and from a calculated juvenile/adult age ratio (Table 5, columns 4 and 5). The lack of an adequate number of recaptures of marked juveniles in late-summer 1967 precluded any direct calculation of both juvenile numbers and the juvenile/adult age ratio. However, on the Camp study area in 1968 we obtained two separate estimates of the juvenile cohort, i.e. 72 on July 25 and 76 on July 30. Comparing the mean estimate of 74 for juveniles (July 28) with that of 43 for adults (June 15) (Table 2), we obtain a fall juvenile/adult age ratio of 1.9:1. Potential adult mortality during the 43-day interval between these two censuses was ignored in this computation. By assuming similar postovulation losses in 1967, we estimated the 1967 juvenile/adult age ratio at 1.4:1.

TABLE 4. Fall age distribution of red squirrels at Rochester, Alberta

Year	Juveniles ^a	Age of adults (years)					Sample size
		1	2	3	4	≥5	
1965.....	47	17	9	2	2	1	78
1966.....	44	24	11	2	3	0	84
1967.....	151	43	37	21	6	1	259
1968.....	209	34	43	20	9	4	319
Totals.....	451	118	100	45	20	6	740

^aSize of juvenile cohort calculated from fall age ratio (Table 5, columns 4 and 5), adults aged by eye-lens weights.

TABLE 5. Juvenile/adult age ratios among red squirrels at Rochester, Alberta 1965-68

Year	Summer age ratio from hare trapping ^a	Relative no. of days juveniles available for capture ^b	Calculated fall age ratio ^c	Estimated fall age ratio ^d
1965	2.4	45	-	1.5
1966	0.5	20	-	0.9
1967	0.8	20	1.4	-
1968	1.9	30	1.9	-

^aTotal juveniles/total adults captured during June 1-September 1.

^bNumber of days prior to September 1 that total juvenile captures exceeded adult captures in hare traps.

^c1968 age ratio calculated from population estimates of juvenile and adult cohorts on the Camp study area (Table 2 and in text). 1967 age ratio calculated from the number of corpora lutea per female, assuming postovulation loss similar to 1968.

^dComputed from the relationship between columns 2, 3 and 4 for 1967 and 1968; procedure explained in text.

Fall age ratios for 1965 and 1966 were computed from age ratios among squirrels taken in summer in hare traps, and from the relative period of time that juveniles were available for capture prior to September 1 (Table 5).

In 1968, with juvenile squirrels available for capture for 30 days (Table 5, column 3), the summer age ratio in hare traps equalled the independently calculated fall age ratio in the population (1.9 juveniles per adult). In 1967, with juveniles available for just 20 days, the summer age ratio underestimated the calculated fall age ratio (0.8 vs. 1.4 juveniles per adult). If we assume a linear relationship between the number of days (*X*) available for capture and the ratio (*Y*) of summer and fall age ratios, we obtain an equation, $Y = .043X - .29$, which can be used to compute *Y* during 1965 (*X* = 45) and 1966 (*X* = 20). When the summer age ratios for 1965 and 1966 are divided by computed *Y* values for these years (i.e. 2.4/1.65 and 0.5/0.57), the result is an estimate of fall age ratios (Table 5, column 5).

Sex ratios

There was no consistent nor significant difference in sex ratios of trapped (*n* = 185) and shot samples (*n* = 404) of adults and juveniles during June 1-September 1, 1967 and 1968. The mean

sex ratio of 52:48 among both cohorts did not differ statistically from a theoretical 50:50 ratio.

Of 47 animals taken early in the breeding season, April 10-22, 1968, 30 were males. The greater proportion of males in this sample is likely due to behavioral differences associated with onset of breeding, females tending to be sedentary and males moving about in pursuit of females.

Mortality rates

Young—The juvenile/adult age ratio of 1.9 (Table 5) in 1968 indicates that each adult female produced 3.8 young which survived till fall. However, since 12% of these females did not breed each breeding female must have raised 4.3 young (i.e. 3.8/.88). This figure is identical to the mean implantation rate (Table 3), and suggests that in utero and preweaning mortality was very low. Such calculations do not of course take into account losses of young associated with adult female mortality prior to time of weaning.

Adults and juveniles.—A time-specific life-table analysis was used to compute mortality rates from population age composition given in Table 4. Age distributions were first converted to percentages to avoid possible errors arising from unequal sample sizes between years. A basic assumption in a life-table approach of this type is that the population is stationary and age stable with fixed rates of birth and death. We realize that our squirrel populations were not stationary, but fluctuating; and that annual changes in birth rate and possibly in age-specific mortality have undoubtedly disrupted age ratios. We feel, nevertheless, that by pooling data spanning 4 years, enough distortions will perhaps cancel out to yield some preliminary estimates of mean annual mortality. Another important assumption is that our age-composition data are representative of the population. There is no reason to suspect sampling bias in the adult cohort; the calculations used to derive the proportion of juveniles in the population have already been discussed, and although admittedly crude, they should, we feel, be utilized.

Average annual mortality (fall to fall) of juveniles was estimated in the life table (Table 6) at 67%. Adult mortality was apparently lower among yearlings (34%) than among older animals (61%).

A time-specific adult mortality rate on the Camp study area between the summers of 1967 and 1968 was calculated from adult population estimates (Table 3) and summer age ratios (Table 6) as follows: adult mortality rate = mean adult population in summer 1968 × percentage of adults 2 years or older in summer 1968 / mean adult population in summer 1967 = 100% - 43 × 68% /

TABLE 6. Time-specific life table analysis of age ratio data in Table 4^a

Interval (years) x	Number alive l_x	Number dying d_x	Mortality rate q_x
0-1.....	236	157	0.67
1-2.....	79	27	0.34
2-3.....	52	33	0.63
3-4.....	19	5	}0.58
≥4.....	14	14	
Totals and means.....	400	236	0.59

^aYearly ratios were converted to percentages in order to negate differences due to sample size, thereby giving each year equal weight in calculating mortality.

37 = 21%. During this same period, 5 of 11 marked territorial adults disappeared from the Camp study area, giving a maximum estimate of mortality of 45%. The latter figure is probably an overestimate of mortality since territorial adult males commonly disperse at the onset of breeding in March (Rusch 1970).

The substantial difference between the computed mean annual mortality rate of 48% for adults and our single time-specific estimate of 21% on one study area may reflect the numerous potential sources of error associated with each estimate. We feel, however, that a more likely explanation rests with real year-to-year variations in mortality both within and between different areas.

Juvenile dispersal

As discussed later, young red squirrels must leave the adult female's territory after weaning. To monitor such movements, we confined the Ca⁴⁵-implantation of adult females in 1967 to a small section of the Camp study area. Eight of nine radioactive juveniles were subsequently captured about 1.6 km from this location, but the implanted adult females remained on their original territories. A juvenile tagged on the Main study area in July 1967 was taken 2.6 km away 12 days later. These data suggest a rather marked post-weaning dispersal of young from natal areas.

In 1968, only one of the three Ca⁴⁵-implanted females on the Camp study area reared a litter. All three radioactive juveniles trapped later were near the perimeter of this female's territory. That juveniles may have dispersed less in 1968 is likewise indicated by relative recapture rates. The study-area trapping program yielded 40 original and 2 (5%) recaptures of juvenile squirrels in summer 1967; there were 46 original and 14 (30%) recaptures in 1968. We have no direct evidence, but believe that this difference may have been food related through the notably larger cone crop of 1968.

TERRITORIALITY, FOOD RELATIONS AND POPULATIONS

From quantitative data obtained in coniferous stands, Smith (1968) concluded that the function of the strong territorial behavior which he observed among red squirrels is to allow each individual optimum conditions for harvesting, storing and defending a seasonal food supply so that it will be available throughout the year. On the other hand Layne (1954), working mainly in deciduous forest, indicated that red squirrels did not establish exclusive property rights over specific areas. We had the opportunity on our two study areas to observe red squirrel territoriality in both coniferous and deciduous stands. The term "territory" as employed by Smith and Layne, and also by us in the following discussion, refers to "any defended area."

A total of 23 squirrel territories were located on the Camp and Main study areas, i.e. 11 and 12 respectively. By late August 1967, 22 of the 23 occupants were individually marked. Territory ownership was determined from defensive vocalization (Smith 1968), from chases of squirrels released after livetrapping, and from recurring localized observations of the marked occupant. For later clarity, these territories will hereafter be called "prime territories." Although no precise quantitative measurements of territory sizes were made, we estimated by repeated observation of marked individuals that these prime territories ranged largely from 1 to 2 acres (0.4-0.8 ha). This is in general agreement with the reports of other workers summarized by Layne (1954). In 1967, 13 of the 23 prime territory owners were males; while in 1968 on the Camp study area, 6 of 11 were males. During summer 1968, two females marked as juveniles in August 1967 occupied prime territories. All prime territories encompassed mature conifers capable of cone production. No territory boundary alterations were noted between 1967 and 1968 when, as shown later, the cone crop recovered from almost nil to medium-heavy. Except for short periods following death of the owner, territories were continuously occupied; and by only one individual at any one time.

Smith (1968) worked with two species of *Tamiasciurus* and found that territories on his study area were contiguous and nonoverlapping. He was also able to determine the age and sex of most territory owners. Of the 22 territories which Smith mapped, only 2 were occupied by juveniles as of late September. If large tracts of land were subject to the strict territorial regime described by Smith and noted also by us in conifers, it is difficult to envision where any appreciable fraction of

a new juvenile cohort could immediately establish itself. It seems reasonable to assume that there are unoccupied areas in which juveniles survive until prime territory sites become vacant.

Comparing the mean adult population estimates on our study areas (Table 2) with numbers of known prime-territorial occupants, we see that 31% of our total adult population was territorial in summer 1967, as was 26% in summer 1968. Smith (1968) referred to the apparently nonterritorial animals as "vagrants." He stated further: ". . . if a squirrel had no territory in the late fall, it would soon starve if it did not find an empty one." The implication here is clearly that squirrels require a food cache for overwinter survival. Presumably this food cache would be defended, and hence all squirrels must to this extent be territorial during at least the winter months.

From data summarized by Layne (1954) regarding density of red squirrels in various habitat types, it is clear that mature coniferous stands generally support the highest densities and hence comprise the best quality habitat. Smith (1968) quantitatively demonstrated that territory size was inversely proportional to the amount of available food; while feeding experiments conducted by Brink and Dean (1966) and M. Smith (1968) showed that red squirrels preferred cones of white spruce over black spruce. On our study areas we would therefore rate white spruce as the best squirrel habitat, followed by black spruce and finally aspen-dominated deciduous stands.

We attempted to evaluate the importance of deciduous areas in squirrel population dynamics. On the Camp study area during 1968 traps were distributed in both spruce and aspen in approximately the same proportion as were active runways. As a result, 60% of the total trap-nights were in deciduous cover. From the outset it was clear that the distribution of conspicuous runways in deciduous areas was strongly associated with the distribution of a hazel understory. This was doubtless in part a function of stem density in hazel clones which discourages lateral movement once runways are established.

Our records of original captures and total captures in spruce and deciduous areas indicated a disproportionately high number of captures in spruce habitat (Table 7). With essentially all of the spruce encompassed in strongly defended prime territories, with prime territorial occupants comprising only 26% of the total adults present, and with only 40% of the total trap-nights in spruce habitat, we might have expected a greater proportion of captures to have occurred in the deciduous cover. These data at first glance appear to refute

TABLE 7. Distribution of red squirrel captures by cover type in Camp study area, 1968. Sixty per cent of the 2,670 trap-nights were in deciduous cover

	Adult captures		Juvenile captures	
	Spruce	Deciduous	Spruce	Deciduous
(Original captures)				
Number	24	12	23	23
Per cent	67%	33%	50%	50%
(Total captures)				
Number	52	19	28	23
Per cent	73%	27%	53%	47%

earlier conclusions about effective and persistent territoriality in high quality habitat.

The large proportion of total captures in the spruce was not due to excessive high rates of recapture there as compared with hazel areas (Table 7), which at least suggests that territorial animals were no more trappable than nonterritorial animals. At no time during the trapping period was a prime-territory owner caught on an adjacent squirrel's territory. The disproportionate number of captures in prime-territory spruce habitat was actually due to intruding free-ranging animals which must then have spent much of the summer foraging in the aspen-dominated areas. Our records of these and other such intruding adults indicated that they were mostly males and nonbreeding or postbreeding females (see Table 8 for example). The sexes were equally represented among intruding juveniles.

Between December 17 and 30, 1967, the spruce cover on the Camp study area was examined after each fresh snowfall for squirrel feeding activity; the best indicator being the piles of stripped bracts from spruce cones. The location of these cutting sites and direct observations of various individuals indicated that the number and distribution of prime-territorial animals was similar to the previous summer. Thus it seems that the free-ranging animals later caught as intruders on prime territories during summer 1968 must have survived the previous winter in predominantly deciduous areas.

In April 1968, three hazelnut middens were discovered in the deciduous cover of the Camp study area. The middens, consisting entirely of hazelnut shells, had been utilized the previous winter. These middens were kept under observation throughout the summer, and only on one occasion was a squirrel seen or heard calling nearby. Calling which would indicate the presence of a territorial animal was infrequently heard in the aspen areas; and when approached such animals would remain quiet and not exhibit the aggressive be-

TABLE 8. Distances moved by nonterritorial adult red squirrels, summer 1968

Toe-clip number	Sex	Condition during original capture	Distance moved (yds.) ^a	Date of original capture	Date of recapture
441.....	F	lactating	175	June 23	Aug. 12 ^b
11.....	F	lactating	200	Aug. 1	Aug. 5 ^b
401.....	F	nonlactating	225	June 21	July 5
401.....	F	nonlactating	125	July 5	July 23
411.....	F	nonlactating	350	June 25	July 13
Average distance moved.....			215		
449.....	M		120	June 25	July 26
741.....	M		400	June 21	June 23
741.....	M		475	June 23	July 3
442.....	M		450	June 24	July 15
479.....	M		725	July 4	July 28
479.....	M		700	July 28	Aug. 2
479.....	M		300	Aug. 2	Aug. 12
Average distance moved.....			453		

^a100 yds=91 m; 400 yds=366 m; 700 yds=640 m.

^bDate of recapture in the postweaning period.

havior characteristic of squirrels occupying prime territories in mature spruce. As a result of these behavioral differences, prime territory owners were much more easily located and observed. Since most of the prime territory owners were marked, the marked-unmarked ratio from general observations resulted in an underestimation of total adult population size when used in a Lincoln-index calculation (Table 2).

The apparent lack of defensive behavior by squirrels residing in deciduous cover in summer, and the fact that these same animals will replace prime-territory owners and then exhibit typical territoriality, leads us to conclude that territories are probably not established during the summer months in deciduous cover because an abundance of food there (fungi, berries, etc.) affords them independence from a cached food supply.

Counts of hazelnuts within 50 paired 3- by 0.75-m quadrats during early August 1968 on the Camp study area gave a mean and standard error of 8.5 ± 4.7 nuts per quadrat, or approximately 6,400 nuts per ha (15,800/acre) in deciduous areas. Nuts which were insect infested or appeared abnormal in any way were not counted. M. Smith (1968) calculated that on an annual basis adult red squirrel required an average of nearly 100 Kg cal/day. Caloric measurements of hazelnuts were not made by us, but Kendeigh and West (1965) and Smith (1968) found a minimum caloric count of about 4.3 Kg cal/g in seeds of 60 different plant species. Assuming very conservatively an average weight of 1 g/nut (Anon. 1948), and a maximum requirement of 100 Kg cal/squirrel per day, 1 acre (0.4 ha) in 1968 could have supplied sufficient food energy from hazelnuts to sustain one squirrel

for 679 days. Although 1968 was a year of excellent hazelnut production, these data suggest that a significant number of squirrels should normally be able to survive over winter in areas of deciduous cover by caching nuts. We do not know how much competition occurs between squirrels and other species for hazelnuts, but blue jays (*Cyanocitta cristata*) are also known to consume them.

Smith (1968) showed that the average total food energy available per territory was very close to the total requirements of the squirrel. On the other hand, M. Smith (1968) demonstrated that in the event of a cone crop failure, cones cached during a year of abundant cone production were utilized for 2 successive winters.

We believe that the fundamental difference between a prime year-round territory and a transient largely winter territory is that the former contains sufficient food resources to permit its occupant to survive for a year or longer without a cone crop, while the latter may or may not guarantee its occupant overwinter survival from one year to the next. Those animals which occupy transient territories over winter evidently abandon these in spring or early summer and attempt to establish themselves on prime territories; hence the observed competition for prime territories and the population mobility noted by us during June-August.

The concept of prime versus transient territories may seem arbitrary, but such a classification is consistent with our field observations and with the marked ecological differences between coniferous and deciduous units of a typical northern mixed-wood forest. We suspect that within extensive

conifer stands there might well be more of a continuum in territory status, which would reflect gradual transitions in habitat quality. The characteristics of territoriality in a red squirrel population as currently envisioned by us are briefly summarized below.

(1)—Prime territory owners defend a given area year-round. These areas are associated with conifers capable of cone production. Between years of drastically changing cone production (e.g. 1967 and 1968) territory size does not change appreciably.

(2)—Transient territory owners, largely juvenile animals, defend a food cache during winter. In the Rochester area these transient territories are largely located in deciduous cover with a hazel understory.

(3)—With the onset of summer and abundant alternate food supplies, breeding females in deciduous areas remain relatively sedentary with their litters, but males and nonbreeding females which occupied a transient territory during the previous winter become freeranging and compete for prime territories. In the postweaning period breeding females may also become freeranging.

(4)—After commencement of food-caching activity in late summer and fall all animals tend to become sedentary. Transient territory owners defend at least a food cache; those squirrels which fail to cache sufficient food to carry them through the winter may starve to death.

DISTRICT AND REGIONAL POPULATION FLUCTUATIONS

We employed fur returns as population indices in examining the synchrony and periodicity of red squirrel fluctuations. Keith (1963, p. 9–12) has reviewed and evaluated the importance of various factors affecting fur returns and their usefulness in depicting population change. Fur harvests and populations are probably not consistently related in some fixed ratio, but most workers agree that changing trends in population size are likely reflected in fur-harvest statistics. Among the predatory furbearers, peak years in fur returns may differ from those in actual populations because of varying trapability associated with prey abundance. Such inaccuracies are improbable with red squirrels where shooting is a common means of taking animals, and where trapping and snaring are not contingent upon attraction to baits.

Our main concern in utilizing fur returns was that harvests might be influenced by annual fluctuations in price, even though prices for red squirrels have been less variable than for other furbearers. (Coefficients of variation in Alberta pelt prices during 1941–65 were 32.7% for squirrels,

but ranged between 33.4% and 99.5% for the five other important furbearers.) However, tests of correlation between fur returns and both the current and the previous year's market price yielded nonsignificant r -values of -0.424 ($P = 0.07$) and 0.350 ($P = 0.12$) respectively. Indeed, the negative correlation coefficient between harvest and price in any one year probably indicates an impact of harvest on price, rather than the reverse situation which was of immediate concern to us.

Synchrony of population fluctuations

District populations.—Fur-return data were obtained directly from the Hudson's Bay Company, Winnipeg, for eight districts covering the northern half of Alberta (Appendix, Table 1). These returns spanned the period 1946–62. They were analyzed to determine whether population increases (I) and decreases (D) tended to be synchronized between districts.

If district populations were fluctuating independently, the degree of interdistrict synchrony observed annually should correspond to probabilities described by expansion of the binomial $(I + D)^8$, where $I = 0.44$ and $D = 0.56$ (increases and decreases totalled 56 and 72 respectively). In any one year, the particular combination of increases and decreases might range from all eight districts exhibiting a population increase ($8I:0D$) to all eight exhibiting a decrease ($0I:8D$). The expected and observed distributions of such I and D combinations over a 16-year period is summarized in Table 9. A Chi-square test showed that these two distributions were significantly different ($P < 0.01$), and hence that district squirrel populations were not fluctuating independently. There was in fact a clear tendency for the majority of districts to exhibit similar population trends each year (Table 13); and in no year did half the districts show an increase and the other half a decrease (i.e. $4I:4D$).

Regional populations.—Total red squirrel fur returns for each of the three Prairie Provinces were obtained from provincial records (Appendix, Table II). Interprovincial synchrony of yearly trends in population was then examined by comparing the three provinces, two at a time, viz. Alberta vs. Saskatchewan, Saskatchewan vs. Manitoba, and Alberta vs. Manitoba. The observed distribution of years of similar and opposite trend in each pair of provinces was tested by Chi-square against the expected distribution. Probabilities for calculating the latter were again based upon a binomial expansion. Two of the three resulting Chi-square values (summarized in Table 10) were significant, indicating that red squirrel population

TABLE 9. Distribution of years of red squirrel population increase or decrease for eight districts in Northern Alberta, 1947-1963, as interpreted from Hudson's Bay Company fur returns

No. of districts with increase or decrease in any one year		Years		$\frac{(O-E)^2}{E}$
Increase (I)	Decrease (D)	Observed (O)	Expected ^a (E)	
0	8	1	1.0	4.0
1	7	2	2.7	2.0
2	6	5	4.3	2.5
3	5	0	4.2	4.2
4	4	3	2.6	0.1
5	3	2	1.3	2.5
6	2	2		
7	1	2		
8	0	0		
Totals		16	16.0	$\chi^2=15.3$ ($P < 0.01$)

^aCalculated from probabilities given in expansion of the binomial $(I+D)^8$, where $I=0.44$ and $D=0.56$. We followed Cochran's (1954) recommendation that minimum expected values in Chi-square tests of unimodal distributions be not less than 1, $df=n-2$.

TABLE 10. Interprovincial relationship between increases and decreases in red squirrel populations

Relationship between provincial fluctuations in the same year	Number of years		
	Alberta vs. Saskatchewan	Saskatchewan vs. Manitoba	Alberta vs. Manitoba
Both increased	10 (7) ^a	9 (4)	6 (3.7)
One increased, the other decreased	9 (16)	2 (10.8)	7 (10.6)
Both decreased	13 (9)	11 (7.2)	9 (7.7)
Chi-square when tested against expected binomial	6.0 ($P=0.04$)	15.5 ($P<0.01$)	3.0 ($P=0.23$)

^aExpected values in parentheses are based on the following ratios:
Alberta vs. Saskatchewan, 1.0:2.3:1.3
Saskatchewan vs. Manitoba, 1.0:2.7:1.8
Alberta vs. Manitoba, 1.0:2.9:2.1

trends are broadly synchronized over a vast region.

Periodicity of population fluctuations

Examining the periodic characteristics of red squirrel fluctuations, we looked first at the length of intervals between population peaks. A peak was arbitrarily defined as any year in which fur returns were higher than in the years immediately preceding and following. The mean intervals, or average distances between all peaks, in population series from Alberta, Saskatchewan and Manitoba were 2.6, 2.8, and 2.9 years respectively.

We then compared the frequency distributions of peak-to-peak intervals in provincial fur data with expected distributions for both serially correlated (Cole 1954) and straight random series (Table 11). There were in each case highly sig-

nificant differences between observed and expected distributions; furthermore, the coefficients of variation of 20-31% between red squirrel peaks were lower than the 35% in serially-correlated and straight-random series. Thus we have annual fluctuations in red squirrel numbers which are significantly more regular than in random series. Davis (1957) and Keith (1963) have suggested that such population fluctuations be termed cyclic.

Another notable characteristic of these fluctuations is that mean intervals have tended to be shorter than in random series of comparable length. An analysis of "runs" as utilized by MacArthur (1958), showed that the 2.6- and 2.8-year periodicities in Alberta and Saskatchewan were significantly shorter ($P < 0.05$); while the 2.9-year periodicity in Manitoba barely lacked statistical significance (Table 12).

The observed synchrony of red squirrel fluctuations over much of the Prairie Provinces suggests a regulating mechanism operating on a regional scale. The progressively increased mean interval from Alberta (2.6) through Saskatchewan (2.8) to Manitoba (2.9) may also indicate a reduced intensity of such regulation from west to east since the latter periodicity approaches that found in random fluctuations.

The importance of conifer seed to red squirrels has been well established through intensive studies by M. Smith (1968) and Smith (1968). Earlier in the present paper we too discussed the obvious orientation of squirrels to conifer stands and the significance of a food cache to overwinter survival. Also striking annual variations in cone crops over sizable areas are well known to foresters. It therefore seemed reasonable to hypothesize that major year-to-year differences in cone production would markedly affect red squirrel population trends.

This idea was indirectly reinforced by MacArthur's (1958) examination of warbler fluctuations. He showed that Myrtle (*Dendroica coronata*), Black-throated Green (*D. virens*) and Bay-breasted (*D. castanea*) Warblers exhibit periodicities which are significantly shorter than expected in random-type fluctuations, viz. 2.6, 2.6 and 2.4 years. The key point here is that these songbirds feed largely on insects associated with conifers, and particularly on the spruce budworm (*Choristoneura fumiferana*) whose population levels seem to be related through some as yet ill-defined mechanism to numbers of staminate flowers (Greenbank 1963). Evidence presented by Fraser (1966) indicated that in black spruce, numbers of male-flower primordia are correlated with female primordia; and hence with the subsequent production of ovulate cones—the red squirrels' chief winter food source. It may thus be that both the red

TABLE 11. Observed frequency distribution of peak-to-peak intervals in provincial red squirrel population fluctuations vs. expected distribution in serially-correlated and straight-random series

Peak-to-peak interval lengths	Observed interval distribution				Expected distribution ^a	
	Alta.	Sask.	Man.	Total	Serially correlated	Straight random
2.....	5	3	3	11	3.3	10.3
3.....	7	6	2	15	8.7	9.0
4.....	0	1	2	3	8.4	4.5
≥ 5.....	0	0	0	0	8.6	5.1
Totals.....	12	10	7	29	29.0	28.9
Mean peak-to-peak intervals.....	2.6	2.8	2.9	2.7	4.0	3.0
Chi-square for total observed.....					34.6	9.2
					(<i>P</i> <0.01)	(<i>P</i> <0.01)
Coefficients of variation.....	20%	23%	31%	25%	35%	35%

^aCalculated from formulae given by Cole (1951, 1954).

TABLE 12. Number of runs of years of either increase or decrease in red squirrel population indices vs. number of runs expected in random series of comparable length

	Number of years	Maximum number of runs		Mean interval between successive peak years ^b
		Observed	Expected ^a	
Alberta	35	27	24	2.6
Saskatchewan	33	23	21	2.8
Manitoba	23	17	18	2.9

^aExpected number of runs at *P*=0.05 (Eisenhart and Swed in Wilks 1949).
^bPeak year is any in which fur returns were higher than in years immediately preceding and following.

squirrel and the warblers have responded, although through different mechanisms, to the common factor of conifer seed production.

Cone crops and squirrel populations

A direct relationship between European red squirrel (*Sciurus vulgaris*) populations and conifer seed production has been suggested by several investigators. To our knowledge, this alleged association has not been statistically evaluated. Thus we find Formosov (1932) commenting,

“With considerable constancy, the decrease in the quantity of squirrel skins brought from the Northern Ural, Western Siberia and Yakutia, correspond to large emigrations of the Siberian Nutcracker . . . The invasions of the nutcracker into Europe are due to a bad crop of cedar nuts in the native country of the bird; it is natural to suppose that the fall in the numbers of the squirrels primarily also depends in these regions upon the same failure of cedar nuts.”

Svärdson (1957) likewise noted the link between cone crops and squirrel populations in Sweden; and in addition he pointed out the possible importance to squirrels of conifer flower buds during the winter preceding cone formation.

The squirrel harvest in Alberta occurs in largely coniferous areas. These extend through much of northern Alberta, and south along the east slopes of the Rocky Mountains. The dominant conifers are white spruce, black spruce, jack pine and lodgepole pine (*Pinus contorta*).

The pines tend to produce relatively stable cone crops from year to year (Baker 1950). While pine stands do support sizable red squirrel populations, densities in pine at Rochester, for example, have been markedly lower than in nearby spruce stands (Rusch 1970). Cone production on black spruce is less variable than on white spruce, but the latter’s cones are definitely preferred by red squirrels and are more nutritious (Brink and Dean 1966). Large annual differences in cone production characterize white spruce, and it is this species which is of primary importance to red squirrels over large sections of Alberta.

White spruce cone crop indices were obtained from the Alberta Forest Service (A.F.S.) and the North Western Pulp and Power (N.W.P.P.) Company at Hinton, Alberta.

A.F.S. reports cover a large segment of the Province ranging from the Crowsnest Forestry District in the south to the Peace River Forestry District in the north (Fig. 2). The cone crop was subjectively rated by A.F.S. personnel as nil, light, medium and heavy. To obtain a numerical index, which was admittedly crude, we arbitrarily assigned values of from 1 to 4 to these categories (i.e. nil = 1, heavy = 4).

N.W.P.P. reports cover an area of 3,000 miles² (ca. 8,000 km²) encompassed by the N.W.P.P. lease. The cone crop classified by N.W.P.P. personnel was rated on a 0–2,500 scale. This rating involves numerous factors such as density of cones and of cone-bearing trees, and height of cone-bearing crown. Since an absolute cone failure never occurs (even though the N.W.P.P. rating

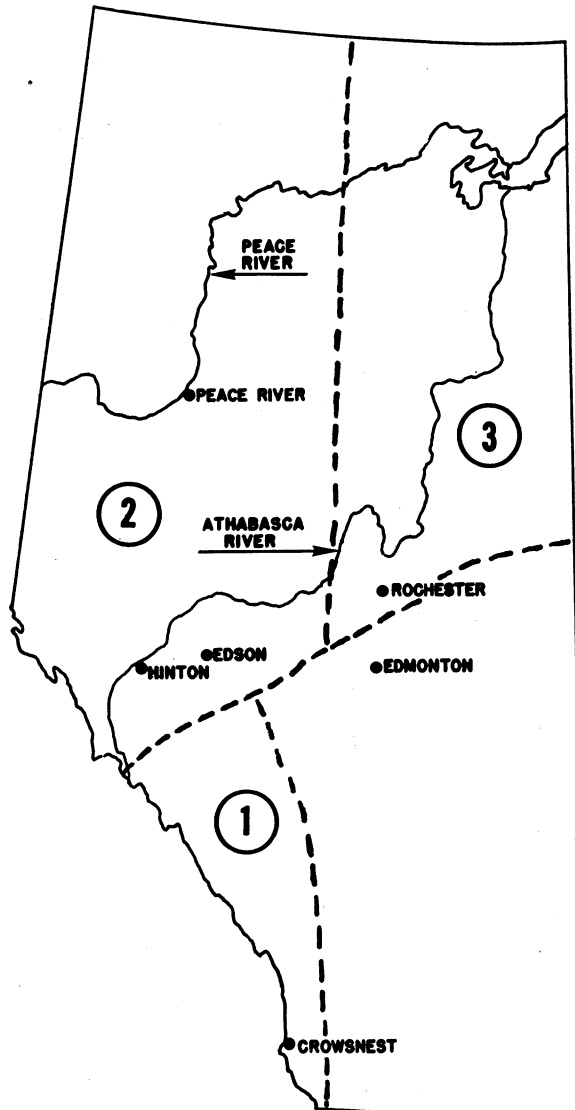


FIG. 2. Map of Alberta indicating locations mentioned in text. Numbers indicate regions used in examining intraprovincial cone production: (1) southwest; (2) northwest; (3) northeast.

scheme yielded "0" values in 2 years), and since zero values are difficult to work with statistically, these values (X) were transformed by $(X + \frac{1}{2})^{\frac{1}{2}}$ to approximate the normal distribution (Steel and Torrie 1960, p. 157). To explore intraprovincial synchrony of white spruce cone production, we divided Alberta into three regions, viz. southwest, northwest and northeast (Fig. 2). The average number of separate A.F.S. cone crop reports available yearly for each region was 31; these reports were given numerical ratings as explained earlier, and a mean cone-crop rating calculated annually for each region (Table 13). Comparable data for all three regions unfortunately span only 4 years, 1959–1962; but do suggest a

tendency for intraprovincial synchrony. A further test of interregional synchrony was possible by comparing 6 years of A.F.S. cone crop indices from the Northeast region with N.W.P.P. data from the Edson-Hinton district of west central Alberta. The correlation coefficient here was almost significant ($r = 0.799$, $P = 0.06$), thus giving additional evidence of widespread synchronization of white spruce cone production.

Crosby (1948) noted that the rhythm of flowering in balsam fir (*Abies balsamea*) is largely coincident over the New England states and the Atlantic Provinces. Cone crop data presented by Svårdson (1957) for three regions in Sweden and spanning 60 years were compared by us to determine if regional increases and decreases in cone crop occurred independently. Our approach was similar to that outlined earlier in Table 10, and this analysis disclosed conclusively that fluctuations in cone crops of Norway spruce (*Picea abies*) have been well synchronized between Northern, Southern and Central Sweden.

Tests of correlation between red squirrel fur returns and the best white spruce cone crop estimates available to us, the N.W.P.P. data, yielded highly significant r values. Correlation coefficients were 0.911 ($P < 0.01$, Fig. 3) with the total Alberta squirrel harvest, and 0.930 ($P < 0.01$) with squirrel fur returns from the nearby Hudson's Bay Company district of Wabasca. We found no significant correlation between A.F.S. cone crop data for 7 years in the Northeastern section of the province and Hudson's Bay Company fur returns from within the same region. This anomaly is probably in part a function of the crude numerical indices derived by us from A.F.S. reports; there may be, however, a more important ecological explanation. Fur harvest trends in several Northeastern districts are not completely synchronous with trends in Alberta as a whole. In the Northeast there are vast lowland areas of predominantly black spruce whose cone crops, fluctuating independently of white spruce, might well have significantly influenced squirrel populations.

Lack (1954, pp. 227–242) summarized relationships between mast-feeding birds and mammals and their principal food sources. Numerical fluctuations comparable to those described above for Alberta red squirrels are common among mast feeders. However, the irruptive mass dispersals noted by Lack in response to sharply declining food supplies are not nearly so frequent nor spectacular among North American red squirrels as among European red squirrels and North American grey squirrels (*Sciurus carolinensis*) (Hatt 1929, Schorger 1949, Lampio 1967). It is noteworthy that neither of the latter two species ex-

TABLE 13. Summary of Alberta Forest Service cone crop reports from three regions of Alberta

Region	Cone crop rating			
	1959	1960	1961	1962
Southwest.....	Light (2.3) ^a	Light (2.4)	Heavy (4.0)	Medium (2.9)
Northwest.....	Light (2.5)	Light (2.0)	Medium (2.7)	Light (1.9)
Northeast.....	Light (2.2)	Light (2.1)	Heavy (4.0)	Light (2.1)

^aDerivation of the numerical rating shown in parentheses is explained in text; nil (1.0-1.5), light (1.6-2.5), medium (2.6-3.5), heavy (3.6-4.0).

hibits territoriality. While we can now only speculate, perhaps the vigorous defense of a food source and/or food cache, coupled with reduced breeding and survival in the nonterritorial cohort, usually keep populations of North American red squirrels well below densities which could evoke mass movements.

Weather, cone crops and squirrel populations

Lester (1967) summarized for several species of pines (*Pinus*) the associations between annual variations in cone production and certain weather conditions. In seven of eight published studies, high temperatures and low precipitation during the summer of bud differentiation were associated with increased cone production. In the Atlantic Provinces, inordinately sunny and dry summers will force flower production and break the 2-year flowering cycle of balsam fir (Greenbank 1963). Such weather thereby tends to synchronize flower production over broad areas. In a comprehensive review of the literature on factors affecting seed production by forest trees, Matthews (1963) noted that a certain minimum degree of heat is apparently necessary for cone initiation, while there may be either a positive or negative association with "water supply." Fraser (1958) reported that higher-than-average day and night temperatures, along with above-average sunshine are conducive to formation of flower primordia in white spruce; but differentiation occurs approximately 1 year prior to maturation of the ovulate cone. The above studies implicate summer weather as an important factor in stimulating and synchronizing flowering among conifers. *Note, however, that such weather effects are not expressed in the cone crop until at least the following year.*

In an attempt to ascertain the effects of weather factors on white spruce cone production, and hence indirectly on squirrel populations, the relationships between mean monthly temperatures and precipitation and the N.W.P.P. cone indices were first tested by simple correlation. Weather records were from Edson, Alberta, near the N.W.P.P. lease. Cone crops were not significantly correlated with mean monthly temperatures for May and June of the preceding year ($r = -0.407$,

$r = -0.331$; $P_{.05} = 0.754$), but they were correlated with July temperatures ($r = 0.807$, $P = 0.04$). Correlation coefficients for July sunshine indices ($r = 0.706$, $P = 0.08$) and precipitation ($r = -0.649$, $P = 0.09$) approached statistical significance. Partial correlation coefficients indicated that the apparent association between cone crop and July sunshine was largely due to a high correlation ($r = 0.928$) between July sunshine and July temperature. Calculated partials between cone crop and July temperature, sunshine and precipitation were $r = 0.894$, $r = -0.195$ and $r = -0.639$ respectively.

To explore the impact of weather on squirrel populations, we examined the relationship between Alberta and Saskatchewan fur returns and temperature and precipitation data. Because of what appears to be a rapidly declining population in the period after 1954, Manitoba fur returns were not included in this analysis.

We suspect that, to a large extent, weather factors have not acted directly on red squirrel populations, but that summer weather and white spruce cone crops are directly linked. Thus because of the strong correlation, noted earlier, between cone production and squirrel population levels, regional weather and red squirrel populations should also be significantly related.

Provincial fur returns were tested against mean monthly temperature and precipitation for both the current year and the preceding year. For example, fur returns for winter 1960-61 were paired with weather data for 1960 and for 1959. Alberta data were for the 34-year period, 1933-1966; Saskatchewan data spanned 33 years, ending in 1965. Weather means were taken from the Monthly Record, Meteorological Observations in Canada (Dept. of Transport.) for two large sections of Alberta, i.e., the Athabasca and Peace River Drainages (Fig. 2). These drainages provide the bulk of the provinces' red squirrel harvest. Saskatchewan fur returns were tested against temperature and precipitation data for the Churchill River Drainage. Before analysis, fur returns were subjected to a log₁₀ transformation to produce additivity and equalize variance.

Alberta fur returns (largely a November-February

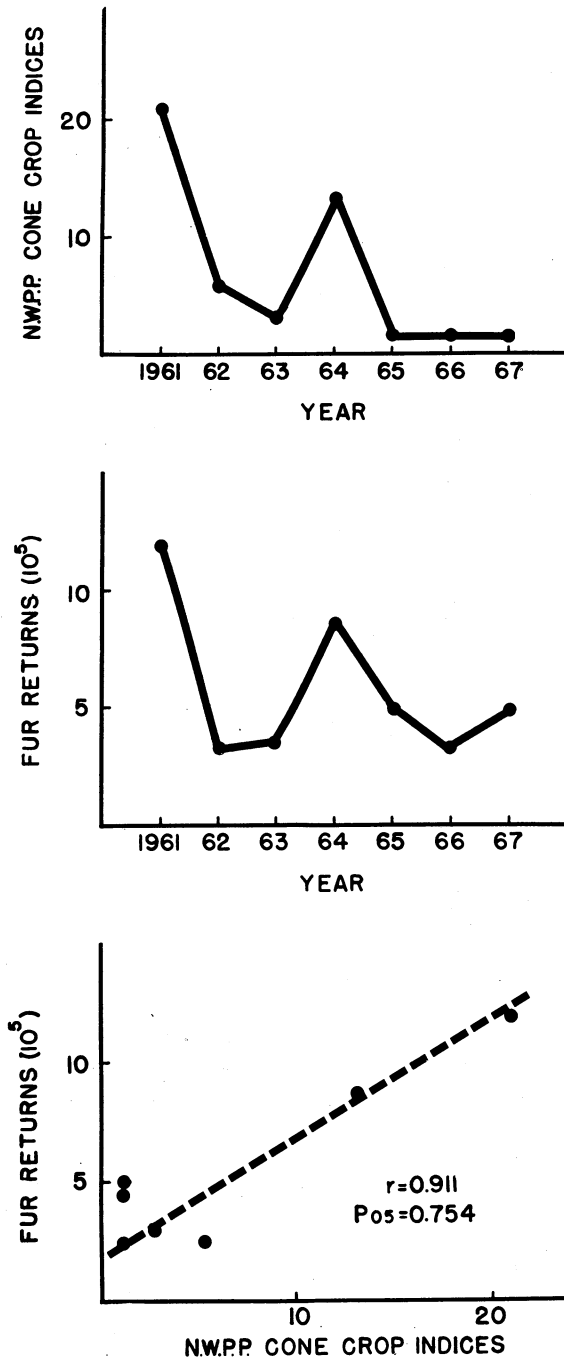


FIG. 3. North Western Pulp and Power (N.W.P.P.) cone-crop indices and Alberta fur returns during 1961-67, and the correlation between these data. Derivation of indices explained in text.

ruary harvest) showed a significant negative correlation with June and July precipitation about a year and a half earlier in the Athabasca River Drainage ($P < 0.01$, Table 14, column 2). A similar relationship emerged between fur harvest and June precipitation in the Peace River Drainage ($P = 0.03$), while the correlation coefficient with

TABLE 14. Correlation between Alberta and Saskatchewan fur returns and the previous year's mean monthly precipitation (water equivalent) records from representative weather stations^a

Month	Athabasca Drainage precipitation vs. Alberta fur returns	Peace River Drainage precipitation vs. Alberta fur returns	Churchill River Drainage precipitation vs. Saskatchewan fur returns
Jan.	-0.137	-0.084	-0.425**
Feb.	-0.171	-0.100	0.013
Mar.	0.343*	0.214	0.011
Apr.	-0.088	-0.155	-0.138
May	-0.237	-0.098	-0.341
June	-0.438**	-0.393*	-0.266
July	-0.421**	-0.319	-0.040
Aug.	-0.306	-0.274	-0.199
Sept.	-0.207	-0.269	-0.027
Oct.	-0.066	-0.122	-0.336
Nov.	0.053	-0.019	-0.213
Dec.	0.067	0.024	-0.151
	$P_{.05}=0.339$	$P_{.05}=0.339$	$P_{.05}=0.342$

^aAlberta data, 1933-1966; Saskatchewan, 1933-1965.

** $P < 0.01$

* $P < 0.05$

July precipitation was nearly significant ($P = 0.06$). In Saskatchewan, the negative correlation between fur returns and May precipitation also approached significance ($P = 0.06$, Table 14, column 4). That the foregoing correlation coefficients have an ecological basis, and are not simply due to chance (i.e. Type I errors in matrix) is supported by: (1) the tendency for r -values to increase and decrease progressively around those having statistical significance, (2) the fact that all 21 r -values in the matrix during April-October are negative (Table 14), and (3) the absence of significant correlations between fur returns and temperature or precipitation during the same year. The coefficients of determination (r^2) here are admittedly low, but this is hardly surprising considering the obvious crudeness of both sets of indices.

These relationships between regional squirrel populations and precipitation tend to corroborate the previously suggested correlation ($P = 0.09$) between N.W.P.P. cone-crop estimates and July rainfall at Edson, Alberta.

We were somewhat surprised to find that provincial fur harvests were not correlated with mean monthly temperatures, since earlier analyses showed that N.W.P.P. cone-crop indices and July temperatures at Edson were significantly correlated. In light of this seeming conflict, and the above described association between precipitation and both cone crops and fur returns, we conclude that summer rainfall is generally the more dominant factor in determining cone production (and hence red squirrel populations). The cone crop-

temperature correlation near Edson may have been fortuitous, but we suspect not. The known effects of temperature on conifer flowering, which were reviewed at the beginning of this section, suggest that temperature acting in concert with moisture might well have a marked effect. In the Edson district, July temperatures and precipitation are negatively correlated, but regionally in the Athabasca and Peace River Drainage no significant correlation exists.

DISCUSSION

Widely separated subpopulations of several species of small mammals commonly fluctuate synchronously over rather broad regions. The microtines and leporids of Arctic and north-temperate latitudes provide numerous well-documented examples of such synchrony (Elton 1942, Siivonen 1948, Keith 1963, etc.). Chitty (1952, 1960) suggested that weather factors play a major role in keeping disjunct populations fluctuating in phase, and Leslie (1959) demonstrated through a generalized mathematical model that operation of a random weather effect could indeed produce synchrony without destroying periodicity. The foregoing analysis of fluctuations involving red squirrels, cone crops, and weather factors support Chitty's view and provides some insight into the mechanism which is operative in this case.

The natural control or regulation of populations is a highly contentious topic, with basic mechanisms subject to continuing dispute and debate (see for example: Birch 1957; Milne 1957; Nicholson 1957; Wynne-Edwards 1965; Lack 1966, pp. 281-312; Chitty 1967). The only point which presently seems clear is that no simple general explanation is likely soon to emerge. Our study of red squirrel populations has disclosed certain local and regional phenomena which may contribute toward a better understanding of population processes in this species.

Several previous workers have suggested, and we concur, that with red squirrels territoriality, food supply and survival are strongly interrelated. We have shown that only about one-quarter to one-third of the adult squirrels in summer occupied "prime territories" capable of assuring sufficient food for year-round survival. We believe that all squirrels must be territorial in winter, at least to the extent that they defend some food cache. Without a cache to carry them over winter, starvation appears inevitable. We cannot demonstrate conclusively that survival rates are highest among prime territory holders; but would note that first-year survival rates for juveniles, few of which hold prime territories, averaged 33% compared to 52% annually for adults (Table 6).

A popular concept of population dynamics is that survival is related directly to habitat quality; and that the number of individuals which can be accommodated in high quality habitats is, due to territoriality, much less variable than elsewhere. Thus overall survival rates may vary density dependently with changing population size, and density independently with factors (largely food and cover) affecting habitat quality. We envision the so-called prime territories at Rochester, associated with mature conifers, as encompassing available high-quality habitat; while habitat of poorer quality is represented by deciduous forest types.

Because of the apparent numerical and spatial stability of prime territories on our study areas, we feel that squirrel population levels from year to year in this predominantly deciduous mixed-forest community are importantly determined by food supplies, and hence overwinter survival, in the deciduous cover. The hazelnut crop would seem to be a highly significant variable in this regard.

If the above assessment of red squirrel population dynamics is correct, why then are there statistically significant correlations between population fluctuations as depicted by fur returns and white spruce cone production and/or weather factors affecting cone production? We believe the answer rests with the fact that the squirrel harvest takes place chiefly in conifer-dominated forest stands where deciduous cover of the aspen-hazel type is much less common than at Rochester. In such coniferous forests, the entire spectrum of habitat quality is largely within a conifer matrix. Here, cone production from year to year can greatly influence survival within the marginal conifer habitats.

Up to this point we have dwelt mainly upon survival as a factor in population change. Yet, as shown earlier, the reproductive rate increased by 66% in 1968 over 1967. The most intriguing aspect of this reproductive increase was that it occurred despite poor cone crops at Rochester in 1966 and 1967, and before the medium-to-heavy cone crop of 1968 appeared. A similar type of anticipatory response was noted by Smith (1968) in 1964 following 2 years of low cone production. An hypothesis which we believe may explain this situation was proposed by Svårdson (1957) for the red squirrel in Sweden. Relative to our own observations, the hypothesis is as follows: during the winters of 1966-67 and 1967-68 squirrels were forced, because of low cone supplies, to utilize white spruce buds extensively for food. [This type of shift in feeding behavior has been noted by Lampio (1967), M. Smith (1968) and other workers]. However, in the winter 1967-68

APPENDIX TABLE 1. Red squirrel fur returns for eight Hudson's Bay Company districts in northern Alberta

Year	Lac La Biche	Keg River	Fort Chipewyan	Fort McMurray	Fort McKay	Wabasca	Whitefish Lake	Sturgeon Lake
1946.....	7,223	7,245	9,356	14,434	14,134	39,733	19,388	47,486
47.....	4,003	15,551	4,484	9,337	21,337	32,071	17,289	29,168
48.....	4,162	9,754	5,739	8,387	36,115	40,711	22,418	40,664
49.....	6,658	4,696	988	3,864	15,632	35,376	29,105	24,764
50.....	8,346	6,559	6,085	7,622	24,677	28,692	5,885	17,746
51.....	5,589	6,381	6,836	8,086	35,064	34,901	15,896	15,912
52.....	6,523	3,865	8,600	4,260	20,863	23,270	13,059	4,007
53.....	1,984	3,308	4,307	1,031	10,075	16,181	7,697	16,478
54.....	5,377	9,174	19,579	4,698	28,143	34,402	23,646	10,575
55.....	1,405	5,569	6,343	1,884	18,741	20,675	6,962	9,717
56.....	1,065	3,872	2,728	173	9,202	5,752	6,098	25,354
57.....	1,525	3,676	5,515	622	12,930	13,793	11,535	12,281
58.....	1,448	3,250	4,957	2,538	18,903	13,942	4,081	4,482
59.....	5,613	10,266	10,876	1,180	15,340	36,552	14,064	22,678
60.....	23,548	11,786	20,643	11,348	22,044	23,306	16,478	9,847
61.....	7,203	5,552	9,464	1,958	19,654	36,354	18,363	9,296
62.....	3,203	5,806	3,607	286	3,441	7,529	16,116	10,226

APPENDIX TABLE II. Red squirrel fur returns from the three Prairie Provinces

Year	Alberta	Saskatchewan	Manitoba
31	288,494		
32	316,333		
33	1,366,326	90,000	
34	1,179,165	50,000	
35	473,898	139,428	
36	1,309,239	811,252	
37	1,024,856	206,696	
38	1,709,152	493,671	
39	3,026,091	560,273	
40	1,534,804	291,845	
41	4,967,933	134,426	
42	1,165,367	248,720	
43	678,039	221,403	326,203
44	1,277,922	304,677	228,803
45	748,671	270,091	445,214
46	1,339,937	379,728	300,847
47	1,300,129	330,757	399,658
48	1,864,547	698,479	224,677
49	1,360,740	353,329	580,707
50	1,165,209	370,292	228,007
51	1,488,240	439,771	378,114
52	976,967	328,698	298,629
53	570,212	178,708	236,870
54	1,003,544	510,520	109,146
55	693,226	250,200	238,959
56	614,812	308,452	121,532
57	688,162	320,736	151,579
58	547,552	310,958	177,436
59	1,153,943	376,136	123,246
60	958,404	449,021	108,399
61	1,149,995	311,567	210,194
62	299,531	169,310	107,683
63	353,425	94,650	86,227
64	866,949	293,110	44,601
65	495,722	149,043	108,244
66	300,408		
67	487,139		

there were many more flower buds present due to differentiation which took place during the preceding summer and which lead to the substantial cone crop in summer 1968. We thus suggest that the higher-quality winter diet provided by these

nutritionally superior flower buds (Kramer and Kozlowski 1960, p. 370; Kupila-Ahvenniemi 1966) subsequently stimulated squirrel reproduction. Svårdson (1957) had also proposed that the observed increases in clutch size of Finnish game birds in years of peak seed production was in response to the previous reproductive "bud-winter."

If the above hypothesis is correct, and red squirrels do characteristically exhibit increased rates of reproduction immediately before a medium-to-heavy cone crop, then the potential for a rapid and marked numerical response to increased cone production would be greatly enhanced. In other words, we could have an anticipatory rise in reproduction coupled later with a higher overwinter survival. Such a mechanism would obviously maximize the red squirrel's ability to utilize a widely fluctuating food supply.

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