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CAN THE SOLAR CYCLE AND CLIMATE SYNCHRONIZE THE SNOWSHOE HARE CYCLE IN CANADA? EVIDENCE FROM TREE RINGS AND ICE CORES

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Abstract.—Dark marks in the rings of white spruce less than 50 yr old in Yukon, Canada, are correlated with the number of stems browsed by snowshoe hares. The frequency of these marks is positively correlated with the density of hares in the same region. The frequency of marks in trees germinating between 1751 and 1983 is positively correlated with the hare fur records of the Hudson Bay Company. Both tree marks and hare numbers are correlated with sunspot numbers, and there is a 10-yr periodicity in the correlograms. Phase analysis shows that tree marks and sunspot numbers have periods of nearly constant phase difference during the years 1751–1787, 1838–1870, and 1948 to the present, and these periods coincide with those of high sunspot maxima. The nearly constant phase relations between the annual net snow accumulation on Mount Logan and (1) tree mark ratios, (2) hare fur records before about 1895, and (3) sunspot number during periods of high amplitude in the cycles suggest there is a solar cycle–climate–hare population and tree mark link. We suggest four ways of testing this hypothesis.

High northern ecosystems are likely to react sensitively to global weather changes. However, northern ecosystems may also be responding to cyclical environmental events in addition to possible global warming (Kane and Teixeira 1990; Friis-Christensen and Larsen 1991). One of the more unusual phenomena in animal ecology, but one that is characteristic of northern ecosystems, is the 10-yr cycle of population numbers shown by several species of mammals and birds in the Canadian and Alaskan boreal forest (Keith 1963; Finerty 1980; Erlien and Tester 1984; Boyce and Miller 1985). The best known of these cycles, that of the snowshoe hare (*Lepus americanus*), has been traced back to the 1790s through the fur records of the Hudson Bay Company (MacLulich 1937, 1957; Elton and Nicholson 1942). Study of the causes of this cycle in particular localities (Keith 1963, 1974; Keith and Windberg 1978; Krebs et al. 1986; Sinclair et al. 1988) has generated two major hypotheses: (1) the cycle is caused by time delays in the interaction of three trophic levels (predators, hares, and their winter food supply); and (2) an interaction of only two trophic levels, that between predators (mam-

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mals such as lynx [*Lynx canadensis*] and birds such as great horned owls [*Bubo virginianus*]) and hares.

The snowshoe hare occurs naturally through the boreal forest from Alaska to Labrador, but the main food types differ between localities and so do the dominant predator species. Thus, paper birch (*Betula papyrifera*) is a main winter food plant in Alaska (Bryant and Kuropat 1980), but it is absent at Kluane, Yukon, only a few hundred km to the east, where it is replaced by grey willow (*Salix glauca*) in the hare's diet (Smith et al. 1988). Lynx are major predators in most of Canada but are absent on the coast of British Columbia and on Anticosti Island, Quebec, where the hare cycle persists (T. Sullivan, personal communication). Thus, one might expect that with different combinations of food species and predators there would be different process rates and time lags in different communities so that localized community cycles might be out of phase. Moreover, even if cycle periods remained the same in different communities, variations in weather regimes might be expected to alter the phasing of the cycle between localities, producing a mosaic of high and low numbers of hares at any instant across the boreal forest.

The Canadian Snowshoe Rabbit Enquiry was a questionnaire survey lasting 17 yr (1931–1948), which asked observers whether the hare population had increased, decreased, or remained the same compared with the previous year. Results were reported by C. S. Elton, D. H. Chitty, and H. Chitty in a series of papers (see Smith 1983 for references). Smith (1983) collated the results to examine spatial differences in the phase of the cycle: in general the cycle was synchronized over the whole of Canada and Alaska within 1–2 yr, contrary to our expectations above. Studies from multiple locations are needed to address what might cause this apparent synchrony. Both Moran (1953) and Leslie (1959) have suggested that an external forcing variable, acting on a continental scale, is needed to synchronize variations in the separate populations: such a synchronizer need act only intermittently to keep the system entrained. For example, natural internal oscillations in the atmosphere of approximately 10 yr could influence ecosystems on a continental scale. Such oscillations have been found by James and James (1989) in numerical simulations of the global atmosphere.

From new evidence found in the rings of white spruce trees (*Picea glauca*) dating back to 1751 at Kluane, southwest Yukon (61°0′N, 138°20′W), we have found a relationship between growth marks produced by hare browsing, hare numbers, the sunspot cycle, and some climate data. We suggest that a climate variable interacting with the sunspot cycle entrains the hare population cycle across the continent during periods when solar activity is unusually high.

METHODS

Tree Data

Snowshoe hares in southern Yukon prefer to eat fast-growing birch and willow shrubs and normally avoid the slow-growing white spruce (Sinclair and Smith 1984; Smith et al. 1988). However, at high hare densities, the apical shoot of

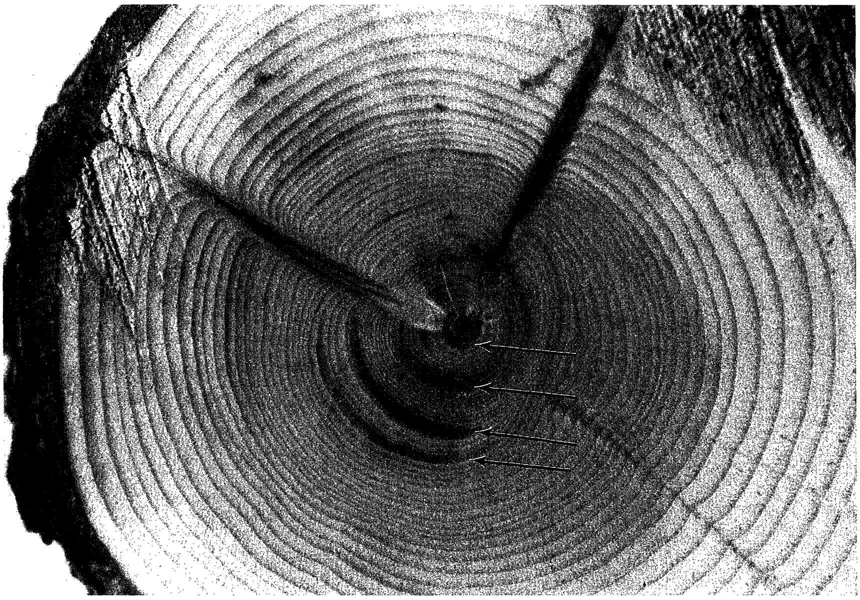

FIG. 1.—Cross-section of base of white spruce showing dark marks (indicated by *arrows*). Where marks covered more than 1 yr, the year of first occurrence was recorded. Marks were identified prior to calculating date by counting growth rings.

small spruce trees (<150 cm high) is commonly eaten. A new apex is then formed from one of the side shoots. Hare browsing can be identified by a clear diagonal cut on the end of the stem. Our observations show that no other browsers make such a cut, and natural or accidental breakage of stems is very rare in our study area. In 1987 we collected a sample of 63 small trees and counted the number of (1) old shoots browsed by hares, (2) growth rings from a cross section of the base to give the age of the tree, and (3) dark bands near the center of the cross section which may be one or several rings thick. These bands are similar in appearance to growth stress marks and are illustrated in figure 1. In 1990 a sample of 157 small trees was scored for the year of the most recent apical browsing.

A 5-km strip of forest, 3 m wide, was cleared in 1987 at Kluane, Yukon. Basal cross sections of all large trees and most small ones were collected (n = 368). The date of germination of each tree was estimated by counting tree rings. From the germination dates, the number of trees available to hares for browsing in this sample was calculated as those less than 50 yr old in each year (trees <50 yr old are usually available to hares, being under 150 cm high). The dates of stress marks in the first 50 yr of life were also scored. Although the oldest tree germinated in 1675, there were too few trees before 1751 to provide useful information.

Hare Data

Population densities of hares at Kluane, in the same region from which the tree data were collected, were measured with live traps set out on grids and monitored at approximately monthly or bimonthly intervals since 1977. Details of the loca-

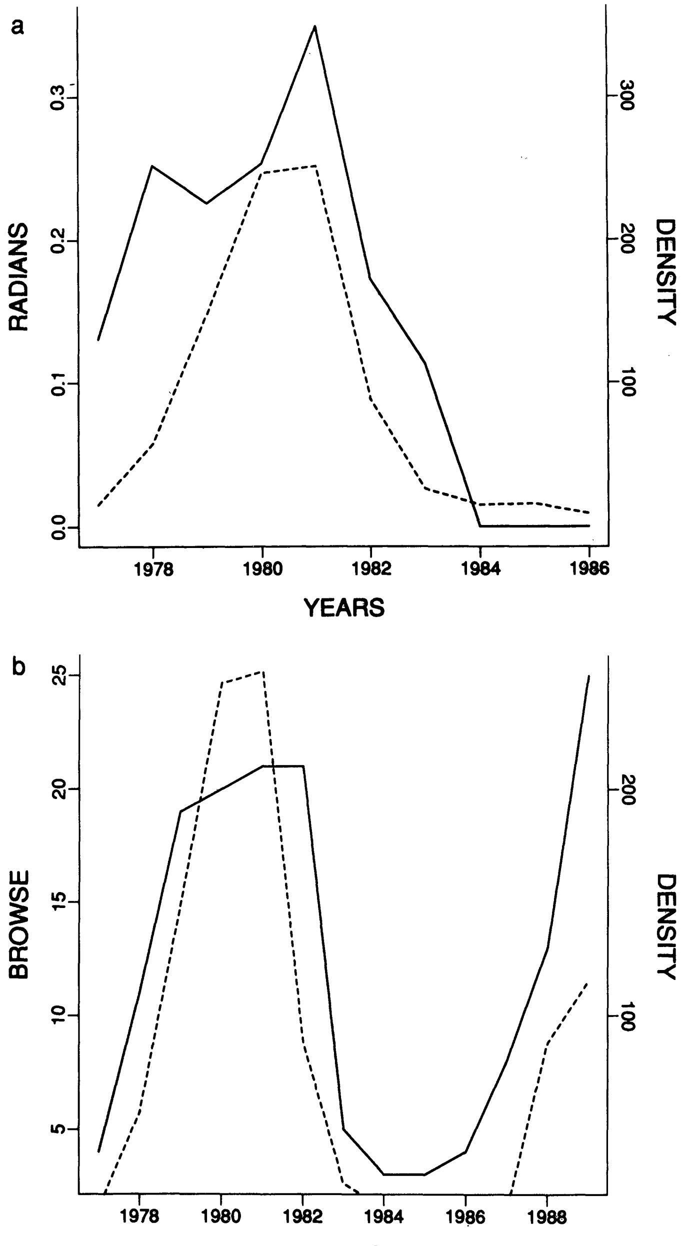

FIG. 2.—*a*, The proportion of marks in white spruce tree rings (arcsine square root transformed) per year (*solid line*) and snowshoe hare density per km^2 for years 1977–1985 (*broken line*). *b*, The frequency of dates when apical shoots of small white spruce were browsed by hares (*solid line*) and hare density per km^2 (*broken line*).

tions, trapping techniques, and population estimation are given in an earlier article (Krebs et al. 1986).

Historical data on snowshoe hare numbers were obtained from the Hudson Bay Company fur records (1844–1904) and from trapper questionnaires (1905–1935; MacLulich 1937). Both data sets were from central Canada (Northwest Territories, Saskatchewan, Manitoba, Ontario).

Climate Data

We used data obtained from a 102.5-m ice core retrieved from the Northwest Col (5,340 m above sea level) of Mount Logan (60°35′ N, 140°30′ W), in Kluane National Park, Yukon. An annual net snow accumulation time series was derived from chemical and isotopic analyses of the core. Annual increments were resolvable from 1736 to 1987. Annual snow or ice increments were converted to water equivalents taking account of layer thinning due to ice flow. Details are given in an earlier article (Holdsworth et al. 1989).

RESULTS

Tree Marks and Hare Browsing

There was a high correlation between the number of shoots on small trees (<150 cm high) browsed by hares and the number of dark marks in the rings (Spearman rank correlation = 0.83, $n = 63$, $P < .001$). These trees can be as old as 50 yr and so could have experienced several peaks in hare numbers. Because the trees came from one small area (approximately 0.5 ha) and the number of marks ranged from zero to six it is unlikely they were caused by stress from weather or other factors affecting trees or hare numbers (hence browsed shoots) independently. Since breakage or other damage was negligible and there were no other browsers, these data suggest a causal relationship between hare browsing and tree marks.

The frequency distribution of dates of tree marks ($n = 1{,}276$) was computed as a ratio of marks per sample of trees available for each year (those <50 yr old at that date) and transformed (arcsine square root). In the hare cycle of 1977–1985 there is a highly significant relationship between hare density and both the untransformed and transformed tree mark ratios (Spearman rank correlation = 0.902 for both, $n = 10$, $P < .01$; fig. 2*a*). In addition, the frequency of years in which the apical shoot was browsed by hares (by dating the browsed shoot itself) also follows closely the hare density in the past two cycles (Spearman rank correlation = 0.825, $n = 13$, $P < .01$; fig. 2*b*). These highly significant relationships between hare density, browsed apical shoots, and stress mark ratios in combination indicate that the frequency of tree marks is a reflection of the hare cycle. This is similar to the relationship between growth scars in pines and the cycle of porcupine (*Erithizon epixanthum*) numbers in Colorado (Spencer 1964).

Tree Mark Ratios

The frequency of tree marks and available trees under 50 yr of age for the whole data set (1751–1983) is shown in figure 3. The untransformed ratios of marks per sample are shown unsmoothed (fig. 4*a*) and smoothed with a 3-yr

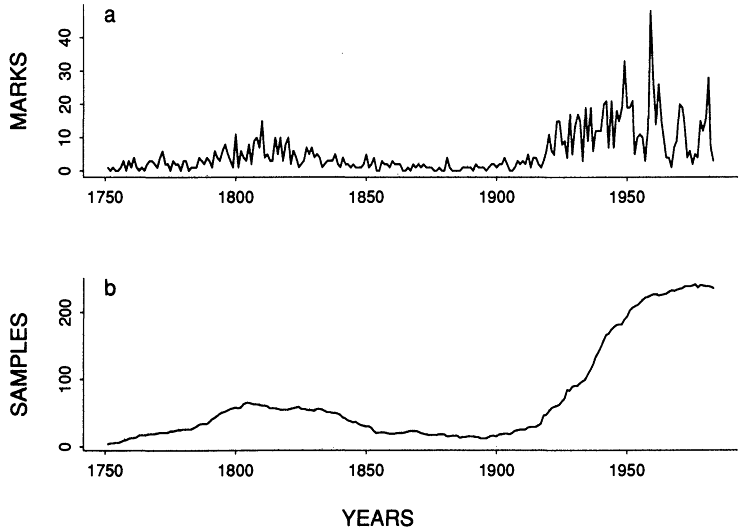

FIG. 3.—*a*, The frequency of marks in tree rings of a given year from the total sample of white spruce; *b*, the frequency of trees <50 yr of age available to be browsed in each year of the sample.

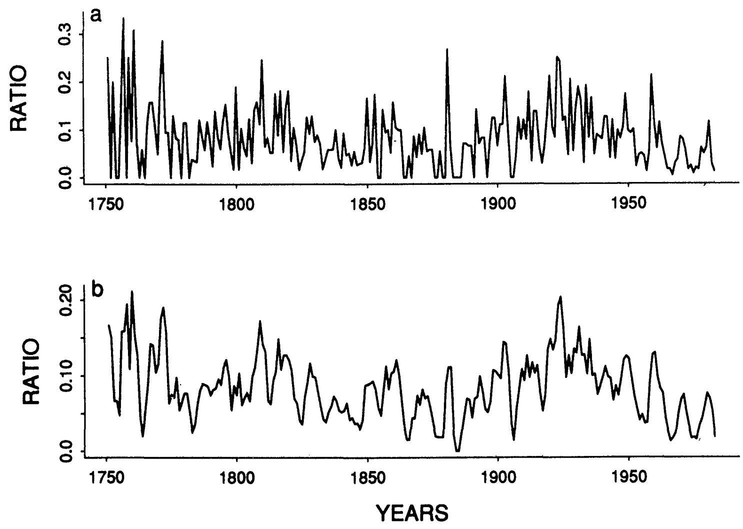

FIG. 4.—*a*, The unsmoothed ratio of marks per sample available for each year; *b*, the same ratio smoothed with a 3-yr running average to remove short-term variations.

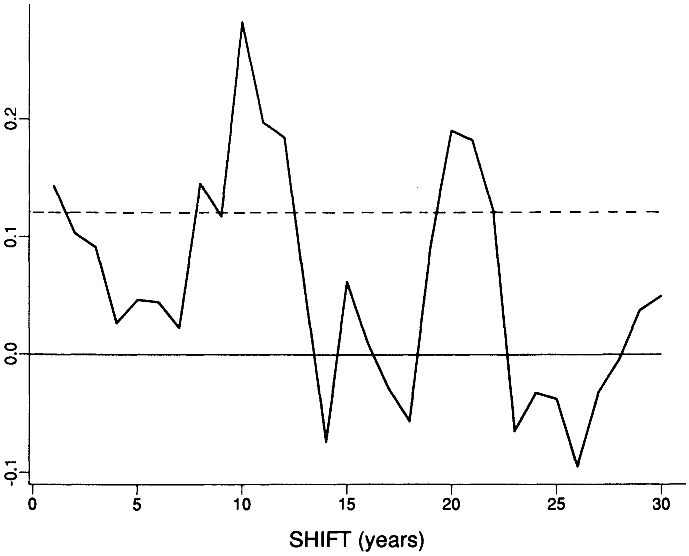

FIG. 5.—Autocorrelation of unsmoothed transformed tree mark ratios in white spruce for 1751–1983. *Broken line* shows the 5% probability value.

running average to remove short term (1–2 yr) fluctuations (fig. 4*b*). The unsmoothed arcsine-transformed data were analyzed by autocorrelation (fig. 5). The smoothed data were analyzed by spectral analysis (fig. 6*a*). Both approaches showed very significant 10–11-yr ($P < .001$) periodicities of marks in trees from 0 to 50 yr of age. The lack of significant negative correlations between the 10-yr peaks in figure 5 is due to noise in the intervening years.

Tree Marks and Sunspot Numbers

The possibility that the hare cycle may be related to the sunspot cycle was originally discounted because the former has a 10-yr mean period, the latter 11 yr (Moran 1949; Keith 1963). Spectral analysis of sunspots by ourselves and others (Waldmeier 1961; U.S. Department of Commerce 1986) showed a peak at 10.6 yr (fig. 6*b*), which overlapped that of the tree marks. Cross-spectral analysis showed high coherence (approximately 80%) at 10 yr as well as at several other frequencies by comparing three-point smoothed spectra. This approach did not provide a clear-cut pattern because the period of the hare cycle varied between 8 and 12 yr and that of the sunspot cycle from 8 to 14 yr during this 230-yr time interval. To determine whether the hare cycle and sunspot cycle varied together it is necessary to subdivide the data set into 30–40-yr periods. However, the frequency resolution of spectral analysis with such short data sets is very reduced, and, therefore, spectral analysis is unlikely to provide an adequate test of our hypothesis.

The sunspot data were, therefore, cross correlated (with successive data shifts up to 30) against the tree mark data, and this produced significant ($P < .01$) negative peaks in the correlation coefficient that are spaced approximately 10 yr

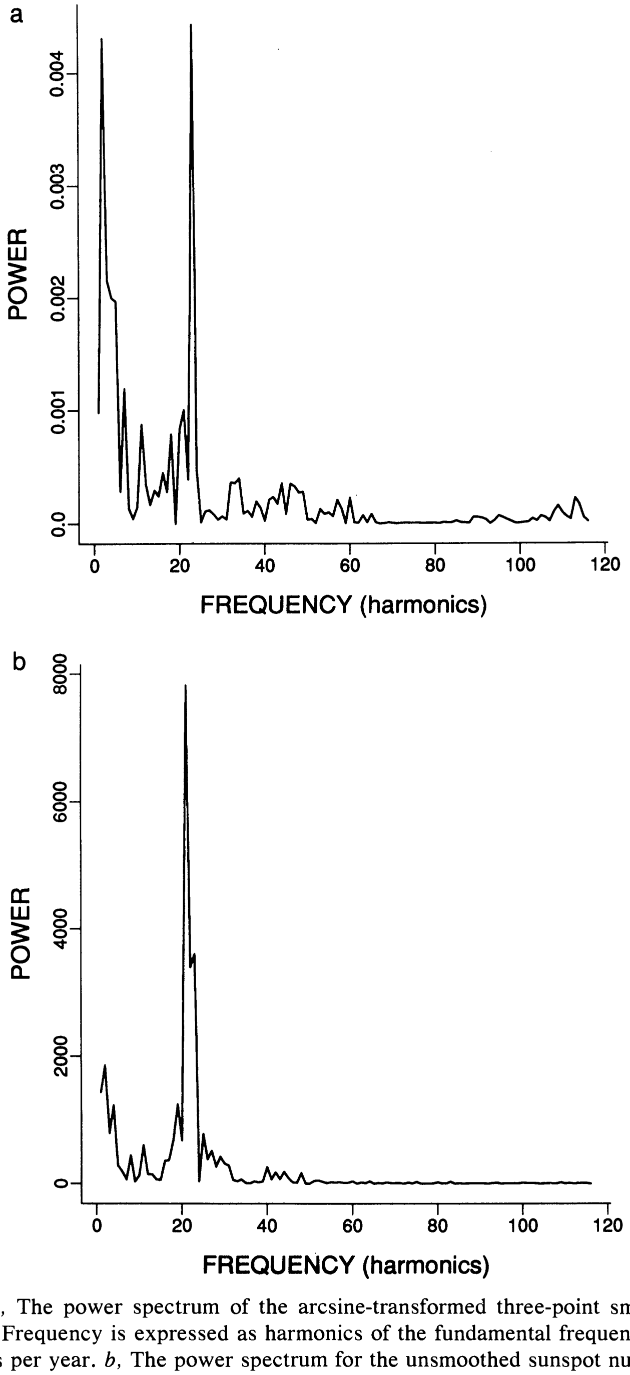

FIG. 6.—*a*, The power spectrum of the arcsine-transformed three-point smoothed tree mark ratios. Frequency is expressed as harmonics of the fundamental frequency, which is 0.0043 cycles per year. *b*, The power spectrum for the unsmoothed sunspot numbers.

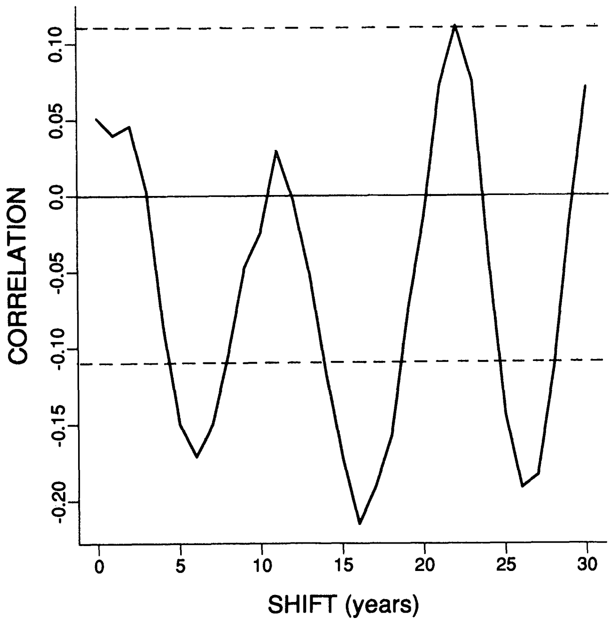

FIG. 7.—Cross correlation of tree mark ratios with sunspot number in previous years, with shifts of 1–30 yr (1721–1983). *Broken lines* show the 5% probability value.

apart (fig. 7). Tree mark peaks were negatively correlated with sunspot minima 6 yr earlier ($P < .01$), or less distinctly with sunspot maxima 2 yr earlier. However, a possible problem with cross-correlation procedures is that spuriously significant correlations can occur in causally unrelated data sets if the periodic functions or processes have a sufficiently similar period. We next explain how we dealt with this problem before interpreting our field data.

Maximum Coefficients in Cross Correlation

If the cycles in two data sets are causally related we expect them to have identical periods. Therefore, in our analyses below we attempt to identify whether cycles in two data sets have identical periods since this is necessary (but not sufficient) evidence to demonstrate causality. Our first simulation examined the cross-correlation results from arbitrary data when similar but not identical periodic functions are compared. For convenience we generated arbitrary sinusoidal data sets, but the results were not dependent on the data's being sinusoidal as opposed to other forms of periodicity. The sinusoidal data were generated as

$$A_n = A_0 \sin 2\pi n/P,$$

where A_n is the annual amplitude, P is the period of the cycle in years, and n is the year.

Two such data sets with nonidentical periods (and approximately 10 data points per cycle) were cross correlated, and the maximum positive correlation coefficient ($r_{\max}$) in the first 20 shifts was identified, as illustrated in the inset of figure

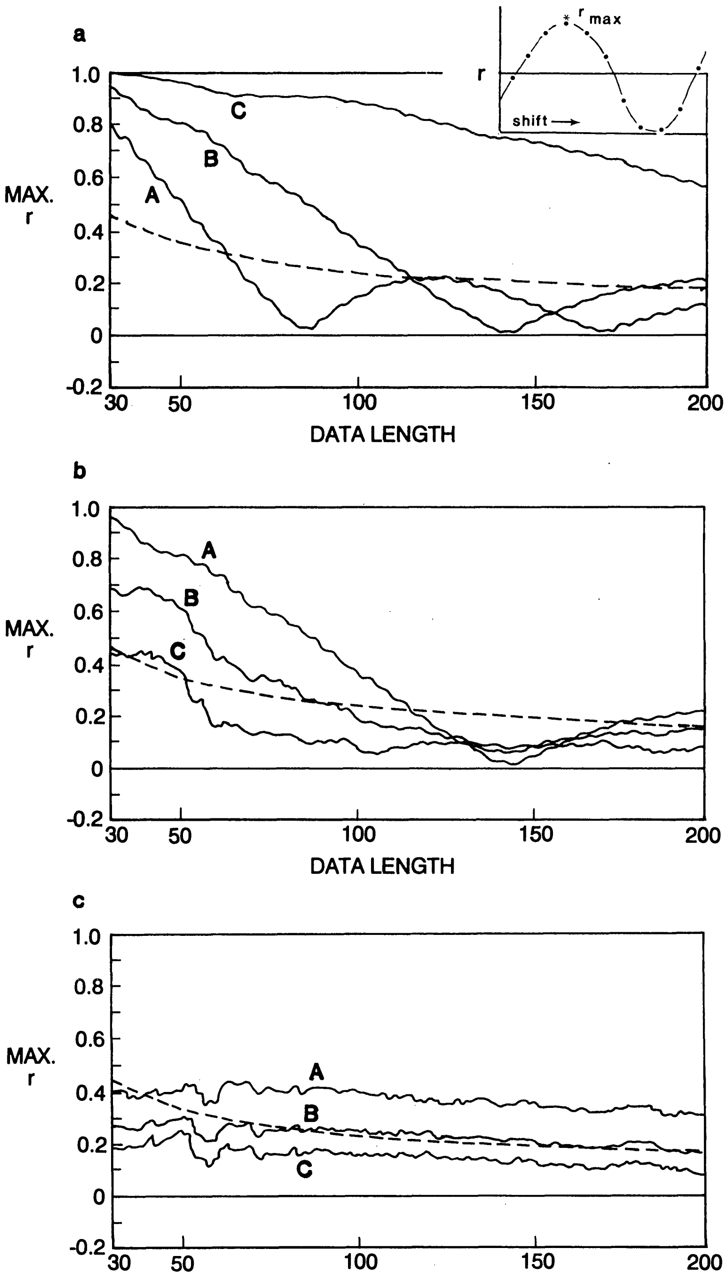

FIG. 8.—*a,* The maximum positive correlation coefficient ($r_{\max}$) produced in the first 20 shifts of a cross correlation of two arbitrary data sets is illustrated in the *inset.* This $r_{\max}$ is plotted against increasing data length, using three pairs of sine waves. Their periods are (*A*) 10.7 and 9.5; (*B*) 10.7 and 9.95; and (*C*) 10.7 and 10.4. *Broken line* shows the 1% probability value. *b,* The effect of noise on the maximum correlation coefficient at different data lengths using two sine waves with periods 10.7 and 9.95: (*A*) correlations from sine waves with no noise, (*B*) those when one wave has a noise: signal ratio of 2, and (*C*) those when the ratio is 10. *c,* The effect of noise on the maximum correlation coefficients from two related data sets, the autocorrelation of sunspot data; noise is added to one data set with noise: signal ratios of (*A*) 5, (*B*) 10, and (*C*) 50.

8*a*. Each $r_{\max}$ was that obtained for a single independent set of data of a given length such as that obtained for $n = 233$ in figure 7. Figure 8*a* shows how the $r_{\max}$ value would be affected if the data set had been of a different length, first for short data lengths (30), then for successively longer lengths up to 200. The first pair of arbitrary data sets (*A*) had periods of 10.7 and 9.5 (i.e., 11% difference in period); two further pairs were successively closer in period, namely, (*B*) 10.7 versus 9.95 (7%), and (*C*) 10.7 versus 10.4 (3%). In each case the maximum correlation was high and significant at $P < .01$ with short data lengths (to be conservative we used the 1% significance level). As data length increased, the maximum correlation fell, the rate of decrease being steeper the greater the difference in period. Thus, the coefficient fell below the 1% probability line at data length 60 in *A* and 120 in *B* but remained above this line in *C* when the periods were only 3% different. A second feature of these cross correlations is that the maximum correlation appeared to go through "nodes" at certain data lengths (*n*). Thus, in *A* the correlation reached a node (i.e., close to zero) at *n* of 90 and then increased again close to the 1% probability line near *n* of 120, before declining to a new node at *n* of 170. As the periods of the arbitrary data sets became more similar the position of the node was reached at a greater data length, being at *n* of 150 in *B,* and no node was reached at all in *C*. Thus, this analysis shows how data sets with nonidentical periods can produce high and significant $r_{\max}$ values even with long data lengths. However, such spurious correlations can be identified either by (1) the appearance of nodes or (2) a declining $r_{\max}$ with data length. In contrast, data sets with identical periods (i.e., from causally related phenomena) have an $r_{\max}$ that is constant with data length (as shown below in fig. 8*c*).

Second, we investigated the effect that noise in one of the arbitrary data sets might have on the maximum correlation coefficients, in order to mimic the apparently noisy tree mark data. Arbitrary data sets with periods of 10.7 and 9.95 (7% difference) were used. The 9.95 sample data were added to noise from a random number generator in the computer to produce root-mean square noise : signal ratios of 2 and 10. These noisy data were then cross correlated with the uncorrupted 10.7 sample data to obtain the maximum correlation coefficients (fig. 8*b*). The same noise data were used for each ratio. As the noise : signal ratio increased, the correlation decreased so that it dropped below the 1% probability line at progressively shorter data lengths. In addition, the node at data length of 140 gradually disappeared, and the rebound giving spuriously significant correlations was progressively eliminated. Thus, the effect of noise in unrelated arbitrary data obscured the appearance of nodes, and $r_{\max}$ became progressively less significant, especially for long data sets.

Third, we examined the effect of noise on the correlation coefficients from sets of data in which the periods were identical (i.e., could be causally related). For this we used the autocorrelation of the sunspot data and added noise as above to one of the copies of the data. Again plotting the maximum correlation against data length, the uncorrupted autocorrelation gave coefficients close to unity for all data lengths, producing a horizontal line. Figure 8*c* shows the effect of increasing noise : signal ratios on the autocorrelation; the horizontal line remained evident

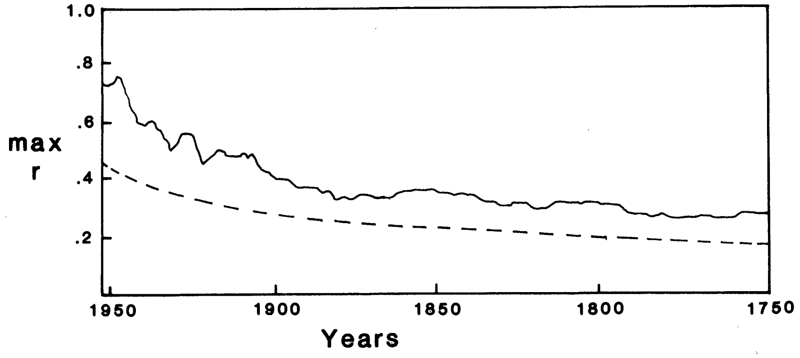

FIG. 9.—The maximum positive correlation coefficient produced in the first 20 shifts of a cross correlation between tree mark ratios and sunspots, plotted against data length. *Broken line* shows the 1% probability level. Data start with the most recent 30 yr and then increase by extending back in time.

but the magnitude of the correlation coefficients decreased with increasing noise. Again, the same noise waveform was used to create the different ratios, so the shape of the line was essentially identical. Short data lengths produced coefficients below the 1% probability line, and there has to be a longer data set for correlations to exceed this 1% value as noise ratios increased from 5 to 10, and at a ratio of 50 the maximum correlation remained below the line. We can conclude, therefore, that if we find significant and constant $r_{\max}$ values at long data lengths, without nodes, then the data sets have identical periods and could be causally related.

In figure 9 we plot $r_{\max}$ against data length for the cross correlation of tree mark ratios and sunspot data. The coefficient declined to about n of 100 and then remained relatively constant. At all data lengths $r_{\max}$ remained above the 1% probability level. By comparing the trends shown in figure 8*a*–*c* with that in figure 9, we can make two inferences about the quality of the correlation between the tree mark data and the sunspot data. First, the lack of any obvious node in $r_{\max}$ while it remained above the 1% probability value throughout a data length of over 230 samples (that spans the period 1751–1983), and, second, the nearly constant $r_{\max}$ above data lengths of 100 suggests that the noisy tree mark data have either (1) identical periods to those of the sunspot data or (2) periods less than about 5% different from each other. Figure 9 does not allow us to distinguish between the two possibilities.

Phase Analysis of Cross Correlation

A more powerful technique for detecting very small differences in the period of two sets of cycles examines phase differences in the cross correlation at different points along the data set. This allowed us to examine subsets of the time series. If two data sets have slightly different periods, then the two sets should gradually drift in their phase relations over the length of the data. The drift in phase difference can be detected by cross correlating short segments of data, for example, blocks of 20, and shifting one set against the other to find the shift in which some reference point such as the maximum correlation coefficient occurs. For example, if the two data sets have identical periods, the shift in which $r_{\max}$ occurs in the 20-yr block 1951–1971 should be the same as that in the 1851–1871 block.

In practice, inspection of the correlograms between tree marks and sunspots showed that the shift in which $r_{\max}$ occurred was not always clear-cut, because the correlograms were sometimes spread over several shifts. Therefore, in this analysis we chose, instead of the maximum coefficient, a more easily identifiable arbitrary point where the correlation coefficient was declining rapidly. Because the peak negative coefficients had a greater magnitude than the peak positive coefficients, we present the results for the crossing at $r = -0.1$, although these results did not differ significantly from those at the $r = 0$ crossing. Further, because the correlation coefficient declined sharply at $r = -0.1$ (see fig. 7), we were able to use linear interpolation to obtain fractional shift values for the analysis of phase.

We tested the prediction that the phase shift was constant for a true causally related periodic process by applying this method to the autocorrelation of the past 200 yr of sunspot data. The analysis used successive blocks of 20 samples, shifting by 15 shifts within each block (fig. 10*a*). As predicted, the shift for the -0.1 correlation crossover (i.e., phase difference) remained essentially constant over the entire data set. The peak at about 1810 reflected several unusually long cycles at that time. Adding noise to one data set did not alter this picture.

If the two data sets were unrelated and had even very small differences in period, then the shift at which the $r = -0.1$ occurred (phase shift) would drift. This prediction is shown diagrammatically in figure 10*a*, in which the broken line gradually increases until it reaches the full cycle then starts again at the bottom. Therefore, a constant phase shift implies that the data sets have identical periods and could be causally related, while drift in phase shift means that they are not related.

We conducted phase analysis of the cross correlations between tree marks and sunspots using data blocks varying from 15 to 70 samples in length. Although short blocks produced more scatter in phase shift and long blocks averaged out some information, they all showed the same picture. We also tried various averaging procedures such as four-point and five-point quadratic windows, but we obtained essentially similar results. All figures shown are for three-point running averages. We show the phase shift plotted against date for blocks of 20 and 40 yr in figures 10*b* and 10*c*, respectively. Two features are apparent: there are periods in which the two data sets appear locked in phase, these being clearer with the longer data blocks; and there are intervening periods when the data sets drift, these being more obvious in figure 10*b*.

The three periods in which data sets have relatively constant phase difference coincide almost exactly with those when the amplitude of the sunspot cycles reach maxima (fig. 11). During the intervening years the sunspot cycles are at low amplitude, and in these periods the two data sets appear to drift in their phase relations. We examined this coincidence more objectively in the following way. The three time periods of high solar activity, defined by peaks of sunspots,

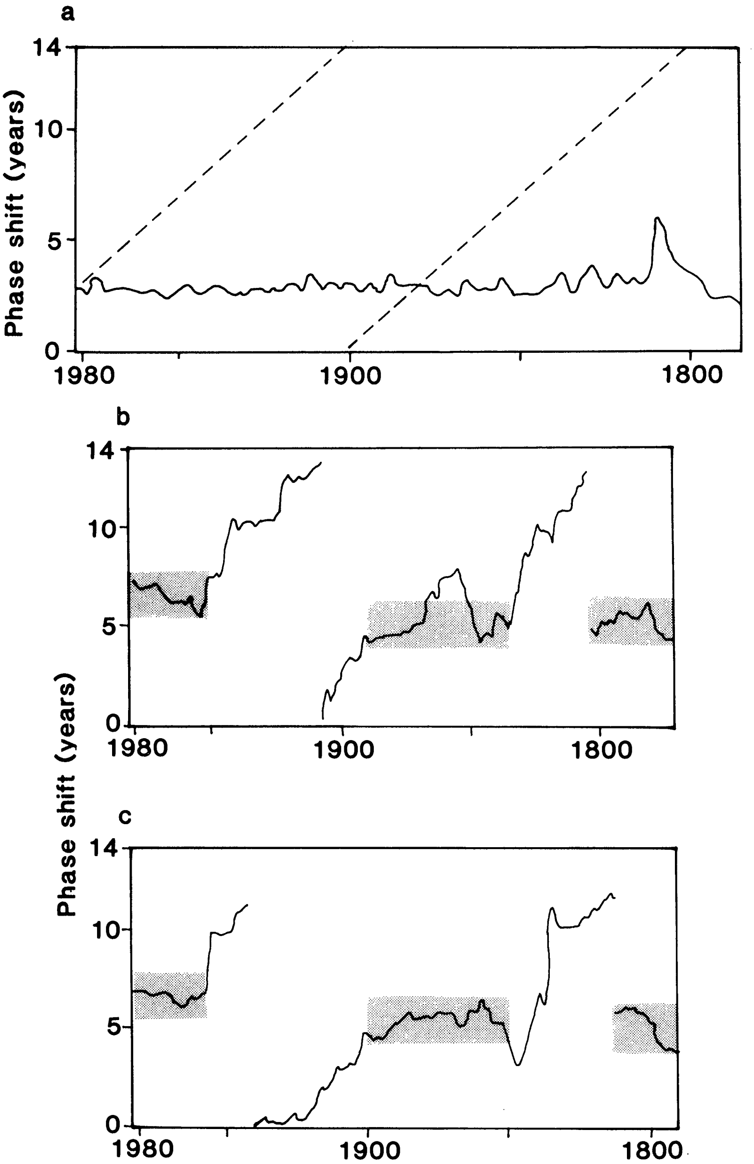

FIG. 10.—Cross correlation of short data blocks, with shifts of 15 yr within each block, and recording the shift at which $r = -0.1$ (phase shift). The block is then moved by 1 yr along the data set to repeat the process. This is a measure of phase difference between the data sets. *a*, Measure is from correlation of identical sets of sunspot data using blocks of 20 to show the shift at which $r = -0.1$ (i.e., phase difference) is constant along the data length. The diagonal *broken lines* predict the trend in phase difference if the data sets have unrelated cycles, in contrast to the horizontal line produced by related data; *b* and *c*, measure is from cross correlation of tree marks and sunspots using blocks of 20 and 40 data points, respectively. The shaded periods are those in which the phase difference is constant. Analysis starts with recent data and moves back in time. The year shown is that of the most recent data in the block (e.g., 1980 refers to a data block of 1980–1961 in *b*, and 1980–1941 in *c*).

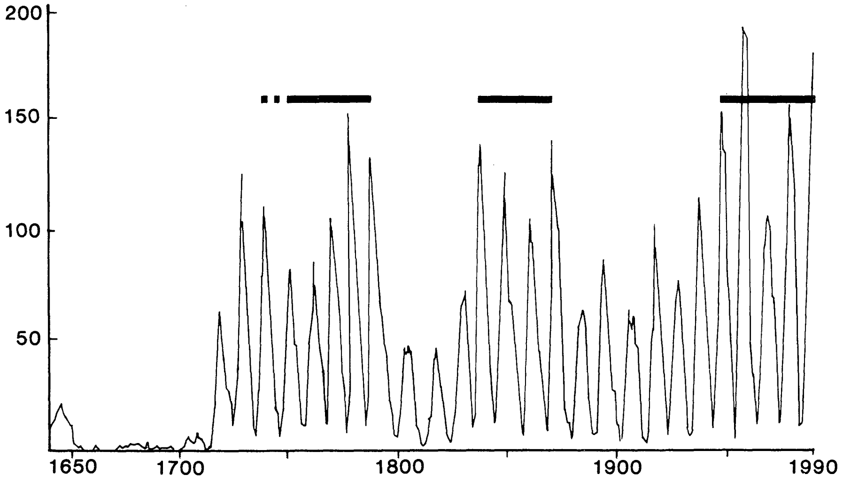

FIG. 11.—Sunspot number (1645–1989) showing the time spans (*horizontal bar*) during which high amplitude cycles coincided with times when tree mark ratios and solar cycles have constant phase differences (see fig. 10*b*). The *broken bar* before 1751 indicates that phase lock may have existed but no data are available.

occurred from the start of the record (1751) to 1787, 1838–1870, and 1948 to the present. Sunspot data for these periods were spliced together. We predicted that these data should show a constant phase shift with the tree mark data for the same time periods. This was indeed the case; the phase analysis showed a constant phase relationship between the data sets, and there was not even a jump where the data had been spliced. Similarly, the data for the two time periods of low solar activity (1788–1837 and 1871–1947), when spliced together, showed a continuous and uninterrupted phase drift. Thus, in the past 230 yr there have been three periods of 30–40 yr each during which the tree mark data and sunspots have been locked in phase. This result is not due to the two series' coinciding as they drift in and out of phase. If this were the case we would not see the episodes of constant phase difference in the two data sets: such episodes were present regardless of the size of data blocks used in our phase analysis.

Tree Marks and Snowshoe Hare Numbers

Given the close synchrony of the hare cycle between different areas of Canada (Smith 1983) and assuming that the fur trade in hare skins is an index of the hare population, we consider that the hare fur records of the Hudson Bay Company are a reasonable index of hare numbers in the Yukon. Some of these data (1844–1870) include part of the period when phase analysis suggests synchrony between tree marks and sunspot data. The historical data on hare fur records were cross correlated with the arcsine-transformed tree mark data, shifting both forward and backward (fig. 12*a*). Tree marks are negatively correlated with hare numbers 2 yr previously, and positively correlated with hare numbers 2 yr ahead for the 92-yr period of the hare data (1844–1935). This suggests that tree marks may be produced during the portion of the hare cycle when numbers are increasing, and

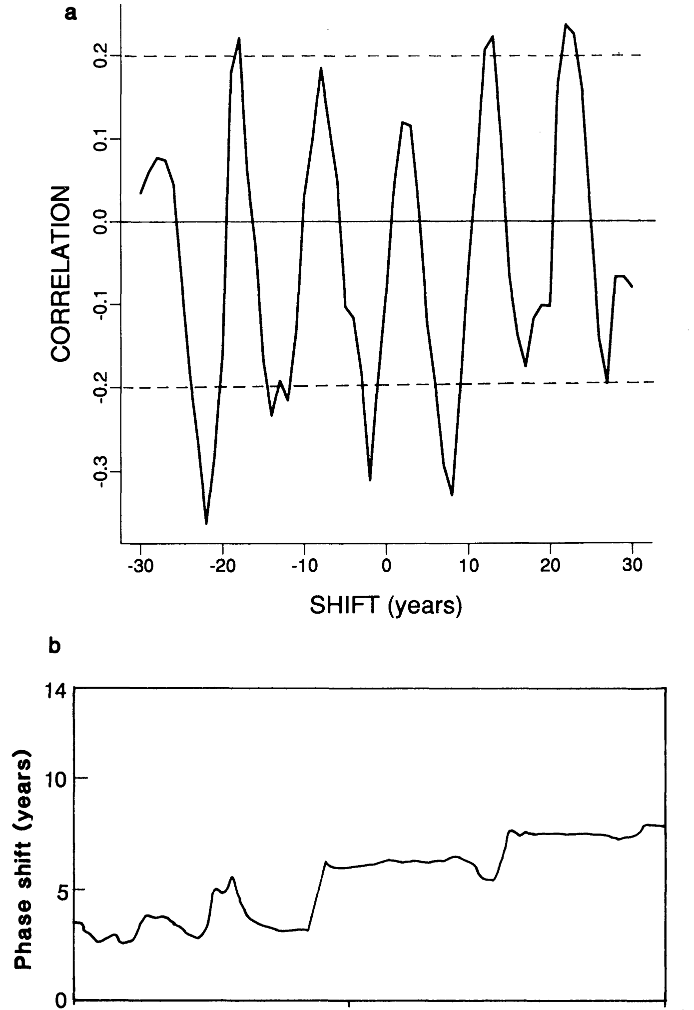

FIG. 12.—*a*, Cross-correlation of tree mark ratios with snowshoe hare records (1844–1935). Positive shift shows the correlation of hare records with tree marks in previous years, while negative shift shows the correlation of tree marks with hare records in previous years. *Broken lines* show the 5% probability value. *b*, Phase analysis of *a* as in fig. 10*b* using blocks of 20 data points.

hence there could be an increasing browsing impact on small trees. There is a clear 10-yr periodicity in the cross correlation.

This cross correlation was examined with the phase analysis procedure described above (fig. 12*b*). Although there are jumps in phase shift around 1904 and 1887, there is no indication of a systematic drift in phase difference. Thus, the hare and tree mark cycles appear to be locked in phase throughout the data length. This evidence, combined with that in figure 2 and the correlation between

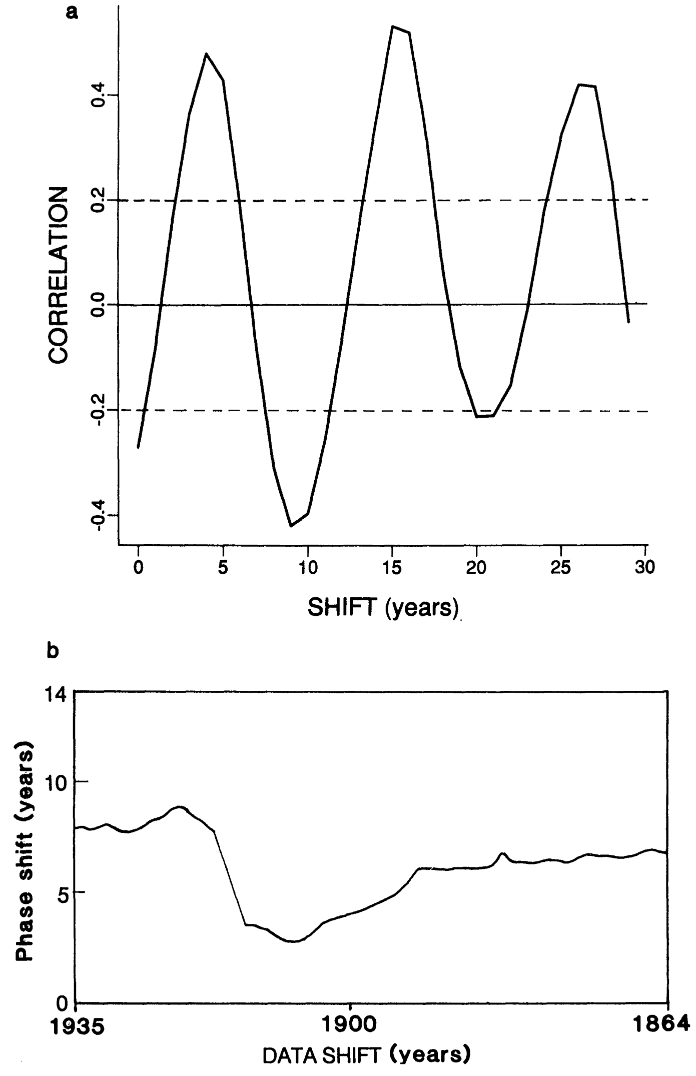

FIG. 13.—*a*, Cross correlation of hare records with sunspot numbers (1844–1935) for shifts of previous 1–30 yr. *Broken lines* show 5% probability value. *b*, Phase analysis of *a*, as in fig. 10*b*, using blocks of 20 data points.

tree marks and hare browsing, leads us to conclude that the marks in the longer tree record are consistent with a hare-browsing hypothesis.

Hare Numbers and the Sunspot Cycle

Hare fur records cross correlated with sunspot data show that peak hare numbers are highly positively correlated ($P < .0001$) with sunspot maxima 4 yr previously (fig. 13*a*). This relationship applies to the second half of last century and early this century. In the most recent three decades sunspot peaks have occurred

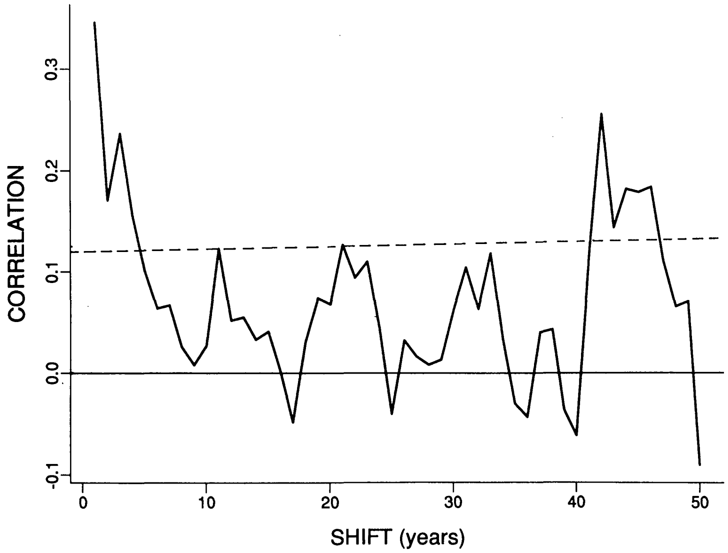

FIG. 14.—Autocorrelation of annual net snow accumulation from Mount Logan with shifts of 1–50 yr. *Broken line* shows the 5% probability value.

in 1969, 1979, and 1990, and hare numbers have peaked in 1971, 1981, and 1990. Of the 15 hare peaks from 1844 to 1991, 11 fall 2–5 yr after sunspot peaks. If there was no correlation they should fall randomly through the years after a sunspot peak, so that of the 15 only five would be expected to fall in the same 2–5 yr; the observations are significantly different from a random distribution ($\chi^2 = 14.4$, $P < .01$).

Phase analysis of the hare record and sunspot cross correlation (fig. 13*b*) shows a jump in phase shift around 1920 and a period during which the phase drifts (1891–1916), indicating uncoupling of sunspots and hare numbers. The period when the phase is effectively constant (1844–1891) is similar to that in the tree mark and sunspot phase analysis, coinciding with the high-amplitude sunspot peaks.

Climate Fluctuations

A 102.5-m continuous ice core from the Northwest Col of Mount Logan has provided an estimate of annual net snow accumulation (ANSA) for the 252-yr period 1736–1987. We use this as an index of precipitation for the Kluane region. The power spectrum has shown a peak in this record between 9 and 11 yr (Holdsworth et al. 1989). Autocorrelation (fig. 14) indicates a cycle with average period of 10.5 yr and with a longer cycle of 42–46 yr superimposed on the shorter one. Maximum entropy analysis of the time series (R. Currie, personal communication) shows that there is a 180-degree phase switch around 1904. Autocorrelation of the ANSA before this date produced a much clearer cycle of 11.0 yr with a major peak at 44 yr.

Cross correlation of ANSA and tree mark ratios produced cycle periods of

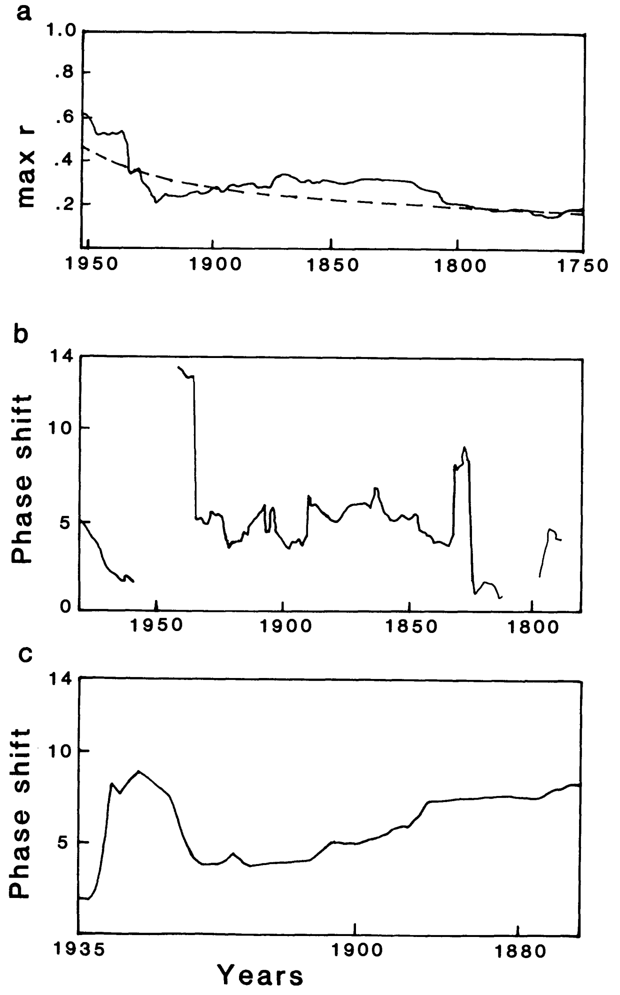

FIG. 15.—*a*, The r_{max} produced in the first 15 shifts of the cross correlation between three-point smoothed annual net snow accumulation (ANSA) and smoothed tree mark ratios, plotted against data length. *Broken line* shows the 1% probability value. *b*, Phase analysis of the cross correlation between ANSA and tree mark ratios, using blocks of 30 data points, 15 shifts within blocks, and recording the shift at which $r = 0$. The gaps indicate no crossing was found. *c*, Phase analysis of the cross correlation between ANSA and hare fur records, using blocks of 30 data points, 15 shifts within blocks, and recording the shift at which $r = 0$.

9–12 yr. The r_{max} values from this cross correlation were plotted against data length using three-point smoothing for both data sets (fig. 15*a*): r_{max} was mostly above or close to the 1% probability value as the data set increased. Also r_{max} remained effectively constant after an initial decline, suggesting that the two data sets had the same period but both were contaminated by noise, as illustrated in our simulation of figure 8*c*. Because of the possible phase reversal in ANSA in

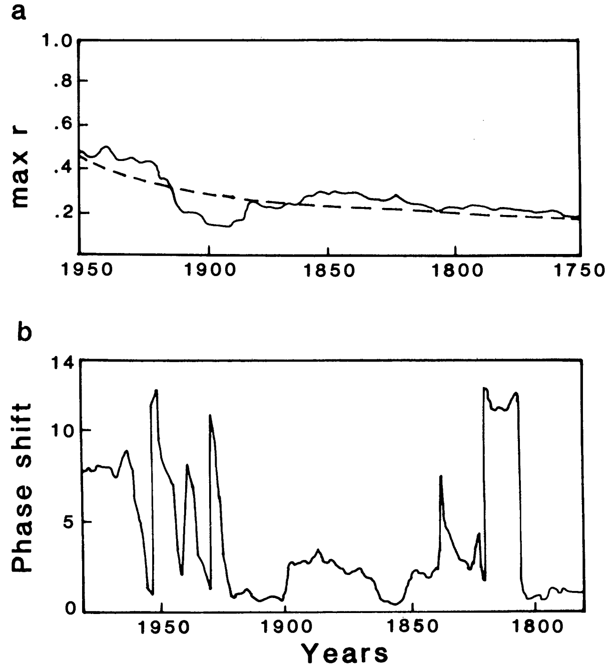

FIG. 16.—*a,* The r_{max} produced in the first 15 shifts of the cross correlation between three-point smoothed ANSA and sunspot numbers, plotted against data length. *Broken line* shows the 1% probability value. *b,* Phase analysis of the cross correlation between ANSA and sunspot number, using blocks of 30 data points, 15 shifts within blocks, and recording the shift at which $r = 0$.

1904, r_{max} was examined for the cross correlation starting in 1903 and extending back to 1751. In this analysis the r_{max} values were constant and considerably higher, with none dropping below the 0.001 probability.

Phase-shift analysis (fig. 15*b*) confirmed that the snow record and tree mark ratios were phase locked over long periods, especially the period 1835–1935. In addition, there is no indication of a regular drift in phase difference over the whole record, which would be expected if the cycles were unrelated. This evidence suggests the strong possibility that the tree mark ratios are related to the snow record either directly (through growth, for example) or indirectly through the effects of hare browsing.

Phase shifts from the cross correlation of ANSA and the hare fur records (fig. 15*c*) are similar to those from the sunspot–hare record analysis (fig. 12*b*): the data sets are phase locked before about 1895, but there is drift in the period 1895–1935.

If the solar cycle is affecting the hare population or the tree marks through climatic influences, then periods of phase lock between ANSA and tree marks should be similar to those seen for sunspots and tree marks (fig. 11). The plot of r_{max} for the ANSA–solar cycle cross correlation (fig. 16*a*) is similar to that for weather and tree marks (fig. 15*a*); namely, there is a decline in correlation from

1983 back to the beginning of the century, but then the correlation becomes nearly constant. When data prior to 1904 are analyzed alone, $r_{\max}$ never falls below a probability of .001.

Phase shift analysis of this cross correlation (fig. 16*b*) suggests that there is phase lock during 1960–1983 (approximately), 1830–1900, and about 1751–1800. This picture is qualitatively similar to that found for the sunspot–tree mark relationship (figs. 10*b,c,* 11). Thus, the data are consistent with the hypothesis that the solar cycle influences climate, which in turn synchronizes the hare population in the boreal forest.

DISCUSSION

Hare Cycles, Tree Marks, and Sunspots: Are They Causally Related?

The evidence from figure 2 showing the very strong correlation between hare numbers and tree marks in the past decade, together with the cross correlation of tree marks and the hare fur records from central Canada (fig. 12*a*) strongly suggests that these two data sets are related. Furthermore, phase analysis of this cross correlation (fig. 12*b*) shows that the two data sets are largely in phase, even though they are derived from different areas of Canada. Evidence that hares cause tree marks comes from the relationship between the number of apical shoots browsed by hares and the number of marks in small trees less than 50 yr old.

There are significant cross correlations between sunspot number and both tree marks and hare fur records. Phase analysis of the sunspot–tree mark cross correlation (fig. 10*b,c*) showed that there are roughly 40-yr blocks of time when the two data sets are locked in phase, and these time periods coincide almost exactly with those in which sunspot cycles are at their greatest amplitude (fig. 11). This is the strongest evidence in support of a causal relationship between sunspots and tree marks. The same phenomena are evident in the phase analysis of sunspot–hare record cross correlation, although the agreement is less marked because of the shorter data length.

Thus, we suggest that periods of high solar activity directly or indirectly entrain either (1) the tree marks through growth or (2) the hare population through survival. We consider the latter case more probable because of the empirical evidence that hares are the direct cause of the dark marks in tree rings. An external forcing variable, like solar variability, must have an effect on a global scale, but such a synchronizer need not influence subsystems continuously or uniformly. It is also possible that the solar cycle is ''beating'' together with a natural decade-long cycle in the earth's atmosphere (Holdsworth 1990). In the 50–70 yr of low sunspot maxima, hare and sunspot cycles drift apart and are then brought back in phase at the next period of high solar activity. These peaks in activity occur with a regular periodicity of 80–90 yr, the Gleissberg period (Friis-Christensen and Larsen 1991). Figure 9 can be interpreted in this light; the data start with the first 30 yr of tree marks and sunspots going back from 1983, when they are highly correlated because they have similar phase difference. Further data are then added back to around 1890, when there is a drift in phase difference, and so the $r_{\max}$ drops. Then earlier data (prior to 1890), when the sets are more constant in phase difference, begin to strengthen the correlation so that $r_{\max}$ stays constant.

Mechanisms Relating Sunspots, Tree Marks, and Hare Cycles

We do not suggest that solar or other environmental events cause the hare cycle, but rather they provide a phase-locking mechanism. A useful analogy can be made with the way the day-night cycle provides the *Zeitgeber* or phase lock for the circadian rhythms of animals; the rhythms themselves are intrinsic to the animal's physiology, and day length merely provides the cue to set the phase. In the present case, the hare cycle probably originates from the dynamics of the ecosystem (Krebs et al. 1986; Sinclair et al. 1988).

We do not yet fully understand the mechanisms that result in the modulation of hare cycles by solar variability. A general scenario would be that solar variability influences weather patterns (and hence climate), which then directly or indirectly (e.g., through precipitation and soil moisture variations) influence food supply that in turn affects hare numbers. To examine climatic influences we have used the annual net snow accumulation record in the Mount Logan ice core, which is the longest available data set for the Yukon. The nearly constant phase relations between (1) the core record and tree mark ratios, (2) the core record and hare fur records before about 1895, and (3) the core record and sunspot number during periods of high amplitude in the cycles are together consistent with a solar cycle–climate–hare population and tree mark link.

Cross correlations between the Mount Logan ice core and precipitation records from local stations are low, although most of these data sets are short. However, the North American precipitation data (Bradley et al. 1985; R. S. Bradley, personal communication) show that the records from the western prairies, British Columbia, Northwest Territories, and Alaska are positively correlated with the Mount Logan ice core. Temperature data also show connections in the northern hemisphere on a continental scale (Jager 1988). This implies that if climate is influencing the hare cycle it is doing so on a continental rather than on a local scale.

There is increasing evidence that sunspots and associated solar activity affect weather systems (Kerr 1988), although some evidence is conflicting (Kerr 1990) and the proposed mechanism (Tinsley et al. 1989) is as yet quantitatively unproven. Sunspots are related both to total irradiance (Foukal and Lean 1990) and to ultraviolet irradiance (Lean 1989; Foukal 1990). North Atlantic winter storms track farther south at solar maxima (Tinsley 1988), and a similar feature could occur in the Pacific, thus modulating precipitation in the Yukon. Also, the solar cycle correlates with Arctic sea ice (Hill and Jones 1990), with northern sea-level atmospheric pressure, both summer and winter temperatures (van Loon and Labitzke 1988), and variation in Northern Hemisphere land air temperatures (Friis-Christensen and Larsen 1991). Moreover, high solar activity is associated with shorter periods in the sunspot cycle (Friis-Christensen and Larsen 1991). This could explain why we see phase lock between sunspots and tree marks during periods of high solar activity.

These climatic influences could affect plant growth and hence animal food supply. The solar magnetic cycle is a double-sunspot cycle (mean of 22 yr; Cole 1973). There are 10–11- and 20–22-yr cycles in temperature, drought, and fire regimes in North America (Mock and Hibler 1976; Siscoe 1978; Mitchell et al. 1979; Clark 1988; van Loon and Labitzke 1988; Barnston and Livezey 1989). Currie and O'Brien (1988, 1990), who so far do not acknowledge the existence of a 22-yr term, report a 10–11-yr and an 18.6-yr cycle in drought indices, tree rings, precipitation, and corn yield data in the United States. This evidence suggests that solar variability effects may be sufficiently amplified in the climate to have marked ecological consequences. It may be significant that the two periods of almost no sunspots and few aurorae, the Sporer Minimum (1400–1510) and the Maunder Minimum (1645–1715), have coincided with the two coldest periods of the past millennium, the "Little Ice Age" (Eddy 1976).

CONCLUSION

Dark marks in the rings of Yukon white spruce when less than 50 yr of age are correlated with the number of stems browsed by snowshow hares. The frequency of these marks is also positively correlated with the density of hares in the same region over one well-documented hare cycle. The frequency of tree ring marks in the first 50 yr of life of trees germinating between 1751 and 1983 is positively correlated with the hare fur records of the Hudson Bay Company. Phase analysis of the cross correlation between tree marks and hare records shows that the two cycles are essentially locked in phase. Together, this evidence suggests that the tree marks are an index of the hare cycle over the past 230 yr.

Both tree marks and hare numbers are correlated with sunspot numbers, and there is a 10–11-yr periodicity in the correlograms. Phase analyses show that tree marks and sunspot numbers have periods of nearly constant phase difference during the years 1751–1787, 1838–1870, and 1948 to the present, and these time spans coincide almost exactly with the time spans of high sunspot maxima. In the intervening years the cycles drift in their phase relations. The hare fur data also appear to be locked in phase with sunspots during some time periods. The nearly constant phase relations between the ANSA on Mount Logan and (1) tree mark ratios, (2) hare fur records before about 1895, and (3) sunspot number during periods of high amplitude in the cycles suggest that there is a solar cycle–climate–hare population and tree mark link.

Therefore, we suggest that the snowshoe hare cycle is modulated indirectly by solar activity through an amplified climate cycle that affects the whole boreal forest ecosystem. Solar variability is hypothesized to be the cause of some climatic variability in the upper atmosphere through complex multistage amplification mechanisms (Tinsley 1988; Tinsley et al. 1989). We do not imply that solar variability (or climate) causes the hare cycle directly; this must be related to the rates of population growth, survival, and mortality, in which time lags and natural resonances operating between the interacting trophic levels are significant.

At present we need more climate data to explore this hypothesis further. The hypothesis can be tested in four ways: (1) by obtaining more tree mark data during the period of the "Maunder Minimum" (1645–1715), when there were few or no sunspots–our hypothesis predicts either no 10-yr cycle in the tree marks during this period or cycles with other periodicities. The hypothesis also predicts that (2) tree marks in spruce trees out of reach of hares should not show 10-yr periodicities since 1751, (3) white spruce in other regions of the boreal forest should show cycles similar to the ones found at Kluane, and (4) hare cycles in Siberia should be in phase with those in Canada.

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