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SYNCHRONY IN OUTBREAKS OF FOREST LEPIDOPTERA: A POSSIBLE EXAMPLE OF THE MORAN EFFECT

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Abstract. I compiled information from the literature on 140 population outbreaks of 26 species of forest Lepidoptera that occurred between the years 1932 and 1992 in the Northern Hemisphere, including Asia, North America, and Europe. Considerable variation in the number of outbreaks occurred among years, with a tendency for outbreaks to be synchronous. Years of numerous outbreaks include 1948, 1956, 1964, the mid-1970s, and the mid-1980s. Published summaries of weather in the Northern Hemisphere indicate the occurrence of above-normal precipitation and cool temperatures between 1954 and 1957, and a high proportion of populations were at peak density in 1954 and 1956. Cool springs in 1964, 1965, and 1976 were also associated with outbreaks in a number of species of forest Lepidoptera. Periods of synchrony of population outbreaks and cool temperatures appear to be associated with troughs in the sunspot cycle. While the details of population dynamics of caterpillars are determined through endogenous processes that influence fecundity and mortality, exogenous forces, such as cool springs, may occasionally play a role in synchronizing populations in the Northern Hemisphere. Thus weather conditions may act as a Moran effect and synchronize fluctuating populations of forest caterpillars over large geographic areas.

Key words: forest Lepidoptera outbreaks; Lepidoptera in the Northern Hemisphere; Moran effect; population cycles; population dynamics; sunspot cycles; synchrony of Lepidoptera outbreaks; weather and populations.

INTRODUCTION

Population fluctuations of many species of forest caterpillars have a periodicity of 8-11 yr and these ‘‘cycles’’ have long fascinated population ecologists. Fluctuations in population density are determined by a suite of biological characteristics. Both fecundity and mortality change with population density (Myers 1988), and these changes determine the details of the population dynamics. Populations tend to increase over 5–7 yr, remain high for 1–2 yr and decline over 2–3 yr. A number of hypotheses have been proposed to explain the fluctuations—maternal effects (Wellington 1965, Rossiter 1994), induced plant defenses (Baltensweiler and Fischlin 1988, Haukioja 1988), parasitoids (Begon et al. 1996, Berryman 1996), and disease (Myers 1993). All of these hypotheses have in common a mechanism that delays the recovery of the population following decline and therefore acts as a delayed density-dependent mechanism.

A fascinating characteristic of cyclic outbreaks is the tendency of geographically separated populations of a species to remain in synchrony even when not all populations necessarily reach high densities in each cycle (Myers 1993). This suggests that either an environmental cue, which has not yet been identified, acts over wide geographic areas to keep populations in phase, or that dispersal is sufficient to reestablish synchrony. Dispersal is hard to quantify. Habitats are often patchy, and female moths or caterpillars of many species have limited movement. Dispersal may not be sufficient to maintain widespread synchrony. However, a strong environmental cue could possibly act sporadically to synchronize populations that are oscillating from similar density-related mechanisms that have a lag. Synchronization of populations by a strong exogenous event was proposed by P. A. P. Moran in 1953 and is now known as the ‘‘Moran Effect.’’

Synchronous outbreaks of different species of forest lepidoptera have been documented. For example, Roland and Embree (1995) recorded the similar pattern of outbreaks of winter moth, Bruce’s spanworm, and

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fall cankerworm in Nova Scotia Canada, and Klimetzek (1990) described a spatial synchronization of outbreaks of four pine-feeding insects in Germany. Other studies have reviewed synchrony within species over geographical scales. Some examples include Williams and Liebhold (1995), who analyzed the pattern of synchrony among gypsy moth populations in New England; Liebhold et al. (1996), who showed a tendency for cyclicity of outbreaks of the beech caterpillar in Japan; Shepherd et al. (1988), who found synchrony among populations of tussock moth in the Pacific Northwest; and Sweetman and Lynch (1993) who analyzed western spruce budworm outbreaks in the southwestern United States through analysis of tree rings.

METHODS AND RESULTS

To determine if widely separated populations of a variety of species of forest Lepidoptera in the Northern Hemisphere fluctuate in a nonrandom pattern, I summarized data from the literature on 140 outbreaks of 26 species between 1932 and 1992 (Table 1). In some cases several data sets were reported in different studies for the same species, but I only included data from populations that were separated by several hundred kilometers. If data on more than one population were recorded in a study, I chose the longest data set for inclusion. An exception was the inclusion of data from two populations of *Bupalus* in Scotland. Although the populations were only several kilometers apart, Barbour (1988) reported them to be out of synchrony. Therefore, I included both sets of data since I did not have a mechanism for distinguishing between them and I did not want to exclude data arbitrarily. Years at the end of the outbreaks were scored. That is, *outbreaks* were defined as ‘‘years in which the populations of caterpillars were high but declined over the larval generation so that densities and/or defoliation were reduced in the next summer.’’ These outbreak years are plotted in Fig. 1, with data from North America, Europe, and Asia indicated. Outbreaks were more common in 1948, 1956, 1964, and in the mid-1970s and mid-1980s. The number of studies varied over time. Therefore, to determine the proportion of populations at peak density for each year I considered each population to be under observation between recorded peaks. The proportion of populations in outbreak for each year was obtained by dividing the number of species recorded as being at peak density by the total number of populations under observation. These data are presented in Fig. 2 and show a similar pattern. Over 40% of the populations had outbreak densities in 1956 and 1964.

DISCUSSION

Weather is a possible synchronizing influence on insect populations, and various combinations of temperature and precipitation have been proposed as having impacts on populations of forest caterpillars (reviews in Martinat [1987], Daniel and Myers [1995]). An analysis of precipitation in the Northern Hemisphere by Bradley et al. (1987) shows that, in the last 100 yr, 1953, 1954, 1956, and 1957 had extremely high precipitation. Over these same years, 1954–1957, March-to-June temperatures in the Northern Hemisphere were also below normal (Jones et al. 1986, Jones 1988) and 1956 was particularly cold. To determine temperature trends during March to June each year, I summed departures in air temperatures from the mean of the reference period (1951–1970) in data reported by Jones (1984, 1988). Years in which the deviation was more than one-degree Celsius below the average are indicated. Of the populations displayed in Fig. 1, 6 outbreaks ceased in 1954 and another 11 in 1956. Therefore the years of high precipitation and cool temperature (1954 and 1955) occurred when 11 populations of forest Lepidoptera were increasing to reach peak densities in 1956. Other years of particularly low spring temperatures in the Northern Hemisphere are shown in Figs. 1 and 2. Since the late 1970s there has been a warming trend in the Northern Hemisphere (Jones 1988). The only year after 1976 with an annual temperature even slightly below the 1951–1970 average was 1986, and February and June of that year were cool. Population outbreaks appear to be less synchronized during the 1980s as compared to the 1950s and 1960s (Fig. 1).

Statistical analysis of these patterns is difficult for several reasons. First, only population outbreaks have been recorded and the sequences of data start and end with outbreaks. Second, the lengths of studies vary and therefore the numbers of populations under investigation vary over time. Third, the years of outbreak are not independent. Once an outbreak of a population is recorded, another is not likely for several years. The highest frequencies of intervals between outbreaks occurred between 9 and 11 yr, but some outbreaks were separated by only 3 yr and others by as much as 21 yr. Fourth, different populations of the same species, even though separated geographically, could share some common feature that would make their dynamics less ‘‘independent.’’ Because of these complications I have used several types of statistical analysis.

In the first analysis a chi-squared test showed that population outbreaks occurred more frequently in cool springs than expected by chance (Table 2). I also determined for each species (Table 1) the proportion of outbreaks that occurred during cold years and then compared the mean of these proportions to the expected based on the number of cold years (7) and number of years of observation (56). Weather data were only published through 1987, so observations after that year

TABLE 1. Species, years of outbreaks, and sources of data on populations of forest Lepidoptera used in the analysis. Because gypsy moth populations in New England are synchronized, only data from Vermont were used, and because populations of beech moth (*Quadricalcarifera punctatella*) in Japan are synchronized, only data from Aomori were used. In both cases these data sets showed the most outbreaks. Two populations of *Bupalus* in Scotland were reported to be out of phase, and both are included.

Species	Years of outbreak	Sunspot trough†	Data source
Malacosoma pluviale californicum	1936, 1945, 1956, 1964, 1970, 1976, 1986	x	Myers 1993
M. disstria			
Ontario (Canada)	1952, 1966, 1978, 1989	x	Myers 1993
British Columbia (Canada)	1954, 1964, 1978, 1985, 1991	x	Turquist 1987
M. neustria	1964	x	Magnoler 1975
Lymantria dispar			
Europe	1934, 1941, 1948, 1956, 1965, 1978, 1985	x	Montgomery and Wallner 1988; B. Schutz, *personal communication*
Vermont (USA)	1941, 1946, 1956, 1964, 1972, 1982, 1990	o	Williams and Liebhold 1995
Zeiraphera diniana	1936, 1946, 1955, 1964, 1975, 1983, 1989	x	Baltensweiler and Fischlin 1988
Orgyia pseudotsugata			
British Columbia (Canada)	1932, 1941, 1950, 1964, 1976, 1983	x	Harris et al. 1985*a*, Myers 1988
Northern Idaho (USA)	1947, 1956, 1964, 1974, 1984	x	A. Berryman, *personal communication*
Oporina (Epirrita) autumnata	1934, 1948, 1956, 1966, 1975, 1985	x	Haukioja et al. 1988
Bupalus piniarius			
Scotland	1957, 1963, 1969, 1977, 1988	x	Barbour 1988
Scotland	1954, 1960, 1964, 1969, 1977	x	Barbour 1988
The Netherlands	1951, 1956, 1962	o	H. Klomp, in Chitty 1971
Germany	1956, 1961, 1967, 1988	x	Klimetzek 1990
Acleris variana	1948, 1956	x	Morris 1959
Zeiraphera griseana	1948, 1956	x	Baltensweiler 1968
Choristoneura fumiferana	1954	x	Royama 1977
Panolis flammea			
Britain	1977, 1986	x	Watt and Leather 1988
Germany	1956, 1967, 1988	x	Klimetzek 1990
Hyphantria cunea	1940, 1949, 1956	o	Morris 1964
Diprion pini	1954, 1961, 1967, 1988	x	Klimetzek 1990
Choristoneura pinus	1966, 1985	x	Howse and Meating 1995
Operophtera bruceata	1976, 1985	x	Roland and Embree 1995
Alsophila pometaria	1976, 1986	x	Roland and Embree 1995
Operophtera brumata			
Nova Scotia (Canada)	1974, 1983, 1991	o	Roland and Embree 1995
British Columbia (Canada)	1990	o	Roland and Embree 1995
Eriocrania spp.	1955, 1965, 1975, 1987	x	Bylund and Tenow 1994
Nepytia freemani	1948, 1964, 1974, 1983	x	Harris et al. 1985*b*
Epinotia tedella	1985	x	Munster-Swendsen 1991
Choristoneura occidentalis			
British Columbia (Canada)	1944, 1958, 1977, 1987, 1992	x	Parfett et al. 1994
New Mexico (USA)	1965, 1985	x	Sweetman and Lynch 1993
Lambdina fiscellaria lugubrosa			
Southwestern British Columbia (Canada)	1947, 1959, 1973, 1987	x	Parfett et al. 1995
Southeastern British Columbia (Canada)	1938, 1958, 1977, 1987, 1992	o	Parfett et al. 1995
Quadricalcarifera punctatella	1941, 1953, 1973, 1982, 1990	o	Liebhold et al. 1996
Dendrolimus punctatus			
Hunan (China)	1954, 1957, 1964, 1972, 1976, 1979, 1984	o	Q. Liang, *personal communication*
Euproctis flava	1932, 1939, 1947, 1954, 1961	o	Miyashita 1964

† In this column, x = at least 50% of the outbreaks were during sunspot troughs.

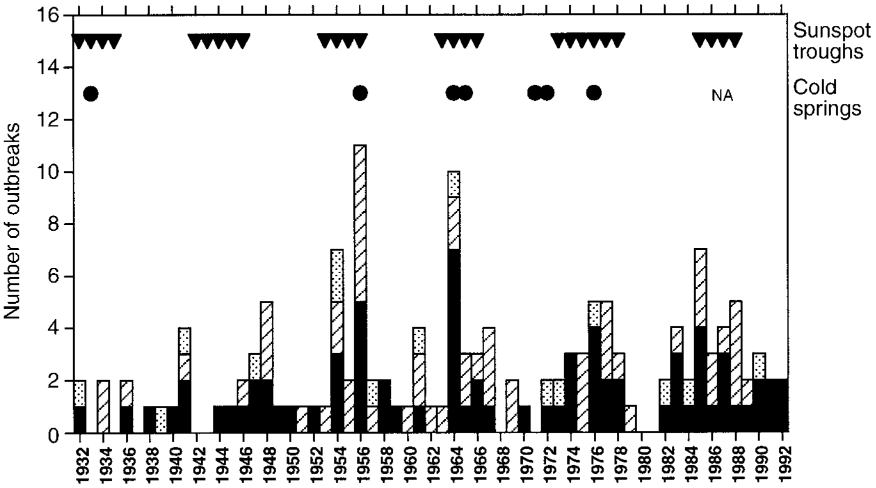

FIG. 1. Number of outbreaks of forest Lepidoptera terminating in years between 1932 and 1992 (solid bars, North America; hatched bars, Europe; and stippled bars, Asia), years in which Northern Hemisphere air surface temperatures were cumulatively >1°C below the mean for the reference period (1951–1970) for the months of March–June (●), and years of sunspot troughs (▼). Temperature data are from Jones et al. (1986) and Jones (1988) and are not available (NA) after 1987. Outbreak data are from Table 1.

were not included, making the sample size for this comparison smaller than the total years of observation. The proportion of outbreaks occurring in cold years for all populations was 0.25 ± 0.08 (mean ± 2 SE). This value is >2 SE above the expected proportion of 0.125. I also compared the proportion of outbreaks occurring in cold years of species for which several populations were included to those with a single population. This was done to determine if the former were biasing the overall results. I combined the data for the three species of *Malacosoma* in this analysis and all populations for the other species with more than one data set. The proportion of outbreaks in cold years for the 7 multiple population studies was 0.24 ± 0.14 (mean ± 2 SE) and for the 17 single population studies was 0.20 ± 0.10. This was not significantly different with a *t* test ($t = 0.44$, df = 22, $P = 0.66$). In addition, a randomization test (Manly 1993) on the proportion of populations in outbreak in each year (Fig. 2) and the pattern of cold years indicated that this pattern would have occurred by random with a probablility of 2.88%.

Another environmental factor that varies, in this case

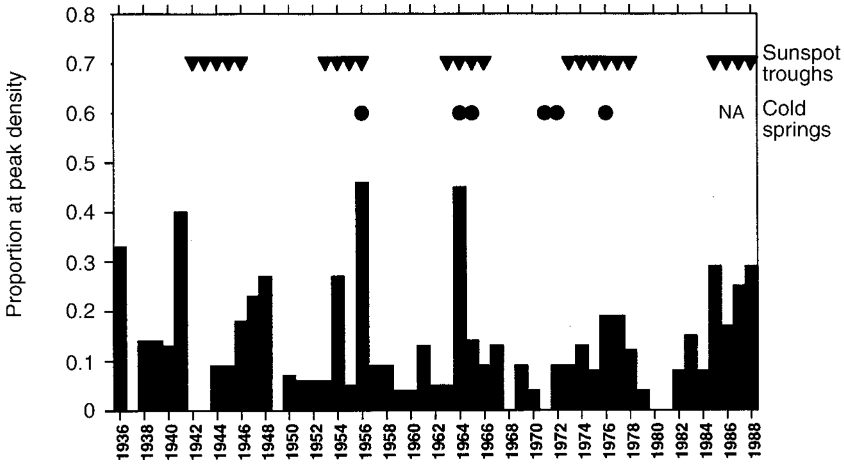

FIG. 2. The proportion of populations under observation that reached peak density in years between 1936 and 1988. To reduce bias associated with the study periods being defined as beginning and ending with outbreaks, data from 1932–1935 and 1989–1992 were not included. Cold springs and sunspot-trough years are as outlined for Fig. 1 and in the text; NA = not available.

TABLE 2. Analysis of number of outbreaks in years with cool and normal springs and in years of peaks and troughs of sunspot cycles.

	Spring temperature†		Sunspot cycle‡	
	Cold	Normal	Trough	Peak
No. of years	7	49	27	34
No. of outbreaks				
Observed	30	97	84	56
Expected	15.9	111.1	61.6	78.4

† In this column, $\chi^2 = 13.5$, df = 1, $P < 0.005$.

‡ $\chi^2 = 14.5$, df = 1, $P < 0.005$.

in a regular pattern, is sunspot activity. Comparison of the number of outbreaks of forest Lepidoptera to sunspot cycles shows that a majority of outbreaks occur during the trough of sunspot activity (Fig. 1). To analyze the possible association between sunspots and the termination of outbreaks of forest Lepidoptera I scored years starting with 1 for the beginning of increase of sunspots through to 10 to 12 for the termination of the cycle. Years 3 to 8 include the peaks of sunspot numbers. In the data set analyzed, 27 yr were in the trough years 1 and 2 (beginning of the cycle) and years 9 to 12 (end of the cycle), and 84 outbreaks ended during these years. Thirty-four years included the peaks of sunspot activity, years 3 to 8, and 56 outbreaks occurred in these. Variation was analyzed with χ^2 analysis in which the expected number of outbreaks per year was determined from the total number of outbreaks (140) divided by the total number of years (61). The variation in the number of outbreaks observed in years of sunspot peaks and troughs is highly significant (Table 2). As with the analysis involving cold years, I compared the mean of the proportions of outbreaks occurring during sunspot troughs for the different populations to the expected based on the 27 years of troughs in sunspot activity over the 61 years of observation. The proportion of outbreaks in trough years for all data sets was 0.63 ± 0.08 (mean ± 2 SE), $n = 36$ data sets, more than 2 SE above the expected proportion of 0.44. The proportion of outbreaks in trough years for the eight groups of multiple populations did not differ significantly from that of the single populations (multiple: 0.57 ± 0.12; single: 0.69 ± 0.14 (mean ± 2 SE); $t = 1.09$, df = 22, $P = 0.29$. A randomization test on the proportion of populations in outbreak in each year (Fig. 2) and troughs of sunspot activity indicated that this pattern would have occurred by random with a probability of 4.5%. The pattern of outbreaks varies significantly from random, with a majority of outbreaks occurring during the trough of sunspot activity.

Populations that had at least half of the outbreaks occurring during troughs of sunspot activity are indicated with an ''x'' in Table 1. Nine populations did not have at least 50% of outbreaks during troughs of sunspot activity, and these show some interesting associations. First, all three of the exotic populations included in the analysis—winter moth, *Operophtera brumata*, in Nova Scotia and British Columbia, and gypsy moth, *Lymantria dispar*, in northeastern North America—failed to show an association with sunspot activity. Second, none of the three species from Asia had more than 50% of the outbreaks during troughs of sunspot activity, and these as well as the introduced gypsy moth and the introduced winter moth in Nova Scotia all occur below 49° latitude. This suggests that the synchrony of populations with sunspot activity may be associated to the geographic location of the populations, and more-northern populations may be more strongly influenced. An exception is the southern population of the western spruce budworm (*Choristoneura occidentalis*) in New Mexico, which had two outbreaks during troughs of sunspot activity.

Whether sunspots and weather are related remains controversial (Kerr 1990). However a period of low sunspot activity between 1640 and 1705 is referred to as the ''Little Ice Age'' because temperatures were so cool (Wilson 1994). This suggests that troughs in the cycles of sunspot activity could be associated with cooler temperatures.

Evidence for cool temperatures being associated with the dynamics of gypsy moth populations has recently been summarized by Williams and Liebhold (1995). Their extensive analysis of weather and defoliation by gypsy moth over 55 yr in Massachusetts, Maine, New Hampshire, and Vermont showed minimum temperatures in December and minimum temperatures in July to be correlated with defoliation residuals. Their interpretation was that warm temperatures in December could increase mortality of overwintering, embryonated eggs, and cool temperatures in July could reduce mating and oviposition success. Miller et al. (1989) also analyzed weather patterns of gypsy moth and reported a positive association between defoliation and minimum temperatures in mid-April through mid-May in both the same year and in the previous year. This result agrees with the pattern indicated in Fig. 1, with cool springs being associated with outbreaks. Population outbreaks of the oriental tussock moth (*Euproctis flava*) in Japan also show an association with low temperature and decreased percentage of sunny hours in spring and summer (Miyashita 1964). While outbreaks of these two species, gypsy moth and oriental tussock moth, are reported to be associated with cold springs, they did not show an association with troughs of sunspot activity (Table 1).

What biological mechanism could explain an association between cool springs and outbreaks of forest

Lepidoptera is not known, but it is possible that egg hatch and leaf development are better synchronized in cool springs. Sweetman and Lynch (1993) found that outbreaks of western spruce budworm tended to be associated with periods of higher precipitation.

Synchronization of populations by a strong environmental cue, the Moran effect, requires no assumptions about periodicity of weather patterns, but does require that insect populations are exposed to a common exogenous factor that can entrain their oscillations. It is likely that the endogenous processes controlling the dynamics of different species of forest Lepidoptera are similar, but vary in details. Perhaps the most parsimonious explanation of the pattern presented in Figs. 1 and 2 is that the abnormal precipitation and temperatures in 1954–1957 entrained the cycles of a number of species and that these remained in synchrony in 1964 and have tended to be synchronized since, simply because the processes driving their dynamics are similar. But if there is even a weak association between a periodic exogenous factor, sunspots and weather patterns, it is possible that fluctuating populations of forest Lepidoptera can be partially and periodically synchronized over large geographic areas. A recent computer simulation by Haydon and Steen (1997) shows that synchrony of populations is most likely to be determined by coefficients of variation of both local and larger stochastic processes. Within a species, migration is only likely to maintain synchrony when local stochastic variation is small, and of course between species it will have no influence. If cool springs have in the past acted to synchronize populations, it will be interesting to follow the potential impact of global warming on synchrony of populations within and between species of Lepidoptera.

Finally, these potential associations between weather and sunspots agree with a previous suggestion that sunspot activity might be related to fluctuations of animal populations (Sinclair et al. 1992). In this situation correlations between sunspots, tree ring scars caused by snowshoe hare feeding, and accumulation of snow on Mount Logan were observed to be in phase during times of high-amplitude sunspot activity. Some climatic factor associated with solar activity was considered to entrain the fluctuations of hares with sunspot cycles.

The potential for large-scale patterns should not be ignored in the study of animal population fluctuations. While the details of mechanisms remain to be worked out, and experiments are difficult, looking for synchronizing signals rather than causal mechanisms may increase success in predicting patterns on a larger geographical scale.

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