

Are North American Populations of Gypsy Moth (*Lepidoptera: Lymantriidae*) Bimodal?

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ABSTRACT Previous studies indicate that North American gypsy moth, *Lymantria dispar* (L.), populations are driven by a numerically bimodal replacement rate model: $N_{t+1}/N_t = f(N)$, where $f(N)$ is bimodal, resulting in two equilibrium densities. Under this theory, populations are regulated about a low density equilibrium for many years until some perturbation (usually mass immigration) elevates populations to high densities, where they are regulated about a high-density equilibrium until crashing. In this paper, the evidence for and against numerical bimodality in gypsy moth populations is reviewed. The Melrose Highlands data (egg mass densities at 83 plots in New England from 1910 to 1931) were reexamined. These analyses indicated bimodality in $f(N)$ when data were expressed as yearly means of several plots in a zone ≈ 30 km in diameter, but there was no clear evidence of bimodality in the dynamics at individual plots. Density fluctuations in these relatively small plots (0.07 ha) were instead dominated by apparently random effects. It is hypothesized that short-range dispersal dominates the dynamics of populations at these spatial scales. These results illustrate the importance of spatial scale in the characterization of ecological processes.

KEY WORDS Insecta, *Lymantria dispar*, density dependence, population dynamics

OVER THE PAST 40 YR, considerable attention has focused on the role of density dependence in the survival and long-term dynamics of insect populations. The universality of density-dependent mortality remains controversial (Stiling 1988, Hassell et al. 1989); it remains unclear whether short-term changes in density are most affected by density-dependent factors or by random effects. Also, there is uncertainty over the relative importance of direct versus time-lagged density-dependent factors (Turchin 1990). Despite this dispute, there is no question that populations are at least sometimes affected by density-related factors that prevent extinction and unlimited population growth.

Ricker (1954) formalized the concept of density-dependent population replacement:

$$N_{t+1}/N_t = f(N_t), \quad (1)$$

where N_t is the population density at time t and N_{t+1}/N_t is the population replacement rate, R (N_t and R are often expressed as log-transformed values). Under Ricker's (1954) model, R is determined by density-dependent negative feedback such that R decreases with increasing values of N_t . Conceptually, there is some equilibrium density, N^* , where $R = 1$. The stability of this equilibrium and population behavior depends on var-

ious characteristics of the replacement rate function, $f(N)$ (May 1974).

Various authors have further developed Ricker's (1954) model of density-dependent regulation by incorporating more than one (usually two) equilibrium points (Morris 1963, Takahashi 1964, Southwood & Comins 1976, Berryman 1978). Under this theory, the curve of R versus N_t is bimodal and there are two stable equilibrium densities, N_1^* and N_2^* , where $R = 1$ (Fig. 1). There also exists an unstable equilibrium density, N' , below which populations are regulated about N_1^* and above which populations are regulated about N_2^* . According to this theory, there is a family of density-dependent mortality factors (typically predators and parasitoids) that is responsible for regulation about the low-density equilibrium and a different set of factors responsible for regulation at high densities. The key aspect of this theory is that populations will remain at low densities for many years, but some perturbation (such as mass immigration) elevates populations over N' . N' functions as a threshold; when densities are elevated over this level, populations equilibrate at high densities and an outbreak results. Again, a major perturbation (such as mass starvation) is necessary to drive densities below N' , where populations will equilibrate at low densities. Southwood & Comins (1976)

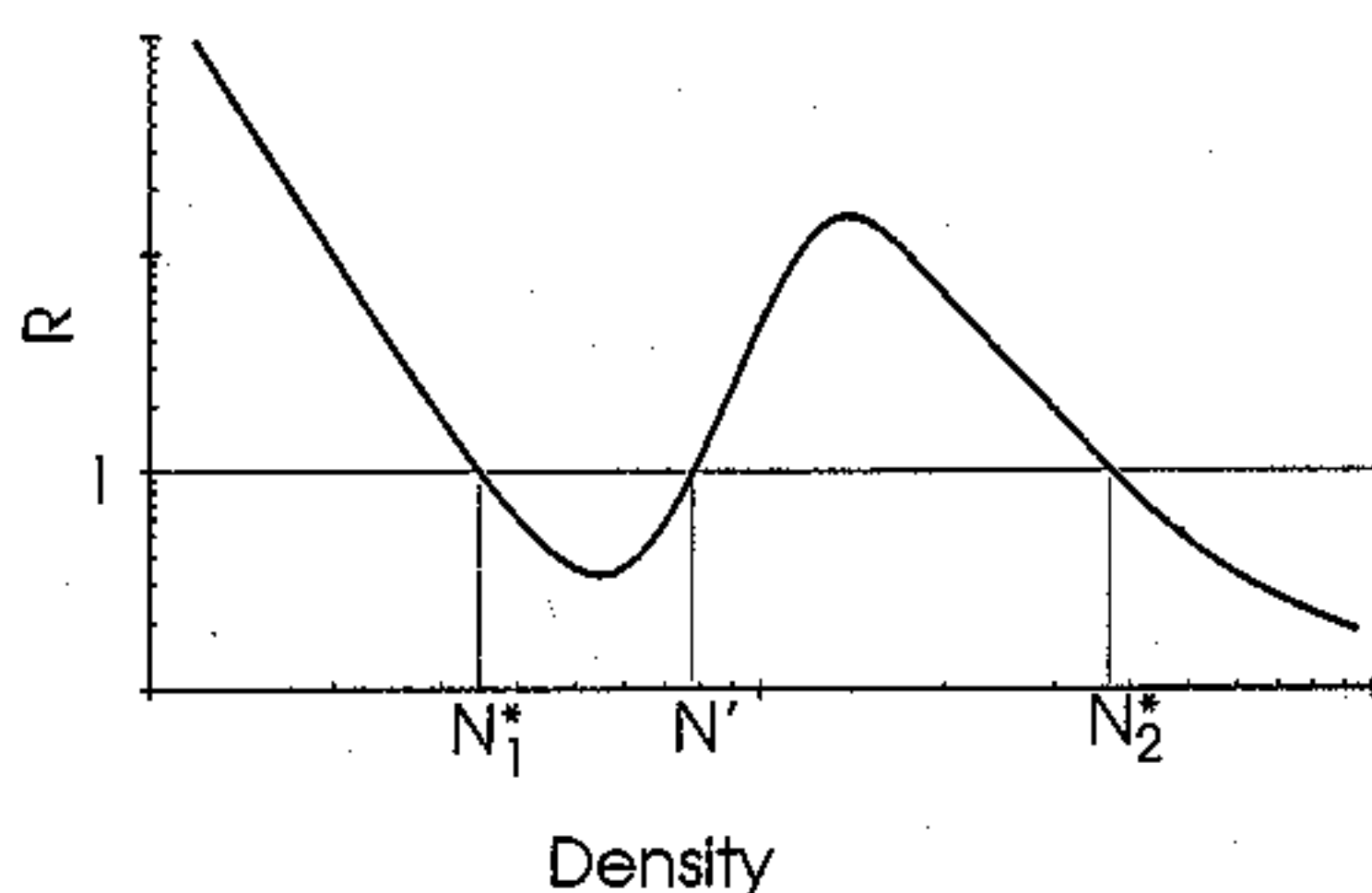


Fig. 1. Conceptual model of a bimodal replacement rate model. R is the replacement rate: N_{t+1}/N_t . N_1^* and N_2^* are stable equilibrium densities and N' is an unstable equilibrium.

added another dimension to this relationship by developing a conceptual framework whereby habitat features may affect the shape of $f(N)$. According to this theory, a species may behave bimodally in some habitats and unimodally in others.

There is considerable evidence of naturally occurring insect populations that behave bimodally. Evidence of this phenomenon has been found in the spruce budworm, *Choristoneura fumiferana* (Clemens) (Morris 1963), the southern pine beetle, *Dendroctonus frontalis* Zimmerman (Mawby et al. 1989), the fir engraver, *Scolytus ventralis* LeConte (Berryman 1973), the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Berryman 1976), and *Cardiaspina albitextura* Taylor (Southwood & Comins 1976). Though these examples are all forest insects, there is no reason not to believe that species from other habitats may also follow this pattern.

The gypsy moth, *Lymantria dispar* (L.), is an example of an eruptive species (Price et al. 1990); population densities vary through several orders of magnitude, often reaching epidemic densities that have spectacular effects on their habitat (i.e., total defoliation of host trees). It is not uncommon for gypsy moth populations to persist for many years at densities so low that it may be difficult to detect any life stages except male moths. Occasionally, for unknown reasons, population densities increase, often to defoliating levels in excess of 6,000 egg masses per hectare, within only a few generations. These outbreak populations may persist for several years before collapsing. It is because of this "boom or bust" characteristic that Campbell & Sloan (1978a) suggested that North American gypsy moth populations are bimodal. In this paper, evidence for and against bimodality in gypsy moth population dynamics is examined.

Earlier Analyses of Bimodality in North American Gypsy Moth Populations

Campbell & Sloan (1978a) quantified the relationship between R and N_t in gypsy moth data collected at various localities and times. Estimates of eggs per acre were collected from 1957 to 1964 at plots in Glenville, N.Y.; from 1965 to 1971 in Eastford, Conn.; and from 1972 to 1974 at "intensive plot system" (IPS) plots located in various parts of New England. They also quantified $f(N)$ from egg mass density estimates in 77 "Melrose Highlands Plots" located through much of coastal New England from 1910 to 1931.

Campbell & Sloan's (1978a) approach to detecting bimodality was first to divide these data into spatial and temporal subsets; each data set was analyzed separately and the IPS and Melrose data were further divided into "outbreak" and "decline" phases. For each data subset, Campbell & Sloan (1978a) used least-squares regression to fit the model

$$\log R = a + b (\log N_t)^3. \quad (2)$$

It is not clear why they chose this particular model, although presumably it provided a better fit than the linear model. Campbell & Sloan's conclusion of bimodality was based upon the finding that the parameters of this model differed among the various spatial and temporal subsets; the slope and intercepts from the Glenville and Eastford data were significantly different. They also found significant differences in the parameters between the Glenville data and the "outbreak phase" of the IPS data (1972–1973) and between the Eastford data and the "decline phase" of the IPS data (1974 only); however, they discounted these differences and concluded that the trends were "similar." Campbell & Sloan (1978a) also found differences in the parameters of equation 2 between the "outbreak phase" (1910–1922) and the "decline phase" (1923–1931) of the Melrose data, and they interpreted this as more evidence of the general bimodality of gypsy moth populations.

Campbell & Sloan (1978a) further developed this theory of numerical bimodality into a generalized qualitative model of gypsy moth numerical behavior (see Fig. 1 of Campbell & Sloan 1978a). They conceptualized gypsy moth populations at any point in time as existing in one of four phases: innocuous, release, outbreak, or decline. They theorized that populations exist in a stable innocuous phase for many years; previous studies (Campbell & Sloan 1977a) indicated that predation may regulate populations at low densities. According to this theory, outbreaks enter the unstable release phase as a result of some perturbation, unusually low predation rates or immigration (Campbell & Sloan 1977b). Campbell & Sloan (1978a) felt that the outbreak mode

was relatively stable, as populations could persist for up to a decade. Finally, according to their theory, populations enter the unstable decline phase as a result of disease, starvation, or reduced fecundity (Campbell & Sloan 1978b).

There are some reasons to question the validity of Campbell & Sloan's (1978a) conclusions. First, the finding that $f(N)$ differs among populations separated by space or time does not necessarily imply an inherent numerical bimodality. Differences among spatially discrete populations probably reflect dissimilarities in the habitats where the populations are located (e.g., Southwood & Comins 1976) rather than an actual difference in the phase of the populations. Furthermore, differences in $f(N)$ within the same population during different time intervals (i.e., "outbreak" versus "declining" years from the IPS and Melrose data) do not necessarily imply an endogenous switch in numerical behavior. Rather, these differences may instead reflect the effect of some exogenous factor(s) such as weather (Miller et al. 1989).

Reexamination of the Melrose Highlands Data

Because there are reasons to question Campbell & Sloan's (1978a) conclusions, it is still unresolved whether North American gypsy moth populations do indeed operate in a numerically bimodal fashion. To answer this question, the Melrose Highlands data was reexamined (the same data that Campbell & Sloan [1978a] used in their analysis). The arbitrary temporal stratification of Campbell & Sloan (1978a) was avoided by pooling all plots in one analysis. Additionally, a graphical display of the frequency distribution of N_t was used rather than relying entirely upon examination of $f(N)$.

The Melrose data are the largest (in terms of numbers of plots and years) set of gypsy moth egg mass data collected in North America and are described in detail by Campbell (1967). In 1910 and 1911, personnel from the Melrose Highlands Gypsy Moth Laboratory established 264 circular plots (0.07 ha) through much of coastal New England. Each year, counts were made of all current egg masses in each plot. Many of the plots were discontinued; data were used in that study only from plots with ≥ 19 yr of consecutive data (83 plots). Nearby plots were assigned to one of five "zones." As much as 40 km separated plots within zones (see Campbell [1973] for a map of zone locations).

Fig. 2 shows plots of yearly population densities in each of the 83 plots, plotted on a logarithmic scale (1 was added to each density). Royama (1984) pointed out that plots of census data should be performed on a logarithmic scale because of the superior resolution at low densities. He showed that historical spruce budworm data showed no clear sign of a low-density equilib-

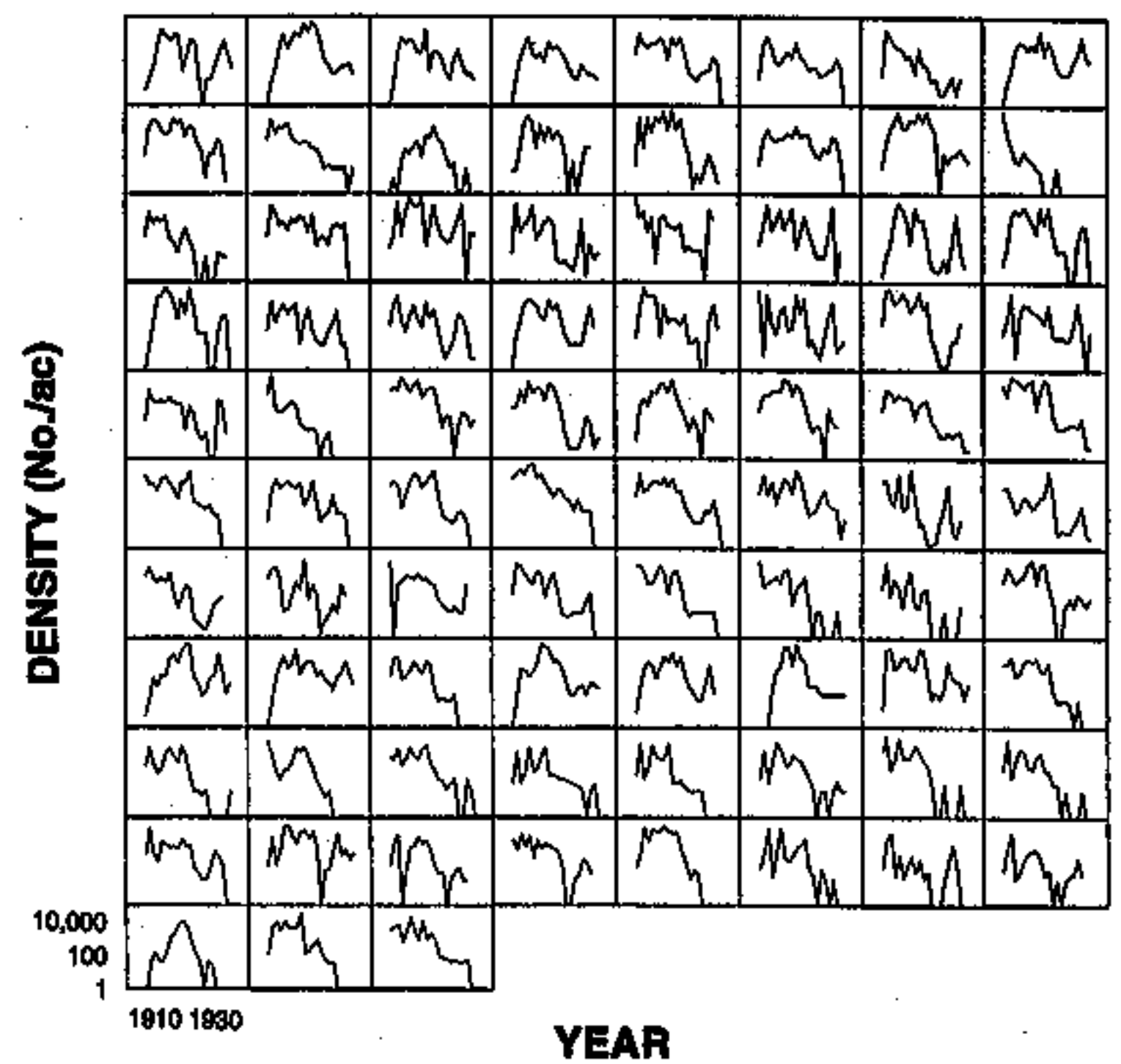


Fig. 2. Yearly egg mass densities at 83 Melrose Highlands plots. (1 ac = 0.4047 ha.)

rium when plotted on a logarithmic scale; the population fluctuated at low densities with no sign of negative feedback. A linear representation of the same data, because of its poorer resolution at low densities, suggested that populations equilibrated about high- and low-density equilibria. The trajectories shown in Fig. 2 show that population densities fluctuated considerably between successive years. In contrast, zone means and grand means of all plots exhibited less abrupt yearly changes in density (Fig. 3). The overall trend for the 22-yr period was of decreasing density.

To examine these data for numerical bimodality, the frequency distributions of N_t were plotted for each spatial scale: plot, zone, and overall. Unlike Campbell & Sloan's (1978a) approach, these frequency distributions of N_t can provide direct evidence of bimodality. The resulting frequency distributions of N_t suggest that the extent of bimodality varies with spatial scale. The distribution of N_t from individual plots is clearly platykurtic, but no distinct modes are evident (Fig. 4A); the frequency of values from 250 to 25,000 egg masses per hectare (100 to 10,000 egg masses per acre) was approximately constant. Bimodality was more distinct in the frequency distribution of yearly zone means (Fig. 4B); modes existed at ≈ 250 and 7,500 egg masses per hectare (100 and 3,000 egg masses per acre). The frequency distribution of yearly grand means (Fig. 4C) also suggested the existence of two modes, although the number of samples was low ($n = 22$).

The plot of R versus N_t for all plots in all years (Fig. 5A) showed little evidence of an $f(N)$ expected under the numerical bimodality hypothesis (i.e., Fig. 1). Instead, these data appeared to

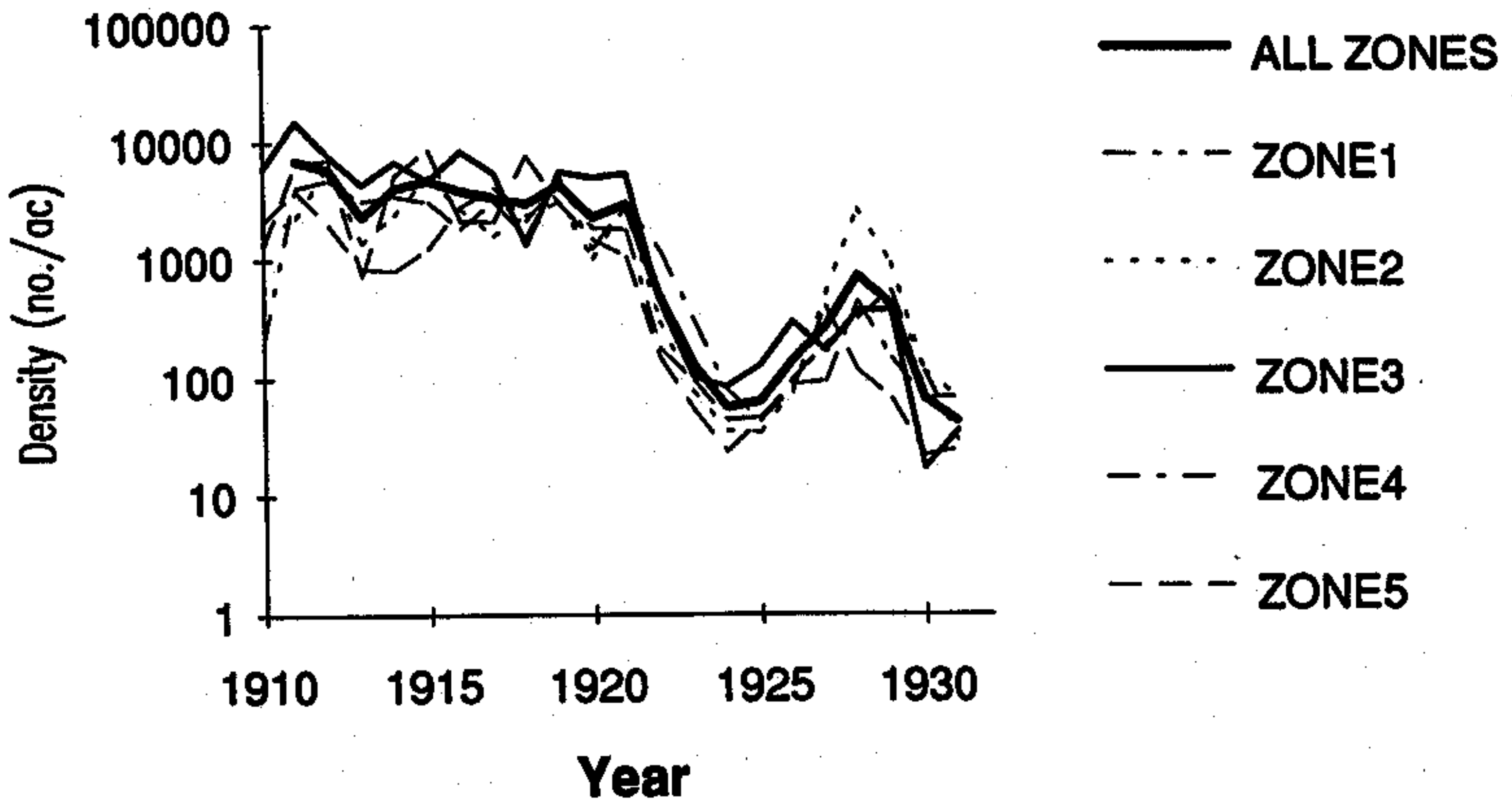


Fig. 3. Yearly mean egg mass density in each of five zones containing Melrose Highlands plots (see Campbe 1973 for location of zones). (1 ac = 0.4047 ha.)

be scattered about a single line of negative slope, crossing the abscissa at $\approx 2,500$ egg masses per hectare (1,000 egg masses per acre). This relationship is indicative of a simple unimodal density-dependent model (i.e., $R = \alpha + \beta N_t$) with an

equilibrium density of $\approx 2,500$ egg masses per hectare (1,000 egg masses per acre). In contrast, the relationship between R and N_t for zone means (Fig. 5B) was less clear. There was a great deal of scatter in the plot, but the data suggested the existence of bimodality (i.e., Fig. 1): for values of $N_t < \approx 2,500$ egg masses per hectare (1,000 egg masses per acre), values were widely scattered about a line of negative slope that crossed the abscissa at 250 egg masses per hectare (100 egg masses per acre); for values of $N_t > 2,500$ egg masses per hectare (1,000 egg masses per acre), points were widely scattered about a line of negative slope that crossed the abscissa at $\approx 7,500$ egg masses per hectare (3,000 egg masses per acre). Plots of yearly grand means (Fig. 5C) also vaguely suggested the existence of the same two zones (above and below 2,500 egg masses per hectare [1,000 egg masses per acre]) of distinct density dependence as observed for the zone means.

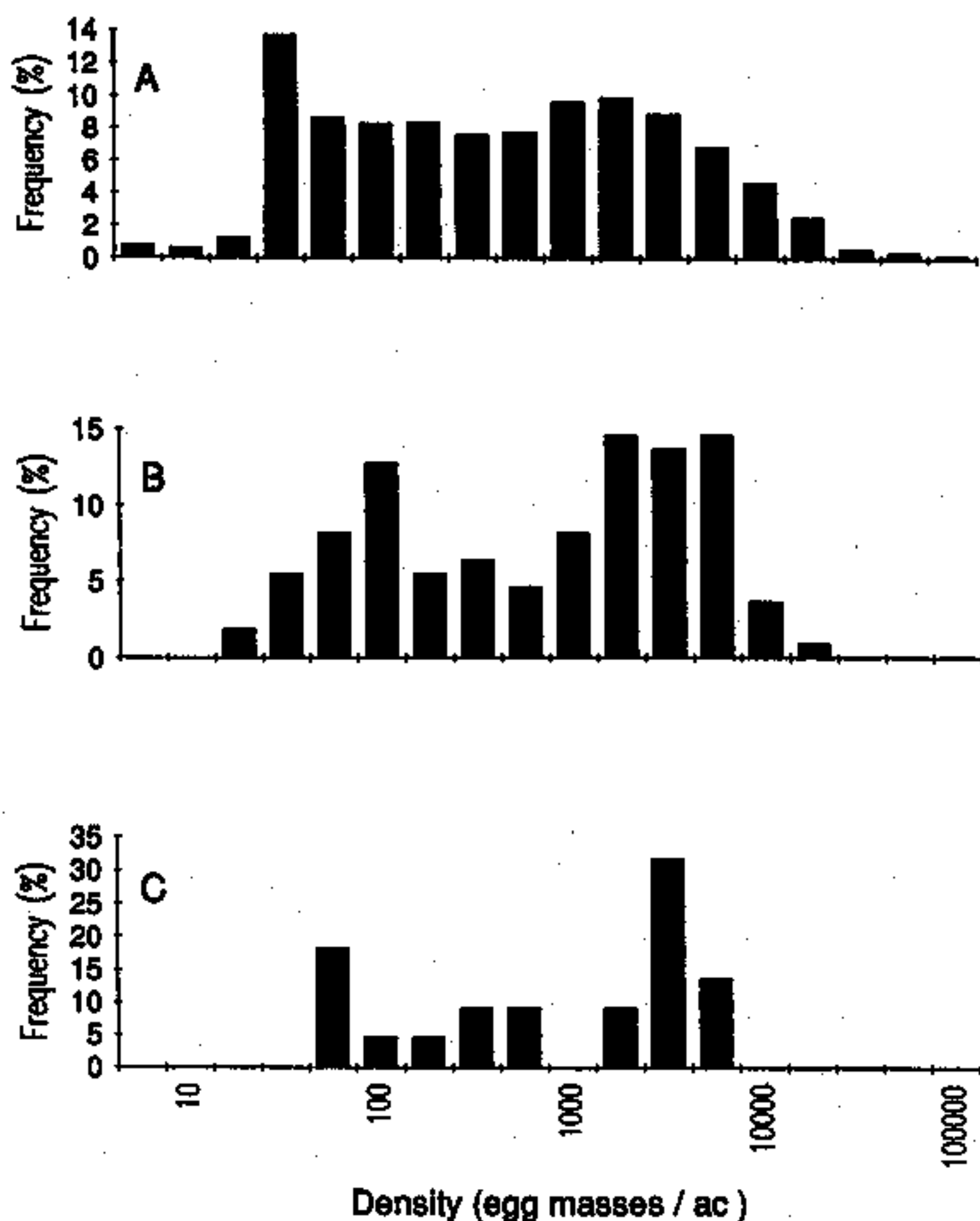


Fig. 4. Frequency distributions for egg mass densities in Melrose Highlands data. (A) Data from individual plots. (B) Yearly zone means. (C) Yearly grand means. (1 ac = 0.4047 ha.)

Parasitism, predation, disease, and delayed fecundity effects can all have delayed or time-lagged effects on replacement rate (Berryman 1978, Royama 1981). Turchin (1990) recently showed that the dynamics of a variety of forest insects are dominated by such delayed-density dependent processes. In such cases, equation (1) can be replaced by

$$N_{t+1}/N_t = f(N_t, N_{t-1}). \quad (3)$$

Therefore, the relationship between R and N_{t-1} was examined because this may be a source of population regulation in the Melrose data (Berryman 1991). For data from individual plots (Fig.

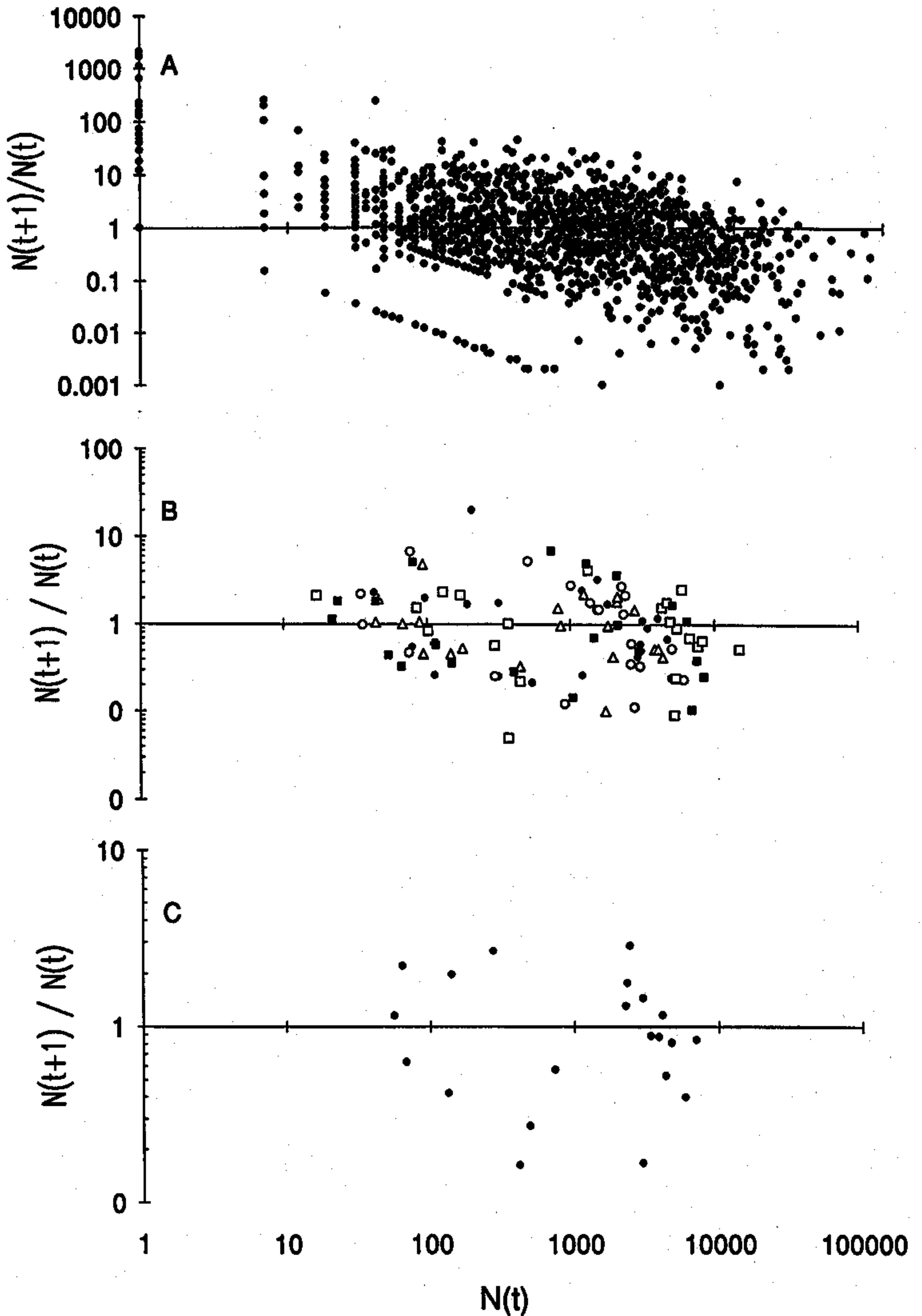


Fig. 5. Replacement rate versus density. (A) Data from individual plots. (B) Yearly zone means; different types of point markers represent the five different zones. (C) Yearly grand means.

6A), there was no evidence of delayed density dependence through any ranges in density; there was no obvious correlation between R and N_{t-1} (see also Liebhold & Elkinton 1991). However, examination of yearly zone means (Fig. 6B) and grand means (Fig. 6C) suggested the existence of a delayed density dependence for values of $N_{t-1} < 2,500$ egg masses per hectare (1,000 egg masses per acre): when N_{t-1} was $< 2,500$ egg masses per hectare (1,000 egg masses per acre), points were widely scattered about a line of negative slope that crossed the abscissa at ≈ 250 egg masses per hectare (100 egg masses per acre). For values of $N_{t-1} > 1,000$, there was no correlation between N_{t-1} and R , indicating an absence of delayed-density dependence (Fig. 6 B and C).

Discussion & Conclusions

In summary, the Melrose Highlands census data exhibit numerical bimodality when expressed as zone or grand means; frequency distributions of densities are bimodal (Fig. 4 B and C), and there is some evidence of bimodality in the direct and delayed replacement rate models (Fig. 5 B and C, 6 B and C). However, there is little indication of bimodality in the individual plot data; frequency distributions are nearly uniform (Fig. 4A), and there is no evidence of bimodality in either the direct or delayed replacement rate models (Fig. 5A, 6A). Eberhardt (1970) and Ito (1972) showed that apparent direct density dependence, such as that seen in the individual plot data (Fig. 5A), can be caused by random factors instead of by a density-dependent factor. It is likely that densities in individual plots are dominated by random effects; immigration and emigration of first instars are likely the cause of these "random" changes in population density, although sampling error may also contribute. Substantial numbers of first instars are capable of dispersing ≈ 50 m (Mason & McManus 1981), thus they could easily move into these relatively small plots (0.07 ha). In contrast, zone means represented populations over as much as 40 km and, over this range of distance, dispersal is likely to be unimportant (Liebhold & McManus 1991).

Campbell & Sloan (1978b) hypothesized that areawide outbreaks can be maintained by dispersal of first instars from stands harboring high-density populations into nearby stands where populations have crashed. A complex mechanism such as this may be responsible for the apparent bimodality in the zone and grand mean data; however, many questions remain unresolved. For example, experimental elevation of gypsy moth egg densities (Gould et al. 1989, Liebhold & Elkinton 1989) demonstrated that populations do not "release" after elevation of populations from low to high densities as hypothesized by Campbell & Sloan (1978b). An-

other problem is that these data indicate a lower equilibrium density of ≈ 250 egg masses per hectare (100 egg masses per acre) (Fig. 5B), yet low-density gypsy moth populations typically remain at densities of < 25 egg masses per hectare (10 egg masses per acre) for many years (e.g., Campbell & Sloan 1978a). Also, the mechanism behind the apparent delayed-density dependence in the zone and grand means (Fig. 6 B and C) is not clear; the numerical response of most gypsy moth parasitoids is highly constrained by hyperparasitoids, and alternate hosts and would thus be unlikely to cause delayed density-dependent mortality (Elkinton & Liebhold 1990).

A key component of Campbell & Sloan's (1978a) theory of numerical bimodality was that a separate family of mortality agents regulated populations at high densities versus those at low densities. There is little question that starvation and disease act in a positive density-dependent fashion at high densities, although these agents typically cause a collapse of populations to very low levels (Doane 1970, Campbell & Sloan 1978b, Woods et al. 1991). At low densities, small mammal predation is important, as Campbell & Sloan (1978a) suggested; however, there is little evidence for density dependence in this predation (Elkinton et al. 1989). Instead, any density dependence in predation at low densities is probably so slight that it is overwhelmed by the yearly fluctuations in small mammal densities (Elkinton et al. 1989).

Campbell & Sloan's (1978a) theory of numerical bimodality and their concept of innocuous release, outbreak, and decline phases in North American gypsy moth populations has considerable appeal because it provides a framework for explaining the eruptive dynamics that result in violent changes in density from one year to the next. Thus, whether gypsy moth populations are bimodal or not is important. Although there is good evidence here of bimodality when populations are averaged over many kilometers, there is no clear evidence of bimodality in populations from individual plots.

Unfortunately, it is at the stand level that management decisions operate. If dynamics at this scale are indeed driven by random processes, it will be difficult to forecast year-to-year changes in density. Ultimately, more information on gypsy moth dynamics is needed at the scale of the individual stand, which probably lies somewhere between the plot and zone levels examined in this study.

There is increasing awareness that landscapes and other ecological systems are scaled in space and time (Allen & Starr 1982, Addicott et al. 1987, Morris 1987). The results reported here reflect a general paradigm for ecological phenomenon: parameters and processes important at one scale are frequently not important or predic-

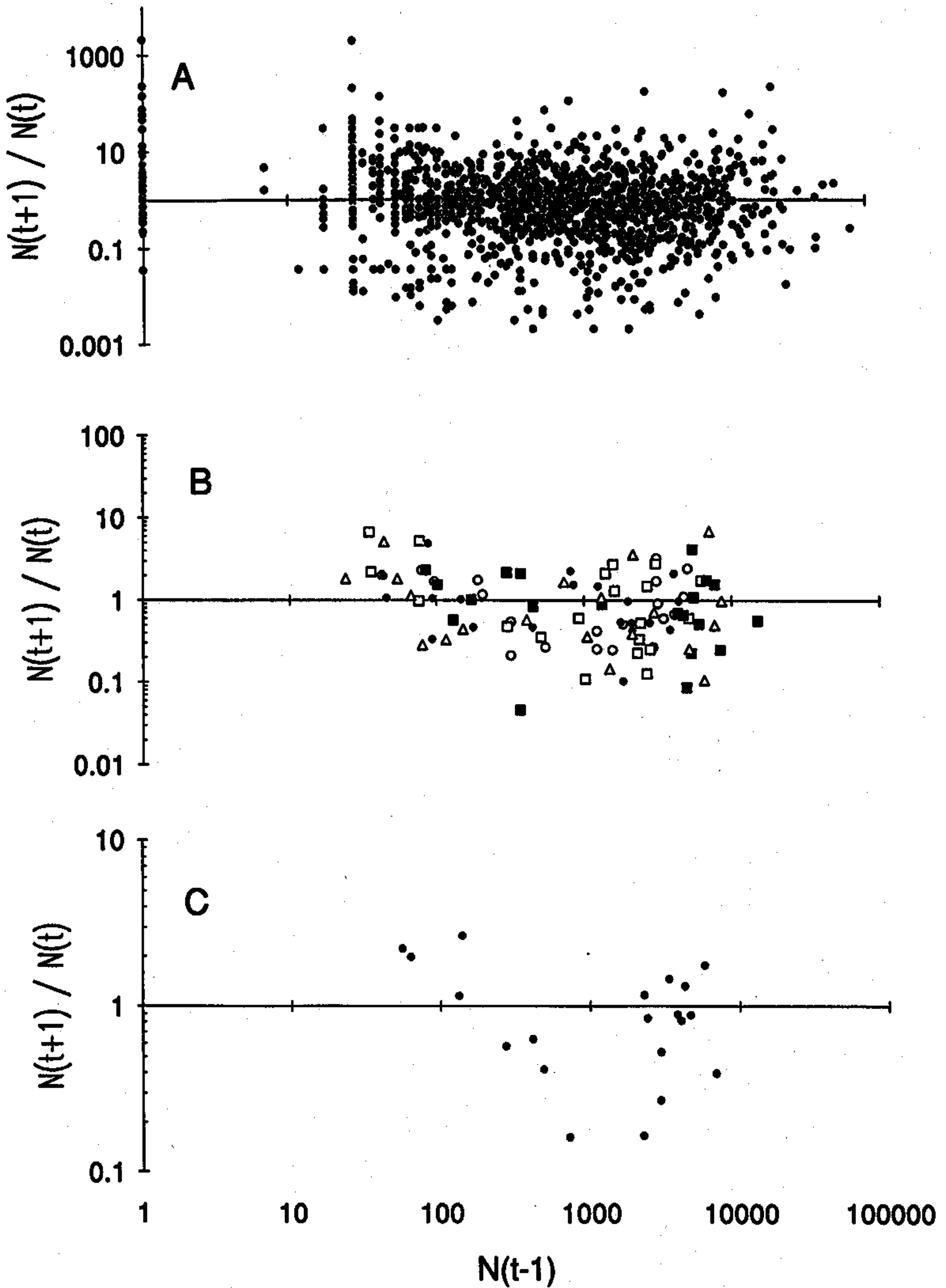


Fig. 6. Replacement rate versus density in the previous year. (A) Data from individual plots. (B) Yearly zone means; different types of point markers represent the five different zones. (C) Yearly grand means.

tive at another scale, and information is often lost as spatial data are considered at coarser scales of resolution (Meentemeyer and Box 1987, Turner et al. 1989). Liebhold et al. (1991) characterized spatial dependence in the Melrose gypsy moth egg mass density data using geostatistical methods and noted two dominant features: there was considerable localized (<5 km) discontinuity in the data, and there was spatial dependence among points separated by as much as 75 km. The apparent dominance of random effects on $f(N)$ at small spatial scales reported here is probably responsible for the high localized discontinuity noted by Liebhold et al. (1991). Further, the existence of spatial dependence in densities at points located as much as 75 km apart explains why zone means exhibit bimodality yet individual plot values do not. This analysis illustrates the caution that must be exercised in extrapolating characterizations of ecological processes across spatial scales.

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