

HABITAT PATCH CONNECTIVITY AND POPULATION SURVIVAL¹

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Abstract. We constructed a patch dynamics model which can be used to simulate the changing sizes of resident populations in a series of interconnected habitat patches. We applied the model to white-footed mice (*Peromyscus leucopus*) inhabiting patches of forest in an agricultural landscape. The model predicts that mouse populations in isolated woodlots have lower growth rates and are thus more prone to extinction than those in connected woodlots. Field data support this prediction.

Key words: connectivity; dispersal; extinction; habitat patch; patch dynamics; *Peromyscus leucopus*; population dynamics; survival; white-footed mouse.

INTRODUCTION

Most models of population dynamics assume that species' resources are homogeneous in space (e.g., see Lotka [1925], Leslie [1945], Wiegert [1974], Beddington et al. [1975], Anderson [1979], Hansen and Tuckwell [1981]). This assumption is made in order to simplify mathematical analysis. However, it is known that resources usually are not uniformly distributed, but generally are "patchy" (Emmel 1976, Cowie and Krebs 1979, McNamara 1982). This lack of uniformity may invalidate predictions of models which assume resource homogeneity (Levin 1976, Goldstein 1977, Southwood 1977).

A common case of resource patchiness occurs when the habitat is divided into useable patches which are separated from one another by nonuseable habitat. For example, dung beetles live in patches of dung, leaf miners live on leaves as patches, bark beetles use trees, and frogs use ponds as patches. It has been suggested (see, for example, Den Boer 1981) that the survival of populations in a group of habitat patches depends on the rate of "local extinctions" (in patches), and the rate of movements of organisms among the patches. If a patch is isolated from other similar patches, so that immigration is minimal, and if there is a high probability of population extinction in the patch, then the probability of survival of a population in the patch will be very low. Therefore, models which make predictions about the dynamics of populations that live in patches should take account of the spatial arrangement of these patches and should do so on the same time scale as local extinctions. These can arise and disappear by recolonization in as little as a few months for organisms with generation lengths of several months to 1 yr (Middleton and Merriam 1981, Henderson et al. 1985). Results on these short time scales cannot necessarily predict species survival on longer ecological or

evolutionary time scales (Middleton and Merriam 1983).

Although some "patch dynamics" models have been developed (Reddingius and Den Boer 1970, Levin 1974, Roff 1974a, b, 1975), they have been proposed primarily for theoretical investigation. The aims of the present study were to: (1) develop a model of patch dynamics that can be applied to field data, and (2) test certain predictions of the model by field work to answer the question: does population survival within a patch depend on the degree to which it is isolated from other patches?

A MODEL OF POPULATIONS IN CONNECTED PATCHES

The model, also presented in Fahrig et al. (1983), follows the population sizes and age structures in a series of interconnected patches through time. A spatial connection means either that the patches are sufficiently close that movement can occur among them, or that there is some "corridor" along which the organisms can move.

There are two components to the population dynamics: (1) within-patch dynamics, and (2) between-patch dynamics. Within a patch, individuals can be added to or lost from each age class. Additions to the youngest age class occur through births, and individuals "graduate" into the other classes by aging. Losses occur through age-specific deaths. Between-patch dynamics consist of additions due to immigration of organisms from adjacent patches, and losses due to emigration of organisms to connected patches. Individuals that emigrate but neither enter another patch nor return to the source patch are also counted as deaths.

We first present the general structure of the model and later will give specifics for this study. The basic operator of the model is a series of transition matrices, one for each time period, whose elements are parameters representing population processes appropriate for a suitable time interval, t .

Each matrix has the following general form:

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$X_t =$

$$1 - \sum_{j=2}^m p_{1,j} + b_1 - d_1 \dots p_{m-1,1} \quad p_{m,1}$$

$$\vdots \quad \vdots \quad \vdots \quad \vdots \quad \vdots$$

$$p_{1,m-1} \quad \dots \quad p_{m,m-1} \quad 1 - \sum_{j=1}^{m-1} p_{m,j} + b_m - d_m$$

where $p_{i,j}$ = the proportion of population in patch i that moves to patch j in time period t , b_i = birth rate in patch i during t , d_i = death rate in patch i during t (d_i includes all emigrants that never reach another patch and do not return to patch i), and m = number of patches.

In order to take account of the age class structure in the populations, each element in X_t is itself a matrix. The diagonal blocks in X_t are essentially Leslie matrices modified by the migration rates.

For three age classes:

$X_{t,i,j} =$

$$1 - \sum_{j=1}^m p_{1,i,j} - d_{1,i} \quad 0 \quad b_{3,i}$$

$$b_{1,i} \quad 1 - \sum_{j=1}^m p_{2,i,j} - d_{2,i} \quad 0$$

$$0 \quad b_{2,i} \quad 1 - \sum_{j=1}^m p_{3,i,j} - d_{3,i}$$

where b accounts for aging of individuals from one age-class to the next (this equals birth rate for $b_{3,i}$).

Off-diagonal elements in X_t account for age-specific and patch-specific movement rates, i.e.,

$$X_{t,i,j(i \neq j)} = \begin{matrix} p_{1,i,j} & 0 & 0 \\ 0 & p_{2,i,j} & 0 \\ 0 & 0 & p_{3,i,j} \end{matrix}$$

The vector of population sizes of the various age classes in the different patches at time $t + 1$ is obtained by multiplying the transition matrix X_t by the transpose of the row vector for the population at time t , i.e.,

$$(N_{1,1}, N_{2,1}, \dots, N_{k,1}, \dots, N_{3,m}).$$

Here, $N_{k,i}$ = number of individuals in age class k in patch i .

Since the values of p , b , and d may be functions of time, several transition matrices are required, one for each time interval. The whole series may be repeated over a longer time period, such as each breeding season. Any density dependence must be incorporated in functions determining specific parameter values.

To test the applicability of the model to a natural situation, and address the question of the effect of isolation on population survival as outlined in the introduction, we chose to apply it to populations of *Peromyscus leucopus* (the white-footed mouse) in wooded patches in southeastern Ontario. There were three main reasons for selecting *P. leucopus*.

First, *P. leucopus* avoids open areas with little cover, such as grassy fields (Bendell 1961, M'Closky and Lajoie 1975, Hansen and Warnock 1978), cultivated fields (Whitaker 1967), and roadways (Oxley et al. 1974), showing a definite preference for habitats with dense cover in the form of shrubs and trees (Whitaker 1967, Myton 1974, M'Closky 1975, Van Duesen and Kaufman 1977, Hansen and Warnock 1978), and debris such as rocks and logs (Bendell 1961, Madison 1977, Miller and Getz 1977, Barry and Francq 1980). The practice of clearing land for agriculture has, therefore, produced a very patchy *P. leucopus* habitat; the pieces of forest which are left form habitat islands surrounded by a sea of inhospitable cleared farmland. These habitat islands are, however, not necessarily completely isolated from each other. Wegner and Merriam (1979) found that *P. leucopus* were readily trapped in fence-rows (fencelines along which trees and shrubs are growing), which implies that they may provide corridors between woodlots along which mice will travel. Beer (1961) also observed that, instead of crossing a small meadow, mice tended to travel around it, "using the brushy edges as lanes." Finally, Sinclair et al. (1967) observed that the activities of *P. leucopus* in a field system were restricted to within 6 m of stone walls, implying that stone fences may also act as corridors through inhospitable fields. All of this evidence suggests that for *P. leucopus* in an agricultural mosaic, isolated woodlots are analogous to the habitat patches in the model; these are separated from each other by uninhabited fields, although sometimes linked by fencerows which are analogous to the connections in the model.

The second reason for choosing *P. leucopus* is that, when populations are confined in small isolated woodlots, their densities decrease with distance of the woodlot from a large forest (Gottfried 1979). This suggests that the presence or absence of connections among woodlots may make a detectable difference to *P. leucopus* population dynamics. Gyug (1978) also found that in small woodlots (<3 ha), autumn emigration decreased populations significantly unless compensated by immigration. Overwintering mortality of these populations can cause local extinctions before spring (Taylor 1978, Middleton and Merriam 1981).

The final reason for using *P. leucopus* is that estimates of the appropriate parameters needed to run the model: birth rates, death rates, dispersal rates, and life history characteristics, are available in the literature.

To apply the model to *P. leucopus*, aging rates through three age classes, weekly birth and death rates, and

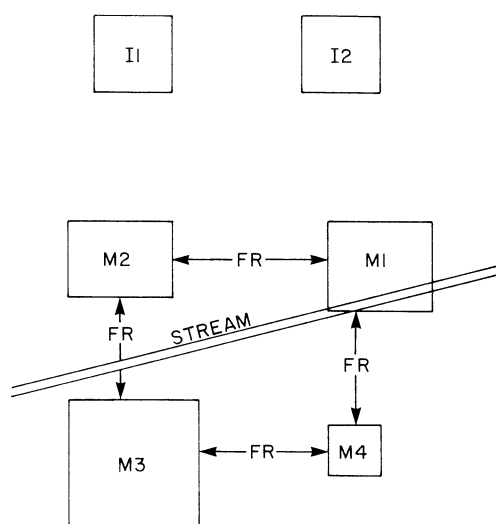


FIG. 1. Schematic representation of study sites. Areas (see Table 3) are to scale. I1, I2 = isolated woodlots; M1, M2, M3, M4 = connected woodlots; FR = fencerow.

weekly, age-specific movement rates were estimated from detailed studies in the literature.² We then chose field study sites (Fig. 1) with two woodlots completely separated by cropland and with four woodlots interconnected by fencerows. We applied the model² in 1-wk intervals to *P. leucopus* populations in spatial arrangements analogous to these woodlots to form predictions concerning the effects of isolation in these woodlots on *P. leucopus* population dynamics. Field data were collected to test the predictions.

To apply the model to a field situation some parameters had to be estimated for our study area. Savidge (1973) found that a stream 3–4 m wide and 10–40 cm deep decreased *P. leucopus* dispersal by about two-thirds. Small streams crossed the fencerows between M1 and M4, and between M2 and M3 (Fig. 1). Savidge's result was used to repropportion the flux of animals along fencerows connecting these woodlots.

Woodlots varied in size but dispersal is apparently density independent (Hansen and Batzli 1978, Nadeau et al. 1981). The maximum population size in any woodlot is known from trapping to be unrelated to woodlot size (Middleton 1979, Fahrig 1983), but since winter resources are relatively scarce, the proportion of mice that survive over winter may depend on woodlot size. We therefore assumed that spring population sizes are proportional to woodlot areas, and starting (March) populations were sized according to areas in Fig. 1.

Simulations of the population dynamics in the iso-

lated woodlots (which were identical) and in each interconnected woodlot were made. Although each simulation considered 28 wk (the 3rd wk in March to the 2nd wk in October), only data for 12 wk corresponding to the field studies were analyzed (2nd wk of June to 1st wk of September). Results were analyzed as follows. A series of increasingly complex least-squares regression models was fitted to the predicted numbers of individuals, and an analysis of variance was constructed. We then determined whether the variances for factors thought relevant were significantly different from random variability. This analysis enabled predictions to be made concerning the effect of increased habitat patch isolation on the population dynamics of *P. leucopus*. These predictions were tested by comparison to field measurements.

MODEL RESULTS

Simulations of mouse populations (Table 1) increase irregularly because birth rate is not constant. Simulation results were analyzed by linear regression analysis to generate predictions concerning the effects of woodlot isolation on population dynamics. The following points (from Table 2) demonstrate the findings.

- 1) There is a significant linear regression of population size on time ($F = 552.2$, $P < .01$), which indicates significant population growth.
- 2) There is no statistical justification for the inclusion of a quadratic term ($F = 2.733$, NS); therefore the population growth rate within a woodlot is constant.
- 3) There is a significant difference between the slopes of the regressions for the isolated and connected woodlots ($F = 26.26$, $P < .01$); the population growth rate in isolated woodlots is lower than that in connected woodlots (Fig. 2).
- 4) There is no significant difference among slopes of regressions for different woodlots within isolated and connected types ($F = 0.869$, NS); population growth rates in woodlots of the same type (isolated vs. connected) do not differ.

TABLE 1. Simulated population sizes in five woodlots (Fig. 1) from the 2nd wk of June to the 1st wk of September.

Week	I1 or I2 (3.75 ha)	M1 (5.3 ha)	M2 (4.5 ha)	M3 (9.8 ha)	M4 (1.5 ha)
1	9	13	13	12	7
2	10	14	14	13	8
3	10	14	14	12	9
4	11	14	14	12	10
5	10	15	15	15	12
6	11	18	18	17	14
7	12	20	20	18	15
8	13	20	20	21	18
9	17	25	25	25	23
10	18	28	28	25	24
11	16	27	27	25	23
12	16	26	26	25	23

² See ESA Supplementary Publication Service document No. 8524 for model computer program listing and parameter estimation (16 pages). For a copy of this document, contact G. Merriam or order from The Ecological Society of America, Cornell University, Ithaca, New York 14853-2701 USA.

TABLE 2. Analysis of variance for regressions of simulated mouse population size on time.

Source	Sum of squares	Degrees of freedom	Mean square	F statistic	Significance level (P)
Total	2048.183	59			
Additional due to different intercepts	414.267	4	103.567	40.365	<.01
Due to types*	286.017	1	286.017	111.365	<.01
Due to woodlots within types	128.250	3	42.75	16.662	<.01
Due to linear and quadratic regression	1423.855	2	711.928	277.473	<.01
Due to linear term alone	1416.842	1	1416.842	552.213	<.01
Additional linear due to types	67.385	1	67.385	26.263	<.01
Additional linear due to woodlots within types	6.691	3	2.230	0.869	NS
Additional due to quadratic term	7.013	1	7.013	2.733	NS
Residual	135.985	53	2.566		

* "Types" means isolated (I1 and I2) vs. connected (M1, M2, M3, and M4) woodlots.

The simulations suggest a mechanism consistent with the dynamics of *P. leucopus* populations studied in patchy environments. A certain number of *P. leucopus* consistently disperse from isolated woodlots (Stickel and Warbach 1960, Gyug 1978, Tardiff and Gray 1978), and the model duplicated this phenomenon. In isolated woodlots this emigration is not balanced by immigration and lower population growth rates result. Taylor (1978) and Middleton (1979) have shown that overwintering mortality rates of 80–90% are common in *P. leucopus* populations in southeastern Ontario, and that many woodlots may begin the spring breeding period with only a few (0–5) reproductive females. Small spring populations were also found by Harland et al. (1979). Local extinctions have been documented (Taylor 1978). It is, therefore, very important that a woodlot population be able to grow quickly during the summer. A large autumn population is necessary to ensure that a breeding nucleus survives until the following spring.

The model predicts that *P. leucopus* populations in isolated woodlots have lower growth rates and consequently have a higher probability of local extinction than those in connected woodlots. This prediction of growth rates was tested by field studies.

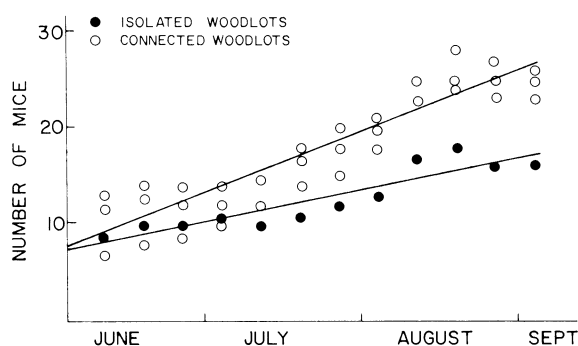


FIG. 2. Regressions of simulated mouse population sizes on time. Isolated: No. mice = $7.591 + .793(\text{time})$. Connected: No. mice = $8.061 + 1.561(\text{time})$. Isolated slope vs. connected slope ($F = 25.44$, $P < .01$).

FIELD METHODS

Seven deciduous woodlots near Ottawa were chosen for the study. I1 and I2 are 3.8 and 3.7 ha, respectively. These woodlots are completely isolated; they are 350 m apart and are both completely surrounded by and separated from each other by alfalfa fields which were harvested twice during the study. The vegetation in I1 and I2 consists of sparsely distributed mature deciduous trees, primarily maple, birch, beech and poplar, and a dense understory of shrubs and saplings. The four connected woodlots, M1, M2, M3, and M4, are 5.3, 4.5, 9.8, and 1.5 ha, respectively. There is a series of fencerows connecting the four woodlots in a ring, and a narrow stream flows through the area (see Fig. 1). The seventh woodlot, FF, is 1.7 ha. M1, M2, M3, M4, and FF are mature deciduous woods, with dense canopies and relatively little understory vegetation. In the areas studied within each of these woodlots, the dominant tree is maple.

The woodlots were studied during the summer of 1982. There were two phases of sampling: tracking and trapping. Weekly from the 2nd wk of June to the 1st wk of September the populations in I1, I2, M2, M3, and M4 were assessed using smoked paper tracking

TABLE 3. Weekly tracking data. Number of tracking records in six woodlots (Fig. 1) from the 2nd wk of June to the 1st wk of September.

Week	I1 (3.8 ha)	I2 (3.7 ha)	M1 (5.3 ha)	M2 (4.5 ha)	M3 (9.8 ha)	M4 (1.5 ha)
1	0	0	0	0	0	1
2	3	1	1	1	2	18
3	6	0	1	2	2	1
4	2	2	1	0	1	2
5	0	5	1	9	5	26
6	4	8	4	19	5	21
7	10	14	5	19	9	8
8	12	15	19	18	10	19
9	2	13	16	14	27	13
10	2	6	5	3	6	2
11	9	6	15	3	8	9
12	8	5	11	20	7	14

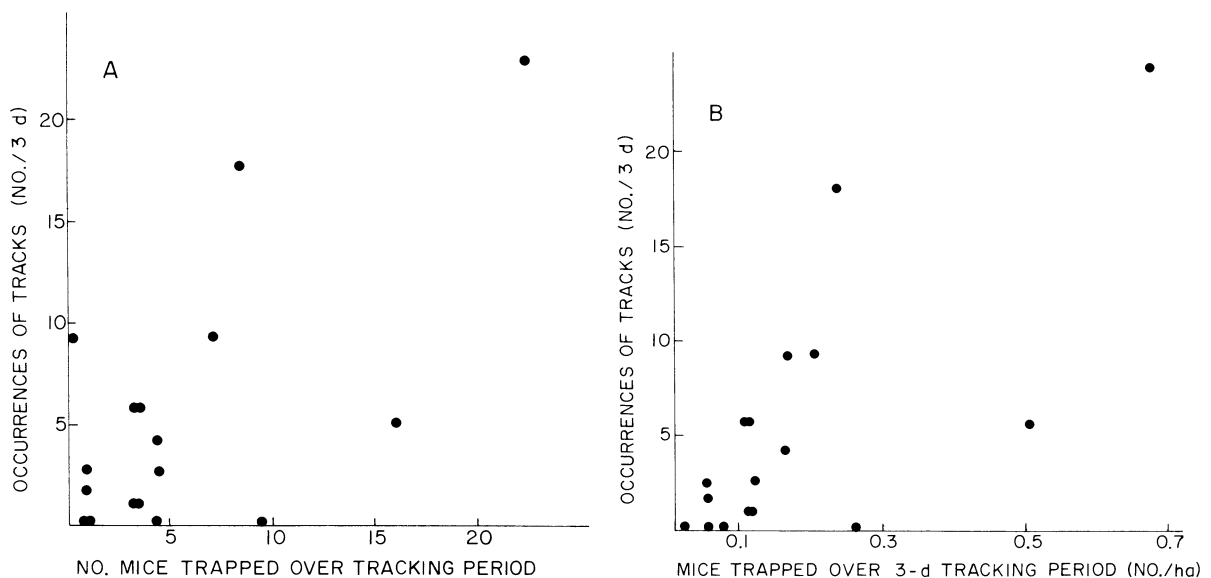


FIG. 3. Correlations between mean number of mice trapped (A) and mean number of mice trapped per hectare (B) over 3-d tracking period, and number of occurrences of tracks in that period. For A, $r = 0.738$ ($P < .01$); for B, $r = 0.596$ ($P < .05$).

(Sheppe 1965). Thirty-centimetre lengths of 3.75 cm (inside diameter) plastic water pipe were lined with glossy paper smoked with carbon black. One hundred tubes were placed in a 100×100 m grid (tubes 10 m apart) in each woodlot. Tubes were checked weekly for *P. leucopus* tracks. The smoked paper was replaced if tracked or smudged. Data were "presence" or "absence" of *P. leucopus* tracks, irrespective of the number of tracks.

During September and October, three of the woodlots, FF, I1, and M4, were live-trapped using Sherman-type live-traps. The traps were placed on 25-m grids

covering the entire woodlots. FF was trapped daily from 4 to 9 September and from 15 to 25 September, I1 was trapped daily from 26 September to 7 October, and M4 was trapped daily from 15 September to 1 October. Trapped animals were removed to woodlots at least 5 km away.

The following analyses were performed.

Relationship between trapping and tracking. — Smoked paper tracking has never been used in this way so it was necessary to relate tracking data to number of mice trapped. Correlations of frequency of tracks present with number of mice live-trapped and of tracks

TABLE 4. Analysis of variance for regressions of mouse tracking data on time.

Source	Sum of squares	Degrees of freedom	Mean square	F statistic	Significance level (P)
Total	163.592	71			
Additional due to different intercepts	16.307	5	3.262	3.190	<.05
Due to types*	6.551	1	6.551	6.407	<.05
Additional due to woodlots within types	9.756	4	2.439	2.385	NS
Due to linear and quadratic regression	74.583	2	37.291	36.472	<.01
Due to linear term	62.513	1	62.513	61.140	<.01
Additional due to quadratic term	12.070	1	12.070	11.805	<.01
Additional due to separate linear and quadratic regressions for types	4.939	2	2.470	2.416	NS
Due to linear term	4.903	1	4.903	4.795	<.05
Additional due to quadratic term	0.0371	1	0.0371	0.0363	NS
Additional due to regression on woodlots within types	12.551	8	1.569	1.535	NS
Due to linear term	9.793	4	2.448	2.394	NS
Additional due to quadratic term	2.779	4	0.6947	0.6794	NS
Residual	55.212	54	1.022		

*Isolated vs. connected woodlots.

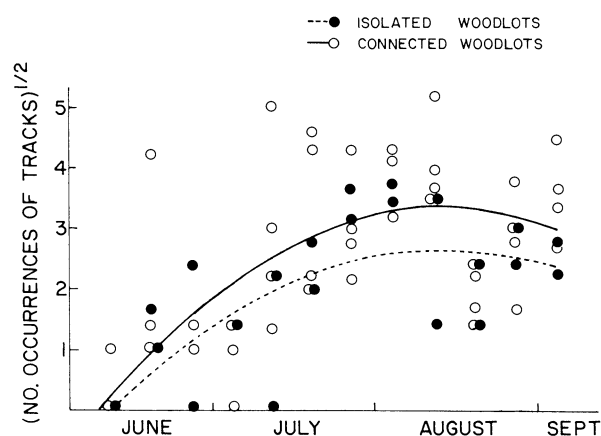


FIG. 4. Regressions of mouse tracking data on time. Isolated: $(\text{no. tracking records})^{1/2} = -0.574 + 0.746(\text{time}) - 0.041(\text{time})^2$. Connected: $(\text{no. tracking records})^{1/2} = -0.427 + 0.818(\text{time}) - 0.044(\text{time})^2$. Isolated slope vs. connected slope ($F = 4.80$, $P < .05$).

present with mice trapped per unit area were compared to show how well tracking measured population size and population density.

Regression analysis of tracking data.—The same method was used to analyze the tracking data for the six woodlots, I1, I2, M1, M2, M3, and M4, as was used in analyzing the simulated data.

TEST RESULTS

The relationships between tracking and trapping data are shown in Fig. 3A and B. A higher correlation was found between the number of tracking records and number of mice trapped ($r = 73.80$) than between number of tracking records and the number of mice trapped per unit area ($r = 59.59$). This indicates that the tracking data are a better measure of absolute population size than of population density.

The tracking results (Table 3) were analyzed by linear regression to test the prediction generated by the simulations, namely, that populations in isolated woodlots have lower growth rates than those in connected woodlots. Note that the dependent variable was transformed to $(\text{tracking records})^{1/2}$ which stabilized the variance, i.e., the variance became approximately constant over the times and woodlots.

The following points (from Table 4) demonstrate the findings.

- 1) There is a significant linear regression ($F = 61.14$, $P < .01$), which indicates significant population growth.
- 2) There is statistical justification for the inclusion of a quadratic term ($F = 11.805$, $P < .01$); therefore, population growth rates were not constant, but reached a maximum during the study period.
- 3) There is a significant difference between the slopes (linear term) of the regressions for the isolated

and connected woodlots ($F = 4.795$, $P < .05$); the population growth rate in isolated woodlots was lower than that in connected woodlots.

- 4) There is no significant difference among slopes of different woodlots within types ($F = 2.394$, NS); growth rates in isolated woodlots can be grouped but differ from those in connected woodlots, which also can be grouped.
- 5) There are no significant differences in the quadratic terms for isolated and connected woodlots ($F = 0.0363$, NS) or for woodlots within types ($F = 0.6794$, NS). This implies that all the woodlots reach their maximum population sizes at approximately the same time; this occurs in the 2nd wk of August (Fig. 4).

DISCUSSION

The model prediction that *P. leucopus* populations in isolated woodlots have lower growth rates than those in connected woodlots is supported by the field results ($F = 4.795$, $P < .05$). As stated earlier, this has important implications for the population survival of *P. leucopus* in fragmented habitat. If populations begin the breeding season with only a few females, and if isolated populations have lower growth rates, they will begin the winter with fewer individuals. The extreme overwintering mortality at our latitudes means that isolated populations have higher probabilities of becoming extinct before the next breeding season. Reestablishment of extinct local populations will take longer in isolated patches than in connected ones. In a whole region, therefore, the frequency and persistence of local extinctions of *P. leucopus* populations depends on the degree to which individual patches are isolated from one another.

Although the model has been applied to *P. leucopus* in woodlots, it may be a useful tool for predicting changes in the population dynamics of any of the many organisms that are found living in habitat patches.

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