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SPITTLEBUG, PHILAENUS SPUMARIUS L.

University of Michigan, Ph.D., 1962
Zoology

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THE EFFECTS OF PERIODIC DESTRUCTION OF HABITAT
ON THE ENERGETICS OF THE MEADOW SPITTLEBUG,
PHILAENUS SPUMARIUS L.

by
Richard George Wiegert

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in the
University of Michigan
1962

Doctoral Committee:

Professor Francis C. Evans, Chairman
Professor William S. Benninghoff
Associate Professor William R. Dawson
Associate Professor Frederick E. Smith

ACKNOWLEDGEMENTS

I am deeply grateful to Dr. Francis C. Evans, the chairman of my doctoral committee, for his stimulating criticism and constant encouragement during all phases of this study. The other members of the committee, Drs. William S. Benninghoff, William R. Dawson, and Frederick E. Smith, advised me concerning certain aspects of the work and reviewed the dissertation.

Dr. Peter M. Ray, Department of Botany, and Dr. Lawrence B. Slobodkin, Department of Zoology, provided both laboratory facilities and valuable guidance. Mr. Richard A. White, Department of Botany, made the tissue sections and Mr. John W. Alley, Department of Zoology, made the photomicrographs. Dr. Don W. Hayne, U. S. Fish and Wildlife Service, Patuxent Research Refuge, Laurel, Md., aided in designing the sampling program and Dr. Thomas E. Moore, Department of Zoology, provided many literature references.

Dr. Evans; Dr. Uri N. Lanham, Wayne State University, Detroit, Michigan; and Dr. Alan T. Marshall of the University of Hong Kong, Hong Kong permitted me to cite from their unpublished data. Mr. Ralph Meyers, Pinckney, Mich., owns the alfalfa fields studied.

The costs of materials and equipment used in this

study were defrayed by the Department of Zoology and by National Science Foundation Grants G-3223 and G-13521 to Dr. Evans. Funds for travel and subsistence were provided by the Horace H. Rackham Graduate Student Research Fund, by the Edwin S. George Reserve Scholarship Fund, and in 1960-61, by a pre-doctoral Fellowship awarded to me by the National Science Foundation.

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INTRODUCTION

The measurement of energy flow has attracted considerable attention in recent years as a supplement to counts of individuals and to measurements of biomass in investigations of laboratory and natural ecosystems. Energy flow is equivalent to the combined rates of production and respiration, i.e. the rate of assimilation of energy by the population or trophic level. Because of the precise physical definition of the calorie, the energy flow in one ecosystem is directly comparable with that in any other ecosystem. Moreover, the transfer of energy from one system to another is quantitative and follows a set of known thermodynamic laws. These properties make energy flow measurement a valuable adjunct to the methods of modern ecology, both theoretical and applied.

The energy flow concept can be applied at the level of the entire ecosystem by measuring the transfer between trophic levels (Odum 1957, Odum and Odum 1955, Teal 1957). Such studies provide an overall view of the energetic processes within the ecosystem and make possible a rough comparison of very different communities according to the rates of energy fixation and utilization, but because of species diversity, the difficulty of delimiting precisely the higher trophic levels, and the complexities of the

physical environment, even the simplest communities present formidable problems. Order of magnitude accuracy in many of the measured parameters must often be accepted.

Some studies have emphasized the measurement of energy flow in single populations or food chains, either in the field (Golley, 1960; Odum and Smalley, 1959; Smalley, 1960; Odum, Connell and Davenport, 1962) or in the laboratory (Richman, 1958; Slobodkin, 1959). Only a start has been made in this line of research, although such a reduction in scope can lead to significant increases in the accuracy of measurement.

Previous field studies have dealt with one or more species of organisms in one ecosystem. This paper compares the energy flow in populations of the meadow spittlebug, Philaenus spumarius L., in two different habitats, (1) a successional old field ecosystem and (2) cultivated alfalfa cropland. Interest developed in this species because of its prominence in the old field insect fauna, and because this prominence seemed to be a result of large seasonal immigrations of adults.

The overall objectives of the study were: (1) to evaluate quantitatively the importance of the spittlebug in the old field ecosystem, (2) to determine the pathways and efficiencies of energy transfer through the populations, and (3) to compare the populations on the two habitats with respect to energy flow, growth, mortality, etc. In addition, the study dealt with the effect of feeding on the primary

production of the vegetation and with the magnitude of energy flow between the two habitats. The latter takes the form of movements of adults from the Alfalfa Field to the Old Field.

Migrations are quite common in nature, especially those of vertebrates, and migrants often have considerable effect upon the structure and function of the invaded community, serving as predators, prey, or both. But the movement of energy into or out of a terrestrial population in the form of migrating organisms has not been evaluated previously, at least not where this movement is a natural and necessary behavior of the migrant organism, and where the magnitude of the energy transfer is large in proportion to the annual energy flow through the "native" part of the population.

The Species Studied

Philaenus spumarius is a species of sucking insect belonging to the order Homoptera, family Cercopidae. It is quite widespread, having been reported from Europe, Asia, North America, and South America. Within the United States the meadow spittlebug is found throughout most of the northeastern, north central, and northwestern parts of the country. It is common over much of this range and in some localities reaches such high densities that it is a serious agricultural pest of legume forage crops (Weaver and King, 1954).

The species shows a high degree of color polymorphism

and many of the color varieties have been named previously as distinct species. Because two species were confused by Linnaeus in his original description of the meadow spittlebug, there has been ground for controversy as to which scientific name should be applied to it. Spumarius has been the name generally used, but for a time the alternative, leucophthalmus, was accepted. However, a recent decision of the International Commission on Zoological Nomenclature (1961) restores the specific name spumarius to this insect.

Because the meadow spittlebug is an important agricultural pest of legume and other crops, a considerable body of information on its life history has accumulated (see Weaver and King, 1954).

The species possesses distinct advantages as the subject of study of energy flow because it produces a single generation annually and overwinters as an egg. Hatching occurs early in May in southern Michigan. The spittlebug feeds on a wide variety of plant species; in the study areas forbs were preferred over grasses. The nymphs climb onto nearby plants and begin to feed, secreting in the process a protective mass of bubble-filled fluid. There are 5 instars and molting takes place within the spittle mass. In June the final molt to the adult takes place. Mating begins soon after adult emergence and can be observed throughout the summer. The adults oviposit during September and by late October are absent from the study areas. In southeastern Michigan the majority of reproduction by the species occurs on legume cropland.

On alfalfa fields high densities of nymphs are permitted by the succulent plant growth made during spring and early summer. A forced exodus of the adults occurs when the hay is cut, with a consequent dispersal of this insect into virtually every type of habitat in the surrounding countryside. With renewed growth of the alfalfa fields, immigration rebuilds their resident populations of adult spittlebugs. This cycle is repeated during the second period of hay cutting, after which overwintering eggs are deposited.

When the adults disperse during the cutting of the legume hayfields, large numbers of them enter the old field ecosystem where the native population of P. spumarius is very small. The migrants at times comprise more than 50% of the total biomass of the above ground insect fauna on the field (Evans and Lanham, 1960 and unpub. data).

The Study Areas

One of the study areas was the 15-acre Evans Old Field, located in the northeast quarter of section 19, Putnam Twp., Livingston Co., Michigan. This field is within the Edwin S. George Reserve of the University of Michigan and is referred to throughout this paper as the "Old Field." The 1200-acre Reserve, originally a farming area, has been enclosed by a seven foot fence since 1928 and allowed to revert to a "natural" condition, subject only to the disturbance caused by a population of whitetail deer maintained within the Reserve.

The topography, soils and vegetation of the field have been described in detail (Evans and Cain, 1952, Evans and Dahl, 1955). Local relief is slight, with gentle contours and several shallow, poorly drained depressions or swales. The soils of the upland areas are mostly of the Fox sandy loam series. Those in the swales are covered by colluvial silt to depths as much as one meter.

The flora of the field is diverse. The swales support a dense growth of Kentucky blue-grass (Poa pratensis), interspersed with milkweed (Asclepias syriaca), foxtail (Setaria glauca), and sorrel (Rumex acetosella). The more complex upland areas are dominated by two species of grass, needlegrass (Aristida purpurascens) and Canada bluegrass (Poa compressa). Witchgrass (Leptoloma cognatum) and panic grass (Panicum depauperatum) occur in patches on the field. The most common forbs include: blazing star (Liatris aspera), goldenrod (Solidago rigida and S. juncea), everlasting (Antennaria neglecta), hawkweed (Hieracium longipilum), bush clover (Lespedeza capitata and L. Virginica), and sorrel (Rumex acetosella). Extensive patches of mosses and lichens occur on the drier sites, often in association with Panicum spp. The general aspect of the field is one of dry soil and sparse vegetation.

One of the two alfalfa fields studied was a 13-acre first year seeding located across the road from the western boundary fence of the Reserve and about one mile southwest of the Old Field. This is the "Small Alfalfa Field." It supported a uniform stand of alfalfa, (Medicago sativa);

several other species were present but in such low densities as to make them of negligible importance in this study.

The second stand of alfalfa was a 25-acre, third year seeding located one mile north of the Small Alfalfa Field and one and one-half mile northwest of the Old Field. This area was used only for samples of the adult spittlebug population in 1960 and is referred to in this paper as the "Large Alfalfa Field."

The topography of these alfalfa fields is similar to that of the Old Field. No soil samples were taken.

The climate of the Reserve was described by Evans and Dahl (1955) as a humid, mesothermal type. They stated that precipitation occurs at all seasons and that the length of the frost-free growing season at Jackson, 30 miles to the southwest, averaged 155 days over a 40 year period as recorded by the U. S. Weather Bureau Station. Published six year averages from the Reserve weather station for the period 1949-1954 (Evans and Dahl, 1955) show an annual range in mean monthly temperature of from 25.3°F. (January) to 70.3°F. (July). The range in mean monthly precipitation was 2.18 inches (August) to 4.10 inches (June).

METHODS

Estimation of Density

During the summers of 1959 and 1960, the numbers of Philaenus nymphs and adults on the Old Field were sampled at intervals of 3 - 7 days. A stratified-random method of sampling was employed. The method of dividing the Old Field into the three categories (strata) has been described elsewhere (Wiegert, 1962). This division and the allocation of samples within each category were primarily aimed at decreasing the sampling variance in a concurrent study of the standing crop of plant biomass on the Old Field. But since the numbers of spittlebugs were directly correlated with the density of green vegetation, the sample allocation increased the accuracy of the spittlebug density estimate over that which simple random sampling would have given. The categories were: (1) upland, (2) bryoid and (3) swale; they occupy respectively, 66.5, 33.9, and 3.6 per cent of the area of the Old Field. Stations were randomly selected within each category, and the same station was used for successive samples throughout the season. The sampling area was a circle of radius 6 paces with the permanent station at its center. Before taking a set of samples, a compass direction and a distance (one to six paces) were selected from a table of random numbers. This direction and distance

from the permanent station located the sample precisely and a given combination was used only once.

The nymphs are slow moving and were easy to sample from a frame quadrat placed on the ground. The first and second instars are quite small and apt to be overlooked, so for the first few sampling periods all forbs within the frame were dug up and dissected in an enameled tray. The older nymphs are easy to detect because of the larger spittle mass they produce.

During 1959 a square wooden frame 0.25 m^2 in area was used to sample the nymphs. The first set of samples, taken on May 12, was from three randomly chosen transects across the field. During the remainder of the 1959 nymph sampling the permanent stations described above were used. Thirty samples were taken in each set.

In 1960 a circular quadrat 0.20 m^2 in area was used. The number of samples taken in a set varied from 7 - 50. The set of 7 samples was taken on May 7 and was randomly chosen from the entire field. For the remainder of the 1960 season the sets contained from 24 to 50 samples each and the permanent stations were used.

For the first two samples of adults (June 19 and 22, 1959) a frame quadrat of area 0.25 m^2 , with sides one foot high, was used. It was placed over the vegetation and all spittlebugs inside the frame were counted. This procedure gave a low estimate of density because some of the insects jumped from the vegetation before being counted and others were missed in counting. I subsequently designed a

cylindrical sampling cage which collected all the adult spittlebugs from an area of 0.20 m^2 (Wiegert, 1961). Throughout the summers of 1959 and 1960, sets of fifty samples each were taken at two-day to one-week intervals at permanent stations as described above.

The 1959 results indicated that a reapportionment of the sampling stations would increase the accuracy of the mean density estimate. In 1959 the allocation of the 50 permanent stations on the Old Field was: upland 28, bryoid 14, swale 8. In 1960 this was changed to: upland 36, bryoid 6, swale 8. The standard errors and the confidence limits of the stratified random samples were calculated according to the method of Snedecor (1956, p. 505).

Because of the relatively uniform stand of vegetation in the Small Alfalfa Field, simple random sampling was used. All samples were taken from an area of approximately one square hectare on the south-central side of the field. The sampling points were located by pacing the distances from marked boundary lines. The nymphs were sampled with the same circular frame used on the Old Field in 1960. On June 20 and again on June 24, 1960, five random samples of the adults were taken with the cylindrical sampling cage. Each time one of these samples was taken I also made 10 sweeps in the general area of the sample with a standard sweep net (15 in. dia. ring). From these data an areal conversion factor was calculated and applied to all subsequent adult samples, which were taken solely with the sweep net, at the rate of 5 samples per set and 10 sweeps per sample.

On the Large Alfalfa Field, only the adult spittlebug populations were sampled. This was also done with a sweep net, and all samples were taken on a transect extending from the southern edge of the field toward the center. I was interested in relative numbers only and so calculated no conversion factor for this field.

Estimation of Mortality

Movement of the nymphs is very restricted, and their immigration and emigration are negligible factors in the population. After the hatching period nymph mortality was calculated from the decrease in density with time. The rate was assumed to be the same during the hatching period.

Adult mortality rates were estimated by placing a large square cage (basal area of 7 m²) over an undisturbed part of the Old Field. The lower edge was sealed with earth and the spittlebug adults in the cage were counted. Successive counts were made at intervals of approximately 10 days from August through October, 1960. In June of 1961 the cage was moved to a new location and the procedure repeated from June through July. No adult mortality rates were measured in the alfalfa field habitats.

Measurement of Biomass

All weights used in this paper were obtained by oven drying the material at 60°C. in a vacuum or at 100°C. without a vacuum. The materials were subsequently stored in desiccators over a drying agent for at least 24 hours before being weighed. All weights were determined on Mettler

automatic analytical balances sensitive to either 0.01 mg or 0.001 mg.

The field collections of nymphs were not weighed directly; instead their weights were calculated by multiplying the number of nymphs by the mean weight for each instar, times the per cent of that instar in the sample. The mean weights of the instars were those of the nymphs used in the respiration experiments.

A mean body weight for adults was calculated from the total weight of all the adult spittlebugs collected in the Old Field samples of 1959 and 1960. The individual samples were also analyzed and, except for a slight increase shortly after emergence, the mean body weight of both females and males remained relatively constant throughout the summer.

A mean weight per egg was obtained from the weight of several hundred fully developed eggs dissected from females collected on both the Old Field and the Large Alfalfa Field in late September and early October, 1960.

The weight of material lost at molting by each instar was determined from field collections of cast exoskeletons. These cast skins were classified by measuring the width of the head capsule and comparing with the instar key of Weaver and King (1954). Weighed exoskeletons from the molt of known fifth instar nymphs served as a check on this procedure.

Determination of the Food Material

To obtain direct evidence of the plant tissues penetrated during feeding carbon dioxide was used to anesthetize nymphs feeding on young tomato plants (Lycopersicon). A section of the plant stem plus attached nymphs was then placed in an alcohol-acetic acid-formalin solution. The material was subsequently cleared, embedded and sectioned. The sections were stained with saffarin and fast green, using the standard graded alcohol-xylene series. They were then mounted under balsam. Most of the nymphs dropped off the stem during the clearing and embedding. The feeding puncture alone, however, was enough to indicate the site of feeding.

Analyses of Xylem Sap and Spittle

Exudate from the bleeding stumps of tomato plants was collected by means of a capillary tube fastened to the stump with a short piece of rubber tubing. Root pressure forced the fluid out of the capillary. This procedure gives a relatively pure sample of the fluid from the xylem elements of the plant (Bollard, 1960).

The spittle samples were collected from fourth and fifth instar nymphs feeding on tomato plants under bell jars. The jars maintained a relative humidity of 100% and prevented evaporation and consequent condensation of the spittle solutes.

The total dry matter, total organic matter and ash content of both xylem sap and spittle were determined by

drying to constant weight in porcelain crucibles at 100°C., weighing, then ashing in a muffle furnace at 600°C. Paper chromatography was used to determine the amino acids.

Whatman No. 1 washed filter paper and solutions of phenol-water and butanol-acetic acid-water (5-1-4 v/v) were used. The papers were air dried for several hours after the runs, then sprayed with a 0.2% solution of ninhydrin in isopropanol and dried at 100°C. for five minutes. The sample amounts applied to the papers were 0.01 ml of 0.2% w/v solutions of the known amino acids, and the equivalent of 0.1 ml of unconcentrated spittle and xylem sap.

For the quantitative determinations a one-way chromatogram was run in phenol-water after applying the above amounts of spittle, xylem sap, and the amino acids known to be present in tomato xylem sap. After development the spots were cut out and eluted in 5 ml of 50% n-propanol. The optical densities of the eluted solutions were read in a Klett-Summerson photometer and the amounts of the unknown acids were determined by comparison with the results from the spots containing the known compounds.

A one-way chromatogram run in butanol-acetic acid-water was used to test for the presence of sugar in the spittle. Anilin phthalate was the developing reagent (0.93 ml aniline and 1.66 gm phthalic acid in 100 ml water-saturated n-butanol) and 0.02 ml of spittle was applied to the paper.

Measurement of Egestion

The rate of spittle production was measured by placing nymphs on tomato plants, letting them feed for a known time, then absorbing the spittle produced on a weighed piece of filter paper. Periodic weighings established a rate of evaporation of spittle from the filter paper and by extrapolation to time zero the total weight of spittle produced was calculated. Because of the small amounts of solute in the spittle and the short time interval involved in the weighings, the error in assuming a constant rate of evaporation was probably not large. Bell jars over the plants maintained the relative humidity at about 100% and prevented evaporation of the spittle during the feeding period.

Although they do not produce spittle, feeding adults forcibly expel small drops of fluid from the anus. The droplets produced by a number of individuals feeding on alfalfa (Medicago sativa) and Kentucky bluegrass (Poa pratensis) were counted and used to calculate a mean rate of droplet production. Several of the flattened droplets were collected on a piece of tinfoil and their diameters measured under the dissecting microscope. A micropipette was used to produce a number of drops with the same mean diameter as those obtained from the spittlebugs. The volume of water used divided by the number of drops produced from the pipette gave a mean volume per drop. This value was checked by weighing a series of droplets from a feeding adult

and extrapolating to time zero in the manner described above for weighing spittle production.

Measurement of Respiration

A modification of the apparatus described by Engelmann (1961) was used for measuring the oxygen consumption of both nymphs and adults. A small glass vial with a ground glass neck held the animals plus a wad of cotton and a piece of filter paper soaked in 10% w/v potassium hydroxide. A pyrex micropipette, graduated in 0.001 ml and taper-ground on one end, fitted into the glass vial. Stop-cock grease was used as a seal. Colored manometer fluid moving down the pipette indicated the volume of oxygen consumed. A vial with filter paper, KOH, and cotton, but without an animal, served as the control. A water bath constant to 0.1°C. held 6 of these instruments. A piece of rubber tubing over the open end of each pipette admitted air to the submerged instruments.

For the variable temperature runs the bath was started at the lowest temperature; this was increased by increments of 5°C. after each determination. An equilibration period of 20 minutes was allowed after each temperature change and before starting the next run. All oxygen consumption data were corrected to standard conditions of temperature, pressure, and humidity.

The respiration of the field populations was corrected for the mean ambient temperature prevailing over each sampling interval. This ambient temperature was calculated

by summing the maximum and minimum temperatures for each day in the interval and dividing by twice the number of days. The max-min. temperature data were recorded at the Reserve weather station, located approximately one-quarter mile south of the Old Field.

Measurement of Caloric Content of Materials

All animal materials were dried in a vacuum oven at 60°C. and burned in a miniature bomb calorimeter (Slobodkin and Richman, 1960). The experimental error of the procedure was approximately one per cent.

The nymphs used in the caloric determinations were collected from an alfalfa field outside the study areas but near the E. S. G. Reserve. The adult material was from the Old Field collections of 1960. Sufficient exoskeleton material from meadow spittlebug nymphs was not available for burning in the calorimeter. Instead, a single determination was made of the caloric content of the cast exoskeleton from the final molt of a cicada (Tibicen sp.). All caloric values from the literature, unless otherwise acknowledged, are from Kharasch (1929).

RESULTS

Population Density

The most striking fact about the nymph populations on the Old Field was the rapid decline from the peak densities of $8.4/\text{m}^2$ in 1959 and $12.0/\text{m}^2$ in 1960 (Figure 1). In each year the nymphal populations declined to a level of less than $1.0/\text{m}^2$ before the first appearance of adults. This high mortality resulted in very low populations of "native" adults ($0.2/\text{m}^2$ in 1959 and $0.4/\text{m}^2$ in 1960). The 95% confidence limits of the mean estimates of nymphal density were generally close to 50%. In a few instances, notably the initial populations of 1959 and 1960 (when the number of samples was low) and some of the last samples in each of these years (when the densities were low), these limits equaled or exceeded the mean.

Shortly after the first appearance of adults on the Old Field the populations increased rapidly to peak densities that in each year exceeded the initial nymph populations (Figure 1). These peaks were followed by a decline in numbers and another rise in midsummer to second peaks which were similar to the first ones. For the adult density estimates the 95% confidence limits were usually 30 - 50% of the mean. A very few samples taken during periods of low density gave limits approaching 100% of the mean. Neither

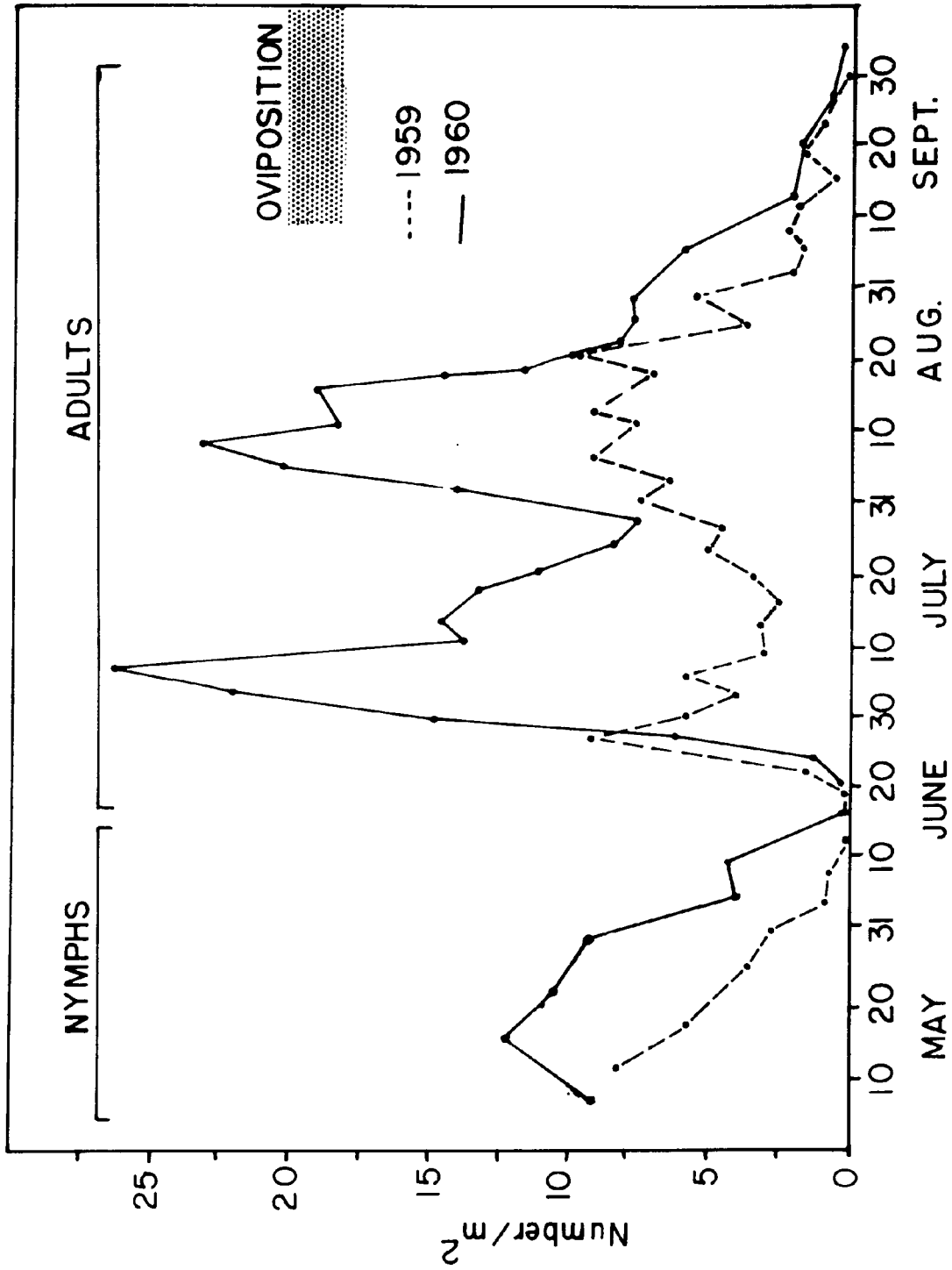


FIGURE 2. PHYLLOPHAGOUS SPIDER POPULATION DENSITIES ON THE OLD FIELD, 1959-1960.

the peaks in Figure 1 nor the lows between them in midsummer can be accounted for on the basis of sampling error. The repetition of the bimodality in successive years is further evidence for the reality of these peaks. The same pattern was noted in the spittlebug population on the Old Field in 1958 (F. C. Evans and U. N. Lanham, Univ. of Mich., unpub. data). Since the adult populations on the Old Field cannot be accounted for by the numbers of nymphs developing on the field, these adults must be immigrants. Changes in the adult population are thus influenced primarily by factors operating outside the Old Field ecosystem and are not directly a consequence of changes in the nymph populations on the Old Field.

Figure 1 shows that in 1960 the spittlebug populations on the Old Field, both nymphs and adults, were approximately twice as great as the corresponding densities in 1959. Insofar as the change in the nymph populations on the Old Field paralleled the change occurring in the outside areas which supply the immigrant adult population, it predicted the resultant increase in the adult population on the Old Field in 1960.

The population densities on the Small Alfalfa Field during the spring and summer of 1960 were very high. The peak nymphal density of $1280/\text{m}^2$ was 100 times as large as the peak density on the Old Field in 1960 (Figure 2). The 95% confidence limits of the Small Alfalfa Field population estimates were in most cases less than 50% of the mean.

By June 28 all nymphs had disappeared from the Small Alfalfa Field and the population density of adults was

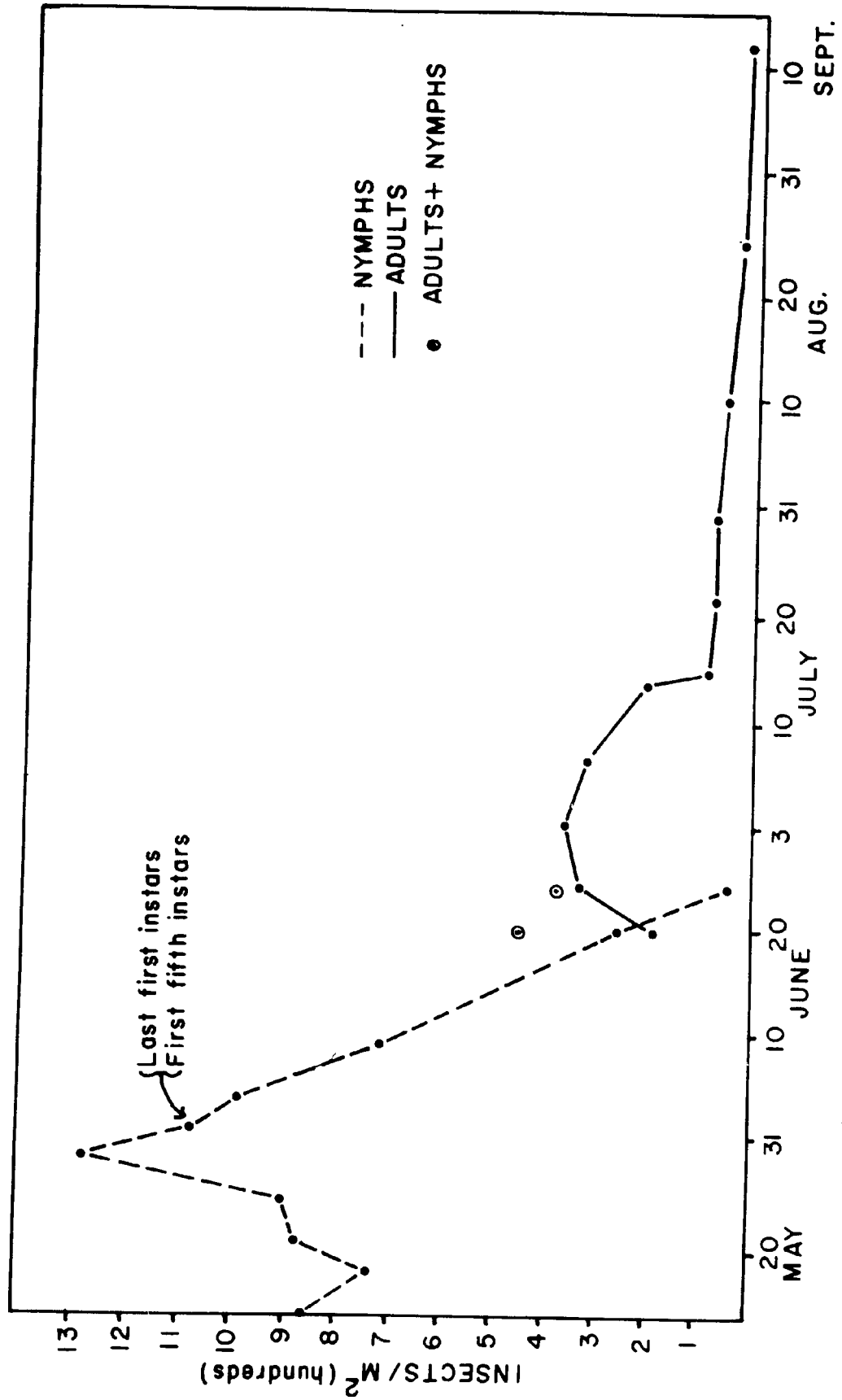


FIGURE 1. QUANTITY OF PHYLLOXERA OPIMARIUS ON THE SMALL ALFALFA FIELD IN 1960.

366/m² (Figure 2). The density of adults decreased steadily throughout the remainder of the season. Such a steady decline in the adult population is in marked contrast to the fluctuations on the Old Field (Figure 1) and on most other legume hayfields. This was because the Small Alfalfa Field was not mowed during the 1960 season. By mid-July the vegetation had matured and begun to die back. Throughout the rest of the summer this field was an unfavorable habitat for insects dependent on a supply of succulent vegetation. The adults on the Small Alfalfa Field were sampled by sweeping and the density per m² was calculated from a conversion factor. The error of the latter is not known, but the 95% confidence limits of the means per set of sweeps were on the order of 25 - 35%.

Population Age Structure

The nymph populations at any given time usually consist of several instars in varying proportions. This is due to a prolonged hatching period and possibly also to some individual variation in rate of development. A comparison of the Old Field in 1959 and 1960 and the Small Alfalfa Field in 1960 shows a similar distribution of instar classes for a given date (Table 1). By the third week of May the first instars were absent from the Old Field population and had all but disappeared from the Small Alfalfa Field. Fifth instars comprised 100% of the population of the Old Field by mid-June and of the Small Alfalfa Field by the latter part of June. There was little difference between the two

TABLE 1

PER CENT REPRESENTATION OF EACH INSTAR CLASS IN
THE PHILAENUS SPUMARIUS NYMPH POPULATIONS OF
THE OLD FIELD, 1959-1960 AND THE SMALL
ALFALFA FIELD, 1960

Date	Instars				
	1	2	3	4	5
Old Field 1959					
5/7	83.3	16.7			
5/12	12.9	74.2	12.9		
5/20		23.1	61.5	15.4	
5/25			26.1	65.2	8.7
5/30			5.6	38.9	55.5
6/3				10.0	90.0
6/7					100.0
Old Field 1960					
5/7	100.0				
5/16	26.0	61.4	12.6		
5/23		27.0	56.6	16.4	
5/30		2.0	23.8	63.3	10.9
6/4		1.4	4.5	54.6	39.5
6/9		1.2	1.9	22.1	74.8
6/16					100.0
Small Alfalfa Field 1960					
5/14	44.1	55.9			
5/18	13.7	84.7	1.6		
5/21	3.6	44.1	52.3		
5/25	4.0	23.7	69.2	3.1	
5/29	2.3	8.4	31.5	57.8	
6/1	0.7	5.9	11.9	80.8	0.7
6/4		1.4	4.5	54.6	39.5
6/9		1.2	1.9	22.1	74.8
6/20				1.2	98.8
6/24					100.0

habitats or between years in the successional changes in instar composition. On the Small Alfalfa Field the hatching period was longer; this in turn prolonged the duration of each instar class in the population.

Mortality

From the end of the hatching period until the first appearance of the adults, the decrease in the nymph populations is equivalent to the mortality. This decrease occurred at a constant percentage rate (Figure 3). The rates of mortality were given by the slopes of the regression lines fitted to these data (Old Field 1959, -0.134; 1960, -0.118; Small Alfalfa Field 1960, -0.047). Because of the relative constancy of these rates in the interval between hatching and the final molt, it seemed reasonable to assume that they held also for the hatching period and the period of adult emergence.

The disparity in mortality rates between habitats in 1960 was much greater than the difference between successive years on the Old Field (Figure 3). The mortality rate on the Small Alfalfa Field was less than one-half that of the Old Field, despite a density on the Alfalfa Field 100 times that of the Old Field. This suggests a basic difference in the carrying capacity of the two habitats.

The mortality rates of the adults confined in the large cage on the Old Field were relatively constant throughout the summer, but increased sharply in early fall (Figure 4). The instantaneous rates derived from these data are:

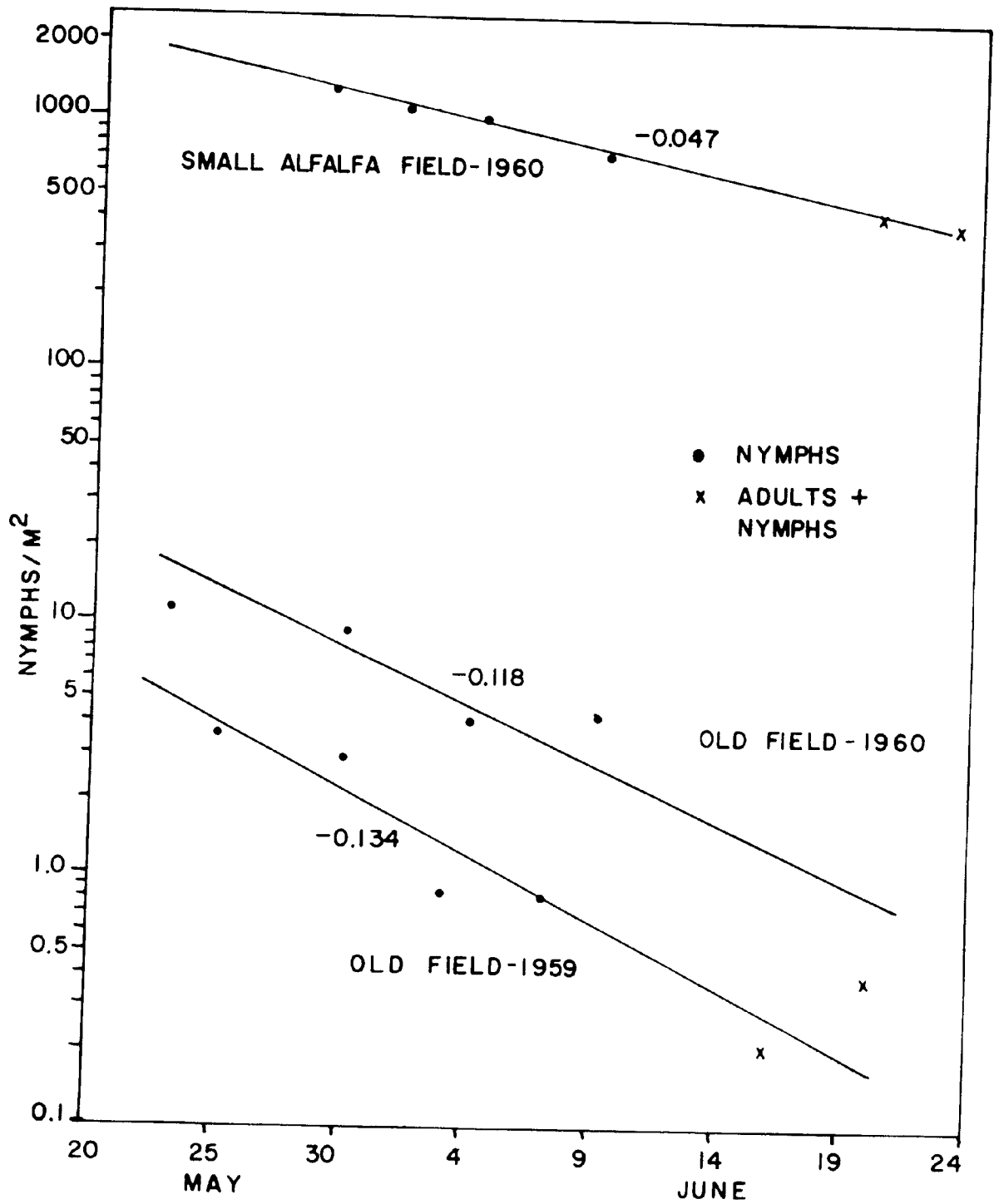


FIGURE 1. SEMILOG PLOT OF PHYLLOPHAGA SPINIGER NYMPH POPULATIONS ON THE SMALL ALFALFA FIELD IN 1960 AND THE OLD FIELD IN 1959 AND 1960. THE SLOPES OF THE REGRESSION LINES ARE THE INSTANTANEOUS MORTALITY RATES AS NYMPH/NYMPH DAY.

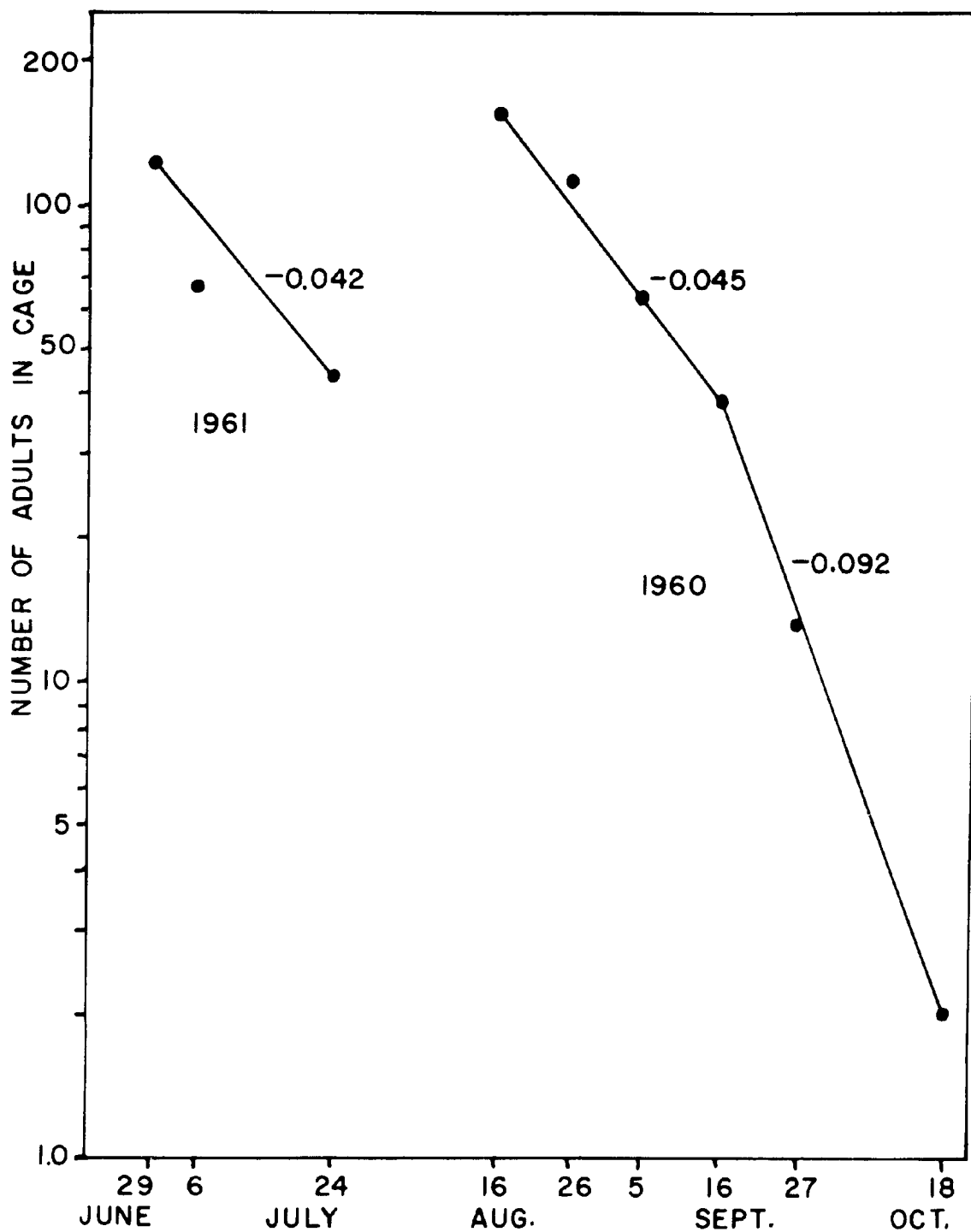


FIGURE 4. MORTALITY RATES OF ADULT *PHILAENUS SPUMARIUS* IN THE LARGE WALK-IN CAGE ON THE OLD FIELD. THE LINES CONNECT THE TWO POINTS USED TO CALCULATE THE INSTANTANEOUS RATES.

June 29 - July 24, 1961, -0.042 adults/adult/day; August 16 - September 16, 1960, -0.045 ; September 16 - October 18, 1960, -0.092 . Because of the uniform rates of decline, regressions were not calculated; instead the lines in Figure 4 connect the two points used in computing the instantaneous rates.

Throughout most of the summer the adult mortality rate in the cage was less than one-half of the mortality rate of the nymphs on the Old Field. The increased rate of mortality in the early fall was coincident with the first light frosts, with the maturation and death of most of the green forbs remaining in the cage, and with the time of oviposition. It is probable that some or all of these factors were involved in the increase in mortality.

Application of these rates of cage mortality to the entire Old Field assumes (1) that all possible sources of mortality were represented within the confines of the cage and (2) that the area enclosed by the cage was representative of the field as a whole. All organisms that were in the cage when it was first placed remained in it for the duration of the experiment, but many flying predators were unavoidably excluded. To the extent that these excluded predators contribute significantly to the spittlebug mortality on the Old Field, the cage data must be regarded as a minimum estimate. Probably the several nesting species of sparrow (Field sparrow, Spizella pusilla; Chipping sparrow, S. passerina; and Vesper sparrow, Poecetes gramineus) constituted the most

important group of predators excluded. Unpublished data on the population densities and stomach contents of these birds on the Old Field, collected by F. C. Evans, University of Michigan, suggest that the number of adult spittlebugs eaten annually may approach 10% of the total mortality on the field. Other possible predators of the meadow spittlebug excluded from the cage were flying insects such as dragonflies and asilid flies.

Immigration-Emigration

Since all of the spittlebug natality took place in the early summer, the decrease in population density on the Old Field following each of the two annual highs (Figure 1) must be due to a combined rate of emigration plus mortality that is greater than the rate of immigration. The adult mortality rates, fitted to semilog plots of the populations of the Old Field in 1959 and 1960, show that mortality alone could account for the observed decline in density (Figure 5). Since the mortality rate changed but little throughout the summer, either the immigration/emigration ratio must be close to unity during the period of declining population density or the immigration and emigration at these times must be small compared with the amount of mortality.

Concurrently with the population fluctuations on the Old Field, changes occurred in the adult spittlebug populations on the managed legume hayfields in the nearby farming areas. The Large Alfalfa Field was sampled just prior to and immediately after each mowing and at intervals between mowings.

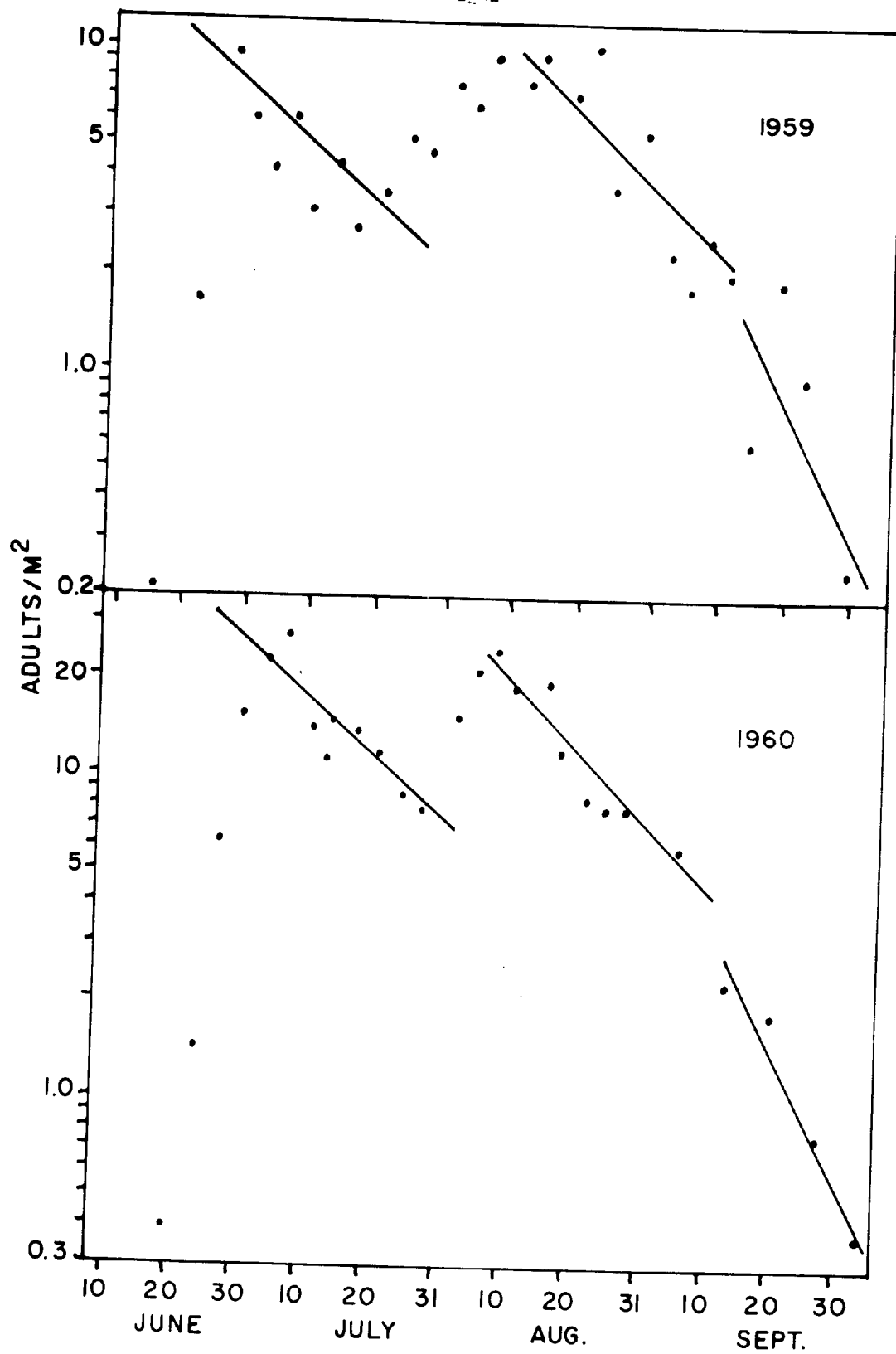


FIGURE 5. ADULT MORTALITY RATES FITTED TO A SEMILOG PLOT OF THE POPULATION DENSITY OF PHILAEUS SPINARIUS ADULTS ON THE OLD FIELD, 1959-1960.

The previous summer this field had been mowed in early September and contained few adults during the period of oviposition. Consequently, the nymph population in the spring of 1960 was low, and prior to the first cutting few adults were present (Figure 6). Twenty-four hours after the first cutting the number of adults per sweep had decreased to one-seventh the previous value. As new growth began on the field the adult population density increased to a high of more than seven per sweep (August 12). The field was then mowed a second time. One day later, on August 13, almost the entire population had disappeared and the sweep sampling gave a value of 0.4 adults/sweep. The mowing produced little mortality; no dead adults were found on the ground beneath the drying hay. An increase in numbers occurred with the resumption of growth by the vegetation. A second peak was reached on September 13, after that the population declined steadily until the end of the season. The magnitude of the increase after the second mowing was somewhat less than one-half the increase that followed the first mowing. This was similar to the population change which occurred on the Old Field (see Figure 1). But in the latter habitat the second increase began on a base population that was considerably higher than the initial population. Thus the second peak in Figure 1 is comparable in height to the first, not considerably lower, as in Figure 6.

Production

Production of the nymphs is of two kinds, (1) that

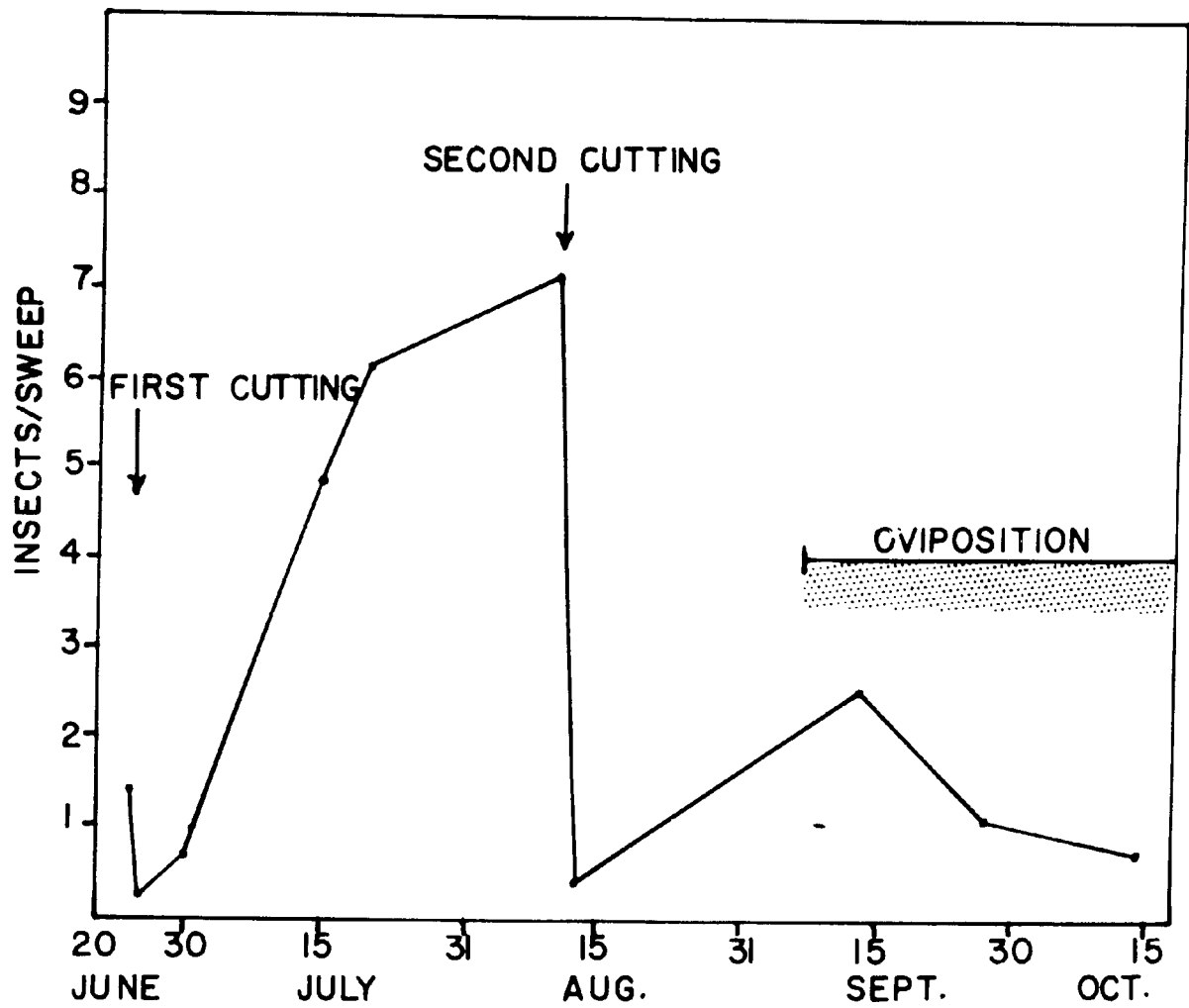


FIGURE 6. POPULATION DENSITY OF ADULT PHILAENUS SPUMARIUS ON THE LARGE ALFALFA FIELD, 1960.

of the body substance of the animal and (2) that of the exoskeleton discarded after each molt. The first of these was calculated from the increase in mean weight per nymph in the field populations (Figure 7). The regression lines show a constant exponential rate of growth in all three habitats. The instantaneous rate on the Small Alfalfa Field in 1960 was identical with the rate on the Old Field in 1960 (0.111 gm/gm day) and differed only slightly from the rate on the Old Field in 1959 (0.120 gm/gm day). Nymphal development on the Old Field in 1959 was about four days ahead of the comparable stage in 1960. Development on the Small Alfalfa Field was a day or two behind that of the Old Field in 1960.

The weights of the exoskeletons molted by the first two instars were estimated by extrapolation from the weights of the weighed exoskeletons of the last three instars (Figure 8). The lines were fitted by eye. The weight of the molted exoskeleton increases at a constant rate, from 0.7 microgram for first instars to 210.0 micrograms for fifth instars. Figure 8 shows that this rate is greater than the rate of increase in the body weight of the nymphs; the body weight/exoskeleton weight ratio of approximately 100:1 for the first instars decreases to 10:1 for fifth instars.

The regression lines of Figure 7, extrapolated back to the weight of a single egg (0.03 mg), gave an estimate of the hatching dates. These were April 29 for the Old

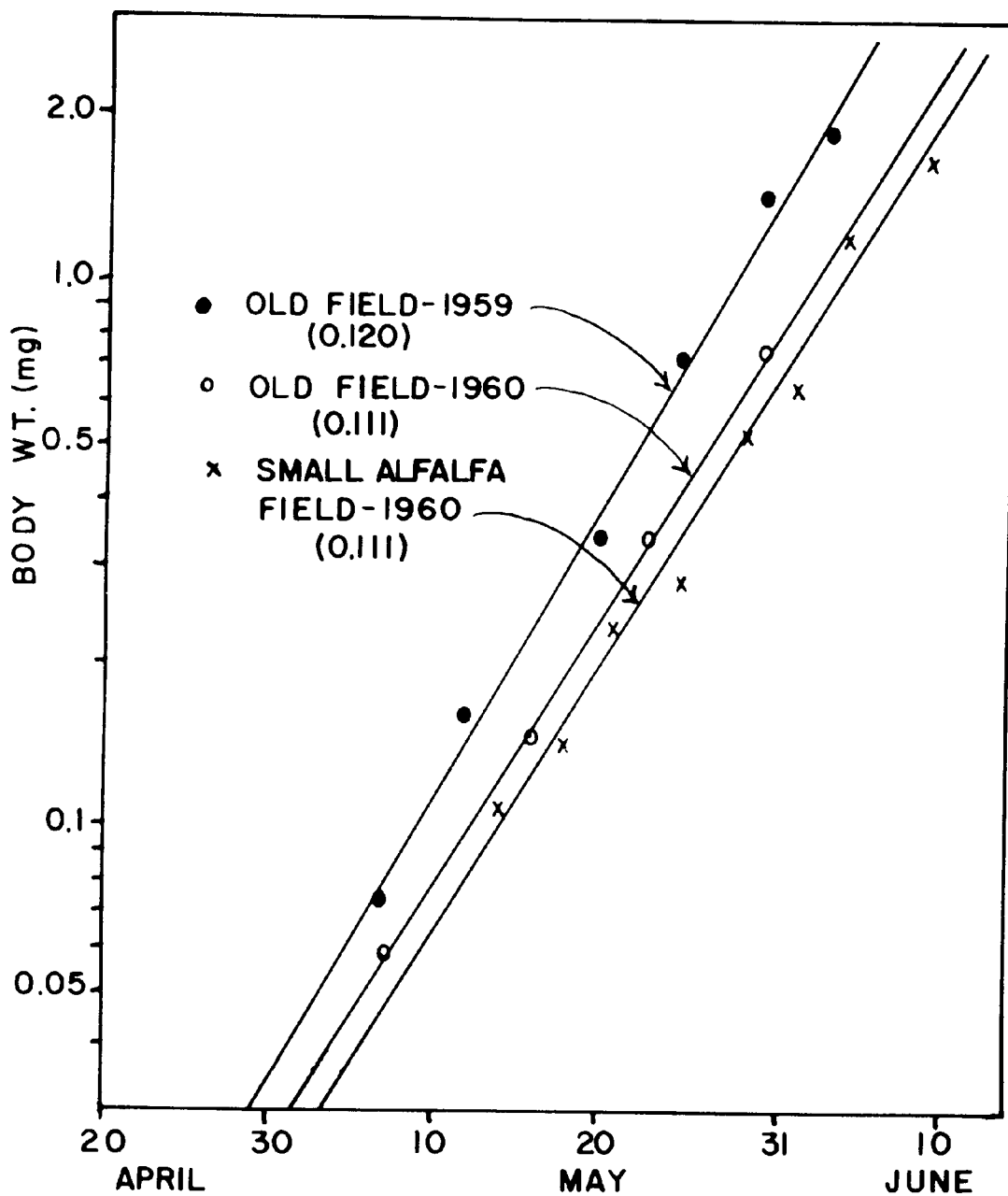


FIGURE 2. SEMILOG PLOT OF *PHILAENUS SPUMARIUS* NYMPH BODY WEIGHT AS A FUNCTION OF TIME. THE SLOPES OF THE REGRESSION LINES GIVE THE INSTANTANEOUS GROWTH RATE AS mg/mg day.

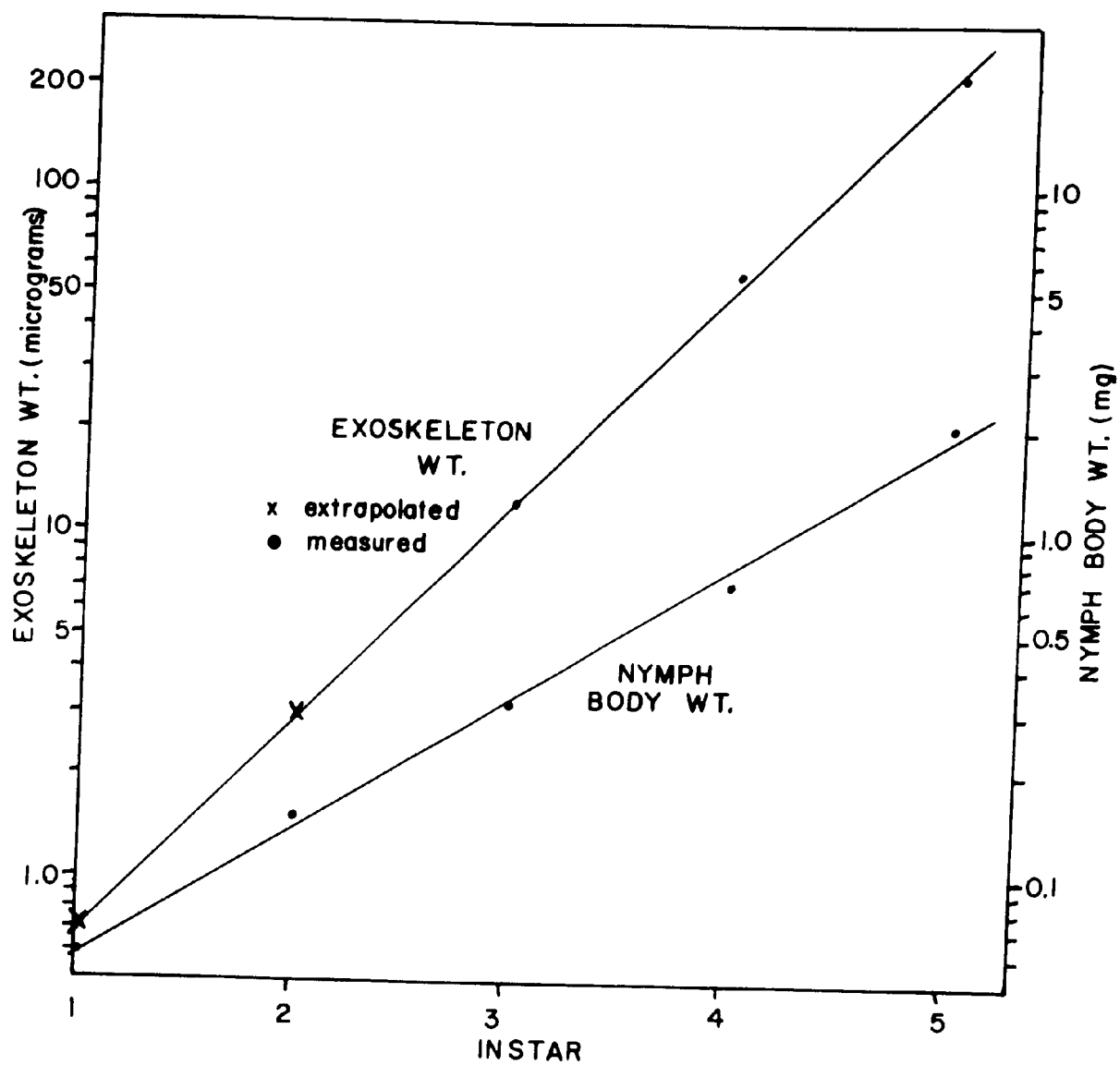


FIGURE 1. SEMILOG GRAPHS OF BODY WEIGHT AND CAST EXOSKELETON WEIGHT OF PHILAEUS SPUMARIUS NYMPHS AS A FUNCTION OF INSTAR CLASS.

Field in 1959, May 1 in 1960, and May 3 for the Small Alfalfa Field in 1960. These values were used in all subsequent calculations of population mortality and energy flow.

Growth ceases with the molt of the fifth instar to the adult. There was a slight rise in the mean weight of both males and females shortly after the first appearance of adults, but no discernable trend in weight change was evident after the first week in July. The egg production of females is apparently at the expense of other body substance and does not result in an increase in weight.

The data used in constructing Figure 8 as well as the mean weights of adults and eggs are shown in Table 2. These values were used in all subsequent computations involving the biomass of a component of the spittlebug populations.

Loss to Molted Exoskeletons

The number of nymphs hatched as first instars equals the number dying plus the number surviving to become adult. In the absence of emigration, the number of first instars dying subtracted from the total hatched equals the number molting to the second instar. Multiplying this number by the weight of exoskeleton molted by the first instar nymph gives the weight of exoskeleton lost by all first instars molting to second instars. Repeating this process for all instar classes and summing gives the total weight of exoskeleton produced by the nymph population. Table 3 shows the results of this procedure for the three populations studied.

TABLE 2
 MEAN WEIGHTS OF PHILAENUS SPUMARIUS EGGS, NYMPHS,
 ADULTS, AND THE EXOSKELETONS MOLTED
 BY THE DIFFERENT INSTARS

Category	Body Weight		Cast Exoskeleton Weight	
	No. Averaged	Mg	No. Averaged	mg
Egg	805	0.030		
1st Instar	16	0.058	-----	0.0007 ¹
2nd Instar	48	0.150	-----	0.0030 ¹
3rd Instar	35	0.315	43	0.0120
4th Instar	24	0.704	30	0.0560
5th Instar	16	1.996	5	0.2100
Adult	3746	3.87		

¹By extrapolation from Figure 8.

TABLE 3

TOTAL EGGS HATCHED, NUMBER OF NYMPHS MOLTING AND DYING, AND PER CENT SURVIVAL OF EGGS TO ADULT ON THE OLD FIELD 1959-1960 AND THE SMALL ALFALFA FIELD 1960. ALL VALUES EXCEPT PER CENT ARE PER M²

Category	Old Field 1959			Old Field 1960			Small Alfalfa Field 1960		
	Mortality	No. Molted	Exoskeleton (mg)	Mortality	No. Molted	Exoskeleton (mg)	Mortality	No. Molted	Exoskeleton (mg)
Instar 1	5.38	17.92	0.013	11.05	30.35	0.021	168.2	1939.0	1.36
Instar 2	7.44	10.48	0.031	9.65	20.70	0.062	408.8	1530.2	4.59
Instar 3	4.82	5.66	0.068	8.32	12.38	0.149	292.7	1237.3	14.85
Instar 4	3.10	2.56	0.143	7.71	4.67	0.262	412.1	825.4	46.22
Instar 5	2.31	0.25	0.053	4.19	0.48	0.101	374.9	450.5	94.61
Adult	0.04		0.308	0.09		0.595	84.5		161.63
Remaining adults	0.21			0.39			356.0		
Total eggs hatched	23.30			41.40			2107.2		
Total adults produced	0.25			0.48			450.5		
Per cent egg survival to adult	1.1			1.1			21.4		

Under the mortality column the number dying in each instar class was calculated by (1) determining the mean density of that instar present over each sampling interval, (2) multiplying each of these values by the instantaneous rate of nymphal mortality for that habitat or year, and (3) summing these products. The "remaining adults" are the numbers present after the disappearance of the nymphs (Figures 1 and 2). Adult mortality was computed as the instantaneous mortality rate for the habitat (one-half the nymph rate was used for the adults in the Small Alfalfa Field), times the mean number of adults present over the interval, from their first appearance to the disappearance of the nymphs, times the number of days in the latter interval. The total eggs hatched was then the sum of nymphal mortality, adult mortality and number of surviving adults. The number molted column was then computed by successively subtracting the number dying in each instar from the total eggs hatched. For example, on the Old Field in 1959, 5.38 first instars died per m^2 . The total number of eggs hatched per m^2 was 23.30, therefore 17.92 first instars molted to second instars. Each molt resulted in 0.0007 mg of exoskeleton being discarded per nymph (Table 2) or a total for that instar class of 0.013 (Table 3). Since 7.44 second instars died, the number molting to third instar was 10.48 (17.92 - 7.44). The per cent survival was computed as the sum of adult mortality plus adult survival, i.e. the number of fifth instars molting to adults, divided by the total eggs hatched (Table 3).

Less than one mg/m^2 of exoskeleton material was produced by the populations on the Old Field, but $162 \text{ mg}/\text{m}^2$ was produced by the population on the Small Alfalfa Field. This was the result of the lower mortality rate on the Alfalfa Field, since a higher proportion of the nymphs survived to the older age classes, where the proportionate production of exoskeleton is much greater (Figure 8). Differences in population density of 100:1 thus resulted in a difference in total exoskeleton molted of more than 162:1.

At the bottom of Table 3 the absolute difference in survival between the two habitats can be seen. For every 100 eggs hatched on the Old Field in both 1959 and 1960 only 1.1 survived to become adult, whereas on the Small Alfalfa Field the comparable figure was 21.4.

Reproduction

Weaver and King (1954) state that eggs of Philaenus spumarius are not found in the field in southern Ohio until after September 7. In the area in and around the E. S. George Reserve, the oviposition period extended from approximately September 10 until the last adults had disappeared. The length of this period plus the high mortality rate of adults in late fall made it difficult to predict the number of eggs that a given number of adults deposited.

The number of eggs carried by a female was estimated from dissections of spittlebugs collected from the Large Alfalfa Field and the Old Field. These specimens were

collected in late September and early October of 1960. The mean number of well-developed eggs per female varied from 9.1 to 17.1 (Table 4). The number of eggs found in individual females ranged from 0 to 30. Since many of the females dissected probably contained fewer than their total production of eggs, the maximum number may be a better estimate of the eggs produced per female than is the mean. The mean maximum of the five samples was 22 (Table 4).

The population of adult spittlebugs confined in the large cage on the Old Field in 1960 (Figure 4) was used to provide an estimate of the number of eggs deposited per adult under "natural" conditions. On May 1, 1961, the eggs deposited the previous fall by this population began to hatch. The hatching period lasted until the latter part of May. The nymphs were not counted during this time, in order not to miss some of the early instars or disturb the remaining eggs. On June 1, 1961 there were 360 nymphs in the cage. The subsequent instantaneous rate of mortality was 0.33 nymphs/nymph day. The mortality that occurred before the first census was estimated by assuming a mean population throughout the hatching period of $360/2 = 180$ nymphs and multiplying by the instantaneous mortality rate. The estimated 190 nymphs that died plus the 360 alive on June 1 indicate that 550 eggs were deposited in the cage the previous fall. Fifty adults were in the cage on September 10, the beginning of the oviposition period (Figure 4). The number of eggs deposited per adult was 11. If half of the adults were females the number of eggs per

TABLE 4
 NUMBERS OF FULLY DEVELOPED EGGS DISSECTED
 FROM FEMALE PHILAENUS SPUMARIUS

Date	Sample location	No. Spittlebugs	No. eggs (mean)	No. eggs (range)
9/22/60	Large Alfalfa Field	13	13.2	0-30
9/27/60	Large Alfalfa Field	30	10.0	0-21
9/27/60	Old Field	18	9.1	0-22
10/4/60	Old Field	4	9.3	6-12
10/6/60	Large Alfalfa Field	19	17.1	6-25
		84	11.9	2.4-22.0

female was 22. The actual sex composition of the population in the cage is unknown, but Old Field collections for September, 1960 contained 47.4% females and a chi-square test showed no significant difference from a 1:1 ratio ($p = 0.60$). The estimate of 22 eggs deposited per female agreed exactly with the mean maximum value obtained from Table 4.

In experiments with caged spittlebugs, Weaver and King (1954) reported 17 eggs per female; Cecil (1930) obtained 16 eggs per female, and Munding (1946) said the number ranged from 18 - 51. Weaver and King also found considerable variation in the number of eggs deposited on different materials; straw was preferred.

Dissections of female spittlebugs made by Weaver and King (1954) showed that the mean number of well-developed eggs per female increased during the summer, from 0.52 in the period August 6 - 12 to 14.82 in the period September 24 - October 1. These values are similar to the data of Table 4.

In view of the above discussion, the value of 11 eggs deposited per adult alive on September 10 seems to be reasonable and is used in this paper as an estimate of the reproductive potential of the meadow spittlebug.

The Food Plants

Philaenus spumarius feeds on a large number of different species of vascular plants. Weaver and King (1954) list over 375 species known to serve as hosts for the nymphs.

The great majority of these are species of forbs; in the field nymphs are only occasionally found feeding on grasses. During the present study I observed nymphs feeding on grass only once, and that instance was under conditions of artificially induced high density in the large cage on the Old Field. I have, however, been able to maintain nymphs on grasses under laboratory conditions. So their unsuitability as food plants does not seem to be due to a lack of essential nutrients.

The vegetation on the swale areas of the Old Field is largely grass or unsuitable forb species (such as Asclepias syriaca, milkweed). Despite the large populations of adult spittlebugs that occur in the swales in the fall, the nymphal densities the following spring are very low; the few nymphs present are found only on the occasional suitable forb. These low nymph populations on the swales may be the result of high mortality of eggs and early instars, or failure of the adults to oviposit there.

Adult spittlebugs on the Old Field fed on as many different species of forbs as did the nymphs, but the adults were also often observed feeding on grasses. In fact, the highest densities of adults on the Old Field were often recorded from the grass-dominated swales. Within the upland parts of the field, however, the densities of adults in the forb dominated areas appeared to be higher than the densities on areas supporting mostly grasses. To test this observation, in 1959 the vegetation under the cylindrical cage sampler was rated according to the dominant vegetation type.

Five categories were used: (1) grass dominant, (2) bryoid species dominant, (3) dominance by a single species of forb, (4) dominance by two species of forb, and (5) dominance by three or more species of forb. Dominance was defined as the contribution of more than half of the total green biomass of vegetation within the area rated. These ratings were completely subjective, but were made before I had any knowledge of the number of insects in the sample. All samples taken on the upland part of the Old Field in 1959 were rated in this manner.

The analyses of the 1022 samples are shown in Table 5. Both frequency of occurrence and density per occupied sample are compared for the different vegetation categories. Frequency is the per cent of the samples that contained one or more Philaenus adults. Density is the number of adults per occupied sample (ecological density).

The three forb classifications differed from both grass and bryoid areas in having consistently higher frequencies and densities (Table 5). Within the forb classification there was little variation, and the grass category was essentially similar to the bryoid category. For statistical comparison the chi-square test was used (Siegel, 1956). In each of the comparisons the null hypothesis that there is no difference between the number expected and the number found is implied. The data used in these comparisons were the number of occupied samples and the number of insects captured in each vegetation category (Table 5). The following comparisons were made: grass

TABLE 5

RELATION OF VEGETATION TYPE TO FREQUENCY OF OCCURRENCE
AND DENSITY OF PHILAENUS SPUMARIUS ADULTS ON
THE OLD FIELD IN 1959

Vegetation type	No. samples	No. of occupied samples	No. of insects captured	Density per occupied sample	Frequency (% of samples containing spittlebugs)
Grass	212	62	91	1.47	29
Bryoid	109	25	34	1.36	23
1 sp. of Forb	222	133	300	2.26	60
2 spp. of Forb	134	72	152	2.11	54
3 or more spp. of Forb	345	193	415	2.15	56
	1022				

versus bryoid, the three forb categories with each other, and the combined data from the grass-bryoid categories with the combined data for the three forb categories. The probabilities that the null hypothesis is true are:

	Grass-bryoid Forbs	Grass-bryoid vs. Forbs	
Number of insects captured	> 0.20	> 0.50	≤ 0.001
Number of occupied samples	> 0.20	> 0.70	≤ 0.001

The high probabilities of the first two sets of comparisons justified combining the data for the third set. The latter showed that there is a highly significant difference between the number of occupied samples and the numbers of insects captured on the forb areas of the upland as opposed to the grass-bryoid dominated areas.

It is tempting to conclude that the densities of Philaenus adults as well as nymphs were correlated with the presence of forbs in the upland habitat. But it was pointed out earlier, that the situation with respect to the adult populations on the swales was just the reverse. Instead of thinking in terms of grasses versus forbs, another explanation is possible. When the samples summarized in Table 5 were taken (July, August, September) the grass dominated areas of the upland consisted mainly of maturing, mature, or dead culms of Poa compressa and Aristida purpurascens. These two grasses exhibit very little new growth during this time of year. Consequently, areas dominated by them have relatively little green vegetation. The bryoid dominated areas have a

low biomass of vascular plant material. The forb dominated parts of the upland and the grassy swales have in common a high biomass of green plant material per unit area. They also contain the highest densities of adult spittlebugs adults. The density of spittlebug adults thus appears to be correlated with a high unit area biomass of green plant material and not necessarily with the growth form or species composition of the vegetation.

The Food Material

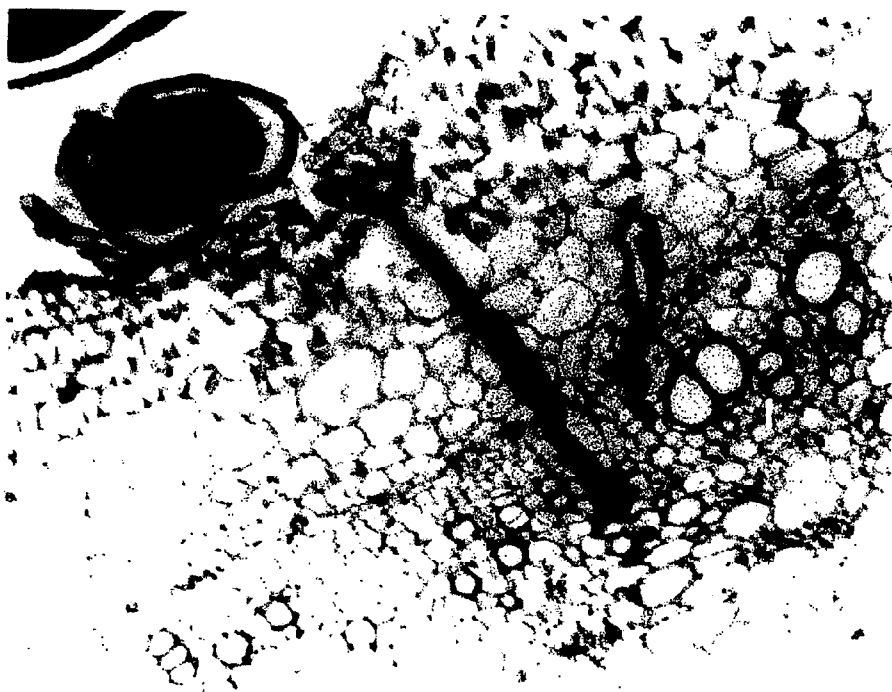
The following observations were important in ascertaining the specific part of the plant fed upon by the spittlebugs: (1) both the nymphs and adults produce fluid when they are feeding. This is expelled from the anus at a fairly rapid rate, and large amounts may be produced from a single feeding puncture. (2) The feeding punctures, even when concentrated on a small area of the plant, seldom produce any obvious necrosis of the tissue around the puncture. (3) The parts of the plant above the feeding site wilt and eventually die if large numbers of spittlebugs are forced to feed from a small section of the stem. The bugs, however, will continue to feed from the living stump of the plant. (4) A paper chromatogram of the spittle showed no traces of sugar.

Observations (1) and (2) do not fit the hypothesis of an insect that feeds from the cell sap of plants. Such an insect typically feeds by inserting the mouthparts, sucking up the contents of a group of cells, withdrawing the

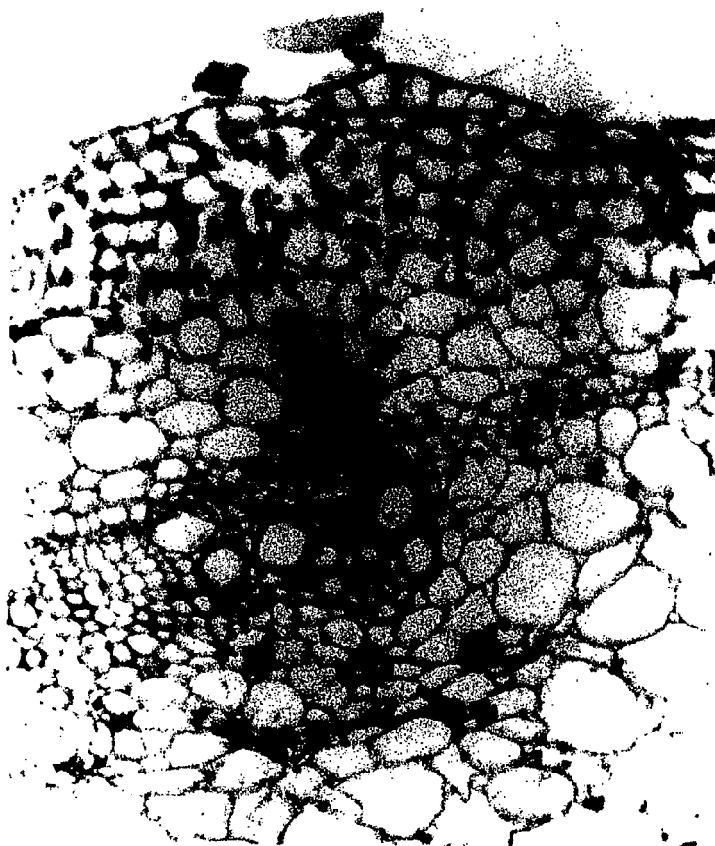
mouthparts, and reinserting them into another part of the plant. A necrotic spot commonly forms at the site of feeding (Flemion, Ledbetter and Kelley, 1954). The material ingested by cell sap feeders is relatively rich in nutrients and large amounts of sap are not needed. Therefore, large volumes of liquid excreta are not expected. Observation (3) indicated a xylem feeder, since the interruption seems to occur in the materials being translocated upward, particularly water, hence the rapid wilting. That the insects can exist even when the plant is decapitated also indicates subsistence from the xylem sap since there would be little of value in the phloem tissue under such circumstances. The final observation (4) is inconsistent with the facts known about phloem feeders. Mittler (1958) showed that aphids, which feed exclusively from the phloem, excrete liquid containing concentrations of from 10 - 25% sugar.

Direct evidence of xylem feeding in Philaenus spumarius was obtained by sectioning a piece of tomato stem from which a number of nymphs had fed (Figure 9). The first photomicrograph (a) shows the partially withdrawn mouthparts and the darkly stained feeding puncture extending to the xylem of the plant. The partial feeding puncture shown on the right of Figure 9a, when traced to its termination, extended to the same group of xylem elements. More than a dozen nymphs had been feeding from this short section of stem and all the remaining feeding punctures stained very deeply red with the saffarin used to dye the xylem elements.

- FIG. 9.--(A) CROSS SECTION OF TOMATO STEM SHOWING FEEDING PUNCTURE AND THE PARTIALLY WITHDRAWN MOUTHPARTS OF A 4TH INSTAR PHILAENUS SPUMARIUS NYMPH. THE PUNCTURE EXTENDS TO THE XYLEM ELEMENTS OF THE VASCULAR BUNDLE.
- (B) CROSS SECTION OF TOMATO STEM SHOWING FEEDING PUNCTURE, WITHOUT MOUTHPARTS, EXTENDING TO LARGE VESSEL.



9-A



9-B

Twenty additional punctures were traced to their terminations (Figure 9b); all but two of them ended in the xylem. The exceptions were punctures that missed the vascular tissue entirely and entered the pith.

Xylem feeding by other members of the Homoptera has been reported. Esau (1961) mentions that leafhoppers and cicadas feed on either phloem or xylem and that spittlebugs of the genus Aphrophora are xylem feeders. Smith (1926) showed that leafhoppers of the genera Eupteryx and Zygina puncture the tracheids of plants. Houston, Esau, and Hewitt (1947) demonstrated with tissue sections that 88% of the feeding punctures of the leafhopper Draeculacephala minerva extend into the xylem, 9.1% into the parenchyma and only 2.1% into the phloem. They also explained that the feeding punctures stain deep red because the saliva lining the walls of the puncture takes saffarin readily.

Composition of the Xylem Sap

The sample of tomato xylem sap that was analyzed contained 10 amino acids and amides, of which seven were identified: glutamine, glutamic acid, asparagine, aspartic acid, leucine, alanine and a fraction identified only to methionine/valine. The three unknowns were present only as trace amounts.

The most important of these were determined quantitatively with a one-way chromatogram (Figure 10). The various fractions and their quantities are listed in Table 6. The glutamine fraction, with 0.25 mg/g of sap, constituted

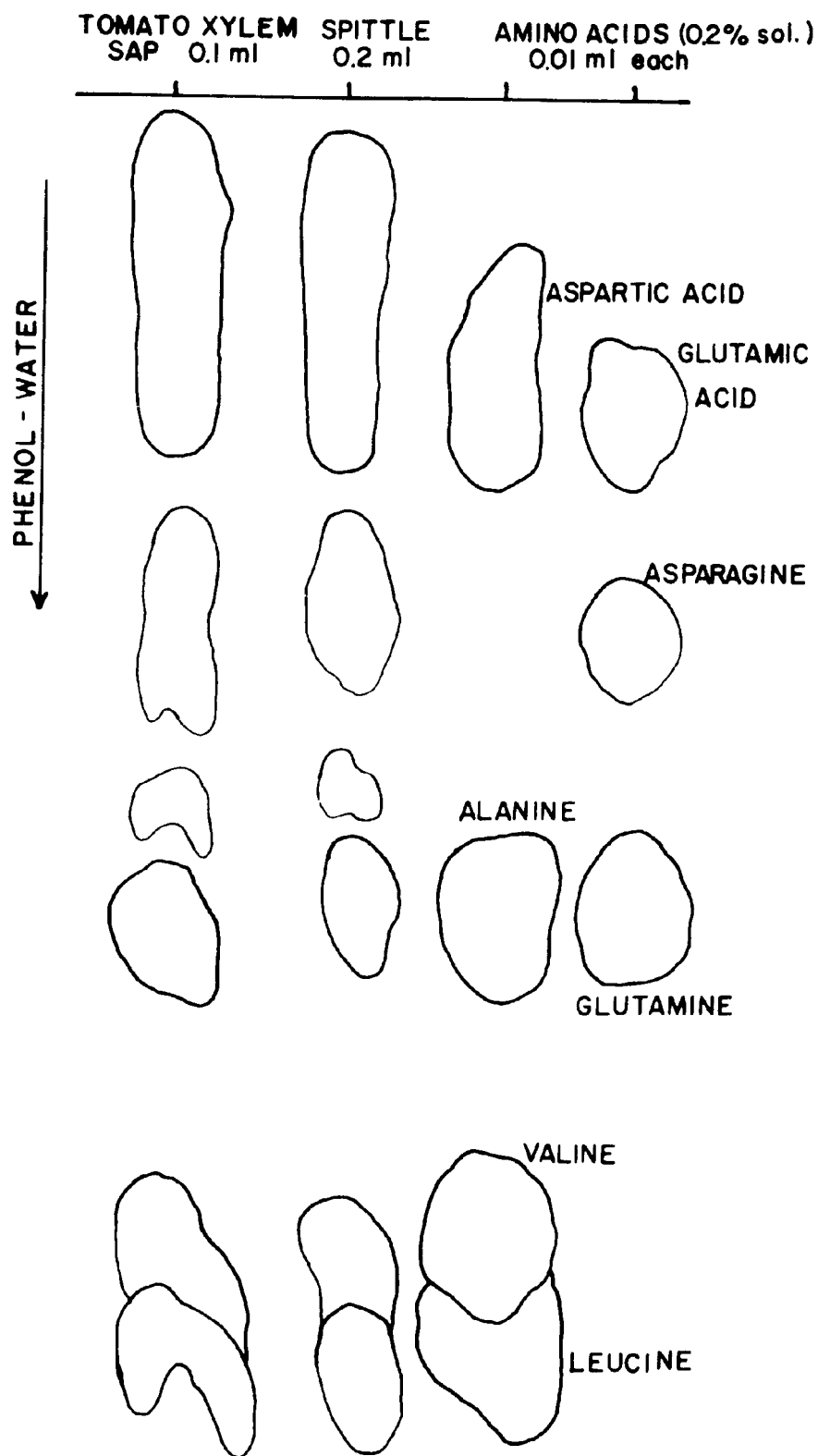


FIGURE 1. PHENOL-WATER SOLUBLE PART OF TOMATO XYLEM SAP, SEPARATED BY
 PAPER CHROMATOGRAPHY. SPOTS OF AMINO ACIDS, AT RIGHT, USED AS STANDARDS.

TABLE 6

COMPOSITION OF TOMATO XYLEM SAP AND SPITTLE OF PHILAENUS
SPUMARIUS NYMPHS FEEDING ON TOMATO. THE SPITTLE
 SAMPLE WAS NOT TAKEN FROM THE SAME PLANT
 AS THE XYLEM SAP SAMPLE

Material	Tomato xylem sap		Spittle	
	mg/g	% of total	mg/g	% of total
Total solids	1.75-3.65	0.18-0.37	1.71	0.17
Ash	1.10-1.53	0.11-0.15	0.69	0.07
Organic	0.65-2.12	0.07-0.21	1.02	0.10
Amino acids				
Glutamine + Alanine*	0.250	39	0.025	22
Asparagine	0.150	23	0.015	13
Glutamic + Aspartic acids	0.140	22	0.050	44
Leucine	0.050	8	0.015	13
Methionine + Valine	0.030	5	0.005	4
Unknowns	0.020	3	0.005	4
		100		100
Total amino acids	0.640	98	0.115	11
Other organic	0.013	2	0.905	89
Total organic det. by ashing in muffle furnace	0.653	100	1.020	100

*Trace.

30% of the total amino acid complex. The unknowns were present in amounts of 0.02 mg/m or 3% of the total. The total organic matter content of the xylem sap sample used in the chromatogram of Figure 10 was 0.653 mg/g. The difference between this value (determined by ashing an aliquot of the sample) and the amino acid component was 0.013 mg/g or 2% of the total organic matter.

The total organic matter content and ash content of several other xylem sap samples from different tomato plants were also determined. Total organic matter content ranged from 0.65-2.12 mg/g and the ash content ranged from 1.10-1.53 mg/g (Table 6). The xylem sap sample used in the chromatogram of Figure 10 had the lowest organic matter content of the various samples.

Since amino acids and their amides accounted for 98% of the organic in the xylem sap sample of Figure 10, they form the bulk of the nutrient substances ingested by spittlebugs feeding on these plants.

Until quite recently the xylem sap of plants was generally regarded as a very dilute water solution of inorganic compounds. Bollard (1957c and 1960) has shown, however, that a substantial amount of organic material is present in the xylem sap of most plants and that amino acids and their amides are the principal constituents. A recent analysis of tomato xylem sap gave a dry matter content of 2.57 mg/g of sap (Van Die, 1958). Van Die found different amino acids and amides; together they accounted for more than 90% of the

total organic matter. Van Die's data corroborate in large part the analyses made during the present study.

Composition of the Spittle

A paper chromatogram of spittle obtained from a nymph feeding on blazing star (Liatris aspera) showed no trace of reducing sugars. Spittle from tomato plants was not tested for the presence of sugars. But since Van Die (1958) found sugars to be present in only extremely minute amounts in tomato xylem sap, it is unlikely that they constitute any significant fraction of the organic matter found in spittle.

The amino acid composition of spittle from nymphs feeding on tomato plants was determined from the one-way chromatogram of Figure 10. The correspondence between the qualitative composition of spittle and tomato xylem sap is striking. All the major groups present in tomato xylem sap were present in the spittle and vice versa. The quantities of amino acids in the spittle, their percentages, and the total organic matter and ash content are shown in Table 6. The ashing determinations were made on the same spittle sample used for the chromatogram. The spittle sample used for the chromatogram was, however, not from the same plant as the xylem sap sample used in Figure 10. Thus the high total organic matter content of the spittle is possible because of the wide range exhibited by xylem sap samples from different plants (see Table 6).

The amino acid fraction of the spittle accounted for

only 11% of the total organic material, as opposed to 98% for xylem sap. This decrease in concentration corresponds to the amino acids assimilated by the nymph. Eighty-nine per cent of the organic matter of the spittle was "other organic matter." This includes the excretory products of nitrogen metabolism as well as the "surface tension depressant" produced by the nymph. The latter substance gives the spittle its foaming property.

There have been a few published analyses of the organic components found in spittle from cercopid nymphs, but unfortunately they disagree about the nature of both the excretory products and the surface tension depressant. Kato (1958) reported ammonia, urea, and uric acid in the spittle of Aphrophora intermedia. Kershaw (1914) found uric acid in the spittle of Tomaspinia saccharina feeding on sugar cane roots. Ziegler and Ziegler (1958) stated that uric acid was not present in the spittle of Philaenus spumarius or Aphrophora salicis but they did not test for urea or ammonia.

The two divergent views of the surface tension depressant are that it is (1) a fatty acid or kind of soap, introduced from the glands of Batelli after the spittle leaves the anus or (2) that it is a proteinaceous substance secreted from the Malpighian tubules. Kato (1958) discusses these two viewpoints in detail. Ziegler and Ziegler (1958) state that the S.T. depressant is a protein whereas Kato (1958) seems inclined toward the lipid theory. A thorough study of this problem is currently being made by Alan T.

Marshall of Hong Kong University. He is convinced that the substance is produced by the proximal segments of the Malpighian tubules and is an acid mucopolysaccharide. (Marshall, pers. comm.)

Composition of the Adult Excreta

I could find no published information on the substances excreted by adult Philaenus spumarius and such an investigation was beyond the scope of this study. Some speculations seem justified, however, on the basis of preliminary findings by Marshall (pers. comm.). His data indicate that the Malpighian tubules degenerate histologically in the adult and that uric acid is excreted via the tracheas. If the surface tension depressant is produced by the proximal segments of the Malpighian tubules it would not be produced by the adult. Because the adult does not produce spittle it certainly has little use for a foaming agent in its liquid excreta. If the bulk of the organic matter excreted by the adult is uric acid (or possibly urea), it is possible to calculate the amount, given the rate of ingestion, the materials ingested, and the rate of respiration.

Table 7 shows the amount of energy that can be derived from the oxidation of one mg of the amino acid complex present in tomato xylem sap if the nitrogen is excreted in the form of either urea or uric acid. The per cent nitrogen in the amino acid complex is the weighted mean of the per cent nitrogen in each amino acid times the

TABLE 7

CALCULATED ENERGY RELEASE ON BURNING ONE MG TOMATO
XYLEM SAP DRY MATTER TO EITHER URIC ACID OR UREA

Material	Gcal. amino acid ingested	Nitrogen excreted (mg)	Waste material excreted (mg)	Gcalories		Per cent retained
				excreted	retained	
Uric acid	3.9	0.165	0.495	1.3	2.6	67
Urea	3.9	0.165	0.356	0.9	3.0	77

TABLE 8

RATE OF SPITTLE PRODUCTION OF PHILAENUS
SPUMARIUS NYMPHS ON TOMATO PLANTS

Instar	Temp. °C.	Relative humidity	Body wt. (mg)	Spittle (mg/hr)	Spittle (mg/mg hr)
4	25	100	1.16	30.2	26.0
3	23	100	0.39	11.7	30.0

relative abundance of that acid in the amino acids of the sap. Thirty-three per cent of the ingested potential energy is excreted when uric acid is the end product of nitrogen metabolism and 23% is excreted when this end product is urea.

Rates of Ingestion and Egestion

The rate of fluid egestion of both nymphs and adults must equal the rate of ingestion, discounting the loss of water from the body surface and tracheal system of the adult. The heavier chitinous exoskeleton of the adult probably reduces the rate of evaporation from the general body surface, but the extent of respiratory water loss is unknown.

Table 8 shows the rate of spittle production of two nymphs under the stated conditions of temperature and relative humidity. The rate per unit body weight increased from 26 to 30 mg/mg hr as the weight of the nymphs decreased from 1.16 to 0.39 mg.

Table 9 shows the rate of fluid production of several adults feeding on grass and alfalfa. The rate of 25 - 26 mg/adult hr is about the same as that of the nymphs, but the rate per mg/mg hr was only 6.5 - 6.8, considerably lower than the nymph rate.

Respiration

The rate of oxygen consumption of Philaenus spumarius varied from 8.70 ml/g/hr for first instar nymphs to 2.70 ml/g/hr for adults (Table 10). The oxygen consumed per

TABLE 9

MEAN RATES OF FLUID EGESTION BY PHILAENUS
SPUMARIUS ADULTS. MAXIMUM RATES ARE
 GIVEN IN PARENTHESES

Food plant	No. insects	Temp. °C.	Droplets/hr.	Mg/droplet	Mg/hr
Grass (<u>Poa pratensis</u>)	8	21	420 (900)	0.06	25.2 (54.0)
Alfalfa	9	21	438 (798)	0.06	26.3 (47.9)

TABLE 10

OXYGEN CONSUMPTION (25°C) AND CALORIC EQUIVALENTS
 OF PHILAENUS SPUMARIUS NYMPHS AND ADULTS

Instar	No. averaged	Mean wt. (mg)	Oxygen Consumption		Gcal/day
			ml/g/hr	mm ³ /hr	
1	16	0.058	8.70	0.50	0.058
2	48	0.150	8.41	1.26	0.147
3	35	0.315	7.89	2.74	0.317
4	24	0.704	6.66	4.68	0.542
5	16	1.996	4.61	9.36	1.084
Adult	23	3.925	2.70	10.58	1.226

insect ranged from $0.50 \text{ mm}^3/\text{hr}$ (first instars) to $10.58 \text{ mm}^3/\text{hr}$ (adults). The double log plot of these data in Figure 11 shows a considerable departure from a straight line relationship to body weight. The lines drawn through the data points (mean values for ml/g hr and mm^3/hr) approximate straight lines only over short intervals. The rate of oxygen consumption for first and second instars is roughly proportional to body weight raised to the power 1.0. This factor decreases with increasing body weight, and between the fifth instar and adult stages the oxygen consumption is proportional to the 0.2 power of body weight. This change is probably best explained by the increasing proportion of metabolically inert chitin in the bodies of the older nymphs and adults. The increase in the chitinized portion of the body is obvious in adults, and the data of Figure 8 indicate that the proportion is increasing gradually throughout the life of the nymph.

Variation in temperature had somewhat more effect on the respiratory rate of the adults than on that of the nymphs, and the adults showed more individual variation in the response of the respiratory rate to temperature changes (Figure 12). The lines on the semilog graph were fitted by eye to the mean rate of oxygen consumption at each temperature. The values were expressed as percentages of the value at 25°C to eliminate individual differences in oxygen consumption. The change in oxygen consumption per $^\circ\text{C}$ remained constant over the temperature interval used in the experiment. The lines of Figure 12 correspond to Q_{10}

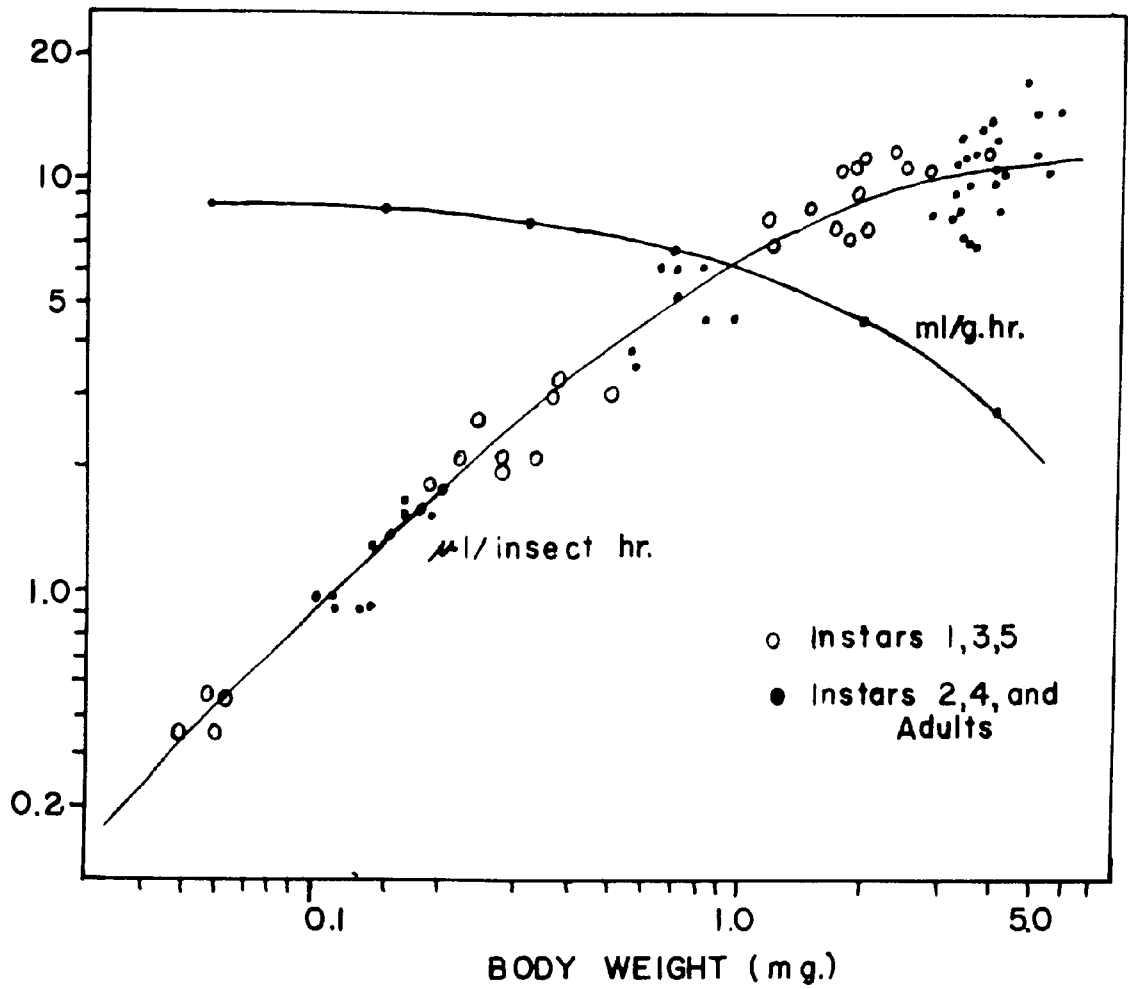


FIGURE 11. OXYGEN CONSUMPTION OF *PHILAENUS SPUMARIUS* AT 20°C, AS A FUNCTION OF BODY WEIGHT. LINES ARE DRAWN THROUGH THE MEAN VALUES FOR EACH AGE CLASS.

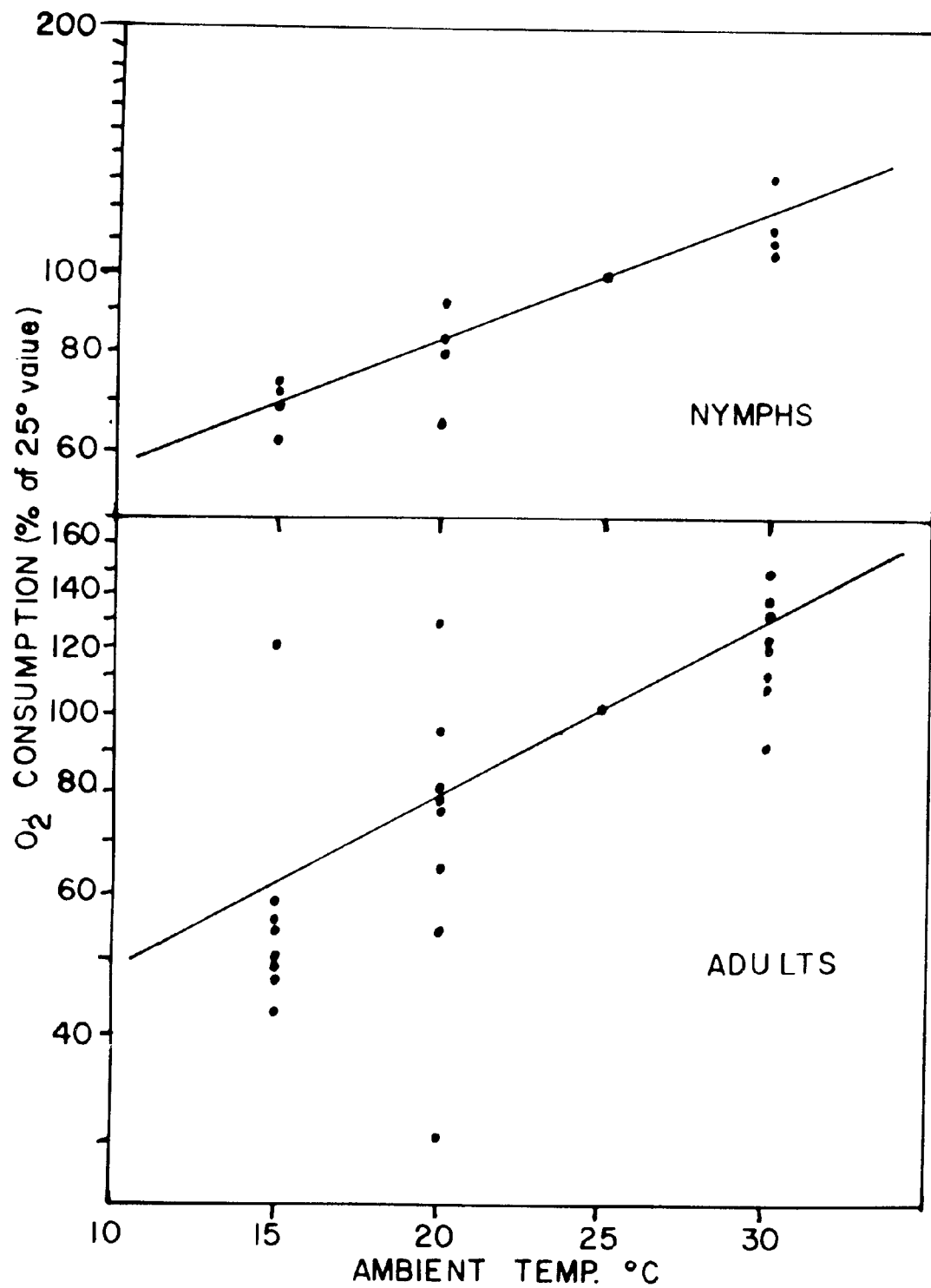


FIGURE 12. OXYGEN CONSUMPTION OF PHILAEUS SPUMARIUS NYMPHS AND ADULTS AT VARIOUS AMBIENT TEMPERATURES. LINES ARE FITTED TO THE MEAN VALUE FOR EACH TEMPERATURE.

values of 1.61 for adults and 1.47 for nymphs.

Oxygen consumption of the field populations was corrected for differences in ambient temperature by multiplying the consumption at 25°C times the appropriate fraction from Figure 12. The effect on the rate of respiratory energy loss due to activity was not evaluated in this study. The nymphs are incapable of rapid movement and are seldom active under field conditions. The adults, although they sometimes fly long distances, spend most of the daylight hours motionless on a suitable food plant. The error involved in extrapolating from small respirometers to field conditions is probably quite small.

Caloric Equivalents

The caloric equivalents of the rate of oxygen consumption are listed in Table 10 for each instar class and the adult. A conversion factor of 4.8 cal/ml of oxygen consumed was used (Brody, 1945, p. 312). The respiratory quotient was not measured, but the conversion factor is appropriate because it is based on an R.Q. of 0.82, approximately that which would result from the catabolic metabolism of amino acids. The values of Table 10, corrected for ambient temperatures different than 25°C., were used in all the calculations of individual and population energy budgets.

The caloric values of all materials involved in ingestion, production, and excretion are listed in Table 11. The number of determinations and the standard deviations are given for all materials burned in the calorimeter.

TABLE 11
CALORIC EQUIVALENTS OF MATERIALS USED IN THE
ENERGY CALCULATIONS

Material	Number of determinations	gcal/gm	Standard deviation
Molted exoskeleton	1	4422	---
Eggs	2	6307	95
Nymphs (instars 3, 4, and 5)	3	5336	232
Adults (♂)	7	5740	177
Adults (♀)	7	5875	179
Adults (mean)	-----	5808	---
Tomato xylem sap (dry organic matter)		3900	
Tomato xylem sap (liquid)		2.5 - 8.3	
Spittle (dry organic matter)		3900	
Spittle (liquid)		4.0	

The caloric content of the nymphs varied with age and the adults showed both seasonal and sex differences in caloric content per mg. The absolute values of the differences were small, however, and in all subsequent computations a mean value of 5336 cal/g has been used for the nymphs and a mean value of 5808 cal/g for adults (Table 11).

The caloric content of the organic matter in tomato xylem sap was calculated by weighting the published values for the different amino acids according to the relative percentages of Table 6. No value for glutamine was available so it was assumed to be the same as that of asparagine, an amide with approximately the same per cent of nitrogen by weight.

The amino acid component of the spittle had the same caloric value (3900 cal/g) as that of the xylem sap organic matter. In the spittle, however, 89% of the organic matter was of unknown composition. Part of this material was the byproduct of nitrogen metabolism, probably uric acid or urea. The remainder was the surface tension depressant, possibly a nitrogenous polysaccharide. Using data on the respiratory rate, ingestion rate, and composition of the ingested xylem sap, I have estimated that each gram of organic matter in the spittle would contain approximately 0.11 g of unassimilated amino acids, 0.20 g of the waste product of amino acid catabolism, and 0.69 g of surface tension depressant. The caloric content of the amino acid

fraction is 3.9 cal/mg, that of excretory waste is 2.7 cal/mg (uric acid), and that of the nitrogenous polysaccharide 4.2 cal/mg (mean of published values for several different polysaccharides). The weighted mean caloric content of the organic matter of spittle was identical with that of the amino acid fraction (3.9 cal/mg). Since a gram of liquid spittle contains 1.02 mg of organic matter, its caloric content is 4.0 cal.

Individual Energy Budgets

Table 12 shows one-day energy budgets for the third and fourth instar nymphs of Table 8 and for an adult (body weight 3.87 mg) feeding at the rates shown in Table 9. All values are in cal/day. 'Growth' and 'respiration' were computed from the rates given in Figures 7 and 11. The 'egestion' of the nymphs was calculated from the caloric values of spittle (Table 11); eleven per cent of the egested energy was amino acids and the remainder 'other organic matter' (Table 6). The 'egestion' of the adults was computed from the amounts of urea and uric acid excreted for a given energy release from the oxidation of amino acids, plus the amount of amino acids unassimilated. The latter value was calculated on the assumption that the per cent unassimilated was the same as that of the nymphs (11%). The 'estimated ingestion' was calculated from the rates of ingestion by multiplying times the caloric content of tomato xylem sap. The range indicated the possible ingestion per day, based on the variation in the energy content of the sap of different

TABLE 12

INDIVIDUAL ENERGY BUDGETS FOR THE NYMPHS AND ADULTS OF PHILAEUS SPUMARIUS.
VALUES IN GCAL/DAY. SEE TEXT FOR EXPLANATION OF CALCULATIONS.

Temp. °C.	Insect	Ingestion	Respiration	Growth	Egestion		% Assimilated
					Amino acids	Other	
23	3rd instar (0.39 mg)	0.7-2.3	0.34	0.25	0.12	1.00	34.5
				0.59		1.12	
				1.71			
25	4th instar (1.16 mg.)	1.8-6.0	0.76	0.74	0.34	2.52	34.4
				1.50		2.86	
				4.36			
21	Adult (3.87 mg) excreting uric acid	1.6-5.2	1.00	----	0.13	0.49	61.7
				1.00		0.62	
				1.62			
21	Adult (3.87 mg) excreting urea	1.6-5.2	1.00	----	0.11	0.30	70.9
				1.00		0.41	
				1.41			

plants (Table 11).

Such terms as egestion, assimilation, etc. are convenient and widely used in ecological energy flow studies. They must at all times be clearly defined. In this paper the following identities are assumed:

- (1) Ingestion = gross energy intake (heat of combustion of food).
- (2) Egestion = ingestion - (respiration + production).
- (3) Assimilation = metabolizable energy (ingestion - egestion).
- (4) Respiration = energy cost of maintenance, work, and 'specific dynamic action.'
- (5) Production = energy contained in organic material synthesized by the organism.
- (6) Growth = that part of production incorporated as an increase in the biomass of the organism.

The gross energy and metabolizable energy categories were proposed by Brody (1945) and have been formally identified by him with the terminology employed in certain thermodynamic equations. A full discussion of the latter terminology is deferred to a subsequent section of this paper.

Table 12 shows that the nymphs assimilated approximately 35% of the ingested energy. The adults assimilated 62 or 71%, depending on whether uric acid or urea was assumed to be the principal excretory product. Nymphs and adults differed in the per cent of the gross energy intake assimilated because of the large amount of organic material egested by the nymphs in the form of the 'surface tension depressant.'

The 'calculated ingestion' was always lower than the maximum value for 'estimated ingestion' (Table 12). Tomato

xylem sap thus contains sufficient energy to account for the ingestion of nutrients and the maintenance of both nymphal and adult spittlebugs. If the per cent assimilated remains constant for all individuals in a given age class feeding on several different tomato plants, then the rate of ingestion must vary with the energy content of the xylem sap of the host plant. In Table 12, for instance, doubling the rate of ingestion would bring the minimum 'estimated ingestion' above the calculated ingestion of energy.

The total energy ingested by a population of spittlebugs can be estimated by multiplying the assimilation of the nymphs by $1.00/0.345 = 2.9$. The ratio for adults is $1.00/0.663 = 1.5$ (the denominator of this ratio is the average of the two assimilation efficiencies from Table 12).

Energy Budgets of the Populations

Table 13 is a summary of the energetics of the populations of Philaenus spumarius studied in 1959 and 1960. All values are in calories and represent a summation for all sampling intervals throughout the season. In calculating these energy budgets the following equalities were used:

<u>Energy in Egg</u>	= (caloric value of egg) . (number of nymphs hatched).
<u>Growth</u>	= (mean biomass/m ² over each sampling interval) . (instantaneous growth rate of nymph).
<u>Loss to molt</u>	= (total weight of exoskeleton produced). (caloric equivalent).
<u>Production</u>	= growth + loss to molt.
<u>Assimilation</u>	= respiration + production (metabolizable energy).

TABLE 13

POPULATION ENERGY BUDGETS FOR PHILAENUS SPUMARIUS ON THE
 OLD FIELD 1959-1960 AND THE SMALL ALFALFA FIELD 1960.
 SEE TEXT FOR METHODS OF COMPUTATION.
 ALL VALUES IN GCALORIES.

Energy category	Small Alfalfa Field		Old Field 1959		Old Field 1960	
	Nymphs	Adults	Nymphs	Adults	Nymphs	Adults
Eggs from prev. Fall	399	----	4.4	---	7.8	----
Growth	15,125	----	46.3	---	92.6	----
Loss to molt	722	----	1.4	---	2.7	----
Production	15,847	----	47.7	---	95.3	----
Respiration	12,216	10,386	38.4	495.6	78.6	992.1
	22,602		534.0		1070.7	
Assimilation	28,063	10,386	86.1	495.6	173.9	992.1
	38,449		581.7		1166.0	
Excretion	53,320	5,193	163.6	247.8	330.4	496.1
	58,513		411.4		826.5	
Ingestion	81,383	15,579	249.7	743.4	504.3	1488.2
	96,962		993.1		1992.5	
Increment to adults	10,120		5.6		10.8	
Mortality	5,005	----	40.7	475.2	81.8	1055.9
			515.9		1137.7	

Ingestion-nymphs = assimilation times 2.9 (gross energy).

Ingestion-adults = assimilation times 1.5 (gross energy).

Mortality-nymphs = growth - energy recruited to adults.

Mortality-adults = (mean energy of adult biomass/m² during sampling interval) . (instantaneous rate of adult mortality).

Increment to adults = (energy per adult) . (number of fifth instars molted to adults).

The energy values of Table 13 for the Old Field in 1960 show approximately a twofold increase over the same values for 1959. The parameters on the field in the two years (mortality rate, growth, etc.) were, with the exception of population density, identical or approximately equal. Therefore, the increase in 1960 is primarily due to the change in population density (Figure 1).

In contrast to the amount of energy transformed by the nymph population on the Small Alfalfa Field, the annual energy flow on the Old Field in 1960 was low. This disparity between the two habitats was due not only to the large difference in population density; it also reflected the greater mortality rate for nymphs on the Old Field. A larger percentage of the nymphs survived to the later instar stages on the Small Alfalfa Field. Since the production per nymph is much greater for the later instars, a population density ratio between the Alfalfa Field and Old Field of approximately 100:1 changes to a ratio of 160:1 when total production on the two areas is considered, and becomes 1000:1 if the increment to adults is compared (Table 13).

On the Old Field adults assimilated approximately 6 times as much energy as did the nymph population. On the Small Alfalfa Field the reverse was true; here the assimilation of nymphs was three times that of the adults. These facts point out the difference in the origin and subsequent history of the adult populations on the two habitats. An immigrant population on the Old Field is continually being replenished while a native population on the Small Alfalfa Field is continually losing individuals through emigration.

DISCUSSION

Energy Flow

In any population of organisms, except primary producers, energy enters the population in the form of ingested nutrients. This gross energy intake ultimately leaves the population by three different pathways: (A) waste materials egested as a byproduct of either the digestion or the metabolism of the food substances, (B) production or storage, by the organism, of energy containing substances that are yielded to a consumer organism of another species, and (C) energy lost as heat. The latter energy loss is often equated with the sum total of the entropy gain from the several transformations which take place in the body during the production and maintenance of the organism. The magnitude of this pathway (C) is estimated by the caloric equivalent of the oxygen consumed by the population (Patten, 1959).

The pathways of energy flow outlined above have been formally identified by Brody (1945) with the components of the Gibbs free energy equation:

$$\Delta F = \Delta H - T\Delta S \quad (1).$$

where: ΔH = change in heat content or ingestion-egestion (metabolizable energy).

ΔF = free energy available for production and the maintenance of the organism. (net energy).

$T\Delta S$ = change in entropy or bound energy
 unavailable for production or
 maintenance (specific dynamic action).

It is not entirely correct to equate respiratory heat loss with $T\Delta S$ of equation (1) since some of this heat results from work performed by the organism on its environment. But for purposes of analogy we can regard the passage of energy through a trophic level or population as a single chemical transformation, in which part of the energy actually assimilated by the organisms (metabolizable energy, ΔH) is passed on to consumer organisms. The part passed on as production is by analogy free energy (ΔF), available for use by the consumer organisms in their own production and maintenance. That part of the energy lost to the atmosphere as heat is unavailable for use by other organisms ($T\Delta S$).

Energy flow is thus measured as the sum of respiration plus production ($T\Delta S + \Delta F$) and equals the assimilation or intake of metabolizable energy (ΔH). This is the generally accepted usage of the term and it is the one followed in this paper. However, it should be pointed out that this concept of energy flow neglects the fact that an 'egested material' can actually be a part of the production of the organism. Therefore the energy flow of the spittlebug nymph population does not account for the 'production' of the surface tension depressant. To that extent the following data are minimum estimates of the true energy flow through the population.

Numbers, biomass and population energy flow of the three populations are compared in Figure 13. The entire nymphal period and the early summer adult densities are

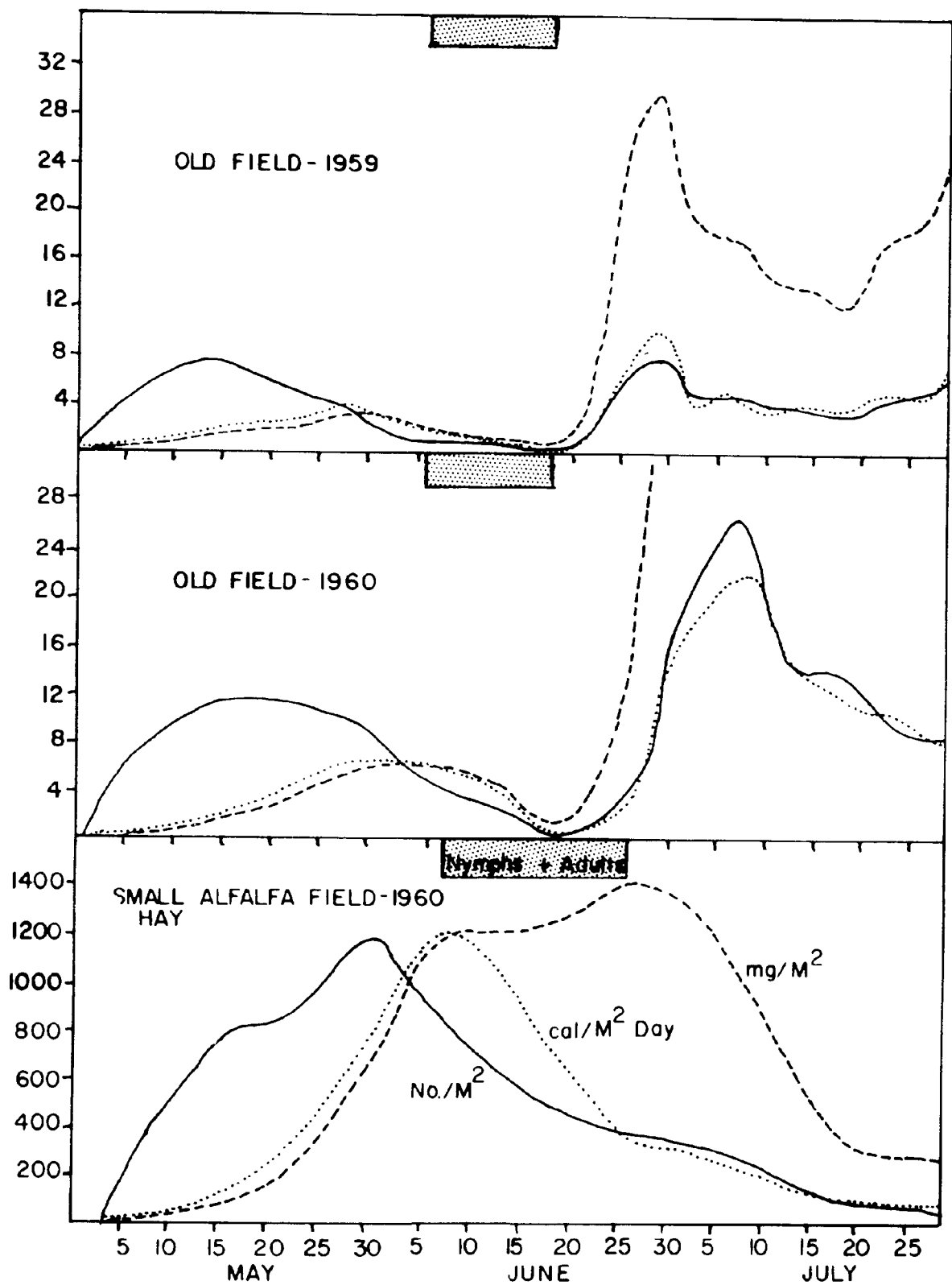


Fig. 1. Population density, energy flow, and energy storage of *P. communis* in the Old Field, 1959 and 1960, and in the Small Alfalfa Field, 1960. The shaded rectangular boxes indicate the periods of high population density.

..... Total population (No./M²)
 ——— Nymphs + Adults (No./M²)
 - - - - - Eggs (No./M²)

included. Assimilation in this graph was calculated as the sum of growth plus respiration. The production of the exoskeleton material was omitted because its rate of production during the different sampling intervals was not known.

The numbers of nymphs increased rapidly and reached a peak early in the season. Because of the constant growth rate, the increase in biomass followed a geometric progression, rising slowly at first, when the nymphs were small, and rapidly building to a peak as the later instars appeared. Since both respiration and growth increased directly with body weight, the energy flow in the nymphal stages changed with biomass, not with numbers. The rate of respiration per unit body weight actually decreases as the weight increases, but the ambient field temperature tends to increase as the season progresses. The net result is a respiratory rate that fluctuates directly with changes in body weight.

Very few nymphs survived to become adult on the Old Field, so biomass, energy flow, and density all declined to very low values as the nymphs disappeared. These parameters fluctuated in a very different manner on the Small Alfalfa Field. During the period of adult appearance biomass remained at a high level and even increased slightly. The energy flow decreased, although at a slower rate than density, because of the cessation of growth when adult metamorphosis occurs.

In the adult population energy flow consists only of respiration, and by definition all three parameters (biomass,

numbers, and energy flow) fluctuate directly with each other. The small discrepancies in Figure 13 between energy flow changes and those of biomass or numbers during this period are due to changes in respiration caused by variation in the ambient field temperatures.

After the disappearance of the nymphs the adult populations of the Old Field and the Small Alfalfa Field differ sharply in the changes that occur in numbers, biomass and energy flow. These parameters decline rapidly on the Small Alfalfa Field. On the Old Field an increase shortly after the appearance of the adults is followed by a decrease and by another rise later in the summer.

The peak energy flow on both the Old Field and the Small Alfalfa Field occurred coincidentally with the periods of highest growth rate of the vegetation. This suggests that a high growth rate in the vegetation may be correlated with increased availability of food materials in the xylem sap.

Bollard (1957a) showed that the amino acid content of xylem sap fluctuates widely through the growing season, being highest during the period of active growth in the spring and decreasing as the plant matures. The availability of food for the spittlebug is thus correlated with the rate of plant production but not necessarily with the standing crop of vegetation. In this respect the meadow spittlebug differs from many phytophagous species in that the latter are often able to exploit the standing crop of green material,

irrespective of when it was produced. Even in phytophagous species, however, behavioral adaptations can restrict the feeding of the growing parts of the plant, and energy flow will still tend to be correlated with the rate of food production (see Odum and Smalley, 1959).

Efficiency of Energy Transfer

Despite recent clarifications of the concepts of energy transfer in populations (Slobodkin, 1960) and in ecosystems (Patten, 1959), the nomenclature of efficiencies remains in a confused state. Speaking of the transfer of energy from one trophic level to the next, Patten (1959) defines one kind of efficiency as the, "Efficiency of transfer to next level in terms of ingested energy." The definition is unambiguous, but is awkward as a reference term. Slobodkin (1960) defined this same efficiency and called it the "ecological efficiency." This designation, also, leaves much to be desired, first because it tells little about the nature of the ratio itself, and second because 'ecological efficiency' has often been used to indicate a general class of efficiencies concerned with energy transfer in living systems. Some standardization of the naming process is needed, in which a concise name not only defines the efficiency but at the same time indicates its relationship to other similar efficiencies.

An efficiency is the ratio of some arbitrarily defined product, (the output) to an expenditure (the input). Therefore, a definitive name must refer first to this product

and second to the expenditure. A modification of the terminology of Brody (1945) seems best for those efficiencies where the input is in the form of food substances ingested by living organisms. My proposed classification proceeds in the following manner: First, a name is given to the product (numerator). Next, the input (denominator) is specified as either, (1) the gross energy of the food (ingestion) or (2) the metabolizable energy (assimilation). Each of these efficiencies is further classified as to whether they include the maintenance cost (gross efficiency) or not (net efficiency). Thus, for a given product (X) four different efficiencies could be computed: (1) Gross efficiency of X/ingestion, (2) Gross efficiency of X/assimilation, (3) Net efficiency of X/ingestion, and (4) Net efficiency of X/assimilation. This nomenclature is followed for all efficiencies discussed in the subsequent sections of this paper.

Gross Efficiencies of Growth

The data of Table 13 were used to calculate various gross efficiencies of growth for the spittlebug populations of the Old Field and Alfalfa Field (Table 14). With respect to the nymph populations the efficiencies varied little between habitats or between years. Approximately 19% of the energy ingested or 54% of the energy assimilated was utilized as increase in biomass. Respiration accounted for 46% of the assimilation. The latter value is relatively low, and it would be even lower if the amount of the surface tension

TABLE 14

VARIOUS GROSS EFFICIENCIES OF ENERGY TRANSFER COMPUTED
FROM THE POPULATION ENERGY BUDGETS OF PHILAENUS
SPUMARIUS ON THE OLD FIELD 1959-1960 AND THE
SMALL ALFALFA FIELD 1960. ALL
VALUES IN PER CENT.

	Small Alfalfa Field 1960	Old Field 1959	Old Field 1960
<u>Nymphs</u>			
Growth/ingestion (Gross)	18.6	18.5	18.4
Growth/assimilation (Gross)	53.9	53.8	53.2
<u>Entire Population</u>			
Growth/ingestion (Gross)	15.6	4.7	4.6
Growth/assimilation (Gross)	39.3	8.0	7.9
Surviving adults/growth	66.9	12.1	11.7

depressant were added to the assimilation of the nymphs. A slight increase in nymph assimilation would also have been effected by including the material lost as molted exoskeleton (Table 13). In the per cent of assimilated energy respired, these spittlebug nymph populations were similar to the planarians studied by Teal (1957). In both instances, the low value for respired energy was caused by a large production of material that did not contribute directly to an increase in biomass (mucus in the case of planarians, 'surface tension depressant' in the case of spittlebugs).

The gross efficiencies of growth for the entire population were quite different in the two habitats (Table 14). Gross efficiency of growth/assimilation on the Alfalfa Field dropped from 18.6% (nymphs) to 15.6% (entire population). On the Old Field in 1960 the decrease was greater from 18.4% (nymphs) to 4.6% (entire population). Similar changes occurred in the gross efficiency of growth/ingestion. On the Old Field, however, there was little change between 1959 and 1960. The cause of the above differences between habitats was the large adult population on the Old Field (relative to the Old Field nymph population) as compared with the adult population on the Small Alfalfa Field. In other words, a net immigration of adults on the Old Field contrasts with a net emigration from the Alfalfa Field.

On the Small Alfalfa Field in 1960, 67% of the energy of growth was recruited to the adult population, but on the Old Field in both 1959 and 1960 only 12% of the total growth 'survived' as adults (Table 14). Thus, survival of individuals

on the Small Alfalfa Field was 20 times that of the Old Field (Table 3), but survival of the energy produced by growth was only 5.5 times greater on the Small Alfalfa Field.

Efficiencies of Yield

That portion of prey production that is ingested by a predator is commonly spoken of as yield. The ratios of this yield to various arbitrarily defined inputs are indices of the efficiency of the yield process. Slobodkin (1960) discussed two useful ratios in this group. One of these, the "ecological efficiency" was discussed above. Applying the nomenclatural method proposed earlier, this efficiency becomes the 'gross efficiency of yield/ingestion.' The other ratio is the "population efficiency," defined by Slobodkin as, "yield to the predator divided by the difference between the energy used in maintaining a population in the absence of predation and that used in maintaining the same population under predation." The denominator is therefore equal to the total ingestion of the prey minus the maintenance. This efficiency is not considered in this paper, except to note that it could be named the 'net efficiency of yield/ingestion; a term that better indicates its relationship to the 'gross efficiency of yield/ingestion.'

Knowledge of the loss to predation is requisite to calculating the gross yield efficiencies of a population. No data on the mortality of adults on legume hayfields nor on the surrounding cropland were available. Nevertheless,

it was possible to compute a 'theoretical maximum' for predation and thus to obtain a maximum value for the gross efficiency of yield/ingestion for Philaenus spumarius.

To compute such a maximum all mortality must be assigned to predation and all the predation must occur at the instant when the gross efficiency of growth/ingestion is at a maximum. Because the meadow spittlebug has only one generation per year and all the eggs are deposited just before death in the fall, the effect on the rate of population increase of removing an individual spittlebug is constant for any age. Since each adult alive on September 10 is assumed to produce 11 eggs, the maintenance of a steady state population density requires that 9.1% of the eggs survive to the following fall. To maximize the gross efficiency of yield/ingestion this 90.9% mortality has been taken at that age when the growth per unit of energy ingested was maximum. The gross efficiency of yield/ingestion is the yield divided by the sum of the total ingestion to the time of yield taking plus the ingestion of the remaining 9.1% of the population to the time of oviposition.

In Table 15 is computed an energy balance sheet for a single meadow spittlebug living on the Small Alfalfa Field in 1960. The rate of ingestion is the mean ingestion rate of the population over the sampling interval divided by the mean number of individuals present. The data are in calories. The columns of cumulative growth, ingestion and the growth efficiency at various times throughout the growing

TABLE 15

CALCULATED ENERGY BUDGET FOR A SINGLE MEADOW SPITTLEBUG ON THE SMALL ALFALFA FIELD, 1960. SHOWS CUMULATIVE GROWTH, GROSS EFFICIENCY OF GROWTH/INGESTION, CUMULATIVE INGESTION AND GROSS EFFICIENCY OF YIELD/INGESTION. GROWTH AND INGESTION IN CALORIES, EFFICIENCIES IN PERCENTAGES. SEE TEXT FOR DESCRIPTION OF COMPUTATIONS.

Date	Cumulative growth	Cumulative ingestion	Growth Efficiency	Yield Efficiency
5/3	0.19(eggs)	----	----	0.8
5/14	0.66	3.96	16.7	2.5
5/18	0.94	5.72	15.9	3.3
5/21	1.27	7.97	15.9	4.2
5/25	1.87	11.57	16.2	5.6
5/29	2.87	17.61	16.3	7.4
6/1	3.89	23.43	16.6	8.8
6/4	5.48	32.31	17.0	10.5
6/9	9.58	52.76	18.2	13.6
6/20	20.91	108.31	19.3	17.4
6/24	"	113.95	18.4	
6/28	"	119.31		
7/6	"	130.03		
7/15	"	142.72		
7/22	"	152.59		
7/30	"	165.79		
8/10	"	181.30		
8/25	"	202.30		
9/13	"	230.04	9.1	9.1

season were obtained by multiplying the growth and ingestion rates of the individual by the days in each sampling interval and summing. On June 20 the total growth reached the caloric content of an adult of 3.5 mg, approximately the mean weight of newly emerged adults. This was also the time of appearance of the first numbers of adults on the Small Alfalfa Field. From this point on, the adult ingestion rate was used in the table.

Because of the constant growth rate and a decrease per unit weight in respiration with increasing body weight, the growth efficiency increases with age, from 16.7% at eleven days after hatching to 19.3% at the time of adult emergence. Growth then ceases and the efficiency decreases to a low of 9.1% on September 13. Since the times of highest growth efficiency and greatest total growth coincide, the most efficient harvest would take 90.9% of the insects immediately prior to adult emergence. The column of yield efficiencies in Table 15 was computed by assuming all yield taken at the same age. A maximum value of 17.4% is realized only if predation is confined to fully grown fifth instar nymphs, and a minimum efficiency of 0.8% is obtained for predation restricted to the eggs. The efficiency for predation on the adults lies between 9.1% and 17.4%, the actual value depending on the age when the yield is taken.

Slobodkin (1960) gave a gross efficiency of yield/ingestion of 12.5% for laboratory populations of Daphnia and stated that the highest conceivable value under experimental conditions would not be expected to exceed 14%.

The data of Table 15 show that this statement is applicable to field populations of the meadow spittlebug. The maximum value of 17.4% would only occur if all mortality occurred at the same age. Since this was not true of the populations studied, the actual value of the gross efficiency of yield/ingestion was probably close to the 12.5% given by Slobodkin (1960).

The Energy Input of Immigration

The necessity of defining carefully the parameters utilized in calculating an efficiency ratio was emphasized in a previous section. It is equally important to define the universe from which these parameters are taken. Both the statement of Slobodkin (1960) about the maximum value for gross efficiency, and the above calculation of this value for the meadow spittlebug (Table 15) were based on laboratory populations, and on field populations qualified by an assumption. The net gain of energy by the populations in any way other than by ingestion was not considered and the loss of energy took place only by excretion and/or mortality. In other words, the possible imbalance of immigration-emigration rates did not enter into the calculations. But in natural ecosystems energy is gained and lost by populations and trophic levels as immigration-emigration, and these pathways must be provided for in any model diagramming the energy transfer through biological systems. Patten (1959) referred to them as "import" and "leakage."

Import/leakage ratios significantly different from

unity are known for number of aquatic ecosystems at the level of the primary producers. These situations generally involve the movement of organic material by water currents, such as the movement of detritus between different parts of a salt marsh community (Odum and Smalley, 1959). Teal (1957) showed a significant interaction between aquatic and terrestrial communities in that a large part of the energy available to the primary consumers of a temperate cold spring was found to have resulted from a net **immigration** of energy into the producer level in the form of leaves from trees. A net import of energy into a community at any level can significantly change the value of ecological efficiencies in comparison to similar communities with an import/leakage ratio close to unity. The unusually high value of 75% for the producer gross efficiency of yield/ingestion of the spring studied by Teal was directly attributable to the unique nature of a large part of the energy input to the producer level (Patten, 1959). Considering the basis of Teal's value, it is not at all surprising, published statements to the contrary notwithstanding.

The present study provided an opportunity to illustrate this point with respect to the gross efficiency of yield/ingestion of a primary consumer population in a terrestrial ecosystem. The calculations of Table 15 showed that the maximum value for this efficiency in the meadow spittlebug could exceed 17.4%. Compare with the actual value as computed from the energy budget data from the Old

Field ecosystem (Table 13). Again we assume that all mortality goes to predation. This is a valid assumption, since all the mortality could conceivably go to predation. Whether it actually does or not is immaterial to the point under discussion. The gross efficiencies of yield/ingestion for the spittlebug populations on the Old Field in 1959 and 1960 are 52 and 59% respectively, considerably greater than the 'theoretical maximum' of 17.4%!

The apparent paradox is resolved by considering the immigration/emigration ratio. On the Old Field in 1959, 91% (470 gcal/m^2) of the total population mortality was composed of immigrant adults (Table 15). In 1960 the comparable figure was 92% (1045 gcal/m^2). Each of these adult immigrants represented from 108 to 230 gcal of total ingested energy, depending on when immigration occurred. But none of this energy was derived from the Old Field ecosystem and consequently it was not included in the denominator of the efficiency ratio. The result was an apparent increase in the efficiency of yield to predation. Those results, regarded uncritically, seem to show Philaenus spumarius to be a remarkably efficient prey species.

The concept of efficiency in energy transfer requires that qualifications as to the applicability of the ratio be explicitly stated. Such qualifications will always be necessary unless the natural area is large enough and/or the mobility of organisms low enough to give an import/leakage ratio of unity. Or at least the magnitude of the imbalance must be reduced to a low value as compared with

energy flow through the system via the more usual route. In view of this, the legume hayfields and the areas around them are each only a part of the total environment of the meadow spittlebug. Neither one alone can provide a complete picture of population energy flow in this species.

Since immigrant Philaenus spumarius represent a significant source of energy inport into the Old Field, they may have considerable importance for those organisms on the field which consume Philaenus. If direct consumption of spittlebugs by predatory or scavenger animals accounts for all, or even a major portion of the mortality, then the energy input of immigration must be supporting populations of these predators or scavengers at much higher levels than would be the case if there were no immigrant spittlebugs. If on the other hand, the dead spittlebugs are usually decomposed first by bacteria and fungi, the effect of the energy input on the ecosystem would be much less. This is because the energy of immigration constitutes a large fraction of the total production of insect biomass (consumer production) on the Old Field, but compared with the production of the vascular plants (primary production) it is insignificant. Since the latter energy source is utilized by the soil decomposers, they would derive little additional benefit from the energy in dead spittlebugs.

Effect of Spittlebugs on the Primary Production

The effect of the consumer on the prey population is usually evaluated only in terms of actual energy consumed;

the potential production that could be realized in the absence of the consumer is ignored. This potential production, because it is unrealized, is thought to have no place in the analysis of the energy balance of a community. This is undoubtedly true for non-photosynthetic prey populations. The consumption of a young growing organism or the growth slowing effect of parasitism, while it reduces the production of the prey species, at the same time frees the food that would have been ingested for consumption by some other organism. If the energy fixed by the producers of a given ecosystem is fully utilized by living organisms (see Hairston, Smith and Slobodkin, 1960) the overall effect on the community is only a change in the pathway of energy flow and not a change in the total energy available for the production and maintenance of protoplasm.

But the primary energy source of photosynthetic organisms is solar radiation. The amount delivered to a unit area of the earth's surface is relatively independent of the living organisms on that surface. Therefore any factor affecting the production by green plants will change both the amount of this energy that is utilized in the production of organic compounds, and the amount of energy supplied to all other organisms in the ecosystem. Factors affecting the potential production of producer organisms can therefore have real significance in the analysis of the energetics of a community.

The effect of consumption on the potential production of the vegetation is difficult to evaluate. It does not always

result in a decreased rate of energy fixation. The retardation of plant maturity under moderate grazing may cause a high growth rate to be maintained over a much longer period than would be the case in the absence of the herbivore.

The meadow spittlebug does, however, decrease the production of the vegetation on which it feeds (Weaver and Hibbs, 1952). Moreover, it will be shown that this effect is all out of proportion to the energy the insect actually removes from the plant. This depression of production must be considered in an evaluation of the importance of this species in the energetics of those communities where it is present as either a native or an immigrant population.

The amino acids found in the xylem elements of plants are probably produced in the roots (see Bollard, 1957c). They are indirect products of photosynthesis being transported through the plant to the sites of protein synthesis. The feeding spittlebug thus removes a portion of the nitrogen essential for the growth of the plant. It is possible that some translocation of nitrogen takes the form of nitrates, although Bollard (1957a, b, c) found few species in which nitrates were important constituents of xylem sap. Nitrates, even if present, would also be removed and excreted by the feeding spittlebugs. If the plant tends to maintain a constant percentage of protein in the organic material synthesized under moderate nitrogen deprivation, then the effect of removing the nitrogen containing compounds will be inversely proportional to the per cent of protein in the plant tissue.

Weaver and Hibbs (1952) investigated the effect of

spittlebug infestations on the yield and nutritive value of alfalfa, red clover and timothy. Using control versus treated plots they found that infestations lowered yields by 13 - 45% and 952 - 2339 pounds per acre (air dry, 20% moisture). The protein and carotenoid concentration of alfalfa from treated (spittlebugs killed) and untreated plots was not significantly different. There was a slight indication of less moisture in the vegetation on the untreated plots. Alfalfa contained 13.8 - 18.2% protein, air dry weight.

It seems that the nitrogen deprivation caused by spittlebug feeding does not produce a change in the protein content per unit weight of vegetation. Instead the total production decreases proportionately to the change in total protein content. Correcting for the 20% moisture, the alfalfa analyzed by Weaver and Hibbs would contain approximately 20% protein by weight (oven dry). The average nitrogen content of mixed protein is 16.5% (Brody, 1945), the same as the value for the amino acid complex in tomato xylem sap. Assuming the nitrogen content of the amino acids in alfalfa xylem sap is equivalent to that of tomato, one gram of amino acids removed from alfalfa by feeding spittlebugs causes a decrease of one gram in the protein produced by the vegetation. At 20% protein per gram, this would be an overall decrease in plant production of 5 g.

The total ingestion of the nymph population on the Small Alfalfa Field in 1960 was 81.4 kcal/m² or 21 g of

amino acids. This would cause a depression of plant production equal to 105 g/m^2 . At a caloric equivalent of 4200 cal/g alfalfa (Miller, 1958), the total decrease in energy fixed by photosynthesis is 441 kcal/m^2 , 5.4 times the energy ingested by the insect population. The losses reported by Weaver and Hibbs (1952), converted to the metric system and corrected to oven dry weights are $86\text{-}210 \text{ g/m}^2$ or $360\text{-}882 \text{ kcal/m}^2$. The losses calculated for the Small Alfalfa Field in 1960 are within this range.

To equal the highest loss reported by Weaver and Hibbs the population density would have to be about twice that of the Small Alfalfa Field in 1960. Although this population was high (2107 eggs/m^2 and a peak of 1280 nymphs/m^2) such levels are not uncommon in cultivated legumes and much higher densities have been reported. Teller (1951) found 351 eggs/ft.^2 ($3780/\text{m}^2$) and an alfalfa field nymph population of 237 nymphs/ft.^2 ($2550/\text{m}^2$). Marshall (1951) cited an undocumented report of a phenomenal 27 million nymphs per acre ($6680/\text{m}^2$)!

The loss of nitrogen due to spittlebug feeding seems sufficient to account for the observed decreases in yields on legume fields infested with these insects. If the calculations made above are reasonably accurate, the overall effect of a population of Philaenus spumarius on the energy balance of the community is to decrease the total fixation of solar radiation by about 5 times the amount of energy actually ingested by the population.

Rate of Population Increase

The intrinsic rate of natural increase of an annual insect species, in which there is but one generation per year and the adults do not overwinter, is calculated as the natural logarithm of the mean number of eggs deposited per egg of the parent generation (Cole, 1954).

Of the 23 and 42 eggs/m² on the Old Field in the spring of 1959 and of 1960 respectively, 1.1% survived to become adult (Table 3). If no immigration had occurred and the adult mortality rates (Figure 4) remained the same, 2.0% of these adults would have survived to oviposit after September 10, 1959, and 2.4% would have survived in 1960. On the Small Alfalfa Field in 1960 nymph survival was much better. Of 2107 eggs hatching per m², 21.4% of the nymphs survived to become adults (Table 3).

Table 16 was computed from these data, starting with equal cohorts of 1000 eggs and assuming a 5% egg mortality between oviposition and hatching. Weaver and King (1954) reported 10% of the eggs they examined were parasitized. Parasites did not emerge from all the eggs they thought parasitized, however, and they felt that 10% was too high an estimate.

Table 16 shows that in the absence of any pre-reproductive mortality the population could increase elevenfold per year, an intrinsic rate of increase per year of 2.40. For an insect this is an extremely low biotic potential. The adaptation of the meadow spittlebug has certainly not been in the direction of increased fecundity as a means of

TABLE 16

INTRINSIC RATE OF INCREASE OF THE MEADOW SPITTLEBUG,
PHILAENUS SPUMARIUS, IN DIFFERENT ENVIRONMENTS

Conditions	Eggs	Nymphs	Adults	Eggs	Ratio	r/year
No pre-reproductive mortality	1000	1000	1000	11,000	11.000	2.4
Old Field 1959	1000	950	11	2.4	0.0024	-6.0
Old Field 1960	1000	950	11	2.9	0.0029	-5.8
Small Alfalfa Field 1960	1000	950	203	---	---	---

species survival.

The population on the Old Field is apparently maintained by the large seasonal immigration of adults. In the absence of such immigration the survival of eggs, nymphs and adults is insufficient to replace the population (Table 16). Thus, in a so-called 'natural' area the dominant species of insect would not even survive or at least would be present in very low numbers, were it not for the action of outside influences.

On legume hayfields the population is obviously maintained and the numbers increase in certain areas from year to year. For every 1000 eggs hatching on the Small Alfalfa Field in 1960, 203 adults were produced (Table 16). Because this field was not managed in 1960 the subsequent history of the adult population is not comparable with legume hayfields in general. On the study area the population declined steadily, due to emigration or death, probably both. I have no data on the mortality rate of adults on cropland. However, for the maintenance of the population, approximately 91 of the 203 adults must survive to oviposit 11 eggs each in the fall. This would be a survival of 45% for the remainder of the summer. This compares with the adult survival on the Old Field of 2.0% in 1959 and 2.4% in 1960. If the nymph mortality on the Small Alfalfa Field was at all typical of legume hayfields in general, then the mortality of most of the emigrant adults must be substantially lower than that of those few (relatively speaking) that enter the Old Field ecosystem.

Successful reproduction can occur only when eggs are deposited on land that is not to be plowed the following spring, i.e. legume hayfields and pastures. The crops on most other fields are either mature or harvested by early fall and such fields do not have large populations of adults. Those legume fields that have sufficient new growth attract large numbers of the adults. First year legume seedlings have especially high nymph densities the following spring because of the availability of straw stubble as oviposition sites (Weaver and King, 1954). As new legume hayfields are established by farmers many old ones are plowed; the nymph populations on the latter are destroyed. The population density maintained over the years will be dependent on the interaction of control factors with the total amount of optimum habitat made available by current agricultural practices.

Seasonal Behavior and Regulation of Numbers

The data on the immigration/emigration ratio and mortality of the meadow spittlebug provided a description of the seasonal behavior of the population and suggested an explanation for the population fluctuations on the Old Field:

Prior to the mowing of alfalfa fields there are few adults on the surrounding cropland. Mowing forces large numbers to emigrate. The dispersal of this migrant population is probably more or less at random, with some influence of factors in the physical environment, such as wind direction. The degree of activity, however, is

inversely proportional to the availability of succulent foliage in the habitat (Weaver and King, 1954). Thus, more insects enter a favorable habitat than leave. The populations density in the favorable habitat increases until the immigration/emigration ratio reaches unity, i.e. a high density of slowly moving insects has an emigration rate equal to the immigration rate from an outside population of low density, fast moving insects.

On the Old Field the initial number of adults is very low. A large increase in the rate of immigration, when it becomes greater than the combined rates of emigration and mortality, results in a population increase. The amount of emigration and mortality also tends to increase proportionately with the increase in density. An equilibrium then becomes established wherein emigration and mortality balance immigration. Concurrent with the population increase on the Old Field, the alfalfa fields are producing new succulent growth. They begin to retain more and more of the adults passing through, thus reducing the numbers in the transient population. This in turn reduces the rate at which the insects enter the Old Field. When the daily immigration declines below the level of the combined daily mortality plus emigration the population begins to decrease until an equilibrium is again established with the new immigration rate. This process is repeated after the second mowing of the alfalfa hayfields. But overall mortality now has reduced the numbers in the transient population, so the magnitude of the second rise on the Old Field is not as large as the first.

The peak density, however, is about the same (Figure 1) because the population on the field does not decrease between peaks to as low a level as at the beginning of the summer.

The Old Field is a reproductive dead end for Philaenus spumarius; factors producing the mortality on the Old Field have little relevance for the survival of the meadow spittlebug as a species. Migrants from legume hay-fields enter many other habitats in addition to the Old Field, however, and Table 16 showed that almost half of them must survive and reproduce. Thus in addition to the mortality of nymphs and eggs, factors operating to cause mortality of migrant adults in areas other than the Old Field could be important in regulating the numbers of meadow spittlebugs. No statements are justified at the present time about the precise methods by which this regulation occurs. But the available data do justify some speculations on the relative importance of weather, predation, and competition.

Weather is undoubtedly important in determining the geographic limits of Philaenus spumarius. Weaver and King (1954) show that high temperatures and low humidity are particularly deleterious to the eggs and young nymphs. It is also reasonable to suppose that 'bad' years (high spring temperatures and low precipitation) can greatly reduce the population density. Within a certain optimum part of the range, however, it is doubtful that bad years would occur often enough to prevent population expansion to the point

where other limiting factors would operate with increasing force.

Weaver and King (1954) found a small percentage of the eggs parasitized and they cited a single instance of parasitism of the adult. I know of no reports of parasitism of the nymphs. Predation was also observed by Teller (1951) and in 1959 I watched a small salticid spider capture and kill a spittlebug adult on the Old Field. The possibility of predation by sparrows on the Old Field was discussed earlier in this paper. Spiders are quite abundant on both the Old Field and the Small Alfalfa Field and they may account for a large portion of the mortality of meadow spittlebugs.

Food limitation may be indirectly involved in causing the mortality on the Small Alfalfa Field. When large numbers of nymphs were confined on a single food plant in the laboratory they quickly caused wilting and death of that part of the plant above the site of feeding. This was probably an effect of removing too much water from the xylem elements. The plants on the Small Alfalfa Field, despite the high density of nymphs, were not wilted to any noticeable degree. However, under experimental conditions the nymphs would, if permitted, leave the plant before it began to wilt and wander around the floor of the cage. Such a behavioral response, operating in the field, might expose them simultaneously to the action of environmental and biotic mortality factors that are not ordinarily operative when the nymph is enclosed in a spittle mass on the plant.

The meadow spittlebug, having adapted successfully

to an entire system of agriculture (the legume hay-feed grain rotation), exists under conditions of extremely strong selection pressures and local instability of habitat, both of human origin. Examples of selection pressures exerted on the population are: (1) The cutting of hay in spring which kills virtually all remaining nymphs and thus selects for early development of the adult. (2) The plowing of cropland and old hayfields early in the spring, which destroys all eggs not deposited on young legume hayfields or pasture land. This would tend to reinforce the observed tendency to oviposit on straw stubble (Weaver and King, 1954) because legume fields with straw are invariably first year seedings, seldom disturbed the following spring.

It is not possible to speak of the 'natural' regulation of such a species population. If we assume that an average hayfield is used for four years and then plowed (a generous estimate) we get some idea of the flux in habitat occurring each year. All the eggs on the plowed field are of course destroyed. This in itself is an important source of mortality. Despite this mortality, the mortality of nymphs, and the low biotic potential, the species has maintained and even increased its numbers in recent years. This is evidenced by the increasing concern with the economic damage to hay crops caused by high densities of nymphs. Most of the increase seems to be consequent on an increased acreage in legume hay. The species is thus constantly invading new environments and may in fact seldom reach the point where ultimate limiting factors become operative.

SUMMARY

The population energetics of the meadow spittlebug, Philaenus spumarius L., were studied in two different habitats in southeastern Michigan, (1) a successional Old Field and (2) a first-year Alfalfa Field. Primary objectives included measurement of the energy flow of the spittlebug populations on the two habitats, measurement of the efficiencies of energy transfer within these populations, and estimation of the energy input to the Old Field contributed by immigrant adult spittlebugs. The effect of spittlebug feeding on the total primary production was also calculated and the net rate of population increase was discussed.

To attain these objectives, determinations were made (a) of the rates of ingestion, respiration, production, egestion, mortality, and reproduction, (b) of population density, and (c) of the specific parts of the plants used for food by spittlebug nymphs.

On the Old Field, peak densities of nymphs declined from 8.4 - 12.0/m² to less than 1.0/m² before the first appearance of the adults. Seasonal changes in density of adults were bimodal, with peaks in early July and mid-August. The majority of the adult population was exogenous in origin. The peak densities were coincident with the mowing of

nearby alfalfa fields and the forced emigration of large numbers of adult spittlebugs.

The Alfalfa Field contained peak densities of 1280 nymphs/m² and 466 adults/m², and the mortality rate of nymphs there was much lower than on the Old Field. Mowing dispersed most of the adults into the surrounding habitats. The density in these 'invaded' areas varied, possibly because of an inverse relationship between the activity of the insect and the suitability of the habitat.

The spittlebugs were found to ingest the xylem sap of plants; the bulk of the energy intake was amino acids. Nymphs egested 65%, and adults egested 30%, of the energy ingested. This difference between nymphs and adults represents the amount of 'surface tension depressant' (organic material) added to the spittle that is produced only by the nymphs. The removal of amino acids from the host plant caused a decrease in the potential fixation of energy of about 5.4 times the total energy ingested by the insects.

Production (growth plus the loss of molted exoskeletons) occurred only in the nymph stages.

The annual energy flow (intake of metabolizable energy) of the spittlebug populations was 38.5 kcal/m² on the Alfalfa Field in 1960, 0.6 kcal/m² on the Old Field in 1959, and 1.2 kcal/m² on the Old Field in 1960. Peak energy flow in both habitats was correlated with the highest growth rate of the vegetation and with the period of greatest concentration of amino acids in the xylem sap.

A standardized method of naming efficiencies was proposed. On the assumption that immigration equaled emigration, the value of one of these efficiencies, the gross efficiency of yield/ingestion (cal ingested by predator/cal ingested by prey), could not exceed 17.4% for a population of meadow spittlebugs. But because of a net gain of energy by immigration, the gross efficiency of yield/ingestion was 59.0% for the spittlebug population on the Old Field in 1960.

Each adult spittlebug that survived to September 10 was estimated to be replaced by 11 eggs. When zero mortality was assumed the intrinsic rate of natural increase was 2.4 per year. Survival on the Old Field was not great enough to provide for replacement in the absence of immigration.

The life of an individual legume hayfield does not often exceed 3 - 4 years. Because of this rapid turnover in habitat and because of the periodic dispersion of the populations by summer mowing, the meadow spittlebug is constantly invading 'virgin' areas. The species may, in fact, seldom reach densities where control factors other than habitat destruction become important.

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