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SOME PRELIMINARY MODELS FOR THE ENERGY FLOW OF A CHORTHIPPUS PARALLELUS (ZETT.) (ORTHOPTERA) POPULATION

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FOREWORD

Dr. Gyllenberg came to the Merlewood Research Station on a Foreign Exchange Fellowship of the Royal Society. His doctoral thesis had been devoted to describing the flow of energy through a population of grasshoppers, and his data seemed well suited to an application of Compartment Modelling. He had very little previous experience of model building or of the use of computers. However, Dr. Gyllenberg had to gain experience of a wide range of modelling tools in a fairly short time; depth was less important than the achievement of a broad understanding of the limitations and potentialities of computer simulation. These requirements could best be met by using the rapidly learned programming language called FOCAL[1].

In accordance with the methods of research organisation presently being used at Merlewood (Jeffers[2]), Dr. Gyllenberg set out his network plan at the beginning of his stay, and it was agreed that he should produce a Research and Development Paper as one of the objectives. The production of this paper has the main function of providing a record of the stages through which Dr. Gyllenberg worked. It is to be hoped that this record will be useful to others having similar problems and starting from a similar background of inexperience in modelling and simulation methods.

It is requested that anyone wishing to quote from this Research and Development Paper should contact either Dr. Gyllenberg at the Zoological Institute of the University of Helsinki, or myself, before doing so.

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Footnotes

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[1] FOCAL is short for Formulating On-line Calculations in Algebraic Language and is a conversational language developed for PDP-8 computers by the manufacturers, Digital Equipment Company.

[2] Jeffers, J. N. R. (1970) Project Planning and Research Administration, Merlewood Research and Development Paper No. 24.

INTRODUCTION

The project plan, which forms the basis for the work on a grasshopper population model, is outlined in Appendix 1. My objective at the beginning was to examine as many techniques of modelling work as possible likely to be useful for studying population numbers, and population energy flow. Some progress was made along these lines, but it was found that it was more relevant to the data to concentrate on a simulation model for the energy flow, omitting numbers. Density dependent models using numbers have already been widely used (for references see Southwood, 1966, Pielou, 1969).

The main emphasis was placed on finding different ways of modelling energy flow, working at first with my own empirical data and especially the 1969 year's data which were the most complete (published in Gyllenberg, 1970).

The computer used was a Digital Equipment Corporation PDP-8/I, and the FOCAL (for Formulating On-line Calculations in Algebraic Language) was chosen for its simplicity and usefulness in simulation as the main language for writing the programmes.

In developing dynamic models in ecology, Jenney, Gessel and Bingham (1949) made the first outlines. I have in my models followed the basic ideas of Olsen (1963) and Gore and Olson (1967) for a compartment model, where the energy change in one compartment (V) is dependent on a constant input (I) and fractional loss from the compartment (kV).

In fact, three types of basic differential equations have been used, in the following sequence:

$$\frac{dV}{dt} = I - (k(t) \times V) \qquad (1)$$

$$\frac{dV}{dt} = I - (k \times V) \qquad (2)$$

$$\frac{dV}{dt^2} = I - (k \times V_1 \times V_2) \qquad (3)$$

The first equation (1) was used to make the compartment values of the simulated fit as close by as possible to the empirical data. This was maintained by changing the k-values at every sample day, i.e. k is time-dependent. The second main procedure was to find a common k-value, either linear to the compartment value (2), or non-linear as a function of two compartment values (3).

The final model was constructed by including environmental factors, by making the k-values functions of these factors, i.e. equation (2), but so that the model would provide estimates for comparison with observations in different years.

I. The Descriptive Model with Changing Coefficient Values, Plot 1 in Figure 2.

In overviewing the simple model of a grasshopper population with 8 compartments (Figure 1), one immediately recognises the input as deriving from solar energy ($k_{12} \times A_1$), whereas all losses from the compartments are worked out as fractions of the compartments. Every one of the compartments should have output ratios at any given time; the reason why no outputs are outlined for the mortality, and losses compartments (7 and 8), is that there was no call for these at this stage of the model. Actual field data are available at each time step for these compartments, however, and one could allow for losses from these compartments due to decomposition, for example, if this was thought to play a role in the subsequent growth of compartment B (grasses). Such a role seems unlikely.

The behaviour of two compartments can be simulated for comparison with observed values, namely 4 (nymphs) and 5 (adults). The observed values are subjected to considerable variation, however, and the mean values of every sample day in 1969 have been accepted on a purely empirical basis. One can, moreover, consider the regression of the decreasing number of individuals on time as an estimator of population density, and the values given by the regression multiplied by mean biomass of each day can be used as a 'best estimate' of total biomass. Knowledge of the energy per unit biomass gives the total energy estimate.

The program for working out the different compartment values at daily steps ($\Delta t = 1$) functions as a coupling pattern between different flow pathways, as seen in Figure 1, and the compartment values can be mathematically expressed through the equations:

$$\frac{\Delta A_2}{\Delta t} = I - A_2\ (k_{23} + k_{24} + k_{25})$$

$$\frac{\Delta A_3}{\Delta t} = k_{23}A_2 - k_{39}A_3$$

$$\frac{\Delta B}{\Delta t} = k_{24}A_2 + k_{64}E - B(k_{45} + k_{47} + k_{48})$$

$$\frac{\Delta C}{\Delta t} = k_{25}A_2 + k_{45}B - C(k_{56} + k_{57} + k_{58})$$

$$\frac{\Delta D_1}{\Delta t} = k_{48}B + k_{58}C$$

$$\frac{\Delta D_2}{\Delta t} = k_{47}B + k_{57}C$$

$$\frac{\Delta D}{\Delta t} = k_{56}C - k_{64}B - (\text{Respiration losses})^{*}$$

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* worked out compactly as 50 per cent of the total egg biomass laid in the autumn.

Estimation of Transfer Coefficients (k_{ij}) - Method 1

Considering the compartment values of nymph or adult biomass (V) in a dynamic model, the biomass change of those compartments equals equation (2). If a steady state is reached, then:

$$\frac{\Delta V}{\Delta t} = 0, \quad \text{and} \quad I = k \times V_{ss} \qquad (4)$$

where: V_{ss} = biomass of nymphs or adults in a steady state.

The equation (4) condition is obtained only at the peak biomass value (V_{max}) of nymphs, or adults, and use can be made of this feature for checking purposes. But because the time periods between the sampling days are rather short, approximate values for any coefficient can be worked out for each time step as losses (L) as per cent of the average biomass value (V_{mean}) of a time period:

$$k = \frac{L}{V_{mean}} \qquad (5a)$$

and with n = number of days in Δt:

$$k = \frac{L}{V_{mean} \times n} \qquad (5b)$$

k having the dimension day^{-1}

Method 2

The transfer coefficients k_{45} and k_{56} can be checked using the numbers of eggs, nymphs and adults known to be present at different times. This is done by calculating the probability of transfer from eggs to nymphs, and from nymphs to adults from time t to time t + 1. Let us assume that these probabilities are expressed as p_{01} and p_{12}, where 0 = eggs, 1 = nymphs, and 2 = adults. In the autumn there should be a transfer from females back to eggs, which can be expressed with p_{20}. Let us, furthermore, assume a probability for each stage remaining in its age class, expressed as p_{00}, p_{11}, p_{22}. Considering the whole year, the total number of eggs at time t + 1 can be expressed from the number of eggs at time t as:

$$p_{00,t} \times n_{0,t} + p_{20,t} \times n_{2,t} = n_{0,t+1}$$

The same equation can be achieved for nymphs and adults, whereas the yearly transfer equations from t to t + 1 can be expressed compactly using matrices as:

$$\begin{bmatrix} p_{00} & 0 & p_{20} \\ p_{01} & p_{11} & 0 \\ 0 & p_{12} & p_{22} \end{bmatrix}_t \times \begin{bmatrix} n_0 \\ n_1 \\ n_2 \end{bmatrix}_t = \begin{bmatrix} n_0 \\ n_1 \\ n_2 \end{bmatrix}_{t+1}$$

From this equation the transfer coefficients k_{45}, k_{64} and k_{56} have been obtained for every time step in calculating the curve with changing coefficient values in Figure 2. (cf. also the example given in Section (3)). The FOCAL program used is added in Appendix II.

Example of Method 1

Assume the following values for the parameters at time t and t + 1, with the dimension kcal x m^{-2}:

parameter/time	t	t + 1	average value for Δ t
veg. standing crop	1200	1300	1250
nymph consumption	0	0.675	
adult consumption	0	1.25	
nymphs biomass	0.75	0.60	0.675
adult biomass	1.1	1.4	1.25
nymph defaecation	0	0.125	
adult defaecation	0	0.25	
nymph mortality	0	0.0125	
adult mortality	0	0.025	

These values give first approximations for the following coefficients:

$$k_{24} = \frac{0.675}{1250} = 0.0005 \qquad k_{25} = \frac{1.25}{1250} = 0.001$$

$$k_{47} = \frac{0.0125}{0.675} = 0.018 \qquad k_{57} = \frac{0.025}{1.25} = 0.02$$

$$k_{48} = \frac{0.125}{0.675} = 0.2 \qquad k_{58} = \frac{0.25}{1.25} = 0.2$$

the dimension of k_{ij} is day^{-1}.

Example of Method 2

To be able to use the matrix probabilities, average biomass for egg, nymph and adult biomass per m^2 must be expressed at time t. These values can be obtained by multiplying numbers/m^2 of eggs, nymphs, adults by the average biomass/individual for each of these compartments at time t.

On the 5th August, there were 4.2 individuals/m^2 of the fourth instar having a mean biomass of 0.034 g (dry weight) and 5.48 kcal/g/individual mean energy value. On the same sample day, there were 12.6 adults/m^2, having a mean biomass of 0.040 g (dry weight) and 5.41 kcal/g/individual mean energy value. On the 8th August, the numbers/m^2 were 1.6 for the fourth instar, and 14.4 for the adults. From these two vector values for population density (on time t = 5.VIII and t + 1 = 8.VIII), a probability matrix for the transfer into adults can be made:

$$\begin{bmatrix} 0 & 0 & 0 \\ 0 & 0.381 & 0 \\ 0 & 0.572 & 0.96 \end{bmatrix}_t \times \begin{bmatrix} 0 \\ 4.2 \\ 12.6 \end{bmatrix}_t = \begin{bmatrix} 0 \\ 1.6 \\ 14.4 \end{bmatrix}_{t+1}$$

$$\begin{bmatrix} 0 & 0 & 0 \\ 0 & 0.381 & 0 \\ 0 & 0.527 & 0.96 \end{bmatrix}_t = \begin{bmatrix} p_{00} & 0 & p_{20} \\ p_{01} & p_{11} & 0 \\ 0 & p_{12} & p_{22} \end{bmatrix}_t$$

The energy vector at time t is obtained by multiplying by mean biomass and energy:

For the fourth instar = 5.48 x 0.034 = 0.238

For the adults = 5.41 x 0.040 = 0.238

which gives the energy vector at time t:

$$\begin{bmatrix} 0 \\ 1.0 \\ 3.0 \end{bmatrix} = \begin{bmatrix} e_0 \\ e_1 \\ e_2 \end{bmatrix}$$

where e_0 = energy of eggs

e_1 = energy of nymphs

e_2 = energy of adults

This gives energy values for the compartments at t + 1:

$$\begin{bmatrix} 0 & 0 & 0 \\ 0 & 0.381 & 0 \\ 0 & 0.572 & 0.96 \end{bmatrix}_t \times \begin{bmatrix} 0 \\ 1.0 \\ 3.0 \end{bmatrix} = \begin{bmatrix} 0 \\ 0.381 \\ 3.428 \end{bmatrix}_{t+1}$$

Moreover, the coefficients k_{47} and k_{57} can be checked from the probability matrix, for a given column as:

$$1 - \sum_{j=1}^{i+1} p_{ij}$$

which gives the following values:

$$k_{47} = 1 - (0.381 + 0.572) = 0.047/(3 \text{ days}) = 0.016 \times \text{day}^{-1}$$

$$k_{57} = 1 - (0.96) = 0.04/(3 \text{ days}) = 0.013 \times \text{day}^{-1}$$

being in reasonably good accord with the values of 0.018 and 0.020 obtained earlier, for k_{47} and k_{57} using Method 1.

If eggs are laid between t and t + 1, p_{20} shall obtain a value, the probability of females laying eggs. This value, however, has to be multiplied by a ratio $\frac{\text{females}}{\text{males}}$, because females and males are combined in the numbers of adults counted.

II. The simulated Model with Constant Coefficients and Linear Equations, Plot 2 in Figure 2

One important aspect is to consider the different coefficients of transfer from one compartment to another. There is evidently an increase and decrease in every ratio value as the season starts or ends, but, in between, the ratio values reach almost a constant level throughout the season. In Figure 2, one of the curves plotted is obtained by keeping the coefficients k_{24}, k_{25}, k_{47}, k_{48}, k_{56}, k_{57} and k_{58}

constant. The maximum biomass values are changed towards the beginning of the season, but otherwise the values of the boxes are fitting reasonably with the obtained field data. As the values for the ratios k_{45} and k_{64} tend to increase throughout the season, they are worked out as an exponential increase from 0 to 1 on a data abscissa (see page). This indicates that all the eggs are used in spring time, constituting an energy reservoir from which the nymphs are hatched, and in the autumn the females replace that energy pool by laying eggs. Throughout the winter, there is a loss in energy from the eggs as respiration and mortality for which reason a value of 90 per cent losses, from the autumn to the spring, from the egg pool has been [illegible].

The program used for the run of the model I and II is added in appendix II.

III. The Continuous Model with Dependent Coefficients and Non-linear Equations, Plot 3 in Figure 2

This model is a direct consequence of the constant coefficient model (II). The main improvements over the previous model is that this model is working purely on a functional feedback basis; i.e. the value of one compartment having reached a certain level will change certain coefficient values. Model II worked only for specific time intervals, and the introduction of a new compartment, e.g. nymph biomass when the season starts, was regulated manually by asking for the different coefficient values at the beginning of each time period.

The main problems in constructing a continuous model with animals are associated with the onset and offset of different coefficient values. These problems are solved mainly by regulating all the k-values through feedback effects. When the standing crop of the plant biomass has reached a certain level, the hatching and growth of the nymphs starts. This means that the coefficients k_{24}, k_{47} and k_{48} receive a constant value. Again, after the plant biomass has reached a second level, the losses from this compartment to standing dead vegetation is introduced, and the emergence of the adults starts. The feedback from the plant biomass compartment on some k-values is obtained through a subroutine in the main programme loop.

The onset of egg laying is regulated through the biomass value of the adults, which is a biologically reasonable assumption. The emergence of macropterous (long-winged) adults (compartment G) depends on the biomass of the adults (C), and also on the biomass of the nymph compartment (B). Thus, the introduction of macropterous adults in the population is regulated by the compartment value of the adults, and the actual transfer rate from nymphs to macropterous adults is a non-linear function of the biomass of nymphs and adults (k_{49} x B x C). When the adult biomass reaches a second level, the actual migration of macropterous adults out of the population starts. This is because the population has now become too dense, and an output is bringing the biomass of the population back to a 'normal' level.

The biological explanation for this feedback is that when the population biomass is too large, hormones from corpora allata are going to be extracted from the adults, and transferred to the nymphs (ecdyson) influencing the balance between juvenile and growth hormone (ecdyson) to the favour of the growth hormone, thereby introducing macropterous individuals. The macropterous individuals are more 'mature' than normally micropterous adults (cf. e.g. [illegible], 1962; Staal and Wilde, 1962; Norris, 1964; Pener, 1965).

The population biomass of adults is thus having an indirect effect on the transfer of nymphs (B) to macropterous adults (G). This indirect effect (dotted line in Figure 3) is one of the main improvements of this model as compared with models I and II.

The other transfer considered to be non-linear is the consumption of plant matter by the animals. In Gyllenberg (1969), it was found that 1968 year's consumption data are proportional in a logarithmic scale to the biomass of the animals (compartments B, C and G). This relationship does not hold for the consumption data of 1969, and a linear relationship is found between the consumption and the biomass of B, C or G.

An explanation to this dissimilarity is that the 1968 results include later data, for August (25.8), when the standing crop of vegetation was decreasing. For 1969, all the values included are for the period when the standing crop of vegetation is remaining more or less constant, and results in a linearity between consumption and animal biomass.

As a conclusion, the consumption is assumed to be a function both of plant and animal biomass, and can be expressed:

$Cs_B = k_{24} \times A_2 \times B$ where Cs_B = consumption by nymphs

$Cs_C = k_{25} \times A_2 \times C$ Cs_C = consumption by adults

$Cs_G = k_{29} \times A_2 \times G$ Cs_G = consumption by macropterous adults

These equations are used in Programme II.

Some of the coefficient values are increasing exponentially from 0 to 1, i.e. the transfer coefficients k_{45} (nymphs to adults) and k_{64} (eggs to nymphs). This means that the further the season is advanced, the greater the probability is that the eggs or nymphs have reached a 'maturity' stage, when they are all going to transfer to nymphs or adults.

To make the point clear, if one looks at the nymphs (Gyllenberg, 1969), there is an easily recognisable pattern of different instars (1st to 4th instar). Through the life cycle the nymphs have to pass through all the instars, to reach the 'maturity' stage or 4th instar, when they are going to moult to adults. At the beginning of the season, the fraction of the nymphs that have reached the 4th instar is small, but as the season advances, this fraction is growing exponentially. The same pattern of stages is recognisable in the egg development from diapausal to post-diapausal stages, although the separation of different stages in this case must be done under microscope.

The changing coefficients (transfer eggs to nymphs, and nymphs to adults) increase each day with a fraction proportional to the value of the coefficients themselves:

$$k_{45} = k_{45} + \mu \times k_{45}$$

$$k_{64} = k_{64} + \sigma \times k_{64}$$

where: μ and σ are the fractional daily increase of the k_{45} and k_{64}.

This is, therefore, a shorthand method which allows in an approximate way for the complex development of the insect.

The incoming solar radiation in Figure 3 is drawn up as a cosine curve (for explanation, see Neel and Olson, 1962). The transfer coefficient k_{12} is calculated empirically for 1969, and a change in this coefficient is introduced, when the standing dead vegetation has reached a certain level (Programme 2 in Appendix II).

The compartment model, with the additional macropterous adult compartment, is outlined in Figure 3. The feedback effect in the programme (Appendix II) from the values of the compartments is obtained through a number of subroutines (3-5), which are executed each day as the indirect programme is passed through. For complete explanation concerning the execution of the programme, see Appendix II.

IV. Component Analysis

The objectives of this component analysis is to find out which of the environmental factors have a significant impact on the values of the parameters. Because some biological factors have not been recorded in field conditions for the Chorthippus parallelus populations, many of the factors suggested in the word model (part I) are related to work done in Canada by Pickford, (1958, 1960, 1962, 1966a, 1966b) and Riegert (1965, 1967). Recently an advanced deterministic model has been constructed by Randell (1970) using these component analyses by Pickford, Riegert and others.

The outlines for the component analysis is a word model, followed by correlation analysis (see e.g. Snedecor, 1956). From the correlation matrix the principal components of the factors are grouped, and multiple regression is performed with the most significant of factors in the relevant components. Basic literature used in the component analysis is Snedecor (1956), Bonnier and Tedin (1962), Hope (1968), Atkins (1969), Sokal and Rohlf (1969) and Sprent (1969). Correlation matrix and eigenvalue extraction programs have been used from the basic FORTRAN programs of Merlewood Systems Unit, and linear and multiple regression analysis programs were written in FOCAL, using Snedecor (1956).

Definition

The word "parameter" is used solely for the energy pathways of the grasshopper population, such as biomass production, consumption, defaecation, respiration, mortality and egg-laying.

A. Word Model of Component Analysis

The following components involved in regulating the energy flow of grasshopper populations have been entered from my own data and the literature -

The Eggs (Riegert, 1967)

1. Desiccation and frost

   If snow cover is absent, frost may injure eggs. Riegert (1967) found that chilling at -12°, -18° and -23°C reduced the viability of some grasshopper eggs by about 10, 20 and 50 per cent respectively. However, the viability was usually high (47 - 94%).

2. Predation

   Mice on eggs. Birds digging out egg pods.

3. Parasitism

   Eggs of Camnula pellucida were rarely parasitized by Scelio calopteni. More parasitism found in Melanoplus bivittatus (Riegert, 1967).

4. The Time when the Bulk of Eggs are laid

If the eggs have reached prediapausal stage before frost occurs, the survival rate is increased (Pickford, 1966b).

On the egg stage, no component analysis has been made for Chorthippus parallelus. The losses due to all factors, including hatching mortality, were calculated compactly as about 50 per cent of the energy deposited by the females in the autumn.

5. Temperature

The duration of the nymphal period varied inversely with the temperature (Pickford, 1960). Because the coefficients have been obtained using empirical data in which effects of temperature are already allowed for, it is not necessary to take separate account of temperature.

6. Rainfall, Humidity

Some behavioural features were observed in the Chorthippus population.

If the grass is totally dry (about 20 per cent R.H.), the grasshoppers were searching ground level, where humidity is higher; they were not feeding.

When the humidity is 35-90 per cent R.H., the grasshoppers are moving upwards and feeding on the leaves. When the humidity is 95-100 per cent R.H., or when rain is falling, the grasshoppers are searching ground level, and feeding is minimised.

Rainfall is built in the model only for mortality, but could be included for consumption.

7. Fungus Disease

The habit of aggregating in a small area has a devastating effect on the later nymphs and adults of the grasshopper Camnula pellucida, when Entomophthora grylli (fungus) appears. The higher density of grasshoppers, the heavier infection, acting as an effective control mechanism. The disease is spread by spores and favoured by heavy rainfall (Riegert, 1967).

The appearance of Entomophthora in the Chorthippus population both in nymphs and adults upset the whole energy flow system in 1967. Sometimes about 50 per cent of the grasshoppers were infested.

The Nymphs

1. Hatching Mortality

The hatching of the eggs and survival of the first instar is very much dependent on the temperature, frost and humidity (Pickford, 1960, 1962). In the Chorthippus population hatching started normally after a slight rainfall in the beginning of June. If temperature is low and frost occurs after that, hatching mortality is high. During the four years 1966-69, no exceptionally low temperatures and frost were recorded, for which reason the 50 per cent losses from egg resources was considered appropriate.

2. Time when the Bulk of Eggs was Laid

Population growth was highest in the earliest-hatched eggs that was laid early in the autumn, and tends to decline progressively as grasshoppers were hatched later (Pickford, 1960, 1966b). From this statement of Pickford, it is not quite clear whether he meant that the relative growth rate, or the peak biomass, was higher in earlier-hatched eggs. No significant differences were observed concerning the growth rate in the Chorthippus population.

3. Food Preference

A combination of plants is the superior food for quick development, survival and mortality (Pickford, 1958, 1962). Because nymphs are not food limited in the Chorthippus population, the choice of food plants was regarded as unsignificant. However, the population becomes food limited late in the autumn, and this could affect the egg laying. For complete analyses, see Gyllenberg (1969).

4. Predators

The losses from the population to predators is found to be very small in terms of energy (Gyllenberg, 1969). Predators are included in the overall mortality.

The Adults

1. Grouping, Pairing and Mating

Females of grouped grasshoppers produced a larger number of eggs per pod and laid a greater total number of eggs that were more viable, and hatched earlier (Riegert, 1965). Because of lack of data, no behavioural aspects have been included for the egg-laying of the Chorthippus population.

2. The Biomass of Macropterous Individuals

Emerging is determined by a non-linear relationship to nymphs and adults. The emergence of macropterous adults is really density dependent, but the same kind of conditions were also observed in terms of biomass.

3. Fungus Disease, related to rainfall (see nymphs).

4. Food Preference (see nymphs)

5. Temperature, Humidity and Rainfall

Affecting the number of eggs laid. The egg-laying in the model is made dependent (in crude way) on temperature multiplied by the percentage of rainy days as an index.

6. Predators (see nymphs)

7. Human Activity

As pointed out in Gyllenberg (1969), this factor may affect the whole energy flow, but as contradictive data were found for 1969, the human activity has not been built in the flow model.

8. Correlation analyses

All correlation analyses have been performed separately for nymphs and adults. The basic pattern of factors involved are the following:

1. Dependent variables

These consisted of the basic parameters involved in component analysis. Most of these parameters are expressed in mg/m^2/day (biomass), because the coefficient for transformation to energy can be regarded as constant. In addition, population density is taken into account (numbers/m^2), but is not used in the framework of the present energy flow model.

2. Independent variables (1)

These were all the main environmental factors significantly regulating the values of the energy flow parameters.

3. Independent variables (2)

These were food preference indices (% eaten/% available food) for some major grass species (for accurate description, see Gyllenberg 1969). Poa pratensis is an early soft grass species, Agrostis tenuis is major food supply occuring over the whole season, and Calamagrostis epigeios is especially abundant late in the season (c.f. Gyllenberg 1969; Figs. [illegible]). As may be expected, a positive correlation is shown in Tables 3-4 for biomass production and consumption (for both nymphs and adults) towards preference for Calamagrostis. This means that the larger the production rate, the later in the season, and accordingly a transfer to a late occuring species of grass.

Both rainfall and temperature have been separated into two sets of variables, the first comprising mean temperatures on the sample day, and the second dealing with temperatures calculated as a mean of the period preceeding the sample day, counted from the previous sample day. It was found that especially rainfall, but also temperature, did not have an immediate effect on the growth of the population, and in all cases, the correlation indices for the preceeding period were higher than for the actual sample day (Tables 3-6).

All the values with a star (*) in Tables 3-6 are those chosen for multiple regression analysis. The significant correlations between food preference indices and parameter values, noted by [illegible], were not used in this model, but could be built at a later stage. This procedure would, however, imply the division of the standing crop compartment into several compartments for the different grass species.

One parameter that was difficult to relate to a common environmental factor was mortality. The nymph mortality for 1968-69 shows a significant correlation to rainfall on preceeding period before sample day (Table 3), but this relationship is not verified for the adults (Table 4). The significant relationship to temperature on sample day could not be used, because of contradictive results in 1968 and 1969. When performing correlation analysis for 1967, which was an extremely rainy year, a high correlation was found between mortality and rainfall on preceeding period. The reason for this high mortality was:

(a) The spreading of fungus disease (Entomophthora) was very efficient in 1967, and sometimes about 50% of the population was infected.

(b) It was observed in the laboratory and in the field that the grasshoppers decrease their feeding rate to a minimal level if the rainfall and humidity was very high. The animals, and especially the more sensitive nymphs, were more likely to die from starvation during long term rainfall.

As a result, mortality was assumed to be correlated to rainfall above a threshold value of 2.0 mm rain/day.

C. Multiple regression analyses

In every case, where at least two highly correlated factors were found for the parameter values, a multiple regression analysis was performed including two of the significant environmental factors. The results of some of these analyses, dealing with temperature, humidity and rainfall, are illustrated in Table 7.

It is evident from Table 7 that when two variables were taken into account, one of them (in this case temperature) was highly correlated with the other one (humidity, or rainfall). The relative weighting of one of the variables in the regression analysis is dependent on the order in which these are taken. Therefore it was concluded that one environmental factor is sufficient in correcting the parameter values, temperature was chosen for this purpose.

One parameter which could be related to two variables is consumption for adults, as the relative weighting of both of them was significant in the multiple regression. In this model, however, only temperature was taken into account, because of the high correlation between temperature and rainfall (Tables 3-6).

D Linear regression analyses

The results from the linear regression analyses for the actual parameter values are listed in Table 8.

If the parameters are correlated with some specific environmental factor, it seems reasonable that the corresponding k-values, being the proportional output from any one compartment should be correlated with the same factor. If one takes nymph consumption, the k-value for a specific time moment is:

$$k_{24} = \frac{\text{nymph consumption}}{\text{standing crop of vegetation}}$$

If it is remembered (p. 4) that the original variation in k-values was obtained by forcing the compartment values of the simulated model to be congruent to every empirical compartment value measured in the field, this variation was achieved by changing the k-values all through the season (model I). The variation in these empirically obtained k-values was assumed to be dependent deterministically on the same environmental factors as the actual parameter values. Through correlation analysis it was found that the standing crop of vegetation was not correlated with any one of the environmental factors used in the component analyses at issue. However, the standing crop of vegetation may be indirectly related to temperature effects, and this would introduce another source of variation in the k-values which it might be necessary to allow for at a later stage when the relationship was known.

In Table 9 a linear regression analysis has been performed for every one of the k-values, corresponding to the parameter regressions. Highly significant regressions were obtained.

One of the k-values that has been correlated to factors (mainly on laboratory results of only one year, and does not have verification from field data) is the k-value for egglaying (k_{56}). It was found that the laboratory data were strongly dependent on temperature and per cent of rainy days, so k_{56} was made a function of both (Table 9):

$$k_{56} = f\left(\text{temperature} \times \frac{\underline{\%\ \text{rainy days out of } 10}}{1000}\right)$$

As the k_{56} in relation to these index values was an exponential curve, it has been divided up in two straight lines, as a matter of simplicity (Fig. 4).

Relating the egglaying to temperature and per cent of rainy days is biologically a reasonable assumption, since it has been found that females lay their eggs only in wet soil (Kennedy 1949), and the rate of egglaying is dependent on temperature. However, as Dempster (1963) has pointed out, laboratory estimation of the number of eggs laid exhibit overestimation in most cases, and further field data are needed

V. The continuous model with k-values corrected for environmental factors

The interesting point of this model is the possibility of comparing model simulation estimates with observations. A X^2-test (a theoretical goodness of fit between observed data) was performed for every one of the compartments for 1966-69, and has been drawn up in Table 10.

As is evident from this table, the main source of variation between simulated and empirical data is derived from the compartments for nymph and adult biomass. Therefore the simulated and empirical curves are presented in Figs. 5-8. The use of the FOCAL programmes for different years is explained in Appendix II (Programme III-VI), and the environmental factors and complete runnings of the programmes are explained in Appendix III.

1967 was, as pointed out earlier, an exceptionally rainy year, and the following factors were found important for explaining the diversion from the empirical data.

(a) Most certainly an underestimation of young nymphs.

(b) The decreasing consumption rate, causing slow development. Rainfall has not been built in the k-values for consumption.

Therefore it is evident that additional factors have to be taken into account to permit the co-ordination of the model with extreme conditions. Models should in fact never be expected to predict outside their intended range. The regression coefficient for k_{24} was, consequently, changed in 1967 to a smaller value (0.000016 in Programme V). Even with this change the deviation from the empirical data for mortality and losses compartments is notable, and further improvements are obviously necessary.

As seen in Table 10, most of the model biomass values for nymphs and adults are significantly differing from the empirical values. However, as the mortality and losses compartments (1966, 1968, 1969) do not show any significant diversion, the actual difference between simulated and field estimated biomass values must be due to the transfer coefficients within the population itself. Most certainly there is an overestimate of the initial egg energy value for some year, and this could explain the overshoot in nymph biomass values for the simulated curves. Furthermore, the exponential increase in the transfer rate from nymphs to adults (k_{45}) is found to be dependent on temperature (Table 9), and this relationship could explain for the overshoot in adult biomass values. The shorthand method is obviously a major oversimplification.

As is felt, the main outcome of the model with corrected k-values are the following:

(a) The procedure of correcting the proportional losses, or k-values, for environmental factors, makes it possible for the model to function in a predictive way, once all the relevant factors are built in. The main reason for constructing this model is to introduce a possible way of setting an energy flow model, by measuring the minimal number of parameters out in the field.

(b) If correction factors for the production of plant biomass could be found, the model could be made to function using only solar energy measurements. In the present shape, the compartment for standing crop of vegetation is made to agree with empirical data by altering the k_{12} values for different years.

(c) In the present form, the model has a correct energy input into the population (standing crop of vegetation), and correct outputs (mortality and losses). It is therefore evident that the disagreement with empirical data lays in the circulation of energy within the population.

VI. Possible future development

The outlines of all the models (I-VII) are mathematically elementary, and even the more complete models (II-VI) still omit much information. For all that, it is felt that the basic ideas could be used for further development, and the models improved for a closer fitness in the following sequence of steps.

1. Field measurements

a. Environmental factors

The lack of agreement between models and observation in some years seems to be due to factors which have not been allowed for over sufficient range. Especially the influence of different factors on the parameters of energy flow has to be studied in the laboratory as well as in the field. As one improvement, the two important features from models II and III, non-linear transfer coefficients for consumption, and the key environmental factors, could of course be united in one model.

b. Developmental stages of the grasshoppers

The egg stage needs a thorough analysis to provide the right energy input to the population at the beginning of the season. Some laboratory studies made by Albrecht (1970) and his school suggest two critical stages in the life cycle of grasshoppers, namely at about 24 hours after hatching (perinatal mortality). and shortly after the final moult (fledging mortality). Particular emphasis should be laid on these critical stages. Furthermore, the field data for numbers of different instars could be used to split the nymph biomass compartment up in four compartments, for each of the instars.

2. Modelling approach

a. Stochastic variation of k-values

The different k-values could, as a first step, be assumed to vary according to a normal distribution within the range of their confidence intervals in the linear regression (Table 8). Model VII takes into account the stochastic variation of k_{24} and k_{25}, the transfer coefficients assumed to have the greatest impact on the whole energy flow model. This preliminary attempt was sufficient to reveal the problems associated with variability in the field data. Basic guides used for penetrating stochastic modelling are Hammersley & Handscomb (1967), and Martin (1968).

b. Matrix approach

One modelling possibility lies in the use of matrices for the probability of transfer from one stage to another (e.g. as explained in Searle 1966). This approach has already been touched in Model I (p. 4, 6). The main advantage of matrices is to find the steady state of a population with overlapping generations, but as the Chorthippus population has a circulating life cycle (no overlapping generations), this procedure is of limited value.

c. Probability model

Another kind of model could be used for the Chorthippus population. If one accepts each hatching day as the offspring of one cohort of the population, one can treat the different cohorts in respect of their developmental cycle. The basic bioenergetic models for cohort development are worked out by Kaczmarek (1967 Fig. 2-4). By plotting biomass against time from empirical data of the Chorthippus population, it is found that in addition to variation on the time axis (i.e. the time of the moults of the grasshoppers is differing), there is variation on the biomass axis (i.e. when moults occur, the grasshoppers have reached different weights). The variation in development is not purely stochastic and determined partly by the availability of superior food (cf. <u>Pickford</u> 1962). If the frequency curve for number of hatchings per day is found, a probabilistic model could be built up for the development of the population as a whole.

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TABLE 1. Coefficient values for the plot curve (Figs. 2 and 2B) with constant coefficient values

t	k_{12}	k_{23}	k_{24}	k_{39}	k_{45}	k_{47}	k_{48}	k_{56}	k_{57}	k_{58}	k_{64}	k_{25}
16.5	0.0055		0			0	0				0	
5.6	0.0055		0.00005			0					0.02	
11.6	0.0052	0			0				0	0	0.044	0
17.6	0.0048										0.087	
23.6	0.0048										0.24	
4.7	0.0026	0.007					0.15				0.55	
8.7	0.0058	0.0027	0.000237	0	0.022	0.0151		0	0.001	0.005	0.9	0.00002
12.7	0.0025	0.003			0.047				0.01			0.00008
16.7	0.0033	0.023			0.07							
20.7	0.0029	0.037			0.138							0.0021
28.7	0.0028	0.056			0.17		0.041					
31.7	0.0039	0.045			0.262		0.031		0.0171	0.131	0	
5.8	0.0047	0.038	0.0001		0.368	0.0015	0.01					
9.8	0.0047	0.026	0.0001		0.516	0.0017	0.01					
13.8	0.0025	0.017			0.9							0.00055
21.8	0.0009	0.014	0			0	0	0.02				
10.9	0.0001	0.033		0.006	0			0.02		0.11		
10.10												

Table 1. Coefficient matrix for the plot curve with constant coefficient values

The matrix being of the general form:

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ k_{12} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & k_{23} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & k_{24} & 0 & 0 & 0 & k_{64} & 0 & 0 & 0 \\ 0 & k_{25} & 0 & k_{45} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & k_{56} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & k_{47} & k_{57} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & k_{48} & k_{58} & 0 & 0 & 0 & 0 \\ 0 & 0 & k_{39} & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}_t$$

For the time periods (t to t + 1), or Δt, the coefficients receive the vollowing values (Table 1).

Table 2. Coefficient matrix for the plot curve with varying coefficient values

The same general matrix is used. For the time periods (Δ t), the coefficients receive the following values (Table 2).

TABLE 2. Coefficient values for the plot curve (Figs. 2 and 2B) with varying coefficient values

t	k_{12}	k_{23}	k_{24}	k_{25}	k_{39}	k_{45}	k_{47}	k_{48}	k_{56}	k_{57}	k_{58}	k_{64}
16.5												
	0.0055	↓	0	↓	↓	↓	0 ↓	0	↓	↓	↓	0
5.6												
	0.0055	↓	0.00003	↓	↓	↓	0 ↓	0 106	↓	↓	↓	0;02
11.6												
	0.0052	0 ↓	0.00019	0 ↓	↓	0 ↓	0.025	0.18	↓	↓	↓	0.066
17.6												
	0.0048	↓	0.00027	↓	↓	↓	0.012	0.184	↓	0 ↓	0 ↓	0.035
23.6												
	0.0048	↓	0.00025	↓	↓	↓	0.016	0.2	↓	↓	↓	0.053
4.7												
	0.0026	0.007	0.00019	↓	↓	↓	0.025	0.2	↓	↓	↓	0.21
8.7												
	0.0058	0.0027	0.00022	0.000015	↓	0.016	0.02	0.18	0 ↓	0.001	0.005	0.9
12.7												
	0.0025	0.003	0.00025	0.00008	0 ↓	0.04	0.022	0.16	↓	0.01	0.1	↓
16.7												
	0.0033	0.023	0.00025	0.00013	↓	0.05	0.01	0.14	↓	0.015	0.18	↓
20.7												
	0.0029	0.057	0.0003	0.00012	↓	0.138	0.008	0.114	↓	0.015	0.2	↓
28.7												
	0.0028	0.056	0.00022	0.00025	↓	0.17	0.01	0.05	↓	0.014	0.14	↓
31.7												
	0.0039	0.0045	0.0002	0.00035	↓	0.22	0.018	0.035	↓	0.022	0.16	0 ↓
5.8												
	0.0047	0.038	0.0001	0.0006	↓	0.275	0.0015	0.01	↓	0.016	0.115	↓
9.8												
	0.0047	0.026	0.0001	0.0006	↓	0.516	0.0017	0.01	↓	0.022	0.11	↓
13.8												
	0.0025	0.017	↓	0.00049	↓	0.9	↓	↓	↓	0.022	0.09	↓
21.8												
	0.0049	0.014	0 ↓	0.00048	↓		0 ↓	0 ↓	0.02	0.018	0.1	↓
10.9												
	0.0001	0.03	↓	0.00048	0.006	0	↓	↓	0.02	0.02	0.1	↓
10.10												

Table 3. Correlation matrix for nymphs 1968-69, including basic parameters, environmental factors and food preference indices

Variable No.	Variables	Mean	S.D.
1	Population density (indiv/m^2)	23.63 ±	10.20
2	Production (mg/m^2/day)	8.42 ±	4.20
3	Respiration (cal/m^2/day)	41.39 ±	23.64
4	Defaecation (mg/m^2/day)	41.89 ±	17.31
5	Consumption (mg/m^2/day)	58.57 ±	24.61
6	Mortality (cal/m^2/day)	21.24 ±	12.81
7	Food preference index for *Agrostis tenuis*	7.03 ±	3.33
8	Food preference index for *Calamagrostis epigeios*	0.95 ±	1.57
9	Food preference index for *Poa pratensis*	7.92 ±	7.90
10	Mean temperature on sample day	15.07 ±	2.08
11	Mean temperature on preseeding period	14.70 ±	1.77
12	Rainfall on sample day	0.36 ±	0.67
13	Rainfall on preceeding period	1.12 ±	1.69
14	Humidity (% R.H.)	86.7 ±	8.3

TABLE 3

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1.0													
2	0.560	1.0												
3	–	0.938	1.0											
4	–	0.510	0.334	1.0										
5	–	0.756	0.538	0.969	1.0									
6	–	0.634	0.631	0.334	0.538	1.0								
7	-0.171	-0.483ø	–	-0.216	-0.314ø	–	1.0							
8	0.325	0.677ø	–	0.368ø	0.518ø	–	-0.809	1.0						
9	-0.224	-0.418ø	–	0.253	0.136	–	0.452	-0.507	1.0					
10	0.484	0.250	0.334	0.557	0.547	-0.038	-0.008	0.266	0.218	1.0				
11	0.582	0.329*	0.333*	0.617*	0.564*	-0.108	0.098	0.139	0.282	0.794	1.0			
12	-0.111	-0.051	-0.152	0.053	0.062	-0.114	-0.175	-0.034	0.421	-0.143	0.044	1.0		
13	-0.540	0.014	-0.109	-0.100	-0.100	0.429*	-0.238	0.118	-0.139	-0.369	-0.462	-0.127	1.0	
14	-0.792	-0.301*	-0.317*	-0.290	-0.364*	-0.186	0.153	-0.300	0.178	-0.352	-0.360	0.094	0.396	1.0

* Significant correlation values chosen for multiple regression analysis

ø Significant correlation values for indices of food preference (see text)

TABLE 4. Correlation matrix for adults 1968-69, including basic parameters, environmental factors and food preference indices

Variable No.	Variables	Mean	S.D.
1	Population density (indiv../m^2)	13.35 ±	5.59
2	Production (mg/m^2/day)	12.11 ±	5.96
3	Respiration (cal/m^2/day)	–	–
4	Defaecation (mg/m^2/day)	63.86 ±	19.89
5	Consumption (mg/m^2/day)	89.77 ±	24.69
6	Mortality (cal/m^2/day)	–	–
7	Food preference index for *Agrostis tenuis*	4.26 ±	3.41
8	Food preference index for *Calamagrostis opigeios*	2.49 ±	2.38
9	Food preference index for *Poa pratensis*	1.69 ±	2.45
10	Mean temperature on sample day	17.59 ±	3.45
11	Mean temperature on preceeding period	16.99 ±	2.50
12	Rainfall on sample day	1.55 ±	3.43
13	Rainfall on preceeding period	1.14 ±	1.16
14	Humidity (% R.H.)	89.9 ±	7.79

TABLE 4

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1.0													
2	0.693	1.0												
3	–	0.704	1.0											
4	–	0.278	-0.104	1.0										
5	–	0.261	0.045	0.881	1.0									
6	–	-0.016	0.306	-0.361	-0.371	1.0								
7	0.023	0.164	–	0.532[ø]	0.267	–	1.0							
8	0.542	0.590[ø]	–	0.721[ø]	0.823[ø]	–	0.250	1.0						
9	-0.154	-0.043	–	0.094	-0.140	–	0.553	-0.288	1.0					
10	0.407	0.491	0.708	0.042	0.142	0.416[1]	-0.461	0.271	-0.470	1.0				
11	0.624	0.529*	0.763*	0.326*	0.472*	0.358	-0.369	0.429	-0.512	0.850	1.0			
12	-0.283	-0.038	-0.046	-0.408	-0.525	-0.279[1]	-0.082	-0.233	0.318	-0.225	-0.435	1.0		
13	-0.399	-0.088	-0.210	-0.612*	-0.528*	-0.181[1]	-0.113	-0.346	0.179	-0.434	-0.611	0.554	1.0	
14	-0.891	-0.746*	-0.835*	-0.270	-0.495*	-0.058	+0.143	-0.414	0.200	-0.476	-0.738	0.355	0.336	1.0

* Significant correlation values chosen for multiple regression analysis

ø Significant correlation values for indices of food preference (see text)

[1] Correlation values for mortality, discussed in the text

TABLE 5. Correlation matrix for nymphs 1966-67, including parameters and environmental factors

Variable No.	Variables	Mean		S.D.
1	Production (mg/m^2/day)	6.38	±	5.32
2	Respiration (cal/m^2/day)	33.9	±	23.3
3	Mortality (cal/m^2/day)	16.84	±	14.50
4	Mean temperature on sample day	15.20	±	2.46
5	Mean temperature on preceeding period	15.00	±	2.21
6	Rainfall on sample day	0.82	±	1.57
7	Rainfall on preceeding period	0.68	±	0.81
8	Humidity	83.9	±	9.12

TABLE 6. Correlation matrix for adults 1966-67, including parameters and environmental factors

Variable No.	Variables	Mean		S.D.
1	Production (mg/m^2/day)	13.29	±	6.00
2	Respiration (cal/m^2/day)	9.23	±	46.8
3	Mortality (cal/m^2/day)	53.57	±	24.68
4	Mean temperature on sample day	17.57	±	3.10
5	Mean temperature on preceeding period	16.45	±	2.68
6	Rainfall on sample day	1.03	±	1.91
7	Rainfall on preceeding period	2.20	±	2.56
8	Humidity	91.6	±	6.27

TABLE 5

	1	2	3	4	5	6	7	8
1	1.0							
2	0.914	1.0						
3	0.632	0.526	1.0					
4	0.509	0.708	0.467	1.0				
5	0.696*	0.835*	0.518	0.785	1.0			
6	-0.242	-0.275	-0.239	-0.482	-0.329	1.0		
7	-0.396	-0.460	-0.169	-0.471	-0.684	0.257	1.0	
8	-0.722*	-0.775*	-0.430	-0.762	-0.820	0.449	0.706	1.0

* Significant correlation values chosen for multiple regression analysis

TABLE 6

	1	2	3	4	5	6	7	8
1	1.0							
2	0.111	1.0						
3	-0.152	0.616	1.0					
4	0.748	0.219	-0.129	1.0				
5	0.637*	0.190	-0.411	0.768	1.0			
6	-0.289	-0.112	0.194	-0.595	-0.523	1.0		
7	-0.126	-0.020	0.337*	-0.48[illegible]	-0.594	0.535	1.0	
8	-0.410*	-0.668*	-0.326	-0.746	-0.526	0.362	0.225	1.0

* Significant correlation values chosen for multiple regression analysis

TABLE 7. Multiple regression analyses, taking into account the variables temperature on preceeding period (TP), humidity (HM) and mean rainfall/day on preceeding period (HR) for some parameters dependent variables). The T-value gives the regression coefficients for the independent variables divided by their standard deviation, and is used to test the goodness of fit of the relation between the parameter value and the two variables.

			T-value and corresponding probability for		
Parameter	Instar	Equation	TP	HM	HR
Consumption (cf. Table 8)	Nymphs	-45.5+7.19xTP-0.0045xHM	2.534 P ≈ 0.02*	-0.076 0.9 < P <1.0	
Defaecation	Nymphs	-38.17+5.58xTP-0.0014xHM	3.0242 0.001 <P < 0.01**	-0.0361 0.9 <0< 1.0	
Respiration 1966-67	Nymphs	-107.68+8.786xTP-0.0025xHM	5.012 P < 0.001 ***	-0.0 0.9 < P <1.0	
Respiration 1968-69	Adults	-141.42+13.52xTP-0.01xHM	4.0836 P≈0.001***	-0.1172 P=0.9	
Consumption 1969	Adults	-44.6+8.57xTP-1.57xHR	2.6744 P ≈ 0.05*		-0.8152 0.4< P <0.

TABLE 8. Linear regression analyses for different parameters in relation to their key environmental factors: temperature on preceeding period (TP), and mean rainfall/day on preceeding period (HR). The t-value gives the regression coefficient divided by its standard deviation, and is used as a goodness of fit for the regression line.

Instar, parameter	Equation	No. of sets	t-value	corresponding probability
Nymphs				
consumption	$-46.+7.2\times\mathrm{TP}$	18	2.6207	$0.01 < P < 0.02$*
Respir.+defaec.	$-65.+7.\times\mathrm{TP}$	32	5.3202	$P < 0.001$***
Mortality	$22.247+1.33\times\mathrm{HR}$	16	2.3221	$0.01 < P < 0.02$*
Adults				
Consumption	$-72.83+10.3\times\mathrm{TP}$	7	4.2662	$0.001 < P < 0.002$*
	$97.094-9.045\times\mathrm{HR}$	15	2.4713	$P \approx 0.02$*
Respir.+defaec.	$-124.85+12.17\times\mathrm{TP}$	22	5.1926	$P < 0.001$***
Mortality				
1966-67	$50.946+5.145\times\mathrm{HR}$	9	3.2646	$0.01 < P < 0.02$*
1968-69	$36.256+11.29\times\mathrm{HR}$	17	3.044	$P \approx 0.01$**

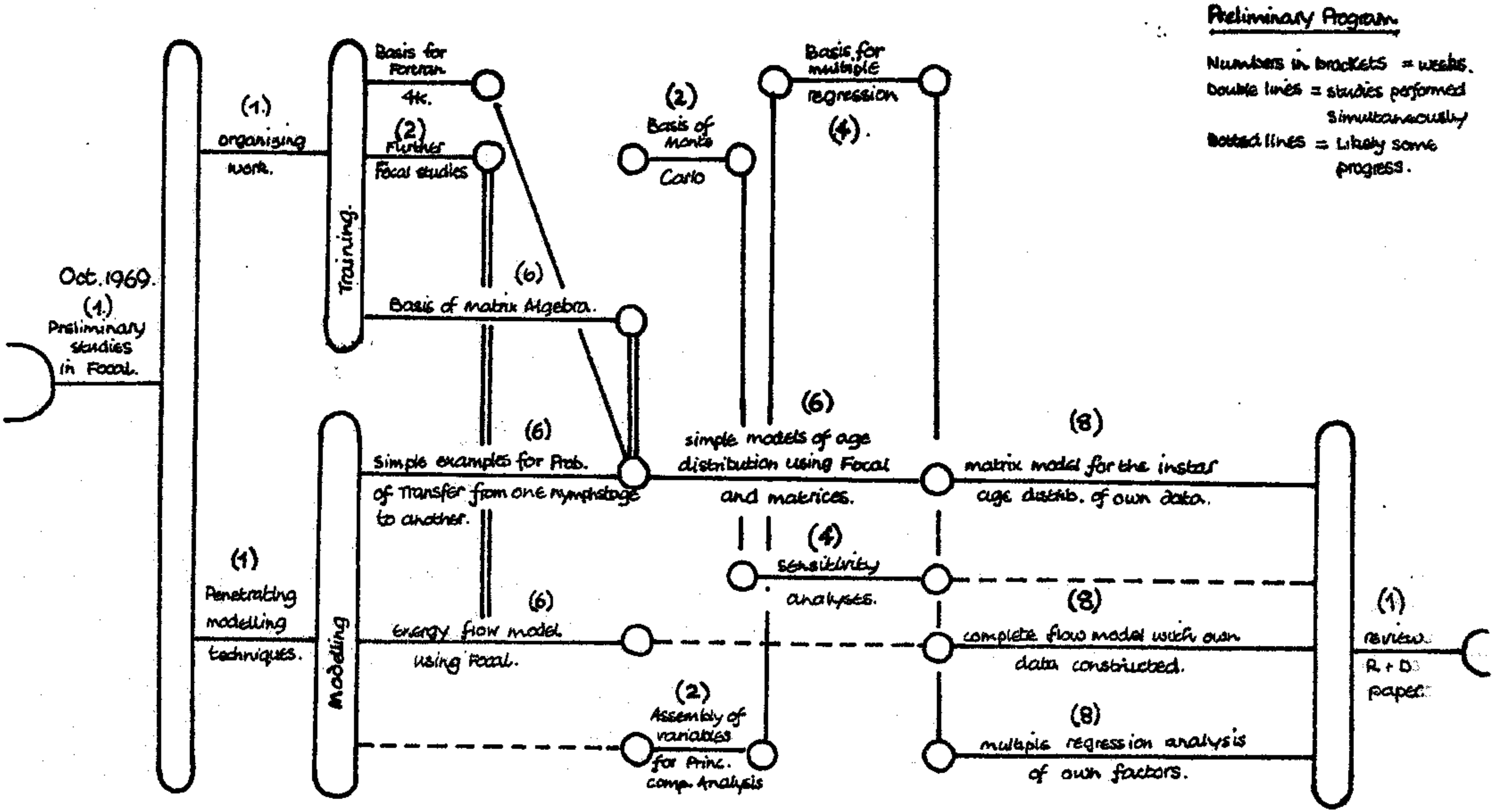
TABLE 9. Linear regression analyses for different k-values in relation to key environmental factors from Table 8: temperature on preceeding period (TP), rainfall (HR), temperature on period preceeding the previous sample day, counted from the actual sample day (TR) and index = temperature x % rainy days (OI). The t-value gives the regression coefficient divided by its standard deviation, and is used as a goodness of fit for the regression line. μ = exponential increase in k_{45}.

Instar, k-value	Equation	No. of sets	t-value	corresponding probability
Nymphs				
k_{24}	-0.000187+0.0000256xTP	11	3.7172	$0.001 < P < 0.01$**
k_{48}	0.057+0.0063xTP	11	8.4124	$P < 0.001$***
k_{47}	0.011+0.0046xHR	12	8.6384	$P < 0.001$***
μ	-0.01+0.0011xTR	8	2.8925	$0.02 < 0 < 0.05$*
	-0.819+0.0411xTR	2	-	
Adults				
k_{25}	-0.00128+0.0000894xTP	11	4.2319	$0.001 < P < 0.01$**
k_{58}	-0 124+0.015xTP	11	29.5097	$P < 0.001$****
k_{57}	0.013+0.0038xTP	12	4.5836	$P \approx 0.001$***
k_{56}	-0.00089+0.00358xOI	6	2.3175	$P \approx 0.05$*
	-0.1125+0.133xOI	12	5.8352	$P < 0.001$***

TABLE 10. A X^2-test between empirical and simulated compartment values for 1966-69. The k-values were corrected on the basis of 1969 year's data, so the compartment values for 1966-68 are predicted on the basis of the variation in k-values with environmental factors. The nymph and adult biomass compartments were tested for actual values as per cent of simulated values (2). In 1967 the regression coefficient for k_{24} was changed (1).

Year	Compartment	X^2-value	d.f.	Corresponding probability
1969	nymph biomass$^{(2)}$	6.68	12	$0.8 < P < 0.9$
	adult biomass$^{(2)}$	28.55	8	$P \approx 0.0005$***
	macr. indiv. biomass	8.77	7	$0.2 < P < 0.3$
	mortality	4.63	13	$0.975 < P < 0.99$
	losses (defaec. + resp.)	4.33	13	$0.975 < P < 0.99$
1968	nymph biomass$^{(2)}$	47.4	14	$P < 0.0005$***
	adult biomass$^{(2)}$	10.8	9	$P \approx 0.3$
	macr. indiv. biomass	7.17	7	$0.3 < P < 0.5$
	mortality	8.3	14	$0.8 < P < 0.9$
	losses (defaec. + resp.)	6.06	14	$0.95 < P < 0.975$
1967$^{(1)}$	nymph biomass$^{(2)}$	102.0	11	$P < 0.0005$***
	adult biomass$^{(2)}$	257.3	9	$P < 0.0005$***
	macr. indiv. biomass	1.64	8	$P \approx 0.99$
	mortality	9.12	11	$0.5 < P < 0.7$
	losses (defaec. + resp.)	15.06	13	$P \approx 0.3$
1966	nymph biomass$^{(2)}$	103.6	14	$P < 0.005$***
	adult biomass$^{(2)}$	58.3	8	$P < 0.0005$***
	macr. indiv. biomass	17.58	10	$0.05 < P < 0.1$
	mortality	3.2	11	$P \approx 0.99$
	losses (defaec. + resp.)	3.74	12	$P \approx 0.99$

APPENDIX I.



Preliminary Program.

Numbers in brackets = weeks.
Double lines = studies performed simultaneously
Dotted lines = Likely some progress.

Appendix II

The different FOCAL programmes developed on a PDP-8/I computer used in constructing the models (I-III, V). Programme I is used for Models I and II, programme II for Model III, and Programmes III-VI for Model V for different years.

Programme I

The programme runs through the main subroutine (2), having asked for the relevant parameter values and some compartment values for each period between sample days. A list of the different parameter values used for Models I and II is given in Table 1 and 2. The programme will print out the values of the compartments for each day, and stops after executing one sample period. After that, all the parameter values have to be re-entered before running through a new period between sample days.

Programme II

Before entering the programme, the initial conditions of the compartment values have to be stated outside the programme, which can be done through a number of SET-statements. This performance has the advantage that the programme can be stopped at any stage, and started again from the same stage. The k-factors which have to be entered outside the main programme are k_{64} and k_{45}. Furthermore, it is preferable to put all k-values equal to zero when entering the initial conditions, since some variabiles may be stored in FOCAL although the programme is erased.

It is most convenient to run the programme in the following sequence of steps:

No. of days	starting day	changed conditions
		SET A2 = 0.; SET B = 0.; SET C = 0.; SET D1 = 0.; SET D2 = 0.; SET E = 0.; SET G = 0.; SET J = 0.0036 SET L2 = 0.; SET M2 = 0. SET K1 = 0.
26	136	
		SET L2 = 0.01; SET E = 1.3
38	163	
		SET L2 = 0.; SET E = 0.; SET M2 = 0.036; SET K1 = 0.026
31	202	
		SET B = 0.; SET M2 = 0.
60	234	
		Season ends

Programme III-VI

The programmes work in the same way as explained for programme II. The initial conditions of the compartments has to be put up before entering the programme routine, in the way explained in Appendix III. This appendix also gives a complete list of environmental factors used for each of the years. The values of the environmental factors are entered through subroutine 6 for each sample period.

The programme prints out the data for each daily step the programme is executed, as the number of days passed from the beginning of the year. The values of the compartments are only printed out at the end of the periods chosen, as a matter of convenience.

Programme VII

This programme contains an extra subroutine (9) for using random number generator, as compared with programme III. This random number is asked for at each run of the main subroutine (2), and a sequence of random numbers could then be used for the periods between sample days. After executing one sample period, the programme jumps automatically to the next period, in which case the user should print "2" for NUMBER OF ITERATIONS. If some variables have to be changed outside the main programme, control returns to the user by printing "1" for NUMBERS OF ITERATIONS.

Programme I.

```
*******************
C-FOCAL,1969

01.01 TYPE "STEPWISE ENERGY FLOW",!
01.02 ASK "J"J; ASK "K1"K1; ASK "A1"A1
01.03 ASK "K2"K2; ASK "L1"L1
01.04 ASK "L2"L2; ASK "M1"M1
01.05 ASK "M2"M2; ASK "R1"R1; ASK "R3"R3
01.06 ASK "R2"R2; ASK "P1"P1
01.07 ASK "P2"P2; ASK "SUN RAD"A1
01.08 ASK "NUMBER OF DAYS"N,!; ASK "E"E,!
01.09 FOR I=1,1,N; DO 02.
01.20 TYPE !!; QUIT

02.01 SET Z=I
02.02 TYPE %2,"DAYS"I
02.03 SET A2=A2+J*A1-M1*A2-L1*A2-M1*A2
02.04 TYPE %7.04,"A2"A2,!
02.05 SET A3=A3+K1*A2-K2*A3
02.06 TYPE %7.04,"A3"A3
02.07 SET B=B+L2*E+L1*A2-M2*B-P2*B-P1*B
02.08 TYPE %7.04,"B"B,!
02.09 SET C=C+M1*A2+M2*B-R2*C-R1*C-R3*C
02.10 TYPE %7.04,"C"C
02.11 SET D1=D1+P1*B+R1*C
02.12 TYPE %7.04,"D1"D1,!
02.13 SET D2=D2+R2*C+P2*B
02.14 TYPE %7.04,"D2"D2
02.15 SET E=E+R3*C-L2*E
02.16 TYPE %7.04,"E"E,!
02.20 RETURN
*************************
```

NOTATIONS:

K12 = J
K23 = K1
K2A = L1
K25 = M1
K39 = K2
K45 = M2
K47 = P2
K48 = P1
K56 = R3
K57 = R2
K58 = R1
K64 = L2

Programme II.

```
@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
C-FOCAL,1969

01.01 TYPE "FLOW MODEL WITH TRANSFER TO MACROPTEROUS ADULTS",!
01.02 ASK "NUMBER OF DAYS"N; ASK "STARTING DAY"V,!!
01.08 FOP I=V,1,V+N; DO 2.
01.10 T %7.04,"SUN RAD"A1,"A2"A2,"A3"A3,!,"B"B,"C"C,!
01.12 T %7.04,"D1"D1,"D2"D2,!,"E"E,"G"G,!!
01.14 QUIT

02.01 SET Z=I; TYPE %3,"DAYS"I,!
02.03 SET Y=0.211*6.2832*(1.-FCOS<6.2832*I/365>)
02.05 SET A1=1500.+Y*1500.
02.08 DO 3.
02.09 SET A2=A2+J*A1-K1*A2-L1*A2*D-M1*A2*C-S2*A2*G
02.11 DO 4.
02.12 SET A3=A3+K1*A2-K2*A3
02.14 SET L2=L2+0.12*L2
02.15 SET B=B+L2*E+L1*A2*B-M2*B-P2*B-P1*B-S1*B*C
02.17 SET M2=M2+0.086*M2
02.18 DO 5.
02.19 SET C=C+M1*A2*C+M2*B-R1*C-R2*C-R3*C
02.22 SET D1=D1+P1*B+R1*C+Q1*G
02.25 SET D2=D2+R2*C+P2*B+Q2*G
02.28 SET E=E+R3*C-L2*E+Q4*G
02.31 SET G=G+S1*B*C+S2*A2*G-Q1*G-Q2*G-Q3*G-Q4*G
02.32 RETURN

03.01 IF (A2-540.) 03.03, 03.10, 03.10
03.03 RETURN
03.10 IF (A2-1300.) 03.12, 03.20 . 03.20
03.12 SET L1=0.000163; SET P1=0.15; SET J=0.0036
03.13 SET P2=0.0151; RETURN
03.20 SET K1=0.026; SET M1=0.00018
03.21 SET R1=0.13; SET R2=0.017; RETURN

04.01 IF (A3-1420.) 04.02, 04.02, 04.10
04.02 SET K2=0.; RETURN
04.10 SET K2=0.006; SET J=0.0006; RETURN

05.01 IF (C-2.0) 05.02, 05.02, 05.10
05.02 RETURN
05.10 IF (C-4.0) 05.12, 05.12, 05.20
05.12 SET S1=0.036; SET S2=0.00025; SET Q1=0.17
05.13 SET 02=0.016; RETURN
05.20 SET Q3=0.1; SET Q4=0.02; SET R3=0.02; RETURN
*@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
```

NOTATIONS:

```
K12 = J     K23 = K1    K24 = L1    K25 = M1    K29 = S2
K30 = K2    K45 = M2    K47 = P2    K48 = P1    K49 = S1
K56 = R3    K57 = R2    K58 = R1    K64 = L2    K97 = Q2
K98 = 01    K96 = Q4    K93 = Q3
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@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
C-8K FOCAL @1969

01.01 TYPE "FLOW MODEL WITH TRANSFER TO MACROPTEROUS ADULTS",!
01.02 ASK "NUMBER OF DAYS"N; ASK "STARTING DAY"V,!!
01.06 FOR I=V,N,V+N; DO 6.
01.08 FOR I=V,1,V+N; DO 2.
01.10 T %7.04,"SUN RAD"A1,"A2"A2,"A3"A3,!,"B"B,"C"C,!
01.12 T %7.04,"D1"D1,"D2"D2,!,"E"E,"G"G,!!
01.14 QUIT

02.01 SET Z=I; TYPE %3,"DAYS"I,!
02.03 SET Y=0.211*6.2832*(1.-FCOS<6.2832*I/365>)
02.05 SET A1=1500.+Y*1500.
02.09 SET A2=A2+J*A1-K1*A2-L1*A2-M1*A2-S2*A2
02.12 SET A3=A3+K1*A2-K2*A3
02.14 SET L2=L2+0.12*L2
02.15 SET B=B+L2*E+L1*A2-M2*B-P2*B-P1*B-S1*B*C
02.17 SET M2=M2+0.086*M2
02.18 DO 5.
02.19 SET C=C+M1*A2+M2*B-R1*C-R2*C-R3*C
02.22 SET D1=D1+P1*B+R1*C+Q1*G
02.25 SET D2=D2+R2*C+P2*B+Q2*G
02.28 SET E=E+R3*C-L2*E+Q4*C
02.31 SET G=G+S1*B*C+S2*A2-Q1*G-Q2*G-Q3*G-Q4*G
02.32 RETURN

04.03 IF (A3-1250.) 04.05, 04.05, 04.10
04.05 SET R3=0.; SET Q4=0.; RETURN
04.10 IF (OI-0.87) 04.12, 04.12, 04.15
04.12 SET R3=-0.0089+0.0358*OI; SET Q4=R3; RETURN
04.15 SET R3=-0.1125+0.133*OI; SET Q4=R3; RETURN

05.01 IF (C-2.0) 05.02, 05.10, 05.10
05.02 SET S1=0.; SET Q3=0.; RETURN
05.10 IF (C-4.0) 05.12, 05.20, 05.20
05.12 SET S1=0.03; RETURN
05.20 SET Q3=0.1; RETURN

06.02 ASK "TEMP"TP; T !; ASK "RAIN"HR; T !
06.03 ASK "INDEX"OI; T !
06.05 IF (B) 06.07, 06.07, 06.10
06.07 SET L1=0.; GOTO 06.13
06.10 SET L1=-0.000187+0.0000256*TP
06.13 SET P1=0.057+0.0063*TP
06.15 SET R1=-0.124+0.015*TP
06.17 SET Q1=-0.124+0.015*TP
06.19 SET P2=0.011+0.0046*HR
06.21 SET R2=0.013+0.0038*HR
06.23 SET Q2=0.013+0.004*HR
06.25 IF (C) 06.30, 06.30, 06.27
06.27 IF (C-2.0) 06.28, 06.28, 06.31
06.28 IF (TP-15) 06.29, 06.29, 06.35
06.29 SET M1=0.00005; RETURN
06.30 SET M1=0.; SET S2=0.; RETURN
06.31 IF (TP-15) 06.32, 06.32, 06.33
06.32 SET S2=0.00005; SET M1=0.00005; RETURN
06.33 SET S2=0.0001; SET M1=-0.00128+0.0000894*TP
06.34 RETURN
06.35 SET M1=-0.00128+0.0000894*TP; RETURN
*@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
```

NOTATIONS:

K12 = J   K23 = K1   K24 = L1   K25 = M1   K89 = S2
K30 = K2   K45 = M2   K47 = P2   K48 = P1   K49 = S1
K56 = R3   K57 = R2   K58 = R1   K64 = L2   K97 = Q2
K98 = Q1   K96 = Q4   K93 = Q3

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C-8K FOCAL @1969

01.01 TYPE "FLOW MODEL WITH TRANSFER TO MACROPTEROUS ADULTS",!
01.02 ASK "NUMBER OF DAYS"N; ASK "STARTING DAY"V,!!
01.06 FOR I=V,N,V+N; DO 6.
01.08 FOR I=V,1,V+N; DO 2.
01.10 T %7.04,"SUN RAD"A1,"A2"A2,"A3"A3,!,"B"B,"C"C,!
01.12 T %7.04,"D1"D1,"D2"D2,!,"E"E,"G"G,!!
01.14 QUIT

02.01 SET Z=I; TYPE %3,"DAYS"I,!
02.03 SET Y=0.211*6.2832*(1.-FCOS<6.2832*I/365>)
02.05 SET A1=1500.+Y*1500.
02.09 SET A2=A2+J*A1-K1*A2-L1*A2-M1*A2-S2*A2
02.10 DO 4.
02.12 SET A3=A3+K1*A2-K2*A3
02.14 SET L2=L2+0.12*L2
02.15 SET B=B+L2*E+L1*A2-M2*B-P2*B-P1*B-S1*B*C
02.17 SET M2=M2+0.086*M2
02.18 DO 5.
02.19 SET C=C+M1*A2+M2*B-R1*C-R2*C-R3*C
02.22 SET D1=D1+P1*B+R1*C+Q1*G
02.25 SET D2=D2+R2*C+P2*B+Q2*G
02.28 SET E=E+R3*C-L2*E+Q4*G
02.31 SET G=G+S1*B*C+S2*A2-Q1*G-Q2*G-Q3*G-Q4*G
02.32 RETURN

04.03 IF (A3-1171.) 04.05, 04.05, 04.10
04.05 SET R3=0.; SET Q4=0.; RETURN
04.10 IF (OI-0.87) 04.12, 04.12, 04.15
04.12 SET R3=-0.0089+0.0358*OI; SET Q4=R3; RETURN
04.15 SET R3=-0.1125+0.133*OI; SET Q4=R3; RETURN

05.01 IF (C-1.4) 05.02, 05.10, 05.10
05.02 SET S1=0.; SET Q3=0.; RETURN
05.10 IF (C-2.0) 05.12, 05.20, 05.20
05.12 SET S1=0.03; RETURN
05.20 SET Q3=0.1; RETURN

06.02 ASK "TEMP"TP; T !; ASK "RAIN"HR; T !
06.03 ASK "INDEX"OI; T !
06.05 IF (B) 06.07, 06.07, 06.10
06.07 SET L1=0.; GOTO 06.13
06.10 SET L1=-0.000187+0.0000256*TP
06.13 SET P1=0.057+0.0063*TP
06.15 SET R1=-0.124+0.015*TP
06.17 SET Q1=-0.124+0.015*TP
06.19 SET P2=0.011+0.0046*HR
06.21 SET R2=0.013+0.0038*HR
06.23 SET Q2=0.013+0.004*HR
06.25 IF (C) 06.30, 06.30, 06.27
06.27 IF (C-1.4) 06.28, 06.28, 06.31
06.28 IF (TP-15) 06.29, 06.29, 06.35
06.29 SET M1=0.00005; RETURN
06.30 SET M1=0.; SET S2=0.; RETURN
06.31 IF (TP-15) 06.32, 06.32, 06.33
06.32 SET S2=0.00005; SET M1=0.00005; RETURN
06.33 SET S2=0.0001; SET M1=-0.00128+0.0000894*TP
06.34 RETURN
06.35 SET M1=-0.00128+0.0000894*TP; RETURN
*@@@@@@@@@@@@@@@@@@@@@@@@@@@@
```

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@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
C-8K FOCAL @1969

01.01 TYPE "FLOW MODEL WITH TRANSFER TO MACROPTEROUS ADULTS",!
01.02 ASK "NUMBER OF DAYS"N; ASK "STARTING DAY"V,!!
01.06 FOR I=V,N,V+N; DO 6.
01.08 FOR I=V,1,V+N; DO 2.
01.10 T %7.04,"SUN RAD"A1,"A2"A2,"A3"A3,!,"B"B,"C"C,!
01.12 T %7.04,"D1"D1,"D2"D2,!,"E"E,"G"G,!!
01.14 QUIT

02.01 SET Z=I; TYPE %3,"DAYS"I,!
02.03 SET Y=0.211*6.2832*(1.-FCOS<6.2832*I/365>)
02.05 SET A1=1500.+Y*1500.
02.09 SET A2=A2+J*A1-K1*A2-L1*A2-M1*A2-S2*A2
02.10 DO 4.
02.12 SET A3=A3+K1*A2-K2*A3
02.14 SET L2=L2+0.12*L2
02.15 SET B=B+L2*E+L1*A2-M2*B-P2*B-P1*B-S1*B*C
02.17 SET M2=M2+0.085*M2
02.18 DO 5.
02.19 SET C=C+M1*A2+M2*B-R1*C-R2*C-R3*C
02.22 SET D1=D1+P1*B+R1*C+Q1*G
02.25 SET D2=D2+R2*C+P2*B+Q2*G
02.28 SET E=E+R3*C-L2*E+Q4*G
02.31 SET G=G+S1*B*C+S2*A2-Q1*G-Q2*G-Q3*G-Q4*G
02.32 RETURN

04.03 IF (A3-1250.) 04.05, 04.05, 04.10
04.05 SET R3=0.; SET Q4=0.; RETURN
04.10 IF (OI-0.87) 04.12, 04.12, 04.15
04.12 SET R3=-0.0089+0.0358*OI; SET Q4=R3; RETURN
04.15 SET R3=-0.1125+0.133*OI; SET Q4=R3; RETURN

05.01 IF (C-2.5) 05.02, 05.10, 05.10
05.02 SET S1=0.; SET Q3=0.; RETURN
05.10 IF (C-3.0) 05.12, 05.20, 05.20
05.12 SET S1=0.03; RETURN
05.20 SET Q3=0.1; RETURN

06.02 ASK "TEMP"TP; T !; ASK "RAIN"HR; T !
06.03 ASK "INDEX"OI; T !
06.05 IF (B) 06.07, 06.07, 06.10
06.07 SET L1=0.; GOTO 06.13
06.10 SET L1=-0.000187+0.0000256*TP
06.13 SET P1=0.057+0.0063*TP
06.15 SET R1=-0.124+0.015*TP
06.17 SET Q1=-0.124+0.015*TP
06.19 SET P2=0.011+0.0046*HR
06.21 SET R2=0.013+0.0033*HR
06.23 SET Q2=0.013+0.004*HR
06.25 IF (C) 06.30, 06.30, 06.27
06.27 IF (C-2.5) 06.28, 06.28, 06.31
06.28 IF (TP-15) 06.29, 06.29, 06.35
06.29 SET M1=0.00005; RETURN
06.30 SET M1=0.; SET S2=0.; RETURN
06.31 IF (TP-15) 06.32, 06.32, 06.33
06.32 SET S2=0.00005; SET M1=0.00005; RETURN
06.33 SET S2=0.0001; SET M1=-0.00128+0.0000394*TP
06.34 RETURN
06.35 SET M1=-0.00128+0.0000394*TP; RETURN

*@@@@@@@@@@@@@@@@@@@@@@@@
```

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L
@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
C-8K FOCAL @1969

01.01 TYPE "FLOW MODEL WITH TRANSFER TO MACROPTEROUS ADULTS",!
01.02 ASK "NUMBER OF DAYS"N; ASK "STARTING DAY"V,!!
01.06 FOR I=V,N,V+N; DO 6.
01.08 FOR I=V,1,V+N; DO 2.
01.10 T %7.04,"SUN RAD"A1,"A2"A2,"A3"A3,!,"B"B,"C"C,!
01.12 T %7.04,"D1"D1,"D2"D2,!,"E"E,"G"G,!!
01.14 QUIT

02.01 SET Z=I; TYPE %3,"DAYS"I,!
02.03 SET Y=0.211*6.2832*(1.-FCOS<6.2832*I/365>)
02.05 SET A1=1500.+Y*1500.
02.09 SET A2=A2+J*A1-K1*A2-L1*A2-M1*A2-S2*A2
02.10 DO 4.
02.12 SET A3=A3+K1*A2-K2*A3
02.14 SET L2=L2+0.12*L2
02.15 SET B=B+L2*E+L1*A2-M2*B-P2*B-P1*B-S1*B*C
02.17 SET M2=M2+0.086*M2
02.18 DO 5.
02.19 SET C=C+M1*A2+M2*B-R1*C-R2*C-R3*C
02.22 SET D1=D1+P1*B+R1*C+Q1*G
02.25 SET D2=D2+R2*C+P2*B+Q2*G
02.28 SET E=E+R3*C-L2*E+Q4*G
02.31 SET G=G+S1*B*C+S2*A2-Q1*G-Q2*G-Q3*G-Q4*G
02.32 RETURN

04.03 IF (A3-1000.) 04.05, 04.05, 04.10
04.05 SET R3=0.; SET Q4=0.; RETURN
04.10 IF (OI-0.07) 04.12, 04.12, 04.15
04.12 SET R3=-0.0089+0.0358*OI; SET Q4=R3; RETURN
04.15 SET R3=-0.1125+0.133*OI; SET Q4=R3; RETURN

05.01 IF (C-1.2) 05.02, 05.10, 05.10
05.02 SET S1=0.; SET Q3=0.; RETURN
05.10 IF (C-3.0) 05.12, 05.20, 05.20
05.12 SET S1=0.03; RETURN
05.20 SET Q3=0.1; RETURN

06.02 ASK "TEMP"TP; T !; ASK "RAIN"HR; T !
06.03 ASK "INDEX"OI; T !
06.05 IF (B) 06.07, 06.07, 06.10
06.07 SET L1=0.; GOTO 06.13
06.10 SET L1=-0.000187+0.0000256*TP
06.13 SET P1=0.057+0.0065*TP
06.15 SET R1=-0.124+0.015*TP
06.17 SET Q1=-0.124+0.015*TP
06.19 SET P2=0.011+0.0046*HR
06.21 SET R2=0.013+0.0038*HR
06.23 SET Q2=0.013+0.004*HR
06.25 IF (C) 06.30, 06.30, 06.27
06.27 IF (C-1.0) 06.28, 06.28, 06.31
06.28 IF (TP-15) 06.29, 06.29, 06.35
06.29 SET M1=0.00005; RETURN
06.30 SET M1=0.; SET S2=0.; RETURN
06.31 IF (TP-15) 06.32, 06.32, 06.33
06.32 SET S2=0.00005; SET M1=0.00005; RETURN
06.33 SET S2=0.0001; SET M1=-0.00128+0.0000894*TP
06.34 RETURN
06.35 SET M1=-0.00128+0.0000894*TP; RETURN

*@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
```

PROGRAMME VII: STOCHASTIC VERSION

```
@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
C-8K FOCAL @1969

01.01 TYPE "FLOW MODEL WITH TRANSFER TO MACROPTEROUS ADULTS",!
01.02 ASK "NUMBER OF DAYS"N; ASK "STARTING DAY"V,!!
01.03 ASK "NUMBER OF ITERATIONS"TZ; T !
01.05 SET TA=1
01.06 FOR I=V,N,V+N; DO 6.
01.07 FOR X=TA; DO 9.
01.08 FOR I=V,1,V+N; DO 2.
01.10 T %7.04,"SUN RAD"A1,"A2"A2,"A3"A3,!,"B"B,"C"C,!
01.12 T %7.04,"D1"D1,"D2"D2,!,"E"E,"G"G,!!
01.14 SET TA=TA+1
01.16 IF (TZ-TA) 01.25, 01.19, 01.19
01.19 GOTO 01.02
01.25 QUIT

02.01 SET Z=I; TYPE %3,"DAYS"I,!
02.03 SET Y=0.211*6.2832*(1.-FCOS<6.2832*I/365>)
02.05 SET A1=1500.+Y*1500.
02.09 SET A2=A2+J*A1-K1*A2-L1*A2-M1*A2-S2*A2
02.10 DO 4.
02.12 SET A3=A3+K1*A2-K2*A3
02.14 SET L2=L2+0.12*L2
02.15 SET B=B+L2*E+L1*A2-M2*B-P2*B-P1*B-S1*B*C
02.17 SET M2=M2+0.086*M2
02.18 DO 5.
02.19 SET C=C+M1*A2+M2*B-R1*C-R2*C-R3*C
02.22 SET D1=D1+P1*B+R1*C+Q1*G
02.25 SET D2=D2+R2*C+P2*B+Q2*G
02.28 SET E=E+R3*C-L2*E+Q4*G
02.31 SET G=G+S1*B*C+S2*A2-Q1*G-Q2*G-Q3*G-Q4*G
02.32 RETURN

04.03 IF (A3-1250.) 04.05, 04.05, 04.10
04.05 SET R3=0.; SET Q4=0.; RETURN
04.10 IF (OI-0.87) 04.12, 04.12, 04.15
04.12 SET R3=-0.0089+0.0358*OI; SET Q4=R3; RETURN
04.15 SET R3=-0.1125+0.133*OI; SET Q4=R3; RETURN

05.01 IF (C-2.0) 05.02, 05.10, 05.10
05.02 SET S1=0.; SET Q3=0.; RETURN
05.10 IF (C-4.0) 05.12, 05.20, 05.20
05.12 SET S1=0.03; RETURN
05.20 SET Q3=0.1; RETURN
```

```
06.02 ASK "TEMP"TP; T !; ASK "RAIN"HP; T !
06.03 ASK "INDEX"OI; T !
06.13 SET P1=0.057+0.0063*TP
06.15 SET R1=-0.124+0.015*TP
06.17 SET Q1=-0.124+0.015*TP
06.19 SET P2=0.011+0.0046*HR
06.21 SET R2=0.013+0.0038*HR
06.23 SET Q2=0.013+0.004*HR
06.27 IF (C-2.0) 06.28, 06.28, 06.31
06.28 SET S2=0.; RETURN
06.31 IF (TP-15) 06.32, 06.32, 06.33
06.32 SET S2=0.00005; RETURN
06.33 SET S2=0.0001; RETURN

09.03 ASK "WX"WX; ASK "WY"WY; T !
09.05 ASK "UX"UX; ASK "UY"UY; T !
09.06 IF (B) 09.07, 09.07, 09.08
09.07 SET L1=0.; GOTO 09.09
09.08 SET L1=(-0.000257+WX*0.00014)+(0.00001+WY*0.0000312)*TP
09.09 IF (C) 09.10, 09.10, 09.15
09.10 SET M1=0.; RETURN
09.15 IF (TP-15) 09.16, 09.16, 09.20
09.16 SET M1=0.00005; RETURN
09.20 SET M1=(-0.00153+UX*0.0005)+(0.0000416+UY*0.000096)*TP
09.21 RETURN
*●●●●●●●●●●●●●●●●●●●●●●●●●●●●●●●●●●●
```

NOTATIONS:

K12 = J K23 = K1 K24 = L1 K25 = M1 K29 = S2
K30 = K2 K45 = M2 K47 = P2 K48 = P1 K49 = S1
K56 = R3 K57 = R2 K58 = R1 K64 = L2 K97 = Q2
K98 = Q1 K96 = Q4 K93 = Q3
WX = LOWER CONFIDENCE FOR Y-INTEPCEPT
WY = RANGE OF VARIATION FOR Y-INTERCEPT OF K24
UX = LOWER CONFIDENCE FOR REGRESSION COEFFICIENT OF K24
UY = RANGE OF VARIATION FOR REGRESSION COEFFICIENT OF K24

Appendix III

Listing of environmental factors used for correcting the k-values: mean temperature of preceeding period counted from sample day (TP), mean value of rainfall per day on preceeding period (HR), and index = temperature x % rainy days (OI).

The programme can be started from the beginning of the grasshopper population season, using the initial values for standing crop of vegetation, egg energy input, and transfer coefficient k_{24}. If some variables have to be changed outside the main programme, this is noted by a number of SET-statements in the list.

YEAR 1969

no. of days	starting day	TP	HR	OI	changed conditions
					SET A2 = 552.133 SET E = 1.3 SET J = 0.0036 SET L2 = 0.01
5	163	12.0	0.7	0.	
5	169	14.4	0.	0.	
5	175	15.9	0.	0.	
10	181	16.0	0.4	0.	
3	192	14.1	0.9	0.	
3	196	13.6	5.3	0.	
					SET E = 0.; SET L2 = 0. SET M2 = 0.036 SET K1 = 0.026
3	200	16.2	0.	0.	
3	204	18.8	0.	0.	
3	208	18.1	0.6	0.	
3	212	18.1	0.6	0.	
2	216	18.1	0.	0.	
4	219	17.5	0.	0.	
3	224	19.5	2.1	0.	
3	228	21.1	0.	0.	
7	232	22.0	0.9	0.	
					SET B = 0.; SET M2 = 0.
7	240	16.2	0.	0.	
					SET J = 0.006
11	248	15.9	0.2	1.36	
9	260	16.5	2.9	0.96	
9	270	14.	3.0	0.7	
10	280	11.	0.9	0.77	
9	291	8.5	7.6	0.28	

YEAR 1968

no. of days	starting day	TP	HR	OI	changed conditions
					SET A2 = 514.0747 SET E = 1.0 SET J = 0.0039 SET L2 = 0.01
6	159	12.9	1.6	0.	
2	166	15.2	0.	0.	
4	169	19.6	0.	0.	
3	174	15.1	0.1	0.	
3	178	15.9	0.	0.	
2	182	13.8	2.7	0.	
3	185	16.1	2.2	0.	
5	189	15.0	0.	0.	
					SET E = 0.; SET L2 = 0. SET M2 = 0.036 SET K1 = 0.026
1	195	13.3	0.	0.	
6	197	12.3	2.6	0;	
2	204	13.8	5.3	0.	
4	207	15.0	0.3	0.	
6	212	13.7	0.2	0.	
5	219	14.0	2.9	0.	

1968 (Cont.)

no. of days	starting day	TP	HR	OI	changed conditions
4	225	14.2	2.3	0.	
6	230	14.1	2.1	0.	
					SET B = 0.; SET M2 = 0.
4	237	16.6	1.7	0.875	
9	242	16.2	0.1	0.875	
9	252	18.	0.5	0.9	
					SET J = 0.0006
9	262	19.2	4.1	1.152	
10	272	18.2	4.7	1.0	
9	283	16.0	2.3	0.96	

YEAR 1967

					SET A2 = 819.8881 SET E = 1.2 SET J = 0.0053 SET L2 = 0.01
9	158	11.8	2.3	0.	
5	168	15.5	0.1	0.	
3	174	13.5	1.1	0.	
6	178	16.5	0.	0.	
3	185	14.1	2.0	0.	
3	189	18.6	0.	0.	
					SET E = 0.; SET L2 = 0. SET M2 = 0.036 SET K1 = 0.028 SET J = 0.0014
3	193	14.9	0.	0.	
3	197	17.9	0.3	0.	
4	201	18.6	0.	0.	
3	206	17.8	0.	0.	
5	210	16.8	0.2	0.	
16	216	21.2	0.	0.4	
3	233	13.8	1.1	1.17	
3	237	12.5	5.9	1.17	
					SET B = 0.; SET M2 = 0.
3	241	12.9	6.7	1.17	
10	245	13.1	1.4	1.26	
					SET J = 0.0005
6	256	15.	5.8	1.35	
9	263	13.	1.5	0.39	
10	273	11.	0.	0.66	
9	284	8.5	3.4	0.6	

YEAR 1966

no. of days	starting day	TP	HR	OI	changed conditions
					SET A2 = 489.6745 SET E = 1.31 SET J = 0.0036 SET L2 = 0.01
5	158	9.7	1.5	0.	
2	164	14.4	0.	0.	
1	167	15.9	0.	0.	
7	169	14.8	0.	0.	
2	177	16.7	0.2	0.	
2	180	15.8	0.	0.	
4	183	15.	0.7	0.	
3	188	22.	0.	0.	
					SET E * 0.; SET L2 = 0. SET M2 = 0.036 SET K1 = 0.025 SET J = 0.0017
4	192	21.	0.	0.	
4	197	21.	1.3	0.	
3	202	16.4	0.8	0.	
4	206	19.4	3.3	0.	
3	211	20.5	7.8	0.	
3	215	22.0	1.9	0.	
3	219	19.6	0.2	0.	
9	223	16.0	2.1	0.	
9	233	15.0	1.2	0.	
					SET B = 0.; SET M2 = 0.
9	243	16.0	0.2	1.4	
9	153	14.	0.	1.4	
					SET J = 0.0008
9	263	15.	3.6	1.05	
10	273	12.	2.4	1.08	
9	284	9.	1.8	0.63	

FIG. 1 STEPWISE ENERGY FLOW, MODEL I AND II

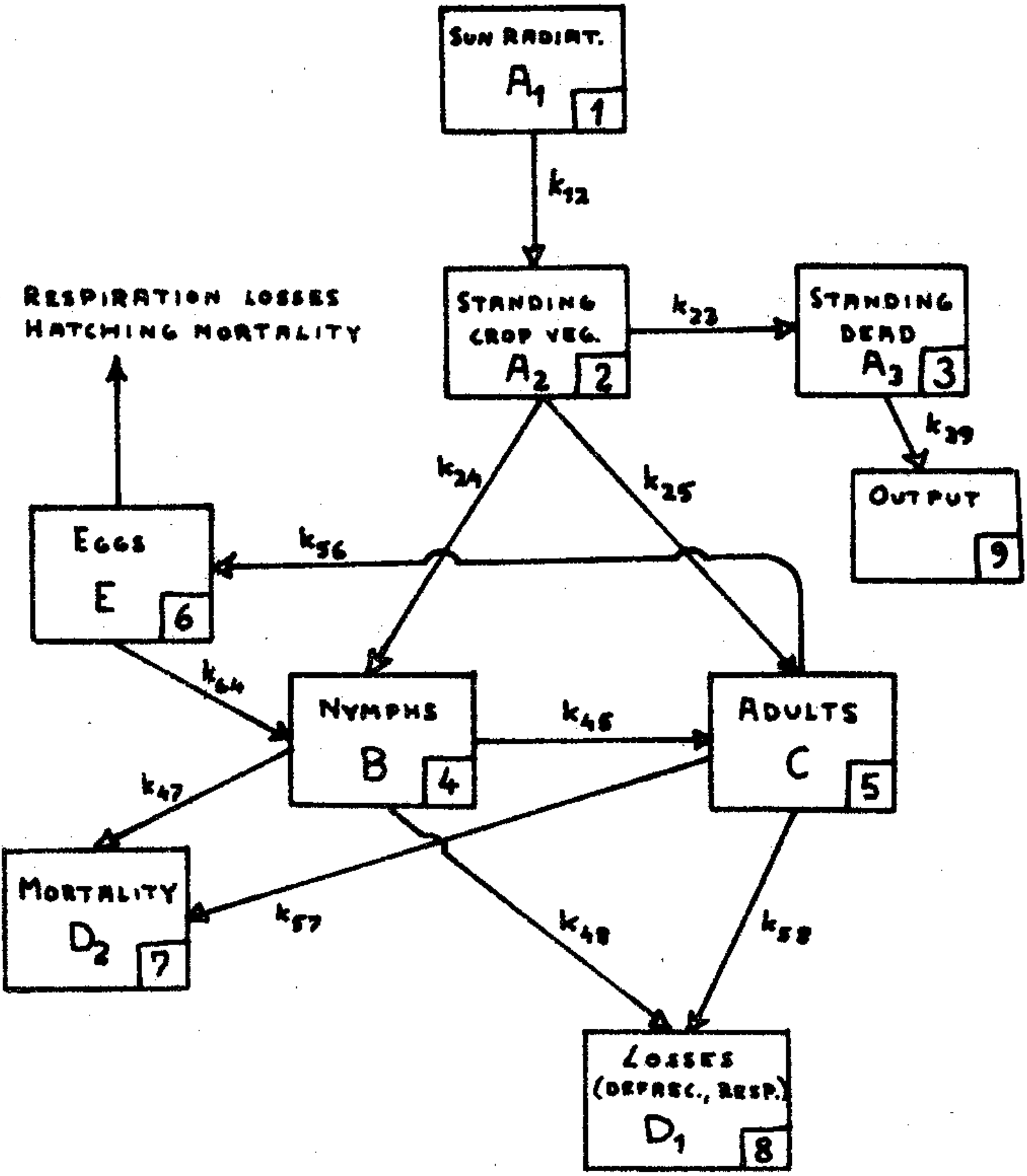


FIG. 2

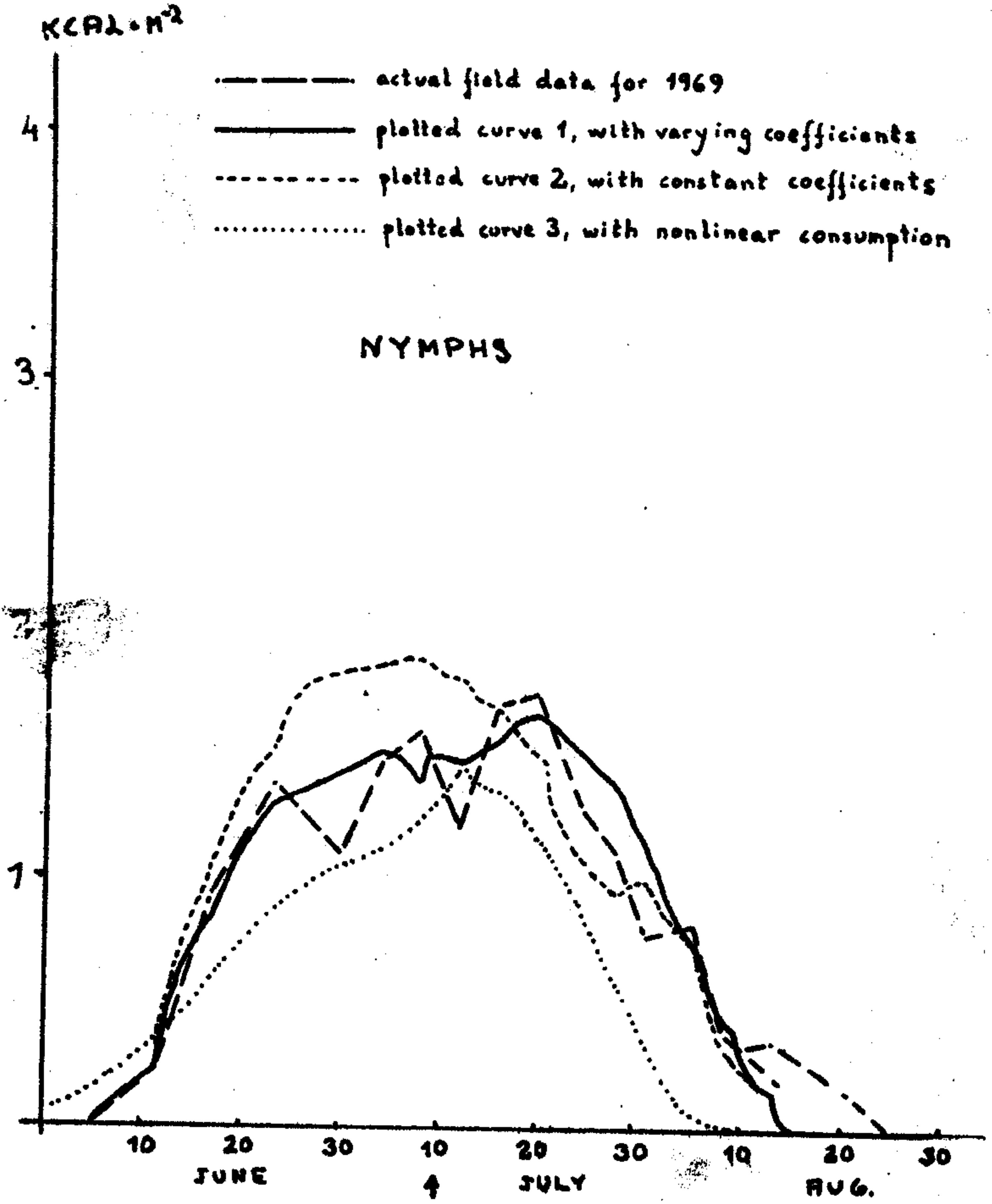

KCAL·M-2
actual field data for 1969
plotted curve 1, with varying coefficients
plotted curve 2, with constant coefficients
plotted curve 3, with nonlinear consumption
NYMPHS
4
3
2
1
10
20
30
10
20
30
10
20
30
JUNE
JULY
AUG.

FIG. 2b

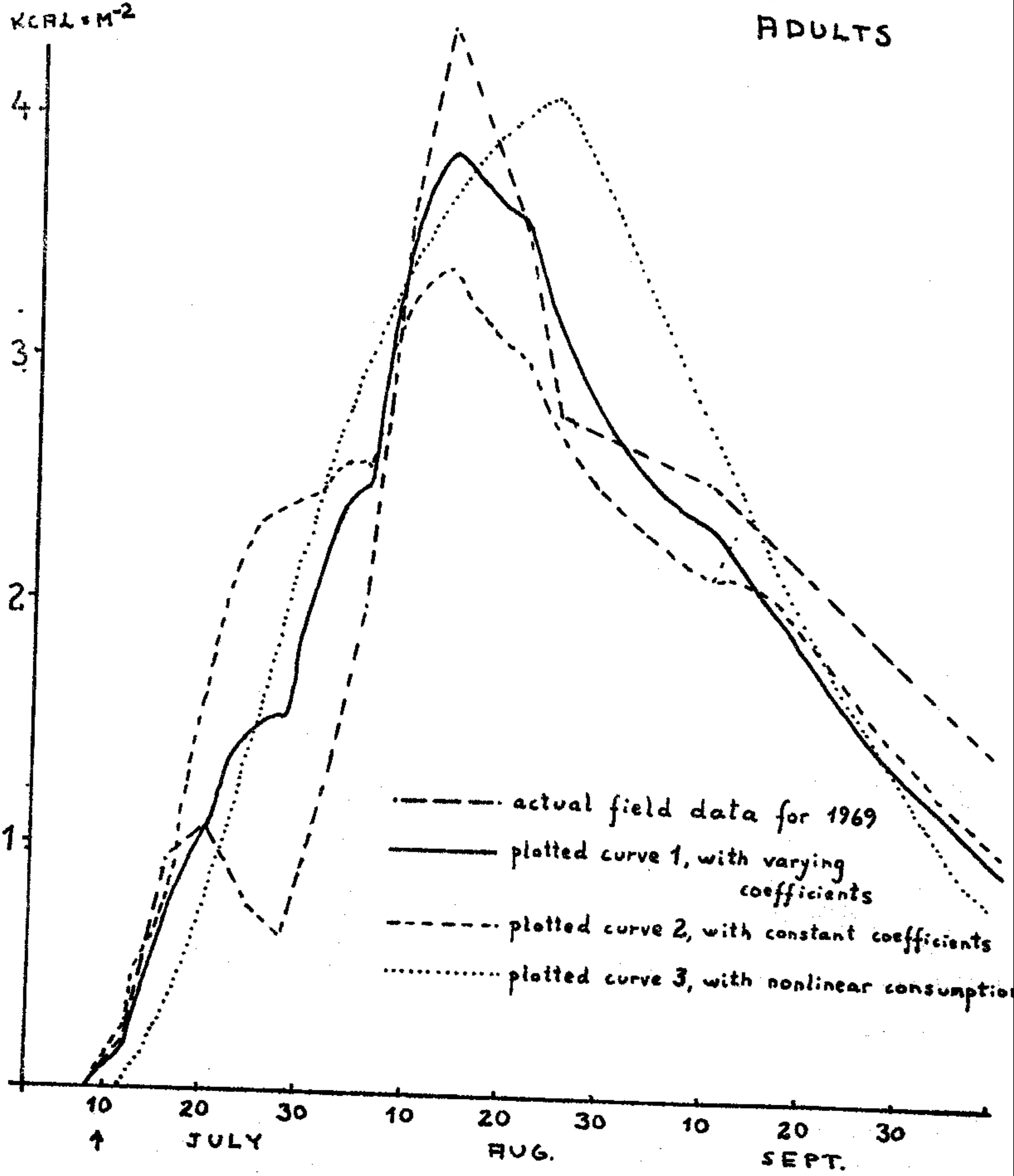

KCAL • M-2
ADULTS
4
3
2
1
10
20
30
10
20
30
10
20
30
JULY
AUG.
SEPT.
actual field data for 1969
plotted curve 1, with varying coefficients
plotted curve 2, with constant coefficients
plotted curve 3, with nonlinear consumptio

FIG. 3 CONTINUOUS MODEL OF ENERGY FLOW, MODEL III

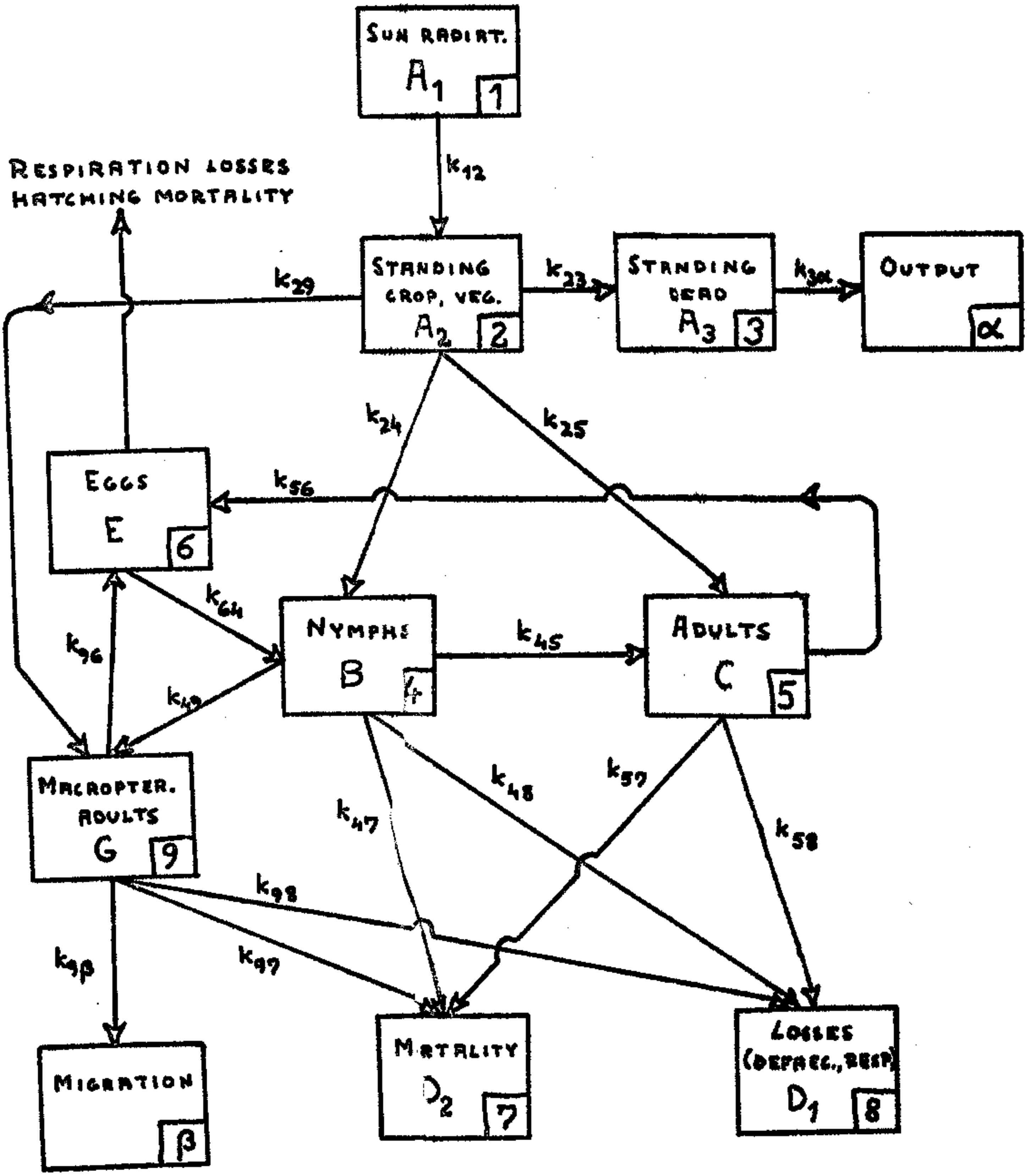
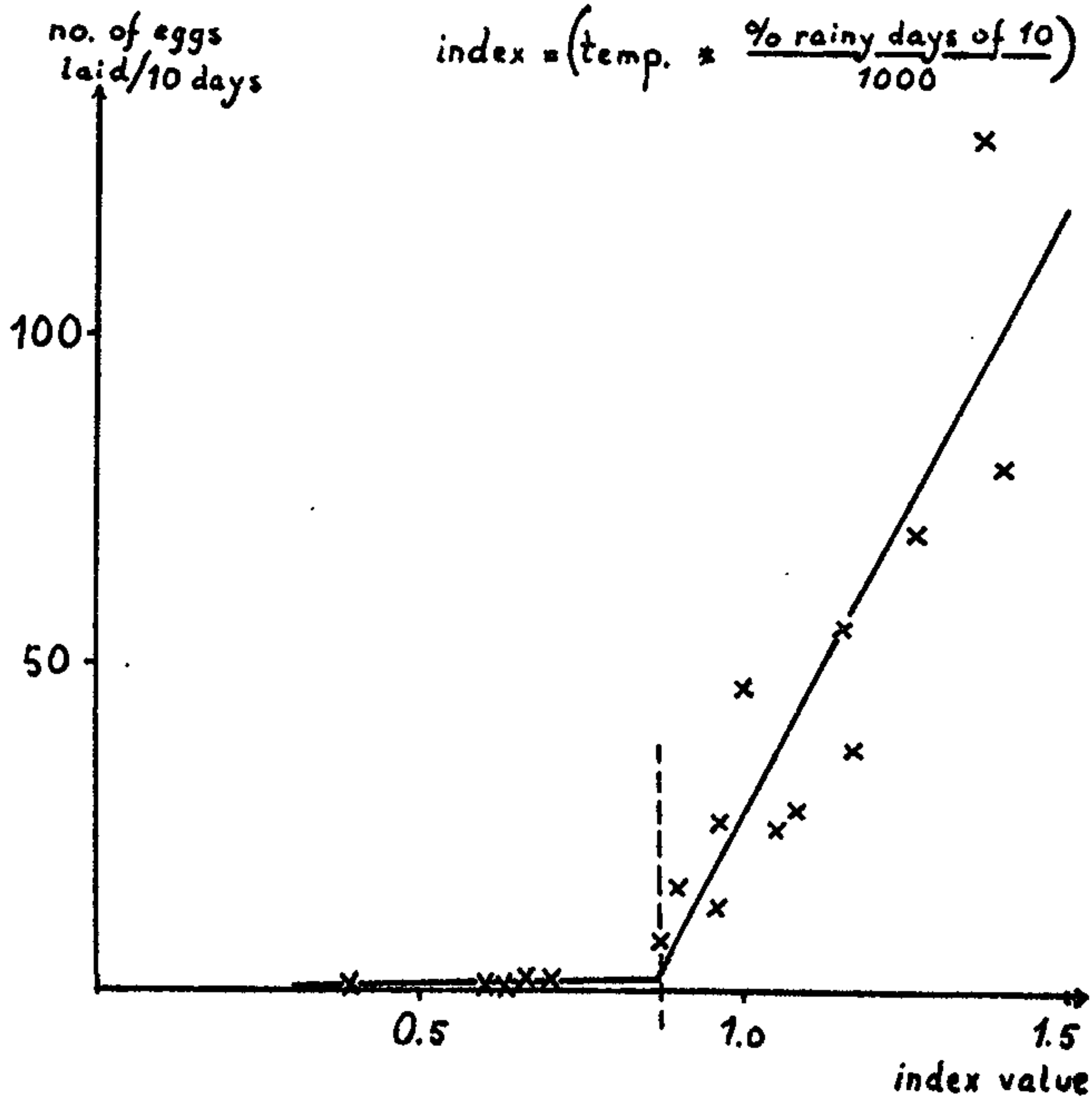


FIG. 4

---- treshold value, changing the equation of the regression line

$k_{56} = f(\text{index})$



$\text{index} = \left(\text{temp.} * \frac{\%\text{ rainy days of } 10}{1000}\right)$

FIG. 5a

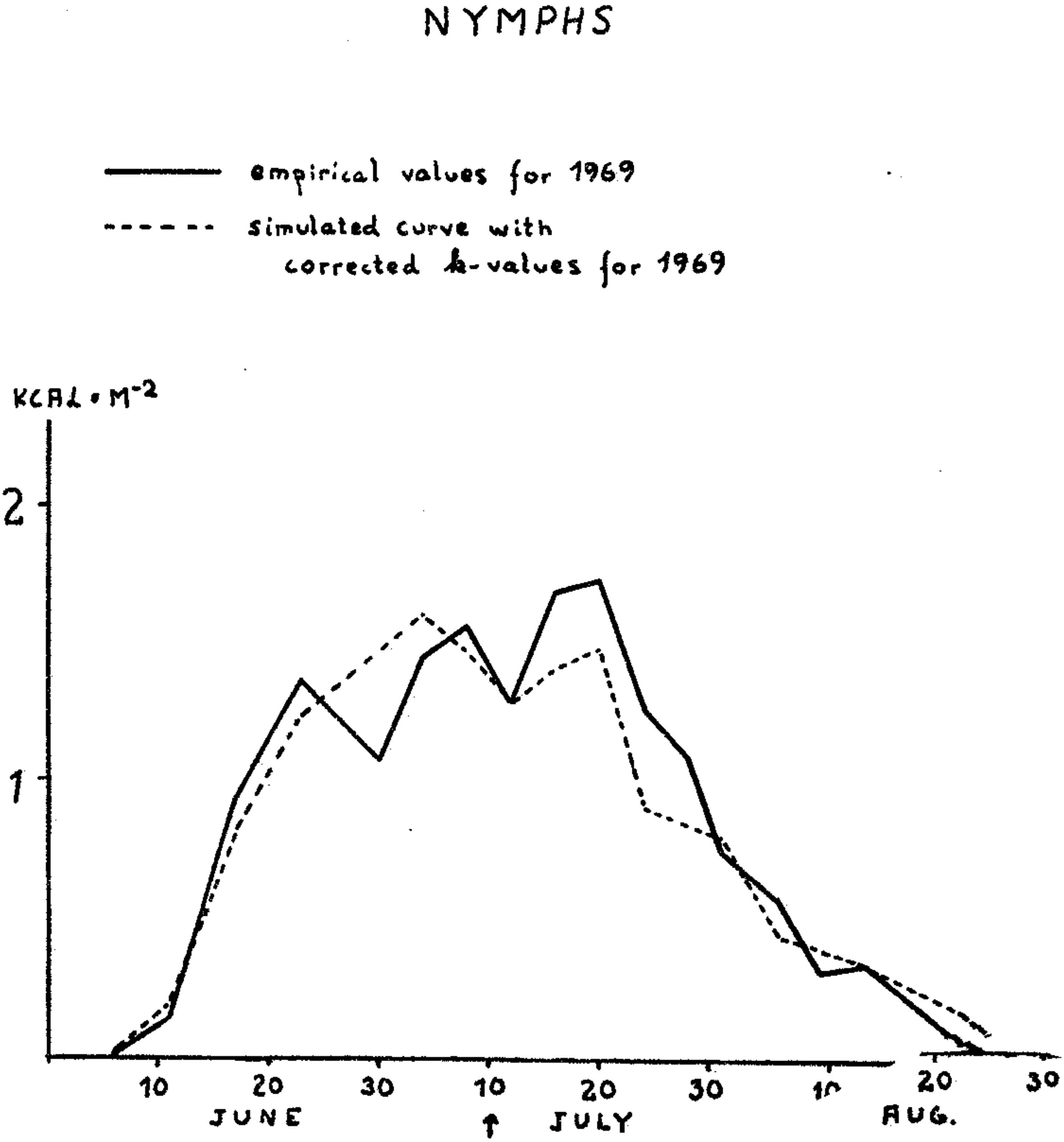

NYMPHS
empirical values for 1969
simulated curve with corrected k-values for 1969
KCAL • M^{-2}
2
1
10
20
30
10
20
30
10
20
30
JUNE
↑
JULY
AUG.

FIG. 5b

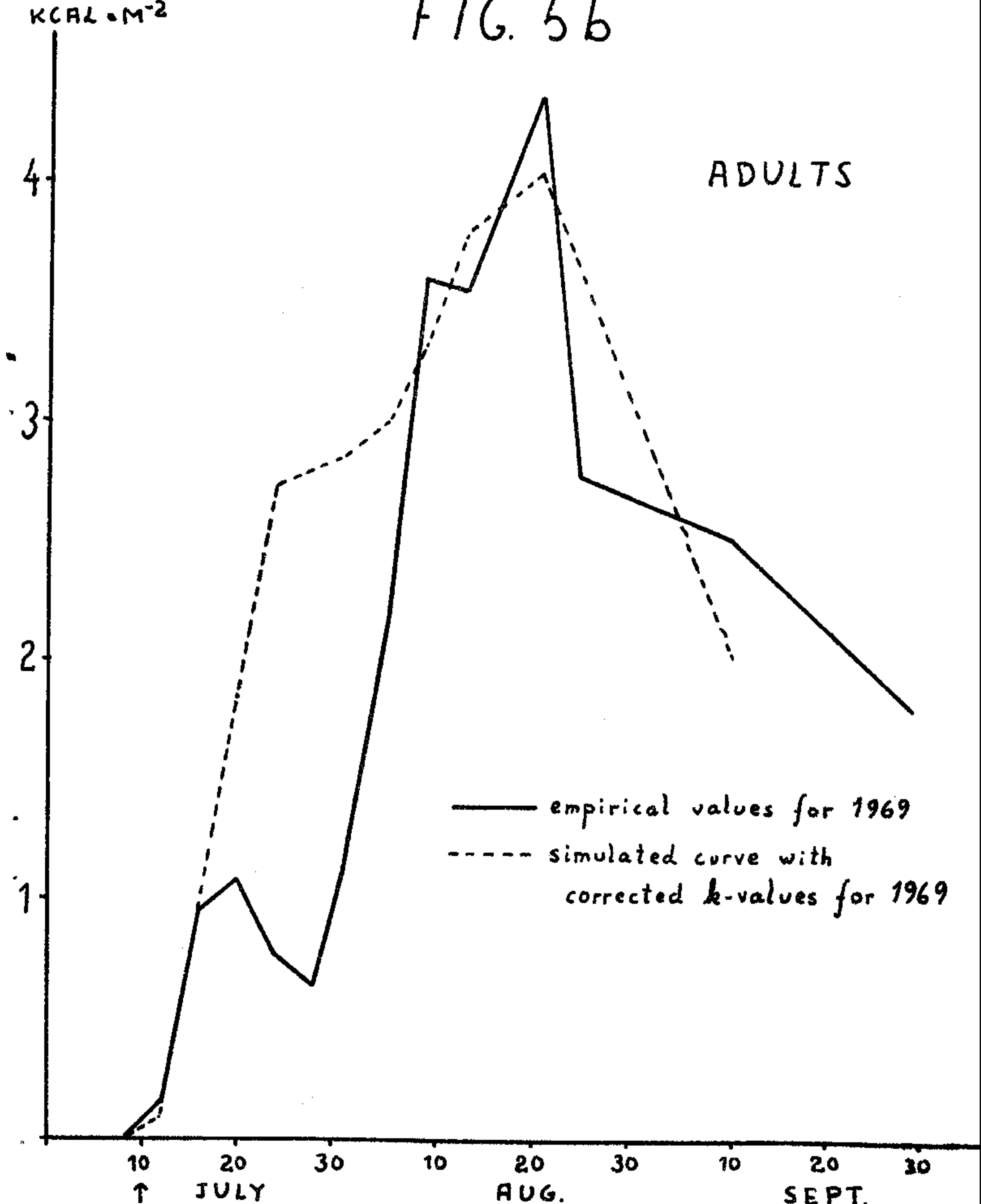

KCAL • M-2
4
3
2
1
ADULTS
empirical values for 1969
simulated curve with corrected k-values for 1969
10
20
30
10
20
30
10
20
30
↑ JULY
AUG.
SEPT.

FIG. 6a

NYMPHS

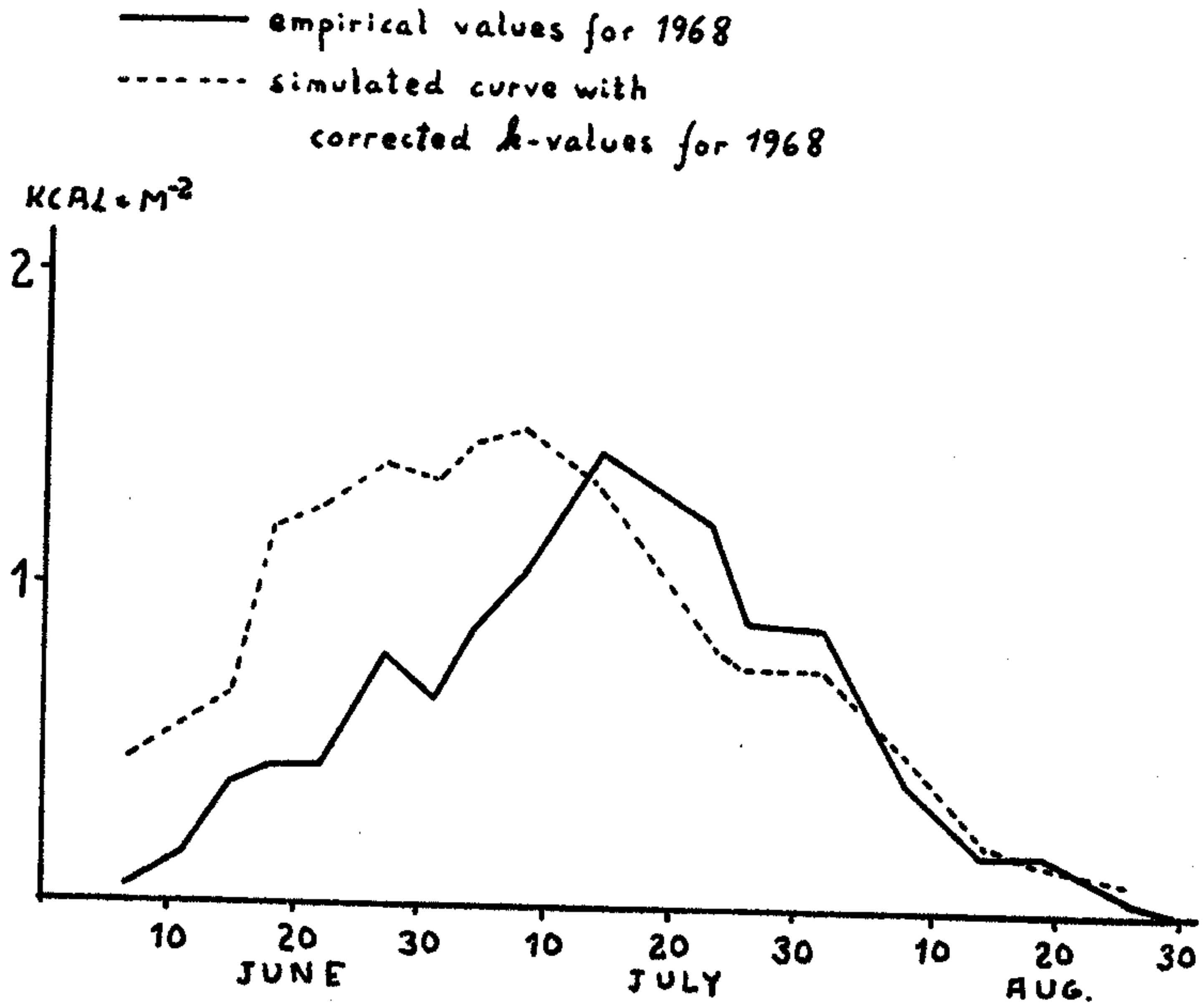


FIG. 6b

ADULTS

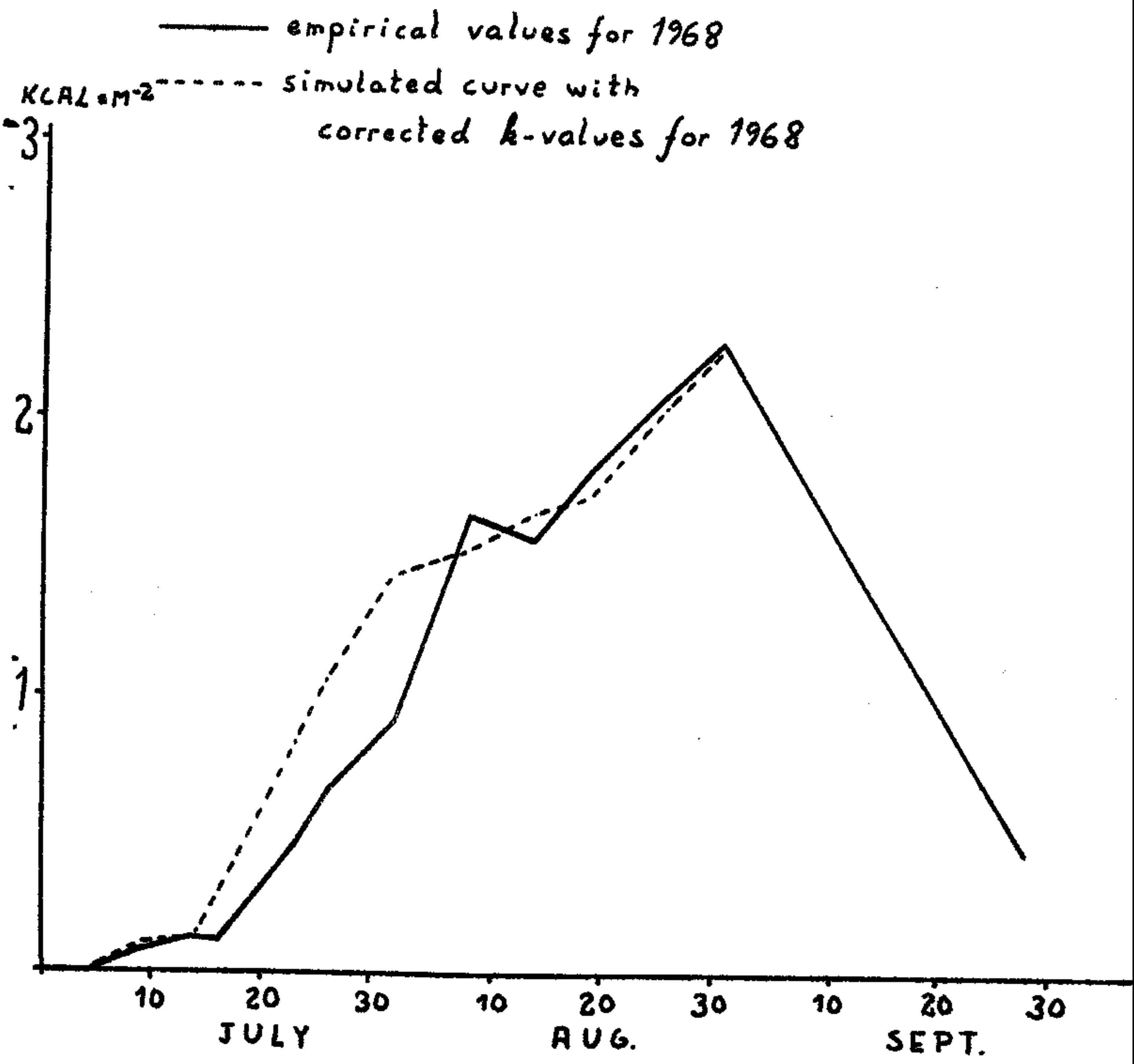
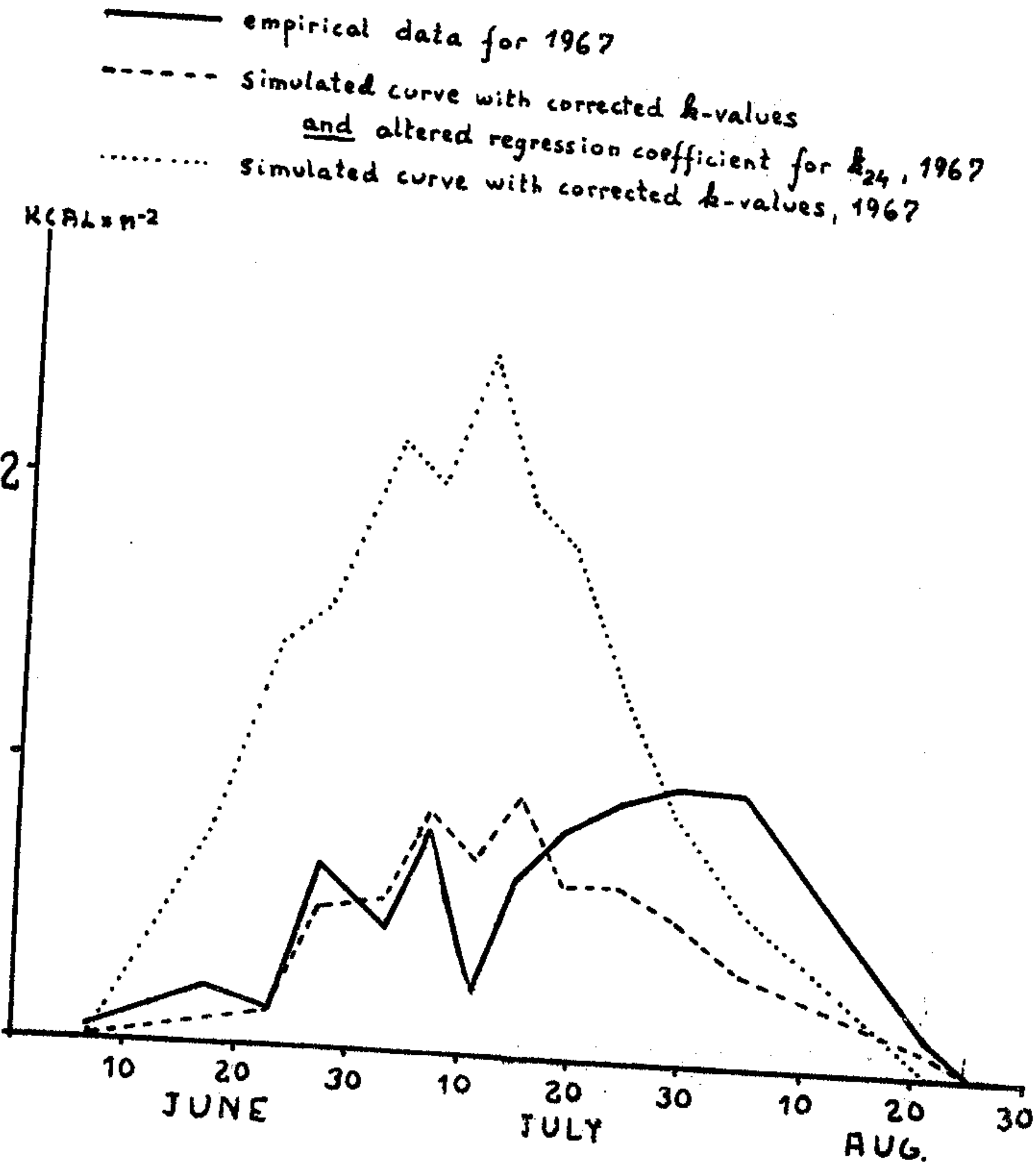


FIG. 7a



NYMPHS

FIG. 7b

ADULTS

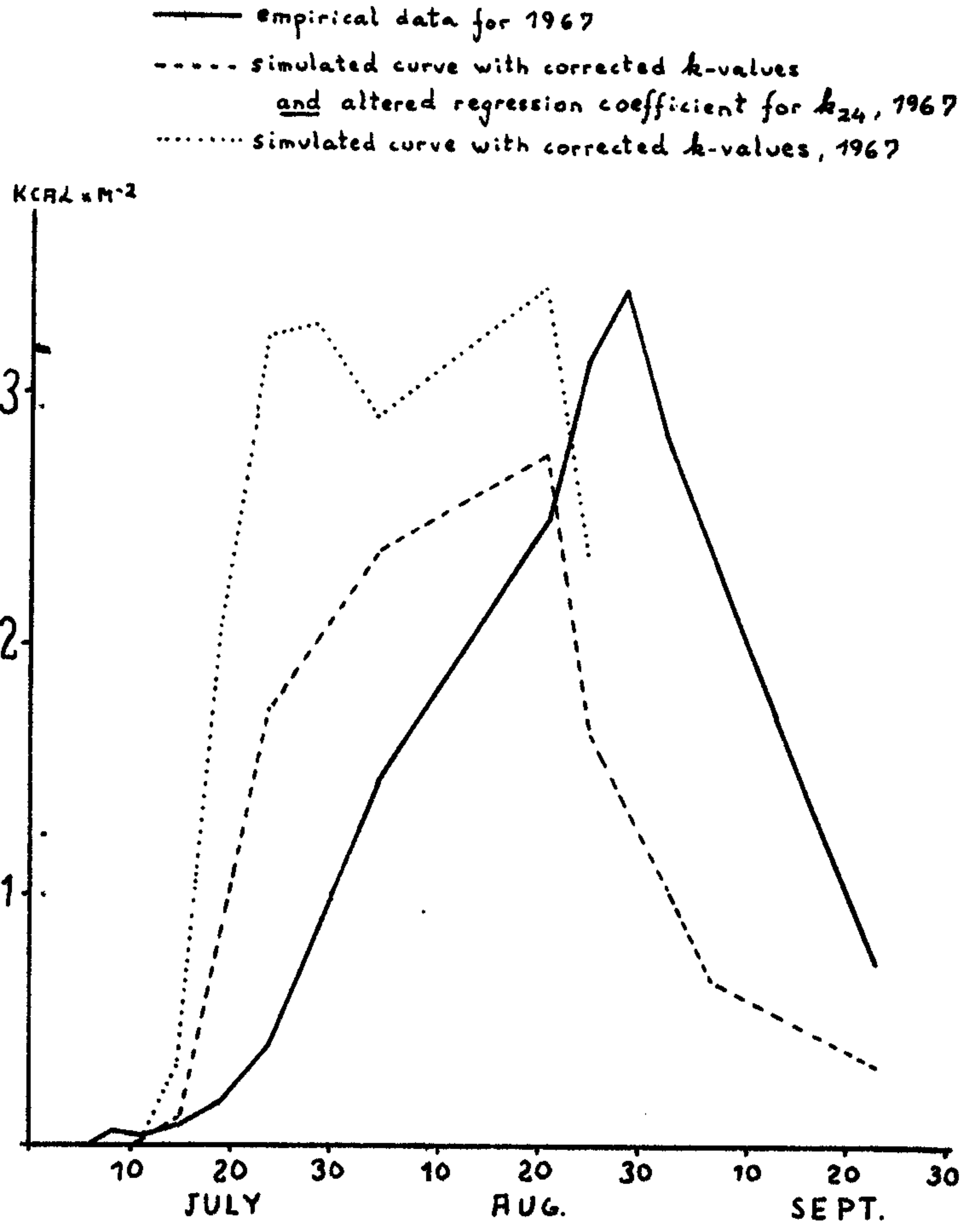
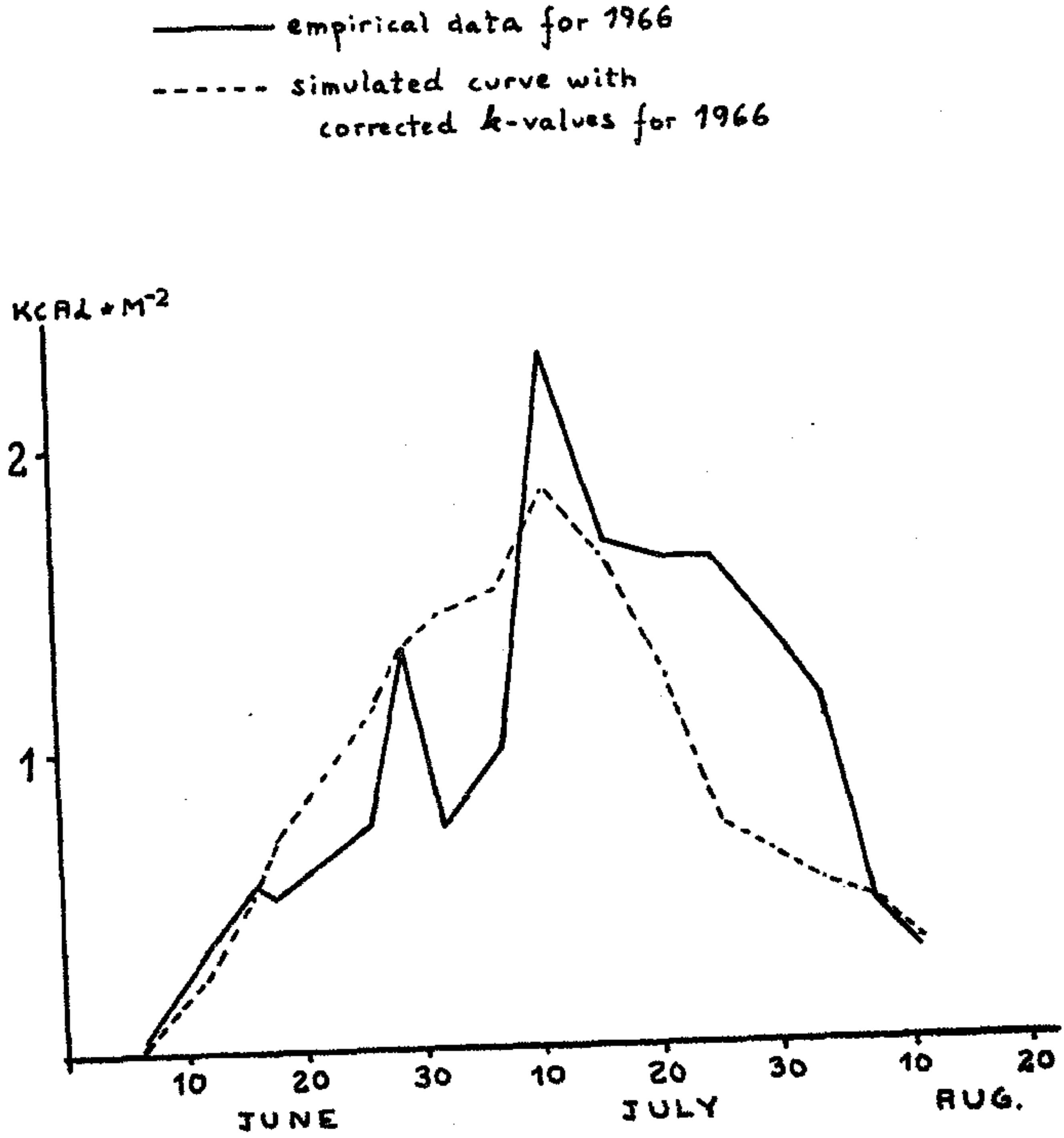
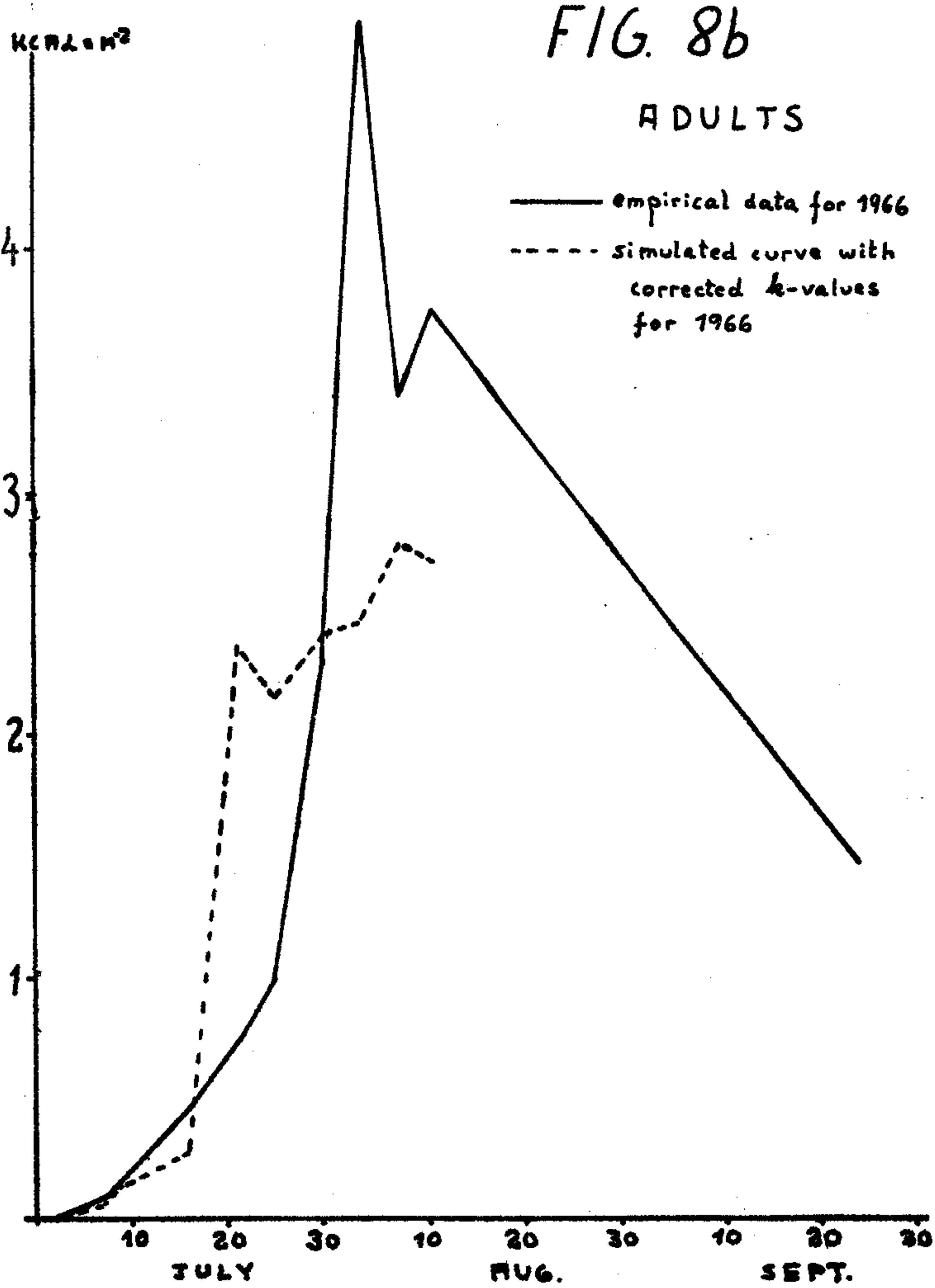


FIG. 8a



NYMPHS

FIG. 8b


ADULTS
empirical data for 1966
simulated curve with corrected k-values for 1966
KCAL m²
4
3
2
1
10
20
30
10
20
30
10
20
30
JULY
AUG.
SEPT.