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The life-system approach: a system paradigm in population ecology

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The life-system concept is a promising theoretical base for the system's approach to population ecology. A revision of the principles of this concept is proposed. To explain population dynamics I examine how quantitative characteristics of its pattern depend on the structure of the life-system. Two aspects of regulation in populations are distinguished: m- and v-stability. The first concerns the stability of the mean value of population density, while the second concerns the stability of density variance. They are characterized by coefficients of m- and v-stability. The contribution of ecological processes and their interactions to these coefficients represents their regulative role in population dynamics. The importance of process interactions is demonstrated using a simulation model of the common pine sawfly *Diprion pini* L. The life-system approach is useful for population management as well. Principles of safety and optimization provide a powerful network for selecting the best control strategy taking into account environmental uncertainty and long-term consequences of applied measures.

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A system is a combination of unity and partition both in space and time: if there is no unity then there are only parts instead of a system, if there is no partition then a system turns into a simple object that can be described externally, but not explained. Explanation differs from description because it has several levels. For example, to explain ecosystem dynamics means to analyze how it depends on the processes going on at the level of its sub-components (they may be individuals, populations, guilds, trophic levels). The main advantage of an explanation as compared with a description is a possibility to consider intermediate processes and stages between cause and effect. Explanations are different from simple predictions as well, for they consider not some specific moment in time but the whole temporal pattern of system dynamics (unity in time dimension). Explanations can be obtained only using the system's approach.

A regression equation, predicting population density on the base of a set of factors is not an explanation because it gives no means to determine what ecological processes are responsible for the revealed correlations between factors and population density. The same is true for the key-factor analysis (Varley and Gradwell 1960): it reveals the correlation between the k-value of some process of death and the k-value per generation, but it tells nothing about the nature of this correlation and what processes are driving population density. Of course, it can be considered as a method obtaining some preliminary suggestions about population dynamics but no more.

The system paradigm is well developed in ecosystem ecology: the notion of the ecosystem has become the main working tool, and principles of the complex interactions between components within an ecosystem have been developed (Odum 1971). However, in population ecology, system ideas have no considerable value. Simulation modeling is highly developed, but these models are used only for prediction and not for explanation. Analytical models are not good for explanation because usually they consider only one (rarely two or three)

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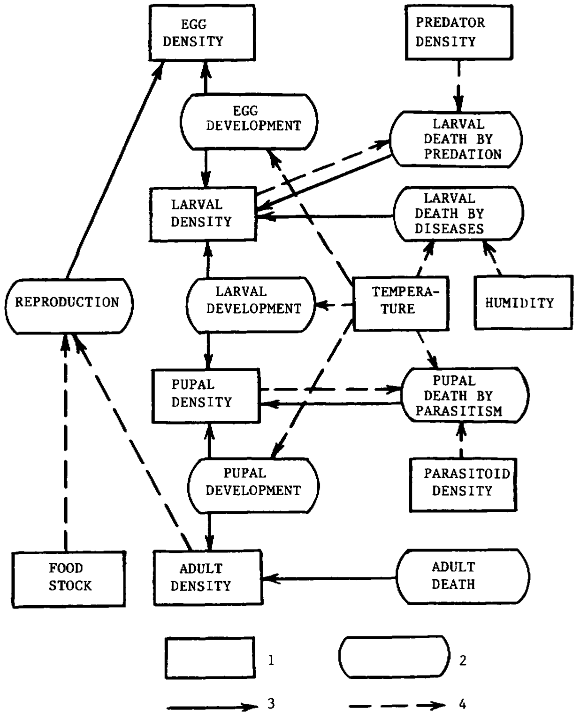

Fig. 1. Diagram of interrelations between factors (1) and ecological processes (2) in a hypothetical insect life-system; 3 – factor change in the course of some ecological process, 4 – factor effect on process rate.

ecological process. This causes a lack of attention towards interactions of processes that drive population dynamics.

In applying a system's approach to population ecology one must decide what is the system. It is not a population, because its dynamics cannot be properly described if its interaction with other components of the ecosystem is ignored (Solomon 1949). On the other hand, if the system considered comprises the whole ecosystem, as Solomon (1949) proposed, then population ecology will be dissolved in ecosystem ecology.

Both these points of view do not allow us to combine population ecology with a system's approach. This combination is possible only in the framework of the life-system concept developed by Australian entomologists Clark (1964) and Geier (1964). Details of this concept were described later (Clark et al. 1967). I consider it to be the most promising theoretical base for population ecology. A life-system was defined as a population taken together with its effective environment i.e. all components of the ecosystem having significant direct or indirect effects on this population. A detailed terminological system has been developed in the framework of this concept that has many advantages compared with traditional terminology.

Clark et al. (1967) applied the life-system approach for an explanation of the population dynamics of several pest insect species. Their main idea was that any feature of the life-system is a product of complex interactions of its parts. A density-dependent process is not a regulative mechanism because its effect can be modified, compensated or even reversed by other processes. Density-independent processes can influence regulation as well. This concept is not realized by many modern ecologists who are still trying to explain regulation by the action of a single density-dependent process.

However, the life-system concept requires some refinement. The idea of an explanation of population dynamics was not formalized. No algorithm was proposed for measuring the contribution of different components of the life-system to the characteristics of population dynamics. Moreover, there were no attempts to use such characteristics. The majority of terms were not exactly defined, some additional terms are needed.

In this paper I first make a revision of main notions of the life-system approach that is necessary to make the terminology clear. Then, I describe the general method of an explanation of population dynamics, and apply it to the problem of population stability. Finally, I describe the application of this approach to the explanation of the population dynamics of the common pine sawfly (*Diprion pini* L.) and to the problem of population management.

Life-system

A *life-system* is a population with its effective environment (Clark et al. 1967). The more important a component of the ecosystem is for this population, the more detailed will be its description as a part of the life-system. For instance, the life-system of an insect pest population usually includes, besides the population, its host plants, natural enemies, competitors, weather and control measures. *Components* of a life-system are organisms, resource items, soil, lower atmosphere layer (weather). Populations will not be considered as components because there are no permanent connections between all members of population. But colonies of social insects are components because of their high integrity.

Each component of the life-system is characterized by its current *state*. The state of an organism can be described by its species name, stage of development and sex. The state of the weather is characterized by air temperature, humidity and so on. The state of the life-system is specified by the composition and states of its components.

An *ecological event* is an elementary change of the life-system state. Birth, death, migration of an organism, contact with food or predator, growth and development are examples of ecological events. Events can be classified: they belong to the same type if components of the life-system involved in these events have the same states. For example, the death of larva and the death of pupa of some insect are events of different types because organisms were at different stages of development at the moment of death. The death of larvae due to parasitism and predation are also events of different types because different inimical agencies caused the death.

An elementary *ecological process* consists of ecological events of the same type. It is also useful to consider complex processes representing several interrelated elementary processes. For example, the process of insect death by parasitism includes the following elementary processes: the meeting of the host and the parasitoid, the stinging of the host by the parasitoid, the development of parasitoid larvae and the death of the host.

Each ecological process has its specific rate measured by a number of ecological events happening in a unit of time per one component of the life-system. Specific mortality and natality, the rate of development are examples of process rates.

Process rates depend upon some characteristics of the current state of the life-system. I will call these characteristics *factors*. Clark et al. (1967) used the term codeterminant instead of factor. I prefer the word factor because it is traditionally used in ecology. Air temperature, population density of a certain life stage, density of predators, parasitoids are examples of factors.

Factors affect process rates (Fig. 1): temperature regulates the rate of insect development; predator and prey densities have their effect on larval death rate by predation and so on. On the other hand, ecological processes change factor values. For instance, the density of eggs decreases and the density of larvae increases in the course of egg development. Death processes decrease the density of insects at various developmental stages and the process of reproduction increases the density of eggs.

The scheme in Fig. 1 represents only a fragment of the life-system. To have the full picture it should be completed with processes determining the dynamics of predator and parasitoid populations and the food supply.

The life-system may include *input factors* the dynamics of which cannot be explained by ecological processes in the given system. For example, temperature dynamics is determined by air movement on the large territory exceeding the boundaries of the ecosystem. Population management (e.g. chemical or biological pest control) is also an input factor. The remaining factors, which can be explained in the framework of the life-system I will call *intrinsic factors*.

The important feature of Fig. 1 is the distinction between factors and processes. No factor can influence another factor directly. Any influence goes through ecological processes. Solomon (1949) was the first who stated that the expression "density dependent factor" must be replaced by "density dependent process". The distinction between factors and processes is particularly important for interpretation of life tables. The widespread term "mortality factor" is not correct because it signifies two different things: a process of death and a factor influencing the rate of this process. As shown in Fig. 1, there is no one-to-one correspondence between factors and processes. Moreover, factors may interact, so that the sufficient amount of mortality cannot be attributed to any individual factor. Thus I reject the term "mortality factor". Inadequate interpretation of life tables by use of this term gives an illusion of dominance of biotic factors because the weather influences on mortality due to predation, parasitism and diseases is ignored.

The *life-system structure* is formed by 1) the set of possible states of life-system components, 2) the set of ecological processes, 3) the influences of factors on the rates of ecological processes and 4) the statistical characteristics of input factor dynamics (mean values, variances, correlations). This structure can be described formally by a simulation model. In the model, factors become variables, processes give their contribution to derivatives of factors (or factor differences in models with discrete time).

It is necessary to emphasize that the model makes no sense if it is considered away from biological interpretation in terms of components, processes and factors of the life-system. It is impossible to reduce ecological theory to mathematics and speak only in terms of variables and differential equations. The same situation exists in physics: physical notions such as energy, mass, time are not reduced to mathematical structures, but only described by them.

Any model may have different theoretical interpretations. For instance, the logistic model has at least two interpretations: resource limited and equilibrium interpretation (Pollard 1981). In the first interpretation carrying capacity represents the amount of resources, while in the second it is determined by the balance of density dependent birth and death rates and has no relation to resources. Theoretical interpretation of the model is quite important for a proper explanation of population dynamics.

Explanation of population dynamics

I propose the following general approach to an explanation of population dynamics. First, a valid simulation model of the life-system must be developed, after which the response of quantitative characteristics of population dynamics pattern to the modification of life-system structure must be revealed using the model. I consider the model as valid if it represents the current knowledge about the life system and mimics main processes with accepted accuracy. Of course, accuracy must be reasonable: if it is too low then there is no prediction, and if it is too high then the appropriate model will never be developed.

The most important population characteristics are the mean value and the variance of log-transformed density. Log-transformation is necessary because of the usual log-normal distribution of population density. Additional characteristics may be used to describe complex patterns of population dynamics with outbreaks: the rate of density increase at the beginning of the outbreak, the duration and frequency of outbreaks, and others. Characteristics of the spatial distribution of organisms may be used as well.

The main ways of modifying the life-system structure are: 1) changing the mean value or the variance of some input factor, 2) addition or exclusion of some ecological processes, 3) fixation of the rate of some ecological process at the equilibrium or mean level.

Two methods, empirical and simulational, are possible in the analysis of the life-system structure influence on population dynamics. The first of them is to modify the structure of the real life-system and then observe the change of quantitative characteristics of population dynamics. For example, we can change the mean temperature in a greenhouse, the intensity or frequency of pesticide spraying or introduce a parasitoid. When using the simulation method, these experiments are simulated by a mathematical computer model. Only the simulation method can be considered as an explanation of population dynamics because the model delivers an opportunity to find processes that are responsible for the change of the life-system dynamical pattern. But the simulation method is indirect and this is its main disadvantage. Its precision depends on the validity of the simulation model. Therefore, the empirical method will be useful for checking the validity of the model.

This general approach allows one to integrate knowledge about all processes in the life system and to examine the role of interactions between factors and processes.

Population stability

In this section I apply the general approach described above to the problem of population stability. First it is necessary to choose quantitative characteristics of stability. In population models an asymptotical stability at equilibrium point in phase space is always analyzed (May 1974, Hassell 1978). Global stability may be determined by the area of convergence of trajectories (Holling 1973). May (1973) suggested to measure stability by the value $\Lambda = -max(Re(\lambda_i))$, where $Re(\lambda_i)$ are the real parts of the characteristic roots of a linearized model at the equilibrium point. This criterion indicates the rate of convergence of trajectories to the steady state. But all these characteristics of stability are oriented to deterministic models. In stochastic models as well as in real populations one cannot observe the convergence rate of population trajectories to the steady state because environmental fluctuations always turn them away from the equilibrium.

I shall use a stochastic approach to measure population stability: the response of the mean value and variance of population log-transformed density to the change of the mean value and variance of input factors will be evaluated, where mean values and variances are estimated for time series. It is important that these changes are considered not in time but in space (or in the greater scale of time). For example, we can compare two populations, one of which is managed and the other is not managed. Management is an input factor that has a non-zero mean value for the first population and a zero mean value for the second.

I define *m-stability* (in previous publications (Sharov 1986a) called buffer ability) as the resistance of mean population log-transformed density y to the change of the mean value of some input factor x. It can be characterized by the coefficient of m-stability:

$$MS = (\partial\bar{y}/\partial\bar{x})^{-1} \tag{1}$$

where $\bar{y}$ is the mean log-transformed population density, and $\bar{x}$ is the mean value of the input factor. If an input factor is a control measure against a pest insect then large absolute values of the coefficient of m-stability implies it is difficult to suppress pest density.

V-stability (in previous publications (Sharov 1986a) called homeostasis) is defined as the resistance of the variance of the log-transformed population density to the change of the variance of some input factor. The coefficient of v-stability is defined as:

$$VS = (\partial s_y^2/\partial s_x^2)^{-1} \tag{2}$$

where s_y^2 and s_x^2 are variances of the log-transformed population density y and of some input factor x, respectively. Any other intrinsic factor of the life-system may be taken as a variable y instead of the log-transformed population density. If x is the only fluctuating input factor, and the life-system state does not go far from the stable equilibrium point, the coefficient of v-stability becomes

$$VS = s_x^2/s_y^2 \tag{3}$$

The greater the coefficient of v-stability, the smaller are the fluctuations in population density for the same fluctuations in the environment.

Besides coefficients of m- and v-stability it is possible to assess the effect of mean input factor on population density variance and the effect of input factor variance on mean population density. But these effects are less important than m- and v-stability because they appear only in non-linear models, while m- and v-stability characterize linear properties of the model.

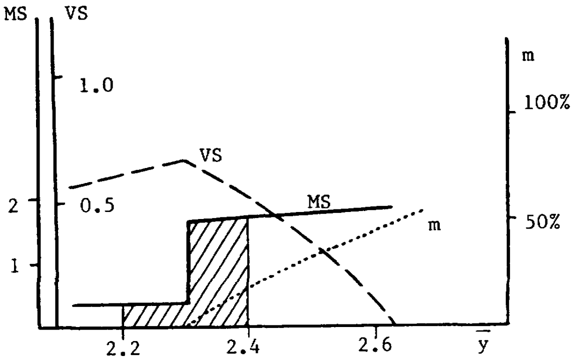

Fig. 2. Coefficients of m-stability (*MS*) and v-stability (*VS*) of host population plotted against its mean log-transformed density ($\bar{y}=\ln H$) for the model of host-parasitoid system (5); *m* – mean percent of parasitism.

M- and v-stability are associated with population regulation. Regulation means the limitation of density fluctuations. The brilliant explication of this idea was done by Chesson (1978) who proposed to examine the confidence interval for population density. Limits of the confidence interval depend on the mean value and the variance of log-transformed density. Coefficients of v-stability and m-stability characterize the effect of input factors on these population parameters and, at the same time, on the position of confidence limits. When these coefficients are high then input factors have little effect on the confidence limits and therefore we can consider the population to be well regulated. Thus we can consider v-stability and m-stability as two aspects of population density regulation.

Coefficients of v-stability and m-stability can be found analytically for simple models such as the model of Morris (1959):

$$\ln N_{t+1} = (1-\alpha)\ln N_t + x_t, \tag{4}$$

where N_t is the population density in the generation t, α is a parameter indicating the strength of the negative feed-back loop and x_t is an input factor. Let $y_t = \ln N_t$. Fluctuations of the input factor are considered to be small enough for the mean log-density $\bar{y}$ to coincide with the equilibrium log-density. It is easy to show that $d\bar{y}/d\bar{x} = \alpha^{-1}$ and $MS = \alpha$. If the dynamics of the input factor has no autocorrelations then the coefficient of v-stability is equal to $1-(1-\alpha)^2$. When $1<\alpha<2$, the coefficient of m-stability increases while the coefficient of v-stability decreases with the value of α because of the overcompensation of the feedback loop.

Coefficients of m-stability and v-stability can be used for prediction of the new mean value and variance of log-transformed population density after a change in life-system structure. This will be shown for the host-parasitoid model proposed by May et al. (1981):

$$\begin{cases} H_{t+1} = H_t exp(-aP_t)exp(r(1-H_t exp(-aP_t)/K))exp(x_t) \\ P_{t+1} = H_t(1-exp(-aP_t)), \end{cases} \tag{5}$$

where H_t and P_t are host and parasitoid population densities in generation t, a is the area of discovery, r is the rate of increase of host population, K is the carrying capacity of the environment for the host population and x_t is the input factor. The value x_t is interpreted as the log-transformed host survival in the course of control actions. The following values of parameters were chosen: $a=0.1$, $r=2$ and $K=50$.

I estimated the mean log-transformed host population density $\bar{y}$ and coefficients *MS* and *VS* for different mean values $\bar{x}$ of the input factor. The coefficients *MS* and *VS* were obtained by the Monte-Carlo method for the low values of variance s_x^2 and by linearization techniques. Both methods gave the same results (Fig. 2). If we want to reduce the mean log-transformed host density $\bar{y}$ from 2.4 to 2.2, we must decrease the mean input factor $\bar{x}$ by the amount given by the shaded area in Fig. 2. The decrease in log-transformed survival of the host $\bar{x}$ is equivalent to the introduction of additional mortality. The higher the coefficient of m-stability, the more additional mortality is needed for the suppression of mean population density.

The ledge on the graph of the function $MS(\bar{y})$ corresponds to the least host density that allows the existence of a parasitoid population (Fig. 2). It is seen that the presence of the parasitoid increases m-stability of host population, but reduces v-stability. The increase of *MS* indicates that it is difficult to change the mean host density in the presence of parasitoids. The explanation of this phenomenon is the following. When additional host mortality is introduced for suppression of its density then the trophic base for the parasitoid is reduced. Consequently, parasitization rate decreases and additional mortality becomes partially compensated.

The decline of *VS* indicates the destabilizing role of the parasitoid in the population dynamics of its host. According to Eq. (3), the variance of log-transformed host density is doubled if the coefficient of v-stability is halved. Reduction of host mortality leads to the increase of mean host log-density $\bar{y}$. Then the coefficient of v-stability will decline according to Fig. 2 and, therefore, the scope of population fluctuations will increase. When $VS=0$ the equilibrium point becomes unstable.

Role of ecological processes in population dynamics

The role of ecological processes can be evaluated by their contribution to integral characteristics of population dynamics. To reveal the regulative role of processes

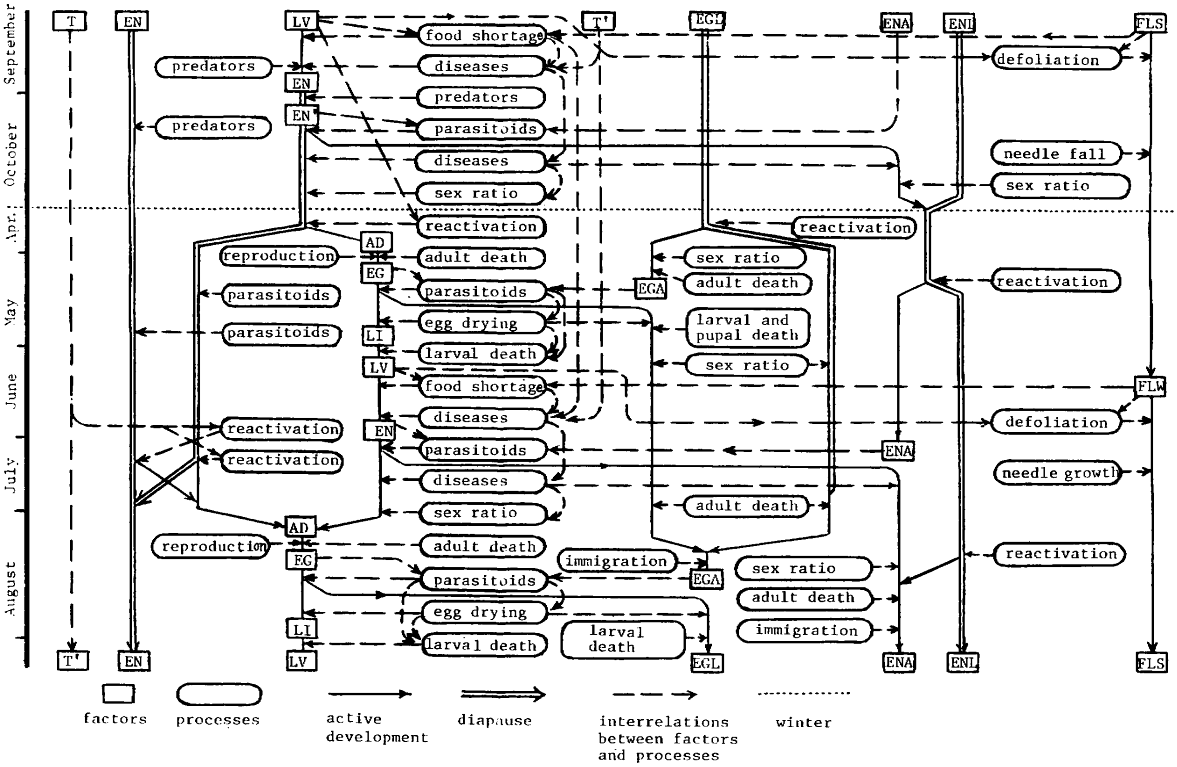

Fig. 3. Scheme of the simulation model of the common pine sawfly. Density of populations: EG – sawfly eggs, LI and LV – sawfly larvae of the 1-st and 5-th stage, EN and EN' – sawfly eonymphs before and after their death due to predation, respectively, AD -sawfly adults, EGL – larvae of egg parasitoids, EGA – adults of egg parasitoids, ENL – larvae of eonymph parasitoids, ENA – adults of eonymph parasitoids, FLW and FLS – foliage biomass in winter and in summer, respectively; T and T' – air temperature in May – September in the current and previous year, respectively.

one should investigate their contribution to the coefficients of m-stability and v-stability. I propose to do this using the polynomial equation:

$$y_i = \beta_0 + \beta_1 z_1 + \beta_2 z_2 + \beta_{12} z_1 z_2 + \beta_3 z_3 + \ldots, \qquad (6)$$

where y_i is the coefficient of m-stability or v-stability (or some other characteristic of population dynamics), z_j is a dummy variable indicating the dependence of the j-th ecological process rate on environmental factors ($z_j=1$ if the rate of the j-th process naturally depends on factors and $z_j=0$ if this rate is fixed at the mean or equilibrium level), β_j is the contribution of the j-th individual process to the value of y_i, and β_{jk} is the contribution of the j-th and k-th process interaction. Coefficients β_j and β_{jk} can be estimated using multiple regressions on the results of simulation of y_i with processes rates being fixed or not fixed in all possible combinations.

In model (5) there are two ecological processes: 1) the death of the host due to parasitism and 2) the density dependent reproduction of the host. The rate of the first process becomes fixed if the expression $exp(-aP_t)$ in (5) is replaced by a constant. Similarly the rate of the second process becomes fixed if the expression $exp(r(1-H_t exp(-aP_t)/K))$ in (5) is replaced by a constant. Coefficients MS and VS were estimated for $\bar{y}=2.5$ and 1) for both processes being naturally dependent on factors, 2) for the first process having a fixed rate, 3) for the second process having a fixed rate, and 4) for both processes having fixed rates. Coefficient of m-stability in these four cases is equal to 1.775, 0.324, 2.146 and 0.0, respectively. As a result, Eq. (6) has the following form:

$$MS = 2.146 z_1 + 0.324 z_2 - 0.695 z_1 z_2, \qquad (7)$$

where −0.695 is the difference: 1.775 - 0.324 - 2.146. Here $\beta_0 = 0$ because in the absence of both density-dependent processes the coefficient of m-stability is equal to zero. The following equation for v-stability was obtained in the same way

$$VS = -0.484 z_1 + 0.543 z_2 + 0.262 z_1 z_2. \qquad (8)$$

The death of the host due to parasitism makes the greatest contribution to the coefficient of m-stability

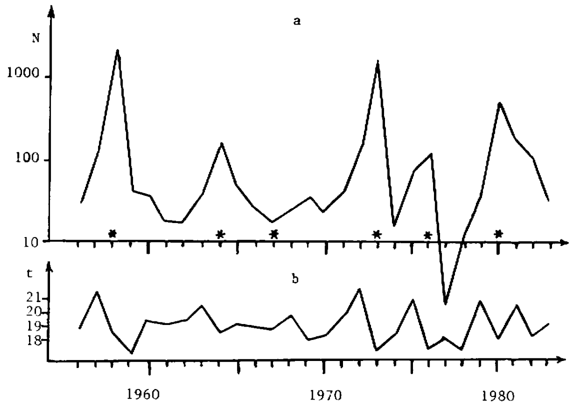

Fig. 4. A simulation of the common pine sawfly larvae density per m^2 in the Rostov region (USSR) in 1956–1983 (a); b – mean air temperature in May-September; * – real sawfly outbreaks.

(2.146) and the host reproduction makes the greatest contribution to the coefficient of v-stability (0.543). Parasitoids destabilize the dynamics of the host population because their contribution to *VS* is negative (−0.484). The interaction of the two processes diminishes the value of *MS* (−0.695).

Analysis of the life-system of the common pine sawfly

The common pine sawfly (*Diprion pini* L.) is a serious pest of plantations of Scotch pine in the steppe zone of the USSR. It overwinters as an eonymph (pre-pupa) in the cocoon in the litter. There are two waves of flight of overwintered sawflies: in the first half of May and in the

Table 1. Contribution of ecological processes in the life-system of the common pine sawfly (coefficients β_j, β_{jk},... in Eq. (6) with confidence intervals (P=0.05)) to the quantitative characteristics of population dynamics y_i.

Numbers of processes (combination of numbers – interaction of processes)*	Characteristics of population dynamics**			
	$y_1 = MS$	$y_2 = VS$	$y_3 = ln \frac{N_o}{N_s}$	$y_4 = ln \frac{N_o}{N_c}$
1	2	3	4	5
–(intercept in Eq. (6))	0	0	0	0.62±0.15
1	0.51±0.17	0.20±0.20	0	−0.83±0.38
2	0.41±0.11	0.68±0.09	0	0.68±0.26
1, 2	−0.22±0.10	−0.59±0.10	0	0.54±0.35
3	−0.01±0.01	−0.02±0.01	0	1.61±0.50
1, 3	0.01±0.01	0.02±0.01	0	1.75±0.52
2, 3	0.01±0.01	0.02±0.01	0	−0.15±0.20
1, 2, 3	−0.01±0.01	−0.02±0.01	0	0.51±0.52
4	0	0	0.35±0.12	0.45±0.15
1, 4	0	0.01±0.01	0.32±0.11	0.12±0.16
2, 4	0	0	0.05±0.03	−0.34±0.15
1, 2, 4	0	0	0.05±0.03	−0.28±0.16
3, 4	0.01±0.01	0.02±0.01	0	−0.36±0.11
1, 3, 4	−0.01±0.01	−0.02±0.01	0	−0.35±0.19
2, 3, 4	−0.01±0.01	−0.02±0.01	0	0.26±0.12
1, 2, 3, 4	0.01±0.01	0.02±0.01	0	0.33±0.26
5	0	0	0.15±0.09	0
1, 5	0	0	0.37±0.27	0
4, 5	0	0	0.13±0.04	0
1, 4, 5	0	0	0.17±0.12	0
6	0	0	0.55±0.15	0
1, 6	0	0	0.46±0.15	0
4, 6	0	0	0.24±0.07	0
1, 4, 6	0	0	0.13±0.12	0
5, 6	0	0	0.20±0.05	0
1, 5, 6	0	0	0.29±0.16	0
4, 5, 6	0	0	−0.05±0.02	0
1, 4, 5, 6	0	0	−0.22±0.07	0
Sum of other coefficients in Eq. (6)	0	0	0.18±0.14	0
Total	0.70±0.12	0.30±0.19	3.37±0.45	4.56±1.08

* 1 – egg death due to parasitism, 2 – eonymph death due to parasitism, 3 – larvae death due to food shortage, 4) reactivation of overwintered sawflies in the first wave, 5) reactivation of overwintered sawflies in the second wave, and 6) sawfly death due to diseases and unidentified causes.

** *MS* and *VS* are coefficients of m- and v-stability of the sawfly population between outbreaks (input factor – larval log-transformed survival in September), N_s is sawfly density in the period of stability, N_o is maximum outbreak density, N_c is density after population collapse (all densities are considered at the September larval stage).

end of July – beginning of August. The second wave is much greater than the first. More than a half of the eonymphs remain in the prolonged diapause for the whole year. The progeny of sawflies, emerged in spring, reach the adult stage by the end of July synchronously with overwintered sawflies, emerging in the second wave.

For a better understanding of the dynamics of sawfly populations a simulation model was created (Sharov 1986b) on the base of original life-table and experimental data obtained in the Rostov region (Sharov and Safonkin 1982, Sharov 1983, 1987). Some data were taken from the literature. The model simulates the interaction of the sawfly with two guilds of parasitoids developing in eggs and eonymphs, respectively, and with the host plant (Fig. 3). Diapause mechanisms and sawfly mortality due to predation and disease are also considered. Weather is characterized by the mean air temperature in May-September. The scheme of the model (Fig. 3) is drawn not exactly in the same manner as the Fig. 1, because there was no room for placing all the processes that are considered in the model (processes of development and some others).

The model was validated using the records of population outbreaks in the Rostov region in 1956–1983. These data were not used for the estimation of model parameters. The model predicted 5 out of 6 real outbreaks (Fig. 4), and no false outbreaks were predicted (Sharov 1986b). So we consider this model to be valid enough on the qualitative level (unfortunately, no quantitative long-term data are available).

Population dynamics of the common pine sawfly in the Rostov region is pulse eruptive according to the classification of Isaev et al. (1984) and Berryman (1987). Outbreaks occur after a hot and dry summer (Fig. 4). I consider 4 periods of an outbreak cycle: 1) stability (between outbreaks), 2) growth (the first year after drought), 3) collapse (the second year after drought), and 4) depression (years after collapse). Each period was described by a specific coefficient and the contribution of ecological processes to these coefficients was estimated using Eq. (6). Coefficients of m- and v-stability were used for the analysis of the period of stability (it is possible to use them for the analysis of global dynamics, but then the result will be less detailed). For other periods additional characteristics were used (see below). I analyzed the role of: 1) egg-parasitoids, 2) parasitoids of eonymphs, 3) food shortage, 4) sawfly reactivation in the first wave, 5) sawfly reactivation in the second wave, and 6) diseases and unidentified causes of death.

For evaluation of confidence intervals 10 modifications of the original model were obtained using independent random variations of the 32 most important model parameters. Standard deviation for random numbers was taken equal to the standard error of these parameters, and therefore the differences between model modifications were rather small. Only valid modifications were selected, validation was the same as for original model. Then, each characteristic of the population dynamics was estimated using all 10 model variants and a standard error was taken equal to their standard deviation (because increasing the number of model variants does not change accuracy). The purpose was to evaluate (at least roughly) the precision of the model. If some effect is obtained using all model modifications then we have more reasons to trust that this effect is not a mathematical accident.

The period of stability was characterized by coefficients of m- and v-stability for larval log-transformed survival taken as a measure of input factor (Table 1). Larval death is a process, and not a factor, but input factors (i.e. intensity of insecticide spray) can be measured in units of additional pest mortality or survival. The temperature in the model was considered to be constant and equal to the mean temperature in non-drought years. M-stability ($MS = 0.7$) is provided mainly by both guilds of parasitoids. V-stability is low ($VS = 0.3$) and provided mainly by parasitoids of eonymphs. Low v-stability indicates that the life-system is sensible to fluctuations of input factors (such as drought).

An outbreak was simulated by increasing temperature for one year (drought simulation). Population growth was characterized by the coefficient $y_3 = ln(N_o/N_s)$ where N_s is population density in the previous period of stability and N_o is the maximum outbreak density (population density is measured at the stage of mature larvae in September). When $z_i=0$ in Eq. (6) then the i-th process rate was fixed at the level peculiar to the period of stability. It appeared that the decrease of sawfly mortality due to diseases and unidentified causes after the drought, that weakened the host plant, has the greatest contribution ($\beta_6=0.55$) to the population growth y_3 (Table 1). Mass reactivation of diapausing sawflies in the second wave (due to increased litter temperature) is also important ($\beta_4=0.35$).

The sum of regression coefficients for individual processes (ignoring interactions) is 1.05 and the sum of coefficients for process interactions is more than twice as great: 2.32. Without interactions, population increases in numbers during an outbreak only 3 times ($e^{1.05}$) while considering interactions it increases 30 times ($e^{1.05+2.32}$). This fact indicates the great importance of process interactions in sawfly population growth at the beginning of an outbreak. The most important is the interaction of egg parasitism (process 1) with mortality due to diseases and unidentified causes (process 6) and reactivation in the second wave (process 4): $\beta_{16}=0.46$, $\beta_{14}=0.32$. It means that initial population growth due to processes 4 and 6 is amplified by escape from egg-parasitoids. An outbreak is impossible without this interaction.

Population collapse was characterized by the coefficient $y_4=ln(N_o/N_c)$ where N_c is the population density after collapse. When $z_i=0$ in Eq. (6) then the rate of the

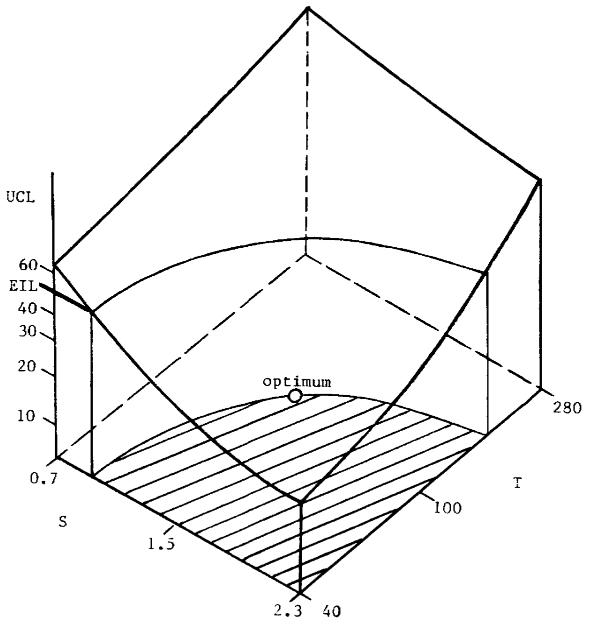

Fig. 5. Optimization of the common pine sawfly chemical control. T – density threshold: the density of sawfly eggs per m^2 in August above which the pesticide is applied; S – intensity of control expressed by k-value of additional larval mortality in September (the logarithm is natural); UCL – simulated upper confidence level for the percent of defoliation caused by the sawfly; EIL – economic injury level (50% defoliation).

i-th process was fixed on the level, peculiar to the period of stability, only in the period of collapse. Food shortage ($\beta_3=1.61$) appeared to be the main cause of population collapse (Table 1). The sum of regression coefficients for process interactions (2.03) is again greater than the sum of the coefficients for individual processes (1.91) indicating the importance of process interactions in this period of an outbreak. The most important is the interaction of egg parasitoids with food shortage ($\beta_{13}=1.75$). This means that food shortage ceased sawfly population growth and that is enough for the parasitoids to increase their relative numbers to the level sufficient for destroying host population.

In the period of depression repeated drought cannot induce another outbreak. It appeared that the increased density of eonymph parasitoids is responsible for this phenomenon (Sharov 1988).

Life-system approach to population management

The purpose of population management is to create with minimum expenses (principle of optimization) such a structure of the life-system that its state will remain in the acceptable region with a certain confidence probability (principle of safety). This formulation differs from the traditional approach to insect pest control where population is suppressed only when its density is high (exceeds the economic injury level, *EIL*). Here the manager does not consider long-term consequences of control measures applied, he is interested only in the current population density. In the life-system approach control measures are considered as a part of the life-system, and their interaction with natural ecological processes determines the probability of the life-system to remain in the acceptable region of the phase space. When using probabilities it is possible to consider future consequences of any control measures.

The density of pest insects is considered as acceptable if it is lower than the *EIL*. *EIL* can be considered either as a constant or as a variable, dependent on prices, yield and so on (see Pedigo et al. 1986). The principle of safety will be expressed by the inequality:

$$UCL \leq EIL \qquad (7)$$

where *UCL* is an upper confidence level of population density, i.e the density does not exceed it with accepted confidence probability (Murdoch 1979). So the purpose of pest management is to reduce *UCL* to *EIL*. This can be done by reducing either the mean density level (especially for stable populations) or the variance of density (especially for unstable populations) or both. Coefficients of m- and v-stability can be used for prediction of the *UCL* change. But for populations with complex dynamics (with outbreaks) direct simulation of the *UCL* will be more easy.

The *UCL* for the common pine sawfly population was simulated under different management strategies characterized by the density threshold (control measures are applied when the pest density is above the threshold) and the intensity of control expressed by the k-value of additional mortality (Fig. 5). The shaded area represents the set of control strategies that satisfy the principle of safety (7). According to the principle of optimization the least expensive strategy has to be selected from this set. It is obvious that the optimal strategy must be located on the boundary of the shaded area in Fig. 5, so it was easy to be found. When comparing chemical and biological control measures it appeared that for pesticide spraying the optimal density threshold is near the *EIL*, but for biological control (parasitoid release) it is much lower, often zero (Sharov 1989). This means that biological control is more effective when applied permanently than according to population density.

Conclusion

The importance of the system's approach in population ecology is still not well realized. Apparently this is the only reason why the life-system concept is rarely used.

There are only few recent works referring to it (Geier et al. 1983, Huffaker et al. 1984, Hughes et al. 1984). No attempts have been undertaken to develop or modify the life-system concept in accordance with modern problems and methods of population ecology.

To investigate the role of ecological processes in population dynamics I propose quantitative methods based on the life-system concept. Without these methods the system's approach in population ecology is non-constructive and is reduced to the statement that everything influences everything. I consider traditional statistical analysis of life tables as only the first step towards the explanation of population dynamics. The second step is the construction of a simulation model using all available information (life tables, results of laboratory and field experiments). The third step is the estimation of integral quantitative characteristics of population dynamics such as coefficients of m-stability and v-stability and analysis of the contribution of individual ecological processes and their interactions to these characteristics. Application of this method to the population of the common pine sawfly revealed that outbreaks of the pest are caused mainly by process interactions and not by individual processes. The importance of process interactions in population dynamics indicates the wholeness of the life-system.

This approach has not only theoretical value for explanation of population dynamics patterns but can be applied to population management as well. Principles of safety and optimization can be used for selecting the best control strategy taking into account stochastic environment fluctuations and long-term consequences of applied measures.

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Reference

Berryman, A. A. 1987. The theory and classification of outbreaks. – In: Barbosa, P. and Schultz, J. C. (eds), Insect outbreaks. Academic Press, New York, pp. 3–30.

Chesson, P. 1978. Predator-prey theory and variability. – Annu. Rev. Ecol. Syst. 9: 323–347.

Clark, L. R. 1964. The population dynamics of *Cardiospina albitextura* (Psyllidae). – Aust. J. Zool. 12: 362–380.

– , Geier, P. W., Hughes, R. D. and Morris, R. F. 1967. The ecology of insect populations. – Methuen, London.

Geier, P. W. 1964. Population dynamics of codling moth *Cydia pomonella* (L.) (Tortricidae), in the Australia Capital territory. – Aust. J. Zool. 12: 381–416.

– , Clark, L. R. and Briese, D. T. 1983. Principles for the control of arthropod pests. 1. Elements and functions involved in pest control. – Prot. Ecol. 5: 1–96.

Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. – Princeton Univ. Press, Princeton, NJ.

Holling, C. S. 1973. Resilience and stability of ecological systems. – Annu. Rev. Ecol. Syst. 4: 1–24.

Huffaker, C. B., Berryman, A. A. and Laing, J. B. 1984. Natural control of insect populations. – In: Huffaker, C. B. and Rabb, R. L. (eds), Ecological entomology. Wiley, New York, pp. 359–398.

Hughes, R. D., Jones, R. E. and Guttierez, A. P. 1984. Short-term pattern of population change: the life-system approach to their study. – In: Huffaker, C. B. and Rabb, R. L. (eds), Ecological entomology. Wiley, New York, pp. 309–357.

Isaev A. S., Khlebopros R. G., Nedorezov L. V., Kondakov Y. P. and Kiselev V. V. 1984. Population dynamics of forest insects. – Nauka, Novosibirsk (in Russian).

May, R. M. 1973. Stability in randomly fluctuating versus deterministic environments. – Am. Nat. 107: 621–650.

– 1974. Stability and complexity in model ecosystems. – Princeton Univ. Press, Princeton, NJ.

– , Hassell, M. P., Anderson, R. M. and Tonkyn, D. W. 1981. Density dependence in host-parasitoid models. – J. Anim. Ecol. 50: 855–865.

Morris, R. F. 1959. Single-factor analysis in population dynamics. – Ecology 40: 580–588.

Murdoch, W. W. 1979. Predation and the dynamics of prey populations. – Fortschr. Zool. 25: 295–310.

Odum, E. P. 1971. Fundamentals of ecology. – Saunders, New York.

Pedigo, L. P., Hutchins S. H. and Higley L. G. 1986. Economic injury levels in theory and practice. – Annu. Rev. Entomol. 31: 341–386.

Pollard, E. 1981. Resource limited and equilibrium models of populations. – Oecologia 49: 377–378.

Sharov A. A. 1983. Parasitoid complex of the common pine sawfly (*Diprion pini* L.) in Rostov region. – Entomologicheskoe Obozrenie (Entomological review) 62: 302–313 (in Russian).

– 1986a. Population buffer ability and homeostasis and their role in population dynamics. – Zhurnal Obshchei Biologii (Journal of General Biology) 47: 183–192 (in Russian).

– 1986b. A simulation model of the common pine sawfly (*Diprion pini* L.) in Rostov region. – Deposited manuscript N7104–B86, Moscow (in Russian).

– 1987. On the role of parasitoids and diseases in population dynamics of common pine sawfly *Diprion pini* L. (Hymenoptera, Diprionidae) in Rostov region. – Zoologicheskii Zhurnal (Zoological Journal) 66: 66–74 (in Russian).

– 1988. Analysis of the role of natural ecological processes in population dynamics of *Diprion pini* L. sawfly in Rostov region using simulation model. – Zhurnal Obshchej Biologii (Journal of General Biology) 49: 653–663 (in Russian).

– 1989. Is the concept of economic injury level universal? – Zashchita Rasteniy (Plant Protection, USSR) N12: 15–17 (in Russian).

– and Safonkin A. F. 1982. Spontaneous and inductive processes in reactivation of common pine sawfly *Diprion pini* (Hymenoptera, Diprionidae). – Zoologicheskii Zhurnal (Zoological Journal) 61: 1171–1179 (in Russian).

Solomon, M. E. 1949. The natural control of animal populations. – J. Anim. Ecol. 18: 1–35.

Varley, G. C. and Gradwell, G. R. 1960. Key factors in population studies. – J. Anim. Ecol. 29: 399–401.