Simulation of the fluctuations of the grey larch bud moth

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Contents

In the summer of 1971 a group of students and accompanying staff from the Entomology Department of the Agricultural University, Wageningen, Netherlands went to Switzerland to take part in a 2-week field course organized by the team of the Alpine Research Centre at Zuoz, studying the population dynamics of the larch bud moth. Discussions with Dr. Auer and Dr. Baltensweiler gave birth to the idea of simulating the gradation cycle of the larch bud moth in the Upper Engadin Valley.

The purpose of simulating was to integrate all the biological data collected so far into a dynamic model to test the validity of different explanations of the mechanism that regulates the numbers of larch bud moth in the Upper Engadin Valley, and to find out what parts of the system are more decisive, in order to suggest priorities for research.

The results of simulation have been discussed with the Swiss research team which we wish to thank for its support and co-operation, and for allowing us to use their sometimes even unpublished data, obtained during many years of painstaking research. However, the responsibility for the content of this monograph is entirely our own.

Collaborating students and research workers of the Agricultural University, Wageningen, were F. H. Rijsdijk, J. Goudriaan and C. T. de Wit.

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1 The grey larch bud moth and its population dynamics

1.1 History

In the Upper Engadin Valley in South East Switzerland, foresters have recorded for many years the recurrence of 'browning' of the canopy and defoliation of the larch (*Larix decidua* Miller) at remarkably regular intervals (6–8 years) (Baltensweiler, 1962; Baltensweiler, 1964). The damage is known to be caused by the grey larch bud moth (*Zeiraphera diniana* Gn.) (Lepidoptera, Tortricidae). In 1948, a comprehensive long-term study of *Z. diniana* was initiated by the Graubünden State Forestry Service and the Entomology Department of the Federal Institute of Technology at Zürich. A scientific working group under the direction of Prof. Dr P. Bovey and Dr W. Baltensweiler is studying the biology of this larch bud moth which involves accurate estimates of larval abundance once a year for each moth generation over the entire Upper Engadin Valley.

The original aims of the study were to assess and explain numerical variations in *Z. diniana*, and to devise methods for preventing serious defoliation of the larch.

1.2 Biology

The grey larch bud moth is univoltine with an obligatory diapause in the egg stage. Two different sympatric biological races are known to exist, one living on larch and the other living on cembran pine (*Pinus cembra*). These races show an effective ecological and sexual isolation (Bovey & Maksymov, 1959).

In the Upper Engadin the eggs of the larch form hatch from mid-May until mid-June. Under normal conditions egg hatching is well synchronized with the sprouting of the larch, so that the first instar larvae have sufficient suitable food (i.e. needles with a length of 6–18 mm) at the time of hatching (Baltensweiler, 1969; Bovey, 1966). When the needles are too short, the larvae are not able to penetrate the short

shoot, and needles that are long are too hard to be a suitable food source for the tiny, freshly hatched larvae (Bovey, 1966).
The larvae pass through five instars in about fifty days. The first four instars feed within the short shoots of the larch, where they spin the needles together to closely webbed tufts. The fifth instar is an open feeder which spins a secondary webbing along the branch axis (Maksymov, 1959).
When feeding is completed, the final instar larvae drop to the ground and pupate in the litter on the forest floor. After a pupation period of 3–4 weeks the moths emerge. They live for about 35 days. The females lay their eggs on the branches of larch trees beneath the protective covering of lichens. Under normal conditions the sex ratio of the adults is about 1:1 (Maksymov, 1959). Under optimum conditions the fecundity amounts to 150–180 eggs per female (Maksymov, 1959). Oviposition mainly occurs during twilight (Meyer, 1969). When the temperature drops below 6 °C active flight and oviposition are interrupted (Maksymov, 1959).

1.3 The population fluctuations in the European Alps

Below an altitude of 1000 m above sea level, for instance on the Swiss Plateau, the density fluctuations of the larch bud moth are of the latent type. Visible damage never occurs there because the climatic conditions do not allow a mass reproduction of the bud moth (Baltensweiler, 1969; Bovey & Baltensweiler, 1970; Bovey, 1966).
The suboptimum zone lies between 1000 and 1300 m altitude; here the density fluctuations of the larch bud moth are of the temporary type. Visible damage occurs at irregular intervals, and only then if the climatic conditions allow a mass reproduction for some years in succession (Baltensweiler, 1966).
The optimum areas are all valleys at high altitudes in different parts of the Alps. In these areas the climate is optimum for the reproduction of the larch bud moth, so here the density fluctuations are mainly determined by density-dependent processes (Bovey, 1958; Baltensweiler 1962), and are of the periodic type. Visible damage occurs at regular intervals of 6 to 8 years. This regularity is most pronounced in the Upper Engadin Valley. This was concluded from forestry reports going back 150 years (Baltensweiler, 1964; Baltensweiler, 1968).

In the Upper Engadin one gradation cycle (defined by the period between two subsequent minima of the population density) lasts 8 to 10 years. The cycle can be divided in a progression phase and a regression phase, both lasting 4 to 5 years. During progression the populations multiply 5 to 10 fold a year, until the food source is exhausted within the larval feeding period. Then regression starts, and the population density is reduced to very low levels again within a few years. Regression changes into progression without any delay. (Auer, 1961; Baltensweiler, 1964; Baltensweiler, 1968; Bovey, 1966).

1.4 The influence of abiotic and biotic factors

1.4.1 Climate and weather

At low altitudes the eggs are laid before August. They have a low survival rate, due to temperature-induced mortality. At high altitudes, on the other hand, the moths generally fly after August and are not able to contribute their full egg potential to population growth, because temperature limits the daily period of oviposition activity (Bassand, 1965; Bovey, 1966). As altitude increases, the heterogeneity of the population structure of the larch bud moth also increases, because the microclimate becomes more variable. Therefore at higher altitudes the populations are better buffered against adverse weather effects, as there is more likelihood that the eggs will hatch at the same time as the larch sprouts (Baltensweiler, 1966; Bovey, 1966). The result is that the physical environment determines an optimum zone (1700–1900 m above sea level) where the population growth is fastest (Auer, 1961; Baltensweiler, 1964; Baltensweiler, 1968; Bovey, 1966).
Baltensweiler *et al.* (1969) showed that extreme weather conditions can influence the population dynamics of the larch bud moth via egg mortality. Baltensweiler (1964) distinguished accelerated, normal and impeded gradations in the Upper Engadin. The differences between these graduation types are probably caused by the variable weather conditions. He mentioned that a dry and warm spring tends to hasten phenological development, thus favouring successful emergence of all the eggs as well as successful establishment of the first instar larvae in the entire area of the valley. He also said that a dry July harmonizes the microclimates of the ground vegetation in pure larch and climax stands and minimizes pupal mortality. The fact that the great bulk

of normal gradations coincides with the average weather conditions in the Upper Engadin is another indication that the climate of this area is very favourable for the larch bud moth (Baltensweiler, 1964).

1.4.2 Quantity and quality of food

During the culmination year, generally complete defoliation occurs within the larval feeding period. Thousands of larvae can then be seen moving on the tree and the forest floor. Most of these larvae die from lack of food, infection by granulosis virus, or from exposure to lethal high temperatures on the soil surface (Baltensweiler, 1964; Baltensweiler, 1968; Bovey, 1966; Maksymov, 1959).
According to Baltensweiler (1968), Baltensweiler (1971), Bovey (1966) and Auer (1968) the quality of the larch needles is reduced for 2–3 years after complete defoliation. According to unpublished data of Benz the quality decrease lasts at least four years. The quality decrease is both mechanical and chemical. The needles hatch later than normal and remain short and hard with an increased content of cellulose and lignine and a decreased nitrogen content (Bovey, 1966; Benz, 1974). The quality of the needles decreases after defoliation levels of 50% or more. This level is reached when the density of the larch bud moth is at least 750 larvae per 7.5 kg of larch branches (Baltensweiler, 1970; Benz, 1974). The decreased food quality strongly affects the larch bud moth populations, especially in the first and second year after complete defoliation. Feeding rate is slowed down, the mean body weight of larvae, pupae and adults decreases, larval and pupal mortality increase, and the fecundity of the females is strongly reduced (Baltensweiler, 1968; Baltensweiler, 1971; Bovey, 1966; Benz, 1974).
Baltensweiler (1968) found some indications that during the regression phase the sex ratio is changed in favour of males. He stated that the homogametic females might succumb more readily to food stress. Benz (1974) showed that the decreased food quality affects the fecundity of the females, but not their mortality rate in proportion to the males. The larval mortality is strongest in the early instars because there is an incoincidence between the egg hatching of the larch bud moth and the sprouting of the larch when needle quality is reduced, and because the needles are too hard then to be a suitable food source for the tiny hatching larvae (Benz, 1974).

1.4.3 Predators, parasites and diseases

The importance of birds and ants as predators of the larch bud moth seems negligible (Bovey, 1958; Bovey, 1966). However, the larch bud moth may be attacked during all its pre-imaginal stages of development by more than 70 different parasite species. Only a few species, all attacking the larval stage, seem to be of real importance as regulators of the larch bud moth.

During progression the parasitism level slowly increases up to 10–20%. Because of the strong reduction of the density of the larch bud moth during the first regression years, the annual increase of the level of larval parasitism is then strongly accelerated. The maximum parasitism level that has been observed in the field was 80%.

During regression the parasite populations are strongly reduced in absolute numbers because of the increased pressure of different forms of intraspecific and interspecific competition. The parasites are unable to inhibit the progression actively as there are insufficient of them left after the density minima of their host (Aeschlimann, 1969; Baltensweiler, 1958; Baltensweiler, 1968; Bovey, 1966). During progression Ichneumonid parasite species, especially *Phytodietus griseanae* Kerrich, are predominant. During the regression phase three Chalcidoid parasite species of the family Eulophidae, are predominant. As parasitism reaches the highest levels during regression, the action of the Eulophids is possibly the most important for the population dynamics of the larch bud moth (Aeschlimann, 1969; Baltensweiler, 1958). Baltensweiler (1958) supposed that only during the regression phase can many Eulophids maintain themselves because the decreased vitality of the larch bud moth increases the effectiveness of parasitism by these species. Aeschlimann (1969) found indications that the Eulophids can maintain themselves quantitatively during both progression and regression. It is not clear whether the effectiveness of the parasite complex as a whole is significantly dependent on the phase of the gradation cycle. Other phytophageous species living on larch can not have any quantitative importance as secondary hosts for the parasites, as their population densities fluctuate at a very low level and usually parallel to that of the larch bud moth. (Baltensweiler, 1958; Auer, 1961; Auer *et al*, 1959).

The quantitative recovery of the parasite populations during the progression phase may be inhibited by the action of Ichneumonid and

Chalcidoid hyperparasite species. In 1964 (the culmination year of the gradation) these species destroyed a considerable part of the primary parasites (Bovey, 1966).
Mortality caused by a granulosis virus was considerable during the culmination year 1954. As the virus remained endozootic during the next two population peaks, its importance as a governing factor for the population dynamics of the larch bud moth seems limited (Martignoni, 1957; Bovey, 1966).

1.5 Spatial distribution within the Upper Engadin

The distribution of the larch bud moth population over the entire Upper Engadin Valley is rather patchy. Statistical research by Auer (1961) shows that significant differences in population density, population development and parasitizing level can be found as a function of exposition, altitude, percentage larches in the stand and the composition of the soil vegetation. The separate effect of each factor is difficult to measure as the different factors strongly interact. Nevertheless it can be stated that the parasitizing level increases when the soil vegetation is more varied, that there is an optimum height for population growth within the valley, and that the annual density increase of the larch bud moth is less when there are less larch trees per unit of surface. The influence of these factors is overwhelmed at higher densities by the very fast population growth of the larch bud moth.
Within the Upper Engadin two different gradation types can be distinguished: an 'early' type in the pure larch stands on the south-facing slopes of the valley, and a 'late' type in the mixed forests on the north-facing slopes. There is a regular, fast increase in the population density of the 'early' type during progression, starting from a relatively high density level. The density level of the 'late' gradation type is low at first, slowly rises during progression and shows a sudden increase in the last year of progression. As the 'late' gradation type generally reaches culmination density one year later than the 'early' type, this fast increase is possibly caused by immigration of adults from stands of the 'early' gradation type (Auer, 1961; Baltensweiler, 1968).

1.6 Explanations of the population dynamics

Since the beginning of the research work in 1948, a number of different theories have been developed to explain the population dynamics of the larch bud moth in the Upper Engadin.
When in 1954, the population density of the larch bud moth was strongly reduced by a granulosis virus, Martignoni (1957) and Bovey (1958) suggested the following explanation for the population dynamics of the larch bud moth.
When the density of the larch bud moth passes a certain level a virus disease breaks out, as the virus spreads readily when the density of the larch bud moth is high. The virus disease together with shortage of food due to overcrowding, destroys a considerable part of the populations. The increase of the level of parasitism and predation is strongly accelerated when the density of the larch bud moth decreases. Below a certain density level the chance for virus infection becomes negligible. Since the virus remained endozootic during the next two density peaks of the larch bud moth, and the regression phase still showed its usual pattern, the above mentioned theory was rejected (Bovey, 1966).
Another hypothesis was put forward by Baltensweiler (1964). In the Upper Engadin and some other valleys at high altitudes in the Alps, the conditions for multiplication are optimum. The average weather conditions and a constant food source guarantee an annual density increase until the food source is exhausted within the period of larval feeding. Processes of intraspecific competition and their various consequences reduce the population density to a very low level again. The ultimate cause of the breakdown of the population is conditioned by processes of overpopulation (shortage of food, reduction of fecundity) and sometimes a virus disease. In a later stage of the regression the parasites reduce the population density still further. Baltensweiler (1968) added that the reduction of fecundity is due not only to food shortage, but also to a change in food quality brought about by defoliation in the previous year. The effects of quality and quantity of food are cumulative in the first regression year. Hence the basic factor that causes the start of the regression is conditioned by the different effects of food quantity and food quality.
A third hypothesis was formulated by Geier (1967). It should be emphasized that his hypothesis is not based on experimental work, but

on discussions with the working group in Switzerland. Geier assumed on the basis of data from Auer (1961) that the reduction of food quantity and quality remains too localized in the Upper Engadin and is therefore insufficient to be the key factor in reducing the density of the larch bud moth during the first regression years over the entire valley. Thus he supposed that the observed differences in vitality of the larch bud moth during progression and regression (expressed in the egg mortality, larval mortality, feeding capacity, mean body weight, pupal mortality, fecundity and the effectiveness of parasitism), have a genetic background. Geier suggested that during the progression phase a 'strong' genetic type is predominant, and during the regression phase a 'weak' type. The 'strong' type would lay 70 eggs per female and would be very susceptible to food stress and to the virus disease. Then selection pressure on the 'strong' type would be very great during the culmination years of the gradation, and therefore the 'strong' type would give way to the 'weak' type during the regression phase. The 'weak' type would lay 30 eggs per female, be more resistent to food stress and be parasitized very easily. Because of the high parasitism level at the end of the regression phase, the 'strong' type would be selected again, and the progression could restart. So according to Geier's hypothesis the gradation cycle of the larch bud moth basically is caused by the mutual competition between two genetic types.

Baltensweiler (1968, 1970) found indications for changes in the genetic composition of the populations of the larch bud moth connected with the phase of the gradation cycle. The treatment of one area with DDT resulted in a mortality of 97% of the larvae. In 1964 the population density showed a 15-fold increase again, but in 1965 regression started simultaneously with the untreated control area. Since the parasitism level in the DDT-treated area was about the same as in the control area all the time, there must have been some density-dependent regulation in this DDT population that had never caused defoliation. This result raises the question of changes in the population quality or genetics during the gradation cycle (Baltensweiler, 1968).

Baltensweiler (1971) assumed that the regression phase lasts longer than could be expected from the effects of food quantity, food quality and parasitism, and suggested that this has a genetic background. He found that the larvae of both the 'larch form' and the 'cembran pine form' show a range of different colour phases from light to dark. The different colour phases can be roughly divided in a 'dark' and an

'intermediate' ecotype. Since crossing experiments between the two extreme forms yielded the full range of intermediate colour phases in the F1 generation, these colour phases in the larvae could not be changed by artificially modifying the density at which they are reared. Moreover rearing experiments on different food qualities resulted in differential mortalities. Therefore Baltensweiler suggested that the ecotypes are genotypes. In laboratory experiments the following properties of the ecotypes were found:

- There is no significant difference in fecundity between the dark and the intermediate ecotype of the larch form. This result contradicts Geier's hypothesis.
- High temperatures (34 °C) during the pre-diapause period of the egg stage kill twice as many eggs of the dark ecotype as those of the intermediate ecotype.
- Eggs of the dark ecotype show a faster post-diapause development than eggs of the intermediate ecotype.
- Larvae of the dark ecotype are more susceptibile to food stress than those of the intermediate ecotype (Day & Baltensweiler, 1972).
- No indications were found that the parasites show a preference for one of the ecotypes. This result also contradicts Geier's hypothesis.

In the latent zone of the larch bud moth (1000 m above sea level or lower) the intermediate ecotype appeared to be predominant. If the colour phases are genetically determined, this predominance could be due to selection against the dark type by high temperatures during the oviposition period. In the Upper Engadin the average weather conditions induce no selection against the dark type. Here the dark type appeared to be predominant during the culmination years of the gradation, and the intermediate ecotype during the regression phase. When it is assumed that the colour phases are genetically determined, this result could be explained by directional selection against the dark type during the culmination year and the regression phase, as the dark ecotype is more susceptible to food stress. If there is alternate directional selection for the colour phases, it is not restricted to climatic and trophic stresses alone. A change in the composition of the larval population towards the light colour phases was observed after the large-scale spray programme (see also Bovey, 1966).

Nevertheless Baltensweiler did not exclude that the observed polymorphism is merely based on modification. There is extensive literature on phenotypic, density-dependent polymorphism associated with

regulation of numbers of gregarious insects, especially amongst noctuid moths (Iwao, 1968). It was found that phenotypic adaptation functions by a change in metabolic rate, i.e. the rate increases in crowded, dark populations, and is low in uncrowded, pale populations. Thus Baltensweiler postulated the following generalization: 'The change in the composition of the larch bud moth populations is an intrinsic mechanism which enables a species to cope with the variability of the environment. This mechanism functions in its most simply conceived form on the basis of two different physiological types and operates either by selection or by modification'.

However Baltensweiler's genetic theory still has several important gaps:

– It has not been proven that the different larval colour types are genetically determined. It is possible that the shifting towards the intermediate ecotype is a phenotypic phenomenon, connected with the quality of food or the population density.

– There is no evidence for the hypothesis that the predominance of the intermediate ecotype lengthens the regression phase.

– The dark ecotype is more susceptible to food stress than the intermediate ecotype (Day & Baltensweiler, 1972). Therefore it can not be excluded that the presence of polymorphism decreases the amplitude of the gradation cycle. The accumulation of the dark ecotypes during progression could hasten the start of regression since the dark ecotypes are selected against as the total density increases.

– The mechanism of directional selection towards the dark ecotypes has not been explained.

– It is unlikely that a shift towards a different ecotype could occur within five generations. Haldane (1957) estimated that an average gene replacement requires 300 generations in nature, although there appear to be many instances where the rates of evolution are higher than could be accomplished by one substitution per 300 generations. It can be stated on theoretical grounds that a shift towards a different ecotype within five generations is only possible if the inheritance of the colour types is monofactorial and if very pronounced differences in fecundity between the different colour types exist. The latter condition has not been met.

2 The application of key factor analysis

Auer (1968, 1969) tried to quantify the influence of the different factors that affect the larch bud moth populations with the help of key factor analysis. By modifying Morris's single factor analysis (Morris, 1959), Auer developed a statistical model for the larch bud moth. Five different factors were taken into account: parasitism, diseases, damage to the tree and loss of food quality, temperature and relative air humidity.
Auer's basic formula reads:

$$Y_{t+1} = aY_t(1-P)^b\,(1-D)^c\,(1/(1+F))^d\,(\Sigma T-36.2)^e\,(RH)^f$$

Y_{t+1} = population density in year $(t+1)$
Y_t = population density in year t
a = factor of proportionality
$(1-P)$ = fraction of the population in year t that is not affected by the parasites
$(1-D)$ = fraction of the population in year t that is not affected by diseases
$1/(1+F)$ = expression for the degree of direct damage to the tree and for the loss of food quality in year t
$(\Sigma T-36.2)$ = the sum of the means of the mean daily temperatures (°C) per month, for the months July, August and September of year t, and the months April, May and June of year $(t+1)$, minus 36.2°C (the weather conditions seem to be the most relevant for the population dynamics of the larch bud moth during these six months; this way of expressing the mean temperature was chosen to avoid negative values)
RH = the mean relative air humidity during the months July, August and September of year t, and the months April, May and June of year $(t+1)$.

By rewriting the basic formula in the regression form the following

expression is obtained:

$$\log(Y_{t+1})-\log(Y_t)=\Delta Y=\log(a)+b\log(1-P)+c\log(1-D)+$$
$$+d\log(1/(1+F))+e\log(\Sigma T-36.2)+f\log(RH)$$

For each successive year the values observed in the field in the year in question are put into the model for P, D, T, and RH. This was not possible for F, as it expresses both the direct damage and the loss of food quality. Auer assumed that the after-effect of the direct damage in year t amounts to 80% in year $(t+1)$, and 20% in year $(t+2)$. F is found by accumulating the direct damage (defoliation as a proportion of the total needle mass) and the after-effects of the direct damage in the two preceding years.

If Δy stands for $\log(y_{t+1})-\log(y_t)$, where y_{t+1} is the observed population density in year $(t+1)$ and y_t is the observed population density in year t, and ΔY stands for $\log(Y_{t+1})-\log(Y_t)$ where Y_{t+1} is the calculated population density in year $(t+1)$ and Y_t is the calculated population in year t, then the optimum values of the regression factors a, b, c, d, e and f can be calculated by minimizing the following expression:

$$\sum_{1}^{n}(\Delta y-\Delta Y)^2\rightarrow\min.$$

(n is the number of successive years for which the calculations are done).

The same procedure is followed for models including 1, 2, 3 or 4 factors. The relative importance of each single factor can be measured by multiplying its mean value in the model by the value of its regression factor.

The most important conclusions from Auer's work were:

The calculations with the 5-factor model resulted in a very high degree of correlation with the observed population density curve. The goodness of fit was 0.98. So according to the results of Auer's calculations, changes in the genetic composition of the populations of the larch bud moth can, at best, play a minor role in their dynamics.

The population dynamics of the larch bud moth cannot be explained by one single key factor, but only by a combination of factors. The more factors that are included in the model, the better the goodness of fit.

The five factors that were considered can be arranged as follows

according to their relative importance for the population dynamics of the larch bud moth:
- parasitism
- damage and loss of food quality
- diseases
- relative air humidity
- temperature.

The model that was developed by Auer was based on regression analysis with empirical data. With this model a satisfactory description of the density fluctuations could be obtained, but this description was not based on the underlying mechanisms at the individual level such as development rates, mortality rates and parasite-host interactions. Errors of the second sort may occur. It could be possible, for instance, to find by chance a high degree of correlation between the density fluctuations of the larch bud moth and some factor that in reality does not affect the larch bud moth at all. The influence of an insignificant factor may also be strongly overestimated when it fluctuates simultaneously with another factor that is important but still unknown. Another shortcoming of Auer's model is that the observed multiplication factors are treated as variables that are independent of the density of the larch bud moth. So the density dependence of the factors parasitism, diseases, and damage and loss of food quality, is not accounted for. Auer (1969) pointed out that it is possible to improve the model in this respect.

Process simulation with the use of computers and special simulation languages is based on quite different starting points. In the computer model, the biological processes that underlie the system are simulated with the help of data that can be obtained from the literature or from experiments. So the description of the density fluctuations of a research object is obtained from the simulation of the underlying processes at the individual level.
The explanatory value of the model is not restricted by limitations of the working method as such, but only by lack of insight in the relevant underlying biological processes. The application of this working method to the population dynamics of the larch bud moth in the Upper Engadin Valley will be explained in the next chapters.

3 The process simulation technique and the simulation of development

A system is a limited part of reality with related elements. The set of relations is called the structure of the system. Examples of a system are a cell, a plant or a field. The boundary between system and environment is preferentially chosen in such a way that the behaviour of the system does not depend on its environment. The system is dynamic, that is it changes with time.
A simplified representation of a dynamic system is a dynamic model. If the model is the same as the original, there is no need to construct it. The model only has to agree with the original on relevant points. The differences between model and original can make the model simpler, easier to handle and more lucid than reality.
A fairly wide definition of simulation is the building of a model and studying its behaviour. Simulation is useful if it increases the insight in reality by extrapolation and analogy, if it is the basis for the design of new experiments and if the model accounts for the most relevant phenomena and contains no assumptions that are proved to be false. Simulation with the help of computers is only useful if the system studied is too complex and an analytical-mathematical approach becomes too difficult. The biological processes that underlie an ecological system can be represented in a simulation model with the help of computer languages that are especially designed for this purpose.

The simulations in this monograph were carried out according to the state variable approach. This approach is based on the use of digital computers. A digital computer, where all executions are discrete and take place in a sequential order, seems to be a most unsuitable instrument for simulating ecological systems, as the changes in this kind of system are parallel and continuous. The main feature of simulation languages is to overcome these limitations. These languages are based on the axiom that changes of the conditions in a system are not mutually dependent, but can be derived separately from the state of the system. All rates of change between time t and time $(t+\Delta t)$ are calcula-

ted from the condition at time t and if necessary data from the past. Only after the calculation of all the rates at the moment of simulation, can the changes be executed by semi-parallel integration over a small time interval.
For practical reasons the time interval for integration cannot be infinitely small. It must be at least so short that the rates can be assumed to be constant during this interval. The simplest integration method available is the Eulerian or rectilinear one, in which the new value of an integral equals the old value plus the product of the time interval and the rate of change. The time interval is kept at a fixed value during simulation when this method is used.
In process simulation models, five different kinds of variables can be distinguished: state variables, driving or forcing variables, auxiliary variables, rate variables and output variables. The state variables characterize and quantify all observed properties of the system, such as number of larvae, number of parasites, amount of food and so on. At the onset of the simulation the values of all state variables have to be known. In mathematical terms they are quantified by the contents of integrals. In relational diagrams they are represented by squares.
Driving or forcing variables are those that are not affected by processes within the system but characterize the influence from outside. These may be for instance the temperature or the temperature sum. Depending on the boundary of the system to be simulated, the same variables may be classified either as state or as driving variables. In relational diagrams driving variables are represented between brackets.
The rates of change of the state variables are quantified by rate variables. Knowledge of the underlying biological and physical processes makes the formulation of rules possible, according to which the values of the rate variables are determined. In relational diagrams rate variables are represented by valves.
For complicated processes the use of properly chosen intermediate auxiliary variables makes the calculation process more lucid. In relational diagrams these variables are represented by circles. Output variables are the quantities that the model produces for the user. They may be state, rate or auxiliary variables.
Parameters, that have a constant value, are underlined in relational diagrams. Flow of material is represented by solid lines, while flow of information is represented by broken lines.
The application of the state variable approach in ecosystem modelling

and the simulation language used here, Continuous System Modelling Program CSMP, is explained in detail in another book of the Simulation Monograph Series (De Wit & Goudriaan, 1974).

The relational diagram in Fig. 1 shows one simple way to simulate hatching, i.e. the development of young larvae from eggs. The amount of eggs, and the amount of young larvae, two state variables, are given within rectangles. They are connected by a solid arrow that designates the flow of individuals from one state to the other. This flow is regulated by the hatching rate, HR, a variable presented within the valve symbol, dependent on a constant, the relative hatching rate RHR, which is underlined and on the amount of eggs; both dependences being presented by broken lines.

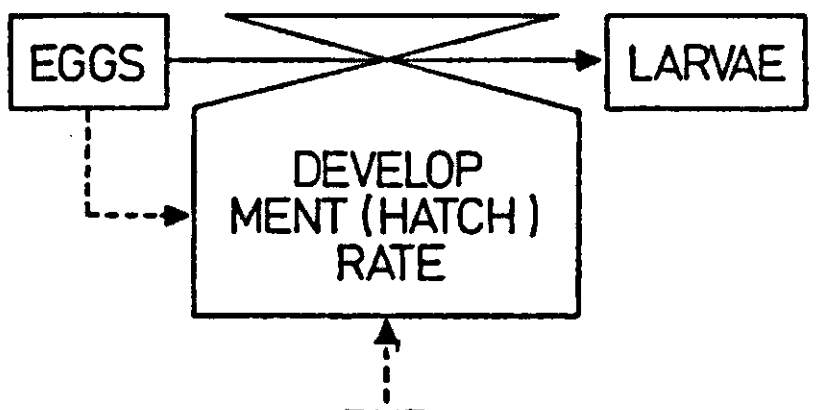

Fig. 1 | Simplest relational diagram for the hatching process of eggs.

In CSMP, the two state variables are presented by integrals.

```
EGGS = INTGRL (100., - HR)
LARV = INTGRL (0., HR)
```

The first number in the argument is the initial value, which is here, of course, zero for the number of larvae, and arbitrarily assumed to be 100 for the number of eggs. The second variable in the argument is the rate of change of the number of larvae. This hatching rate may be equal to HR = RHR * EGGS in which the relative hatching rate is defined as a parameter at, for instance, 0.1 day^{-1} with

```
PARAMETER RHR = 0.1
```

The actual simulation program is completed with a statement that specifies the time period over which the system is simulated and the

TIME	EGG	MINIMUM 4.9787E+00 I	MAXIMUM 1.0000E+02 I
0.0000E-01	1.0000E+02		
1.0000E+00	9.0484E+01		
2.0000E+00	8.1873E+01		
3.0000E+00	7.4082E+01		
4.0000E+00	6.7032E+01		
5.0000E+00	6.0653E+01		
6.0000E+00	5.4881E+01		
7.0000E+00	4.9659E+01		
8.0000E+00	4.4933E+01		
9.0000E+00	4.0657E+01		
1.0000E+01	3.6788E+01		
1.1000E+01	3.3287E+01		
1.2000E+01	3.0119E+01		
1.3000E+01	2.7253E+01		
1.4000E+01	2.4660E+01		
1.5000E+01	2.2313E+01		
1.6000E+01	2.0190E+01		
1.7000E+01	1.8268E+01		
1.8000E+01	1.6530E+01		
1.9000E+01	1.4957E+01		
2.0000E+01	1.3534E+01		
2.1000E+01	1.2246E+01		
2.2000E+01	1.1080E+01		
2.3000E+01	1.0026E+01		
2.4000E+01	9.0718E+00		
2.5000E+01	8.2085E+00		
2.6000E+01	7.4274E+00		
2.7000E+01	6.7206E+00		
2.8000E+01	6.0810E+00		
2.9000E+01	5.5023E+00		
3.0000E+01	4.9787E+00		

TIME	LARV	MINIMUM 0.0000E-01 I	MAXIMUM 9.5021E+01 I
0.0000E-01	0.0000E-01		
1.0000E+00	9.5163E+00		
2.0000E+00	1.8127E+01		
3.0000E+00	2.5918E+01		
4.0000E+00	3.2968E+01		
5.0000E+00	3.9347E+01		
6.0000E+00	4.5119E+01		
7.0000E+00	5.0341E+01		
8.0000E+00	5.5067E+01		
9.0000E+00	5.9343E+01		
1.0000E+01	6.3212E+01		
1.1000E+01	6.6713E+01		
1.2000E+01	6.9881E+01		
1.3000E+01	7.2747E+01		
1.4000E+01	7.5340E+01		
1.5000E+01	7.7687E+01		
1.6000E+01	7.9810E+01		
1.7000E+01	8.1732E+01		
1.8000E+01	8.3470E+01		
1.9000E+01	8.5043E+01		
2.0000E+01	8.6466E+01		
2.1000E+01	8.7754E+01		
2.2000E+01	8.8920E+01		
2.3000E+01	8.9974E+01		
2.4000E+01	9.0928E+01		
2.5000E+01	9.1791E+01		
2.6000E+01	9.2573E+01		
2.7000E+01	9.3279E+01		
2.8000E+01	9.3919E+01		
2.9000E+01	9.4498E+01		
3.0000E+01	9.5021E+01		

Fig. 2 | Simulated hatching curve of eggs and corresponding emergence of larvae, when only one integral is used (Poisson process).

interval at which output is wanted:

```
TIMER FINTIM = 30., OUTDEL = 1.
```

a statement that specifies the output:

```
PRTPLT EGGS, LARV
```

The output is given in Fig. 2.
Obviously there is an exponential decrease in the number of eggs and a corresponding increase in the number of larvae.
The hatching rate may also be a function of temperature. If a birth rate, BR, and a death rate of eggs, DR, is added the first integral becomes

```
EGGS = INTGRL (100., BR - DR - HR)
```

and the hatching rate becomes

```
HR = EGGS * AFGEN (RHRT,TEMP)
```

The AFGEN function (Arbitrary Function GENerator) makes linear interpolation possible between given values for RHR as a function of the temperature TEMP.
The other rates, birth rate and death rate should, of course, also be quantified.
It is well known that the average residence time in the egg stage is the inverse of the relative hatching rate, i.e. 10 days for Fig. 2. Hence the duration of the process is controlled by the relative hatching rate.
The form of the resulting curve, however, is still unrealistic. Actual experiments show that for some days after the onset of hatching small numbers of larvae appear. Then the hatching rate increases and decreases again. The complexity of the hatching process and the many subprocesses concerned, obviously causes a bell-shaped hatching curve.

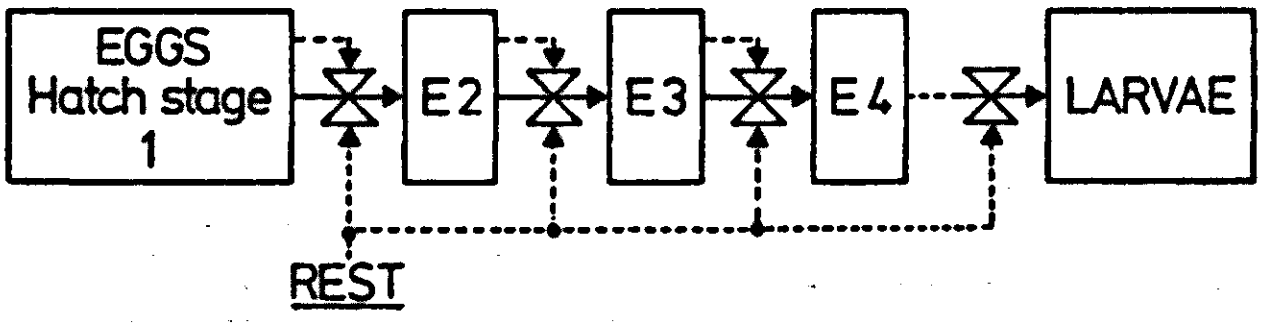

Fig. 3 | Relational diagram of the hatching process of eggs, application of the boxcar train or age classes approach.

Without analysing these underlying processes in detail, they may be mimicked by constructing a number of development classes according to the relational diagram of Fig. 3.
In each class the residence time, RT, is 1/N of the total residence time (hatching time) REST, N being the number of classes (N = 10). This is programmed as follows:

```
EGG1 = INTGRL (100., - EGG1/RT)
EGG '2,10' = INTGRL
  (0., (EGG '1,9' - EGG '2.10')/RT)
LARV = INTGRL (0., EGG10/RT)
```

The second integral statement stands for the 9 integrals EGG2–EGG10. For instance:

```
EGG5 = INTGRL (0.,(EGG4 - EGG5)/RT)
```

The residence time in each class, being defined by:

```
RT = 1/N*REST
REST = 1/RHR
PARAMETER RHR = .1, N = 10,
```

The resulting emergence curve of larvae is presented in Fig. 4. A Gaussian distribution function with its maximum at 10 days (1/RHR) is obtained.
Goudriaan (1973) showed that the variance of this Gaussian distribution function is defined as:

$$S^2 = N \times (RT)^2$$

$N \times RT$ representing the average total residence time REST.
Hence the relative standard deviation is constant according to:

$$S/REST = S/(N \times RT) = (1/\sqrt{N})$$

and only dependent on the number of development classes.
So a relative standard deviation of 0.2 is realized when 25 classes are distinguished, and for a relative standard deviation of 0.1, 100 hatching (development) classes must be distinguished.
This large number of classes takes too much computing time and moreover, once the number of classes is chosen, the relative standard deviation is fixed.
It is possible that the relative standard deviation depends on the abiotic

	MINIMUM 7.137AE-04 EGG VERS TIME	MAXIMUM 1.0000E+02
TIME	EGG	I
0.0000E-01	1.0000E+02	----------+
1.0000E+00	1.0000E+02	----------+
2.0000E+00	9.9995E+01	----------+
3.0000E+00	9.9890E+01	----------+
4.0000E+00	9.9187E+01	----------+
5.0000E+00	9.6817E+01	----------+
6.0000E+00	9.1608E+01	---------+
7.0000E+00	8.3050E+01	--------+
8.0000E+00	7.1663E+01	-------+
9.0000E+00	5.8741E+01	------+
1.0000E+01	4.5793E+01	-----+
1.1000E+01	3.4051E+01	----+
1.2000E+01	2.4239E+01	---+
1.3000E+01	1.6581E+01	--+
1.4000E+01	1.0939E+01	-+
1.5000E+01	6.9851E+00	+
1.6000E+01	4.3297E+00	+
1.7000E+01	2.6125E+00	+
1.8000E+01	1.5382E+00	+
1.9000E+01	8.8565E-01	+
2.0000E+01	4.9964E-01	+
2.1000E+01	2.7664E-01	+
2.2000E+01	1.5056E-01	+
2.3000E+01	8.0649E-02	+
2.4000E+01	4.2572E-02	+
2.5000E+01	2.2169E-02	+
2.6000E+01	1.1399E-02	+
2.7000E+01	5.7929E-03	+
2.8000E+01	2.9114E-03	+
2.9000E+01	1.4486E-03	+
3.0000E+01	7.137AE-04	+

	MINIMUM 0.0000E-01 LARV VERS TIME	MAXIMUM 9.9999E+01
TIME	LARV	I
0.0000E-01	0.0000E-01	+
1.0000E+00	1.0945E-05	+
2.0000E+00	4.6453E-03	+
3.0000E+00	1.1024E-01	+
4.0000E+00	8.1328E-01	+
5.0000E+00	3.1629E+00	-+
6.0000E+00	8.3924E+00	----+
7.0000E+00	1.6950E+01	--------+
8.0000E+00	2.8337E+01	----------+
9.0000E+00	4.1259E+01	----------+
1.0000E+01	5.4207E+01	----------+
1.1000E+01	6.5949E+01	----------+
1.2000E+01	7.5761E+01	----------+
1.3000E+01	8.3419E+01	----------+
1.4000E+01	8.9061E+01	----------+
1.5000E+01	9.3015E+01	----------+
1.6000E+01	9.5670E+01	----------+
1.7000E+01	9.7388E+01	----------+
1.8000E+01	9.8462E+01	----------+
1.9000E+01	9.9114E+01	----------+
2.0000E+01	9.9500E+01	----------+
2.1000E+01	9.9723E+01	----------+
2.2000E+01	9.9849E+01	----------+
2.3000E+01	9.9919E+01	----------+
2.4000E+01	9.9957E+01	----------+
2.5000E+01	9.9978E+01	----------+
2.6000E+01	9.9989E+01	----------+
2.7000E+01	9.9994E+01	----------+
2.8000E+01	9.9997E+01	----------+
2.9000E+01	9.9999E+01	----------+
3.0000E+01	9.9999E+01	----------+

Fig. 4 | Simulated hatching curve and corresponding emergence of larvae with several development classes and the 'continuous' method of simulation of development.

conditions for growth and development. A solution for this problem is found by a versatile combination of the presented method with a modelling system which moves the eggs through the development classes without dispersion, like the contents of the boxcars of a train moving along a track.
To achieve movement without dispersion the whole contents of the development classes are shifted at the moment that one residence time is passed. This is done as follows:

```
EGG1 = INTGRL (100., -PUSH * EGG1)
EGG '2,10' = INTGRL (0.,
  PUSH * (EGG '1,9' - EGG '2,10'))
LARV = INTGRL (0., PUSH * EGG10)
```

The variable PUSH is always zero, except at the moment when the residence time is passed. Then it has the value 1/DELT, in which DELT is the small time step of integration. At that moment the rate of change of, for instance, the integral EGG1 becomes EGG1/DELT, the content of the integral changes with numerical integration to:

$$EGG1_{T+DELT} = EGG1_T - (1/DELT) \times EGG1 \times DELT = 0$$

In this way the first development class is completely emptied. Similar shifts occur in the other classes.
The control of the value of PUSH requires two additional statements

```
PUSH = INSW (HST - 1/N, 0., 1/DELT)
HST = INTGRL (0., (RHR - PUSH/N))
```

The hatching stage, HST, is the integral of the relative hatching rate. HST accumulates until it exceeds 1/N. Then 1/N is subtracted. PUSH is set at zero by the INSWitch as long as HST is smaller than 1/N and equals 1/DELT when HST is larger. In Fig. 5 the result of this way of modelling is given, with $N = 10$ and a hatching rate of 0.1 day^{-2}.
Hence there are now two programming systems available. One, the continuous one, which generates a constant relative standard deviation and the other, the discontinuous method, that generates no standard deviation at all. A combination of both methods for which the relative standard deviation is not constant can be mimicked by an intermediate method. A fraction F of the content of the development classes is shifted with a frequency which is 1/F time larger. F may

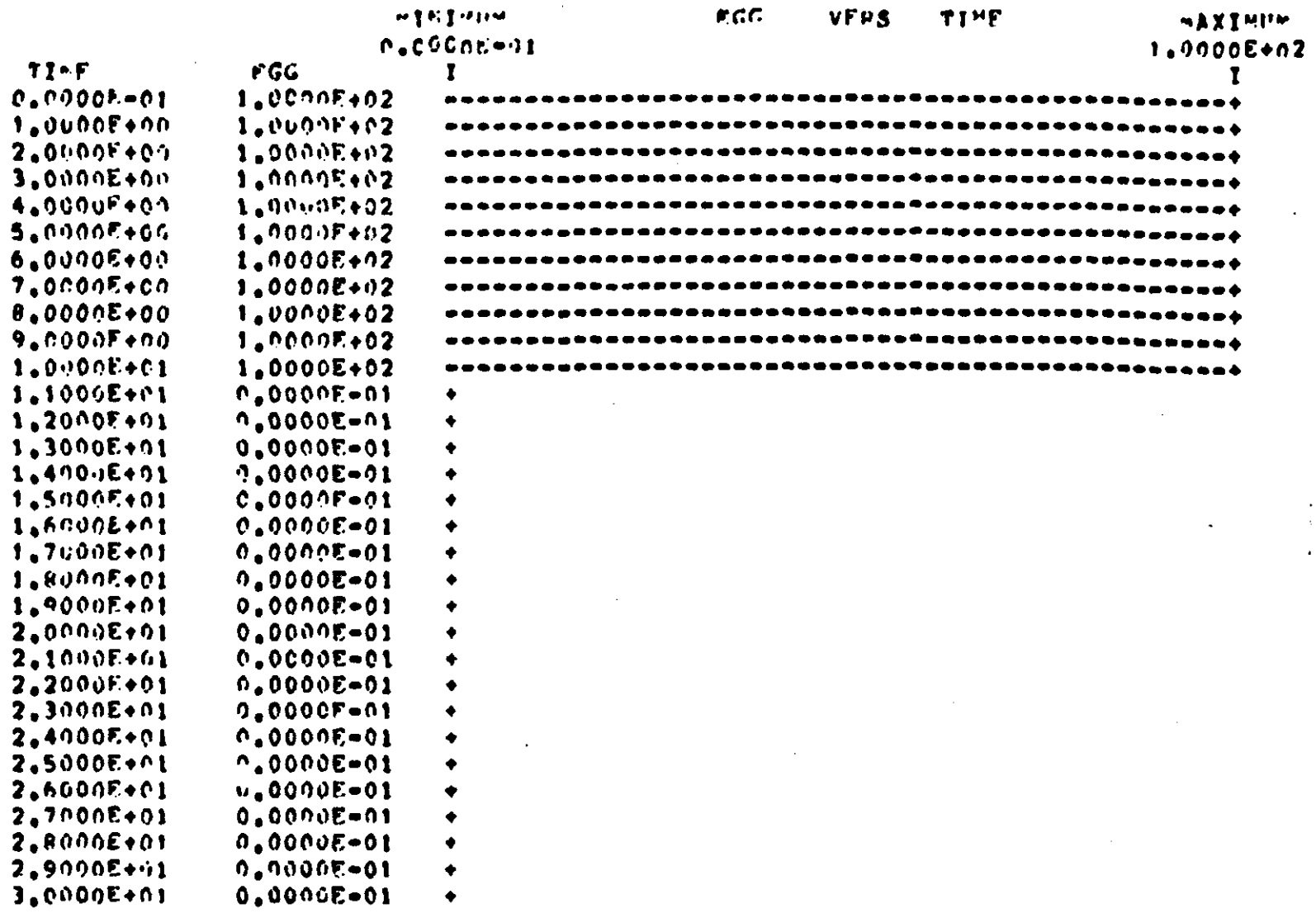

Fig. 5 | Simulated heatching curve with the 'discontinuous' method of simulation.

depend on abiotic conditions or on other driving variables. This fraction is 1 when complete 'discontinuous' simulation is required and is DELT/RT when complete 'continuous' simulation suffices to mimic the dispersion.
This is shown in the following notations:
Continuous:

$$F = DELT/RT$$
$$HR = -EGG1 \times PUSH \times DELT/RT$$

As PUSH is 1/DELT:

$$HR = -EGG1 \times 1/RT$$

Discontinuous:

$$F = 1$$
$$HR = -EGG1 \times PUSH \times 1$$

In the intermediate cases the fraction F equals

$$1 - N \times (S/REST)^2$$

so the size of the fraction is determined by the deviation from the 'continuous' situation, i.e. $N = (S/REST)^2$. Thus the value of F can be adjusted to give different values of the relative standard deviation. When the standard deviation becomes relatively small, the size of the fraction increases until the extreme case of complete 'discontinuous' simulation without any dispersion occurs.
In CSMP this is written:

```
EGG1 = INTGRL (100., - PUSH * EGG1 * F)
EGG '2,10' = INTGRL (0., PUSH *
  (EGG '1,9' - EGG '2,10') * F)
LARV = INTGRL (0., PUSH * EGG10 * F)
PUSH = INSW (HST - 1.,0., 1./DELT)
HST = INTGRL (0., 1/RT - PUSH)
F = AMAX1 (DELT/RT, 1. - N *
   ((S/REST)** 2))
```

The expression AMAX1 (––, ––) is a CSMP function that takes the largest of the two arguments between the brackets.
The resulting birth curve is given in Fig. 6. It can be shown that the resulting variance is given by

	MINIMUM 2.1180E+00	EGG VERS TIME	MAXIMUM 1.0000E+02
TIME	EGG	I	I
0.0000E-01	1.0000E+02	----------	+
1.0000E+00	1.0000E+02	----------	+
2.0000E+00	1.0000E+02	----------	+
3.0000E+00	1.0000E+02	----------	+
4.0000E+00	1.0000E+02	----------	+
5.0000E+00	1.0000E+02	----------	+
6.0000E+00	1.0000E+02	----------	+
7.0000E+00	1.0000E+02	----------	+
8.0000E+00	1.0000E+02	----------	+
9.0000E+00	1.0000E+02	----------	+
1.0000E+01	1.0000E+02	----------	+
1.1000E+01	1.0000E+02	----------	+
1.2000E+01	1.0000E+02	----------	+
1.3000E+01	1.0000E+02	----------	+
1.4000E+01	1.0000E+02	----------	+
1.5000E+01	1.0000E+02	----------	+
1.6000E+01	1.0000E+02	----------	+
1.7000E+01	9.9979E+01	----------	+
1.8000E+01	9.9761E+01	----------	+
1.9000E+01	9.8777E+01	----------	+
2.0000E+01	9.6059E+01	----------	+
2.1000E+01	8.7061E+01	----------	+
2.2000E+01	7.3130E+01	----------	+
2.3000E+01	5.6943E+01	----------	+
2.4000E+01	4.1363E+01	----------	+
2.5000E+01	2.8253E+01	----------	+
2.6000E+01	1.8287E+01	----------	+
2.7000E+01	1.1293E+01	----------	+
2.8000E+01	6.6929E+00	----------	+
2.9000E+01	3.8257E+00	+	
3.0000E+01	2.1180E+00	+	

	MINIMUM 0.0000E-01	LARV VERS TIME	MAXIMUM 9.7882E+01
TIME	LARV	I	I
0.0000E-01	0.0000E-01	+	
1.0000E+00	0.0000E-01	+	
2.0000E+00	0.0000E-01	+	
3.0000E+00	0.0000E-01	+	
4.0000E+00	0.0000E-01	+	
5.0000E+00	0.0000E-01	+	
6.0000E+00	0.0000E-01	+	
7.0000E+00	0.0000E-01	+	
8.0000E+00	0.0000E-01	+	
9.0000E+00	0.0000E-01	+	
1.0000E+01	0.0000E-01	+	
1.1000E+01	0.0000E-01	+	
1.2000E+01	0.0000E-01	+	
1.3000E+01	0.0000E-01	+	
1.4000E+01	0.0000E-01	+	
1.5000E+01	0.0000E-01	+	
1.6000E+01	0.0000E-01	+	
1.7000E+01	2.1475E-02	+	
1.8000E+01	2.3894E-01	+	
1.9000E+01	1.2229E+00	+	
2.0000E+01	3.9408E+00	---+	
2.1000E+01	1.2939E+01	---------+	
2.2000E+01	2.6870E+01	----------	+
2.3000E+01	4.3057E+01	----------	+
2.4000E+01	5.8637E+01	----------	+
2.5000E+01	7.1747E+01	----------	+
2.6000E+01	8.1713E+01	----------	+
2.7000E+01	8.8707E+01	----------	+
2.8000E+01	9.3307E+01	----------	+
2.9000E+01	9.6174E+01	----------	+
3.0000E+01	9.7882E+01	----------	+

Fig. 6 | Simulated hatching curve and corresponding emergence with the method of 'controlled' dispersion.

$$(S)^2 = N \times RT^2 \times (1-F)$$

In this way $(S)^2$ equals zero when $F = 1$, and whole contents of the classes are shifted. It approaches its maximum value when F approaches zero.
As has been said F and the relative hatching rate are often the functions of biotic and abiotic conditions. This combined method of modelling is used in this monograph to simulate the development of the larval, pupal and adult stages of the larch bud moth. However the lumping of populations into development classes introduces errors of approximation. In the most extreme case when $F = 1$, the contents of the classes are shifted as a whole and when a limited number of classes is distinguished the approximation errors can be considerable. For instance, in a development model of eggs at a constant temperature of 15°C, age classes of 0–2, 2–4, 4–6, 6–8 days may be distinguished. Every two days the contents of the classes (as $F = 1$) are shifted one place, so that generally the residence time in each class is two days. This does not hold however for the first development class, as it has a continuous inflow, formed by the birth rate. Only individuals born just after a shift will stay here for two days. As time proceeds the residence time of individuals born later will become progressively shorter. On the average the residence time in the first class will be half of the interval of pushing. So the average age of the eggs pushed from the first age class to the second is not 2 days, but 1 day, and this means that the next age classes are 1–3, 3–5, 5–7 days, instead of 2–4, 4–6, 6–8 days, respectively.

A solution for this error is found by placing a preclass before the different development classes. This class is filled continuously by the birth rate and emptied continuously with a rate that is half the residence time of the considered age class multiplied by the content of this class, so:

```
EGGO = INTGRL (0., BR -
  (1/(RT * .5)) * EGGO)
```

and as $F = 1$

```
EGG1 = INTGRL (0., (1/(RT * .5)) *
  EGGO - PUSH * EGG1 * 1.)
```

In this way the first development class is filled with a continuous rate of eggs with an average age of one day. The average age of the eggs in the first age class at the moment of shifting is then two days instead of one day.
When F = 1, error occurs and the given solution for this problem should be applied, but, when F = DELT/RT, there is no error of approximation. Therefore in the intermediate cases and when F = DELT/RT, an additional correction should be introduced. This is done by multiplying the rate of transfer from the preclass to the first development class by the reciprocal of the fraction F. Thus a preclass with an outflow of 2/RT when F = 1, and of (2/RT) × (1/F) in the intermediate cases, synchronizes the ages in the development classes. When F = DELT/RT in the case of 'continuous' simulation, the residence time in the preclass is negligible but then very small time steps are necessary and this requires too much computer time. Waste of computer time is prevented by choosing the number of classes not too close to that number with which continuous simulation mimics the dispersion correctly.
In this way growth and development of populations is simulated with incorporation of the dispersion in development, due to the underlying physiological processes, and without losing any accuracy in the age structure of the population.

4 The model

In this chapter the structure of the simulation model that was designed for the population dynamics of the larch bud moth, is explained. In the first section some general remarks on the structure of the model are made. In the second section the relational diagrams for the three subsystems that were simulated in the model, are given. These diagrams are meant to give a general idea, but are not in detail. The structure of the model is explained on the basis of a number of detailed sub-diagrams. In the third section the technical details of the simulation program are explained. The appendixes give a list of abbreviations, an explanation of the symbols used in the relational diagrams, and the complete simulation program.

4.1 The general design of the model

The mean population density curve of the larch bud moth in the Upper Engadin Valley was simulated. Although within the Valley different gradation types can be distinguished, the Upper Engadin as a whole is considered an autochtonous ecological entity. Migration of adults into or from the area seems not to be of importance for the population dynamics of the larch bud moth inside the valley (Auer, 1961). Therefore the Upper Engadin was taken as the spatial limit for simulation. In the model three different subsystems were simulated: the larch bud moth, the larch and the parasite complex. The virus disease was left out as the virus remained endozootic during the last two density peaks of the larch bud moth (Bovey, 1966; Baltensweiler pers. commun.). Predators and hyperparasites were omitted because generally they are not of quantitative importance (Bovey, 1966). Moreover the research data were insufficient. Only the effect of egg predation was introduced in the form of a certain percentage egg mortality (see Section 4.2.8). The simulation program (see Appendix C) is divided in an INITIAL, a DYNAMIC, and a TERMINAL part so that the calculations can be repeated for a number of successive years during one run of the program. In the INITIAL part the initial amounts needed to start the

calculations, are given. These are: the initial number of female parasites NPARI, the initial needle mass WENEI, and the number of larch bud moth eggs after winter EW. In the DYNAMIC part, the text of the proper simulation program is given, and the TERMINAL part calculates the amounts that are needed to start the simulation for the next year.
A period of 30 years was simulated. Simulation starts with 0.06 parasites per 7.5 kg larch branches, an initial needle mass of 3.314 kg per 7.5 kg larch branches, and with 0.37 eggs per 7.5 kg larch branches. All amounts in the model are expressed per 7.5 kg larch branches as this was the sample unit formerly used by the research team in Switzerland.
The same temperature table was used for every year. In this table the mean daily values of the temperature are given every day from 1 May until 6 November. These values are based on data of 1963 from the meteorological station at Bever (Upper Engadin). This way of introducing the temperature seemed acceptable as the regularity of the outbreaks of the larch bud moth in the Upper Engadin indicates that the variations in weather conditions between the years in this area are relatively unimportant for the population dynamics of the larch bud moth. Bovey (1958) and Baltensweiler (1962) pointed out that in the optimum areas such as the Upper Engadin the climate always allows a mass reproduction of the larch bud moth, so that the density fluctuations in these areas are mainly determined by density-dependent processes. As soon as more data on the influence of the temperature on the mortality of the larch bud moth are available, it might be useful to give different temperature data for each successive year.
Simulation starts on 1 May and ends on 6 November for each successive year. The rectilinear integration method was used. The time step for integration was fixed at 0.1 days as further shortening of the time step had no significant influence on the results of simulation.

4.2 Relational diagrams

In Figs. 7, 8 and 9 the general concept of the model is presented. These diagrams are treated in more detail in the next sections.

4.2.1 The development of the larch bud moth

The larval stage, the pupal stage PU, and the adult stage AD, are simulated separately. The development of each stage is divided into four classes: 0, 1, 2 and 3, as can be seen in the relational diagram Fig. 10. Each zero-class is a pre-class as described in Chapter 3. The unparasitized larvae, LAU, and the parasitized larvae, LAP, are kept in two separate series of parallel development classes.
The rate of change of the number of individuals in a certain development class at a certain moment equals the rate of inflow minus the rates of outflow and mortality. The rate of inflow equals the rate of outflow of the preceding development class.
The rates of inflow and of outflow are modified by the temperature

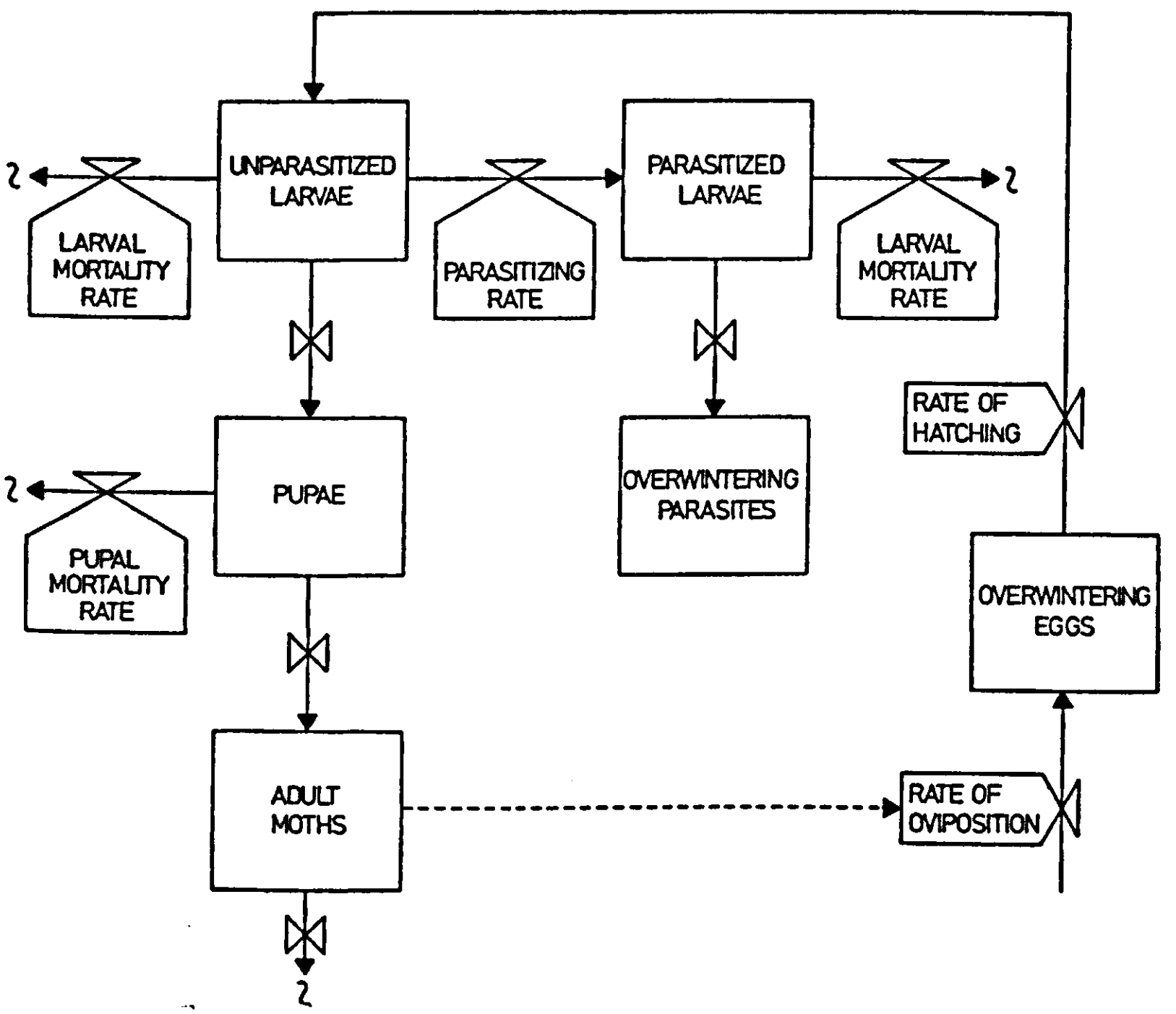

Fig. 7 | Relational diagram of the larch bud moth.

TEMP. Each stage is simulated with its own temperature dependence. Data on the development duration and its standard deviation at different temperatures were taken from thermostat experiments of Maksymov (1959). In the model, the development threshold of the larval stage is 2°C. The threshold of the pupal stage is 7.5°C. No

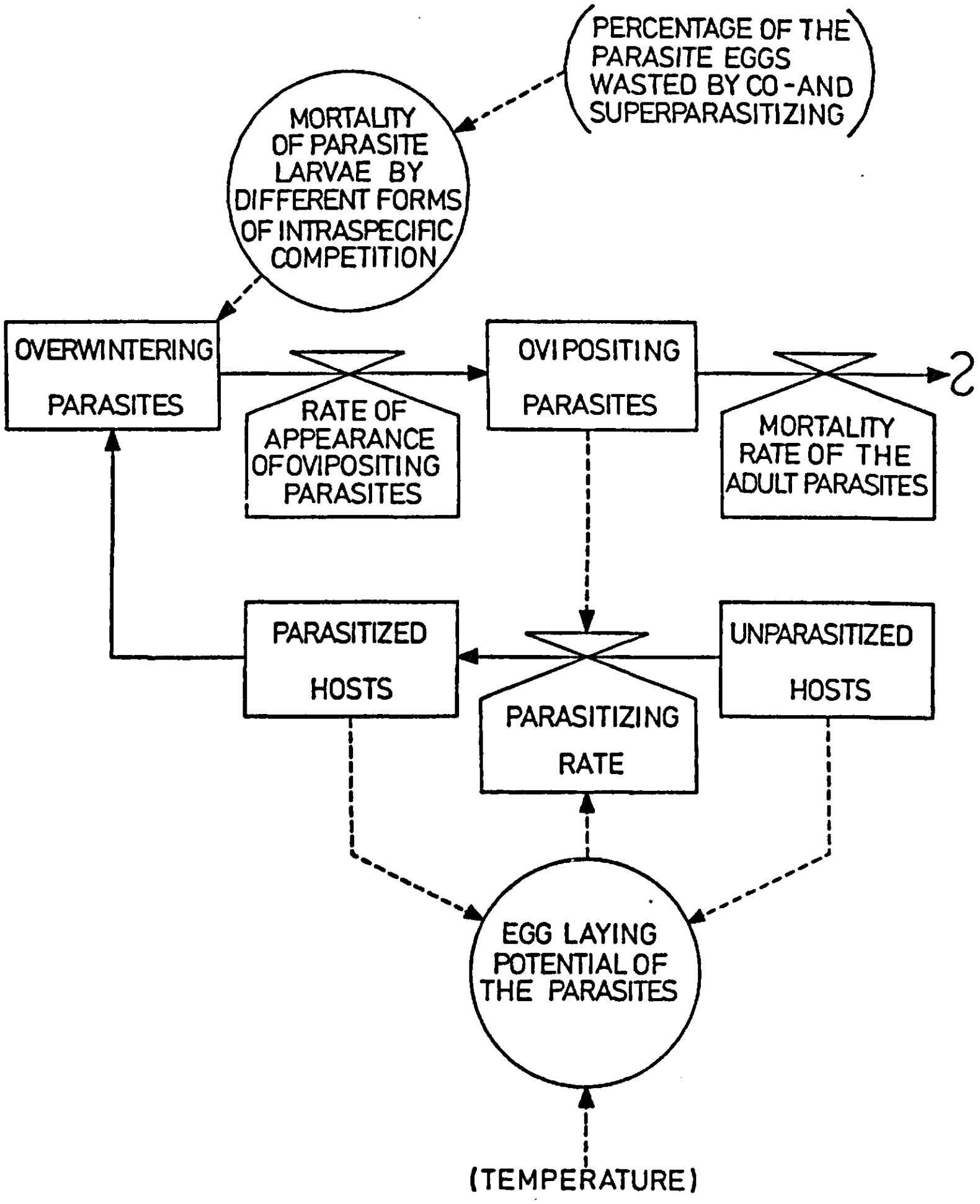

Fig. 8 | Relational diagram of the parasite complex.

experiments have been done on the longevity of the adults at different temperatures. Maksymov (1959) mentioned that under the mean climatic conditions of the Upper Engadin their longevity is 35 days. The females live for about three weeks under laboratory conditions (Baltensweiler, pers. commun.). In the model, the adults live 35 days at 11 °C, and 21 days at 20 °C. The development threshold of the adults is assumed to be 2 °C.

4.2.2 The damage to the tree

The damage to the tree has two aspects:
– the damage that is caused directly by larval feeding and that can be expressed as percentage defoliation;

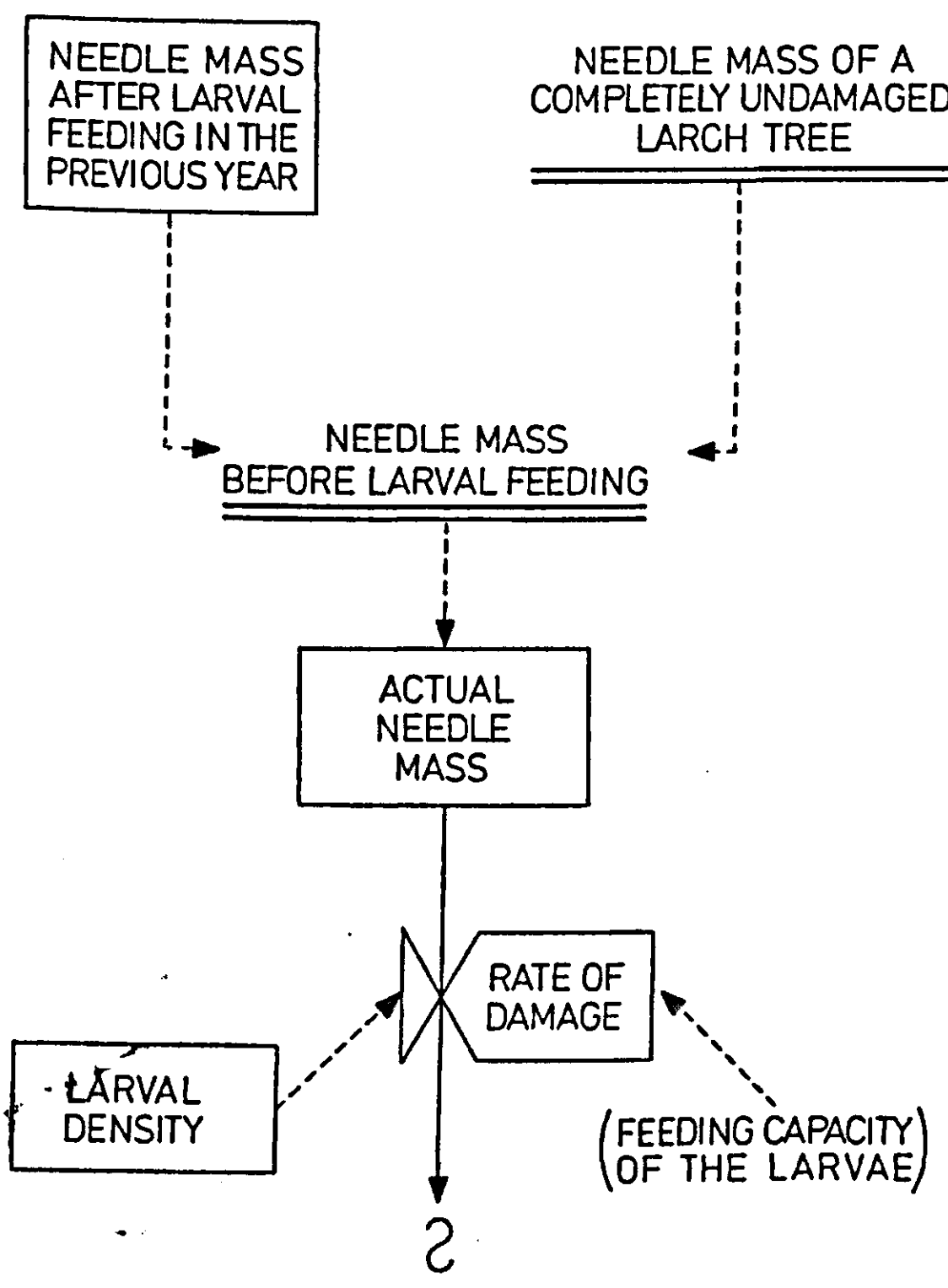

Fig. 9 | Relational diagram of the tree as food source for the larch bud moth.

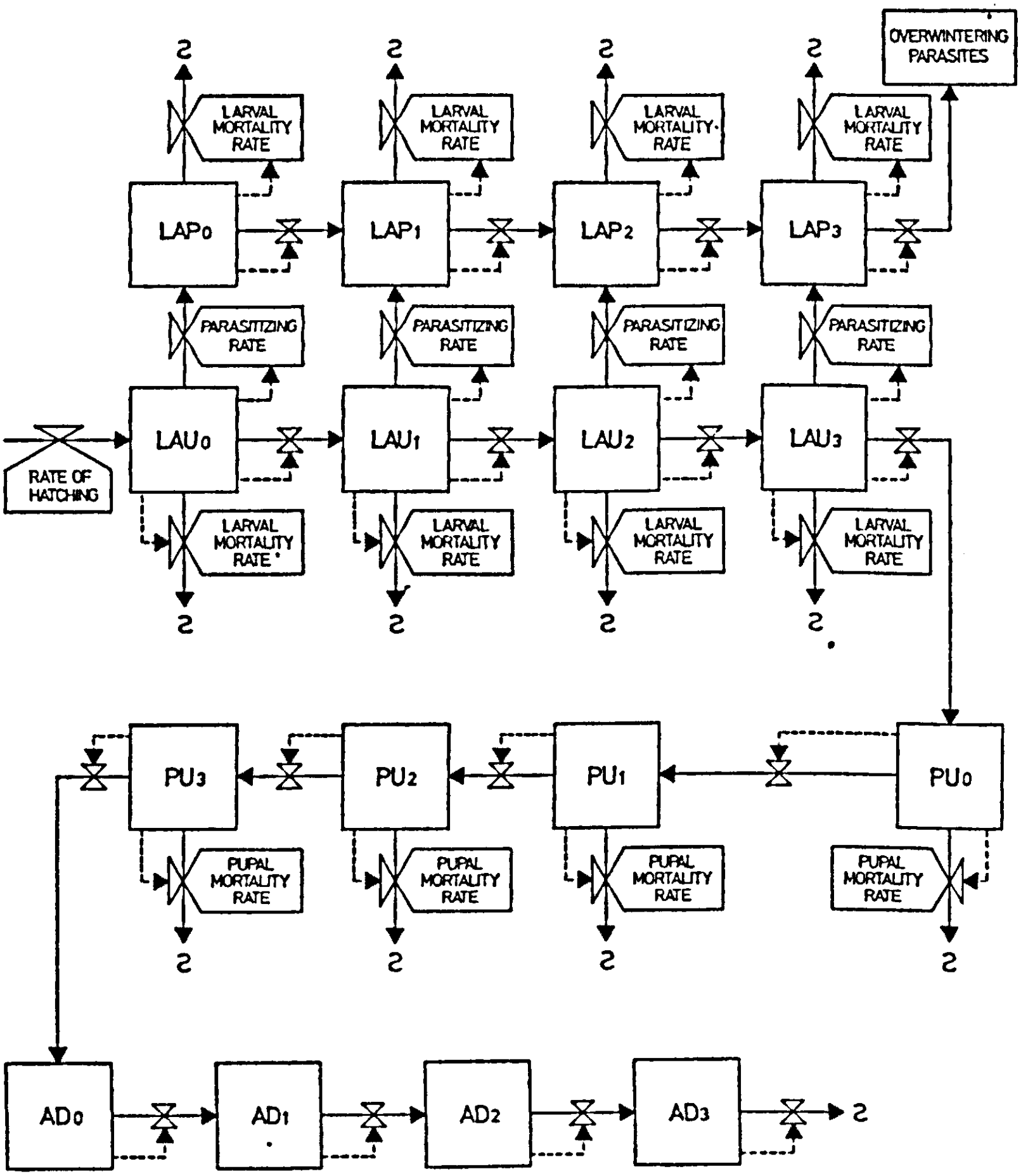

Fig. 10 | Relational diagram of the development of the larch bud moth.

– the physiological damage (decreased needle quality) that is caused by the larval feeding in the preceding years.

The best procedure is to simulate both these aspects with the state variable approach—not a difficult task with direct damage. As soon as the larvae start feeding, the needle mass WENE decreases at a rate of damage RDAM; this rate is determined by the number of larvae and by their feeding rate FEDR, and is independent of

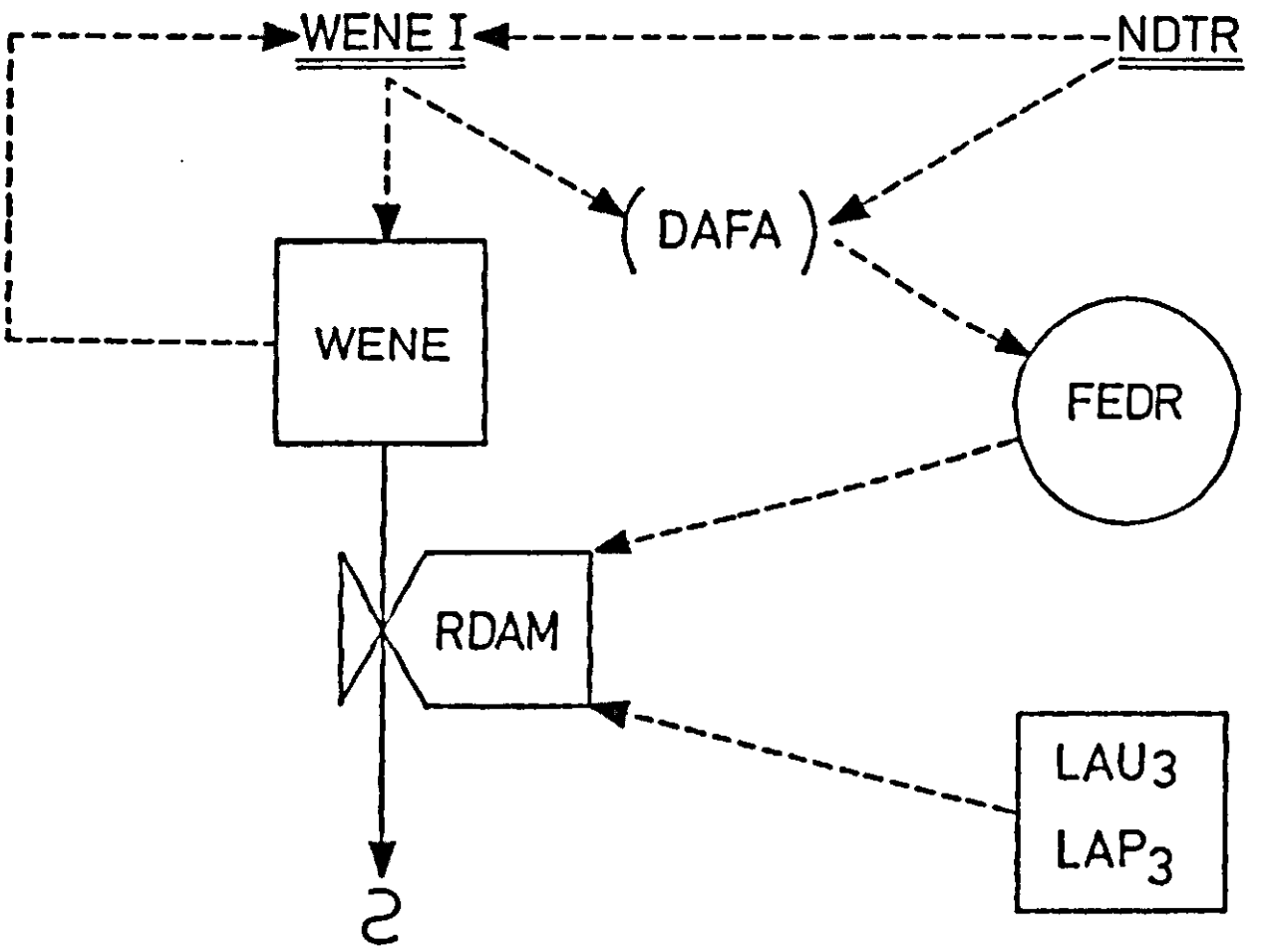

Fig. 11 | Relational diagram of the damaging effects of the tree.

the availability of food as long as the food source is not exhausted. Feeding is assumed to be concentrated in the last development class of both the parasitized and the unparasitized larvae (LAP3 and LAU3). This seems justified as the damage is mainly caused by the oldest larval instars (Gerig, 1967, Baltensweiler, pers. commun.). The parasitized larvae were assumed to have the same feeding rate as the unparasitized larvae.

It was not possible, however, to simulate the quality decrease of the needles properly, as no information was available about the physiological processes that underlie this quality decrease. One of the ways in which the physiological damage is expressed is in short and hard needles of reduced weight (see Section 1.4.2). Therefore in the model the physiological damage for each successive year is measured by the value of the parameter WENEI, which represents the weight of the needles per 7.5 kg larch branches before larval feeding. The value of WENEI is for each successive year calculated as follows: WENEI equals the needle mass of a completely undamaged tree (NDTR) if the quality of the needles is normal, but is smaller than NDTR if the quality of the needles is reduced.

For the next year WENEI is calculated as the mean of the actual needle mass WENE at the end of the year (after larval feeding) and the needle mass of a completely undamaged tree NDTR. So after complete

defoliation, WENEI for the next year amounts only to 0.5 × NDTR. If after one year of complete defoliation there was no more larval feeding, the reduction of WENEI would be halved every year. This is in agreement with the observation that it takes about 4 years for a larch stand to recover from complete defoliation.
For the parameter NDTR the value of 3.314 kg needles per 7.5 kg larch branches was chosen according to data of Auer (pers. commun.). The physiological damage during a certain year is now expressed in the model by the damage factor DAFA. The value of DAFA ranges between 0 and 1, and is determined by WENEI and NDTR according to the following formula:

$$DAFA = 1 - (NDTR - WENEI)/(0.5 \times NDTR)$$

When the quality of the needles is optimum, DAFA has the value 1, and when the quality decrease is maximum (WENEI = 0.5 × NDTR), DAFA has the value 0.
The feeding capacity of the larvae FEDR is a function of the damage factor DAFA. As Auer (1961) and Baltensweiler (1964) attributed complete defoliation to a density of 1250 larvae per 7.5 kg larch branches, the value of FEDR under optimum conditions (DAFA = 1) was chosen in such a way that at a density of 1250 complete defoliation occurs just within the larval feeding period. In the model, the larval feeding period is identical to the mean residence time in the last larval development class. The residence time could easily be calculated, since the same temperature table is given for every year, and the relation between development duration and temperature is known. The residence time in the last larval development class is one third of the mean development duration of the larvae. The calculation of the mean development duration is described in Chapter 5.
In the first year after complete defoliation (DAFA = 0), FEDR is assumed to be reduced by 50%. If after complete defoliation there is no more larval feeding in the following years, the recovery would occur as follows: 37.5% reduction in the second year after complete defoliation (WENEI = 0.75 × NDTR, DAFA = 0.5), 25% in the third year (WENEI = 0.875 × NDTR, DAFA = 0.75), 12.5% in the fourth year (WENEI = 0.9375 × NDTR, DAFA = 0.875), and in the fifth year after complete defoliation (WENEI = 0.96875 × NDTR, DAFA = 0.937), the feeding capacity of the larvae would be back to normal again. An after-effect of complete defoliation that lasts four years was

chosen as the quality decrease of the larch needles lasts at least four years after complete defoliation according to unpublished data of Benz.
The reduction of the feeding capacity of the larvae and all the other effects of food quality that are described in the next sections, are put into the model as functions of the damage factor DAFA. They were not simulated as a process with the state variable approach, as only empirical data were available and no information was available about the physiological processes in the larch bud moth that underlie these effects.

4.2.3 The hatching of the eggs of the larch bud moth

There is a certain number of unhatched eggs, NEG. As long as no eggs have hatched, NEG equals the number of eggs that are ready

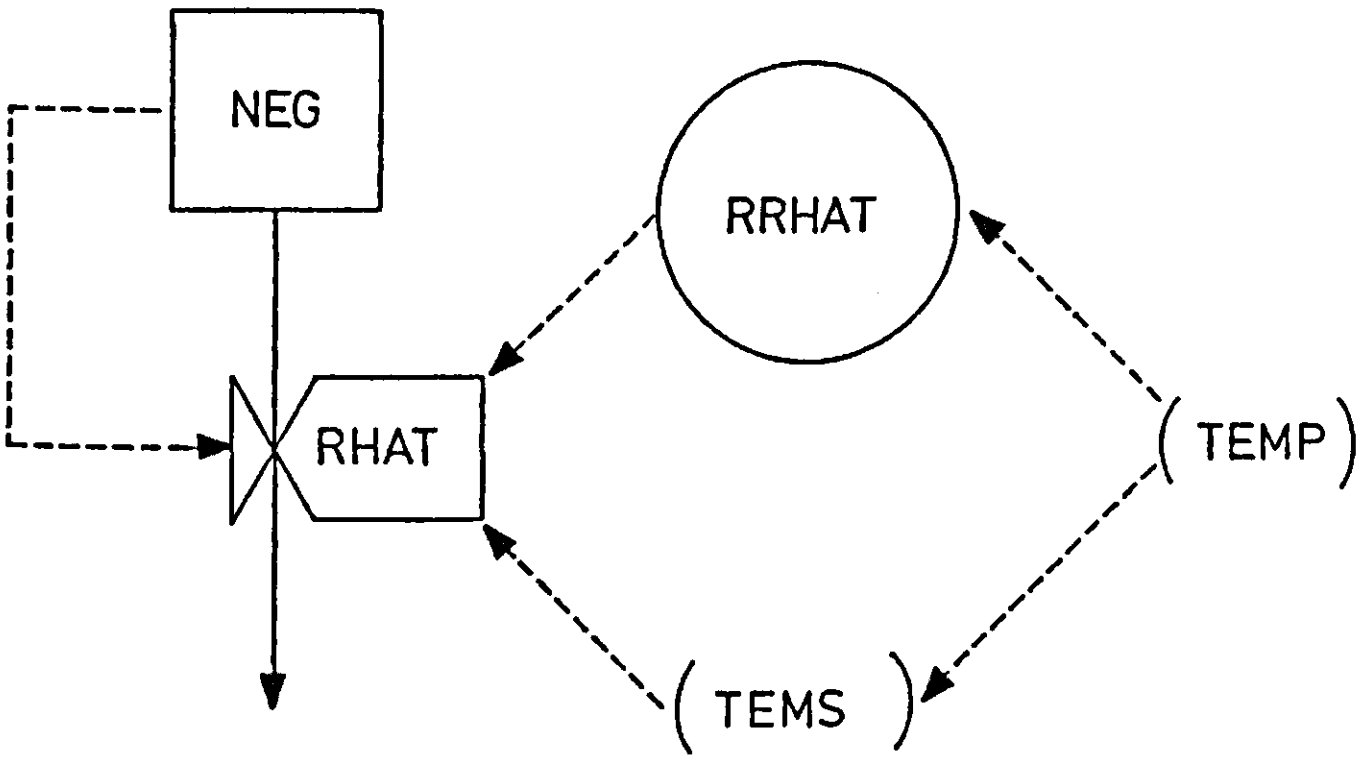

Fig. 12 | Relational diagram of the hatching process of larch bud moth eggs.

to hatch after winter. Egg hatching starts as soon as the temperature sum in °C, TEMS, has passed the value 45 (TEMS is zero when the simulation starts, i.e. on 1 May). Then the integral NEG is emptied at the rate of hatching RHAT. This rate is the product of NEG and the relative rate of hatching RRHAT. This relative rate is a function of the temperature TEMP. This function was globally estimated from data of Baltensweiler (1972), about the duration of the hatching period

and the temperature during this period at different locations. The temperature threshold for egg hatching was assumed to be 5°C, according to data of Bassand (1965)

4.2.4 Mortality by incoincidence

The reduced rate of hatching RHATR equals the rate of hatching RHAT multiplied by a reduction factor (1 – RDM). The factor RDM represents the proportion of hatching larvae that is not able to penetrate a short shoot and so dies at once. The reduced rate of hatching RHATR forms the rate of inflow of the first development class of unparasitized larvae, LAUO.

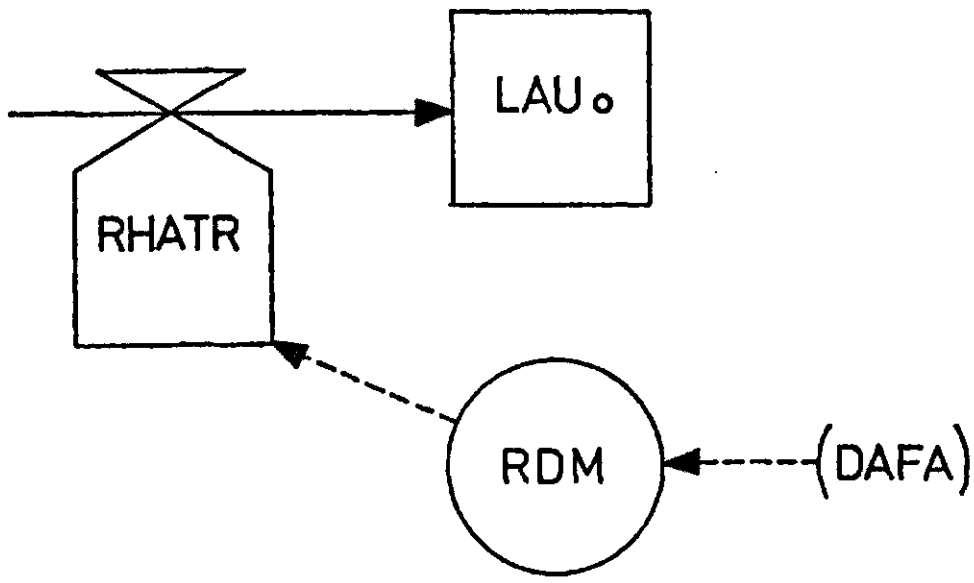

Fig. 13 | Relational diagram of the mortality by incoincidence of hatching eggs and sprouting needles.

RDM is a function of the damage factor DAFA. The data on the mortality by incoincidence between the sprouting of the larch and the hatching of the eggs of the larch bud moth are rather vague. According to Baltensweiler (pers. commun.), the total mortality in the first and the second instar amounts to 80–90% in the first year after complete defoliation. It is assumed that in the first year after complete defoliation (DAFA = 0), 65% of the larvae is not able to penetrate a short shoot and so dies at once. The remaining 15–25% mortality in the first and the second instar are assumed to be due to other causes, such as physiological weakening because of decreased food quality (see 4.2.5). If after complete defoliation there is no more larval feeding in the following years, the recovery would take place as follows:

31.1% of the hatching larvae would die at once in the second year after complete defoliation (DAFA = 0.5), 14.0% in the third year (DAFA = 0.75), 5.9% in the fourth year (DAFA = 0.875), 1.5% in the fifth year (DAFA = 0.9375) and in the sixth year after complete defoliation the mortality by incoincidence would be back to zero again.

4.2.5 Mortality from physiological weakening due to decreased food quality

The relative rate of mortality from physiological weakening RPHM is caused by the decreased mechanical and chemical food quality. RPHM affects all the larval and pupal development classes and is a function of the damage factor DAFA. The values of this function were chosen in such a way that RPHM causes a mortality of 75% in the first year after complete defoliation (DAFA = 0). If after complete defoliation there is no larval feeding in the following years, the recovery would take place as follows: 45% mortality in the second year after complete defoliation (DAFA = 0.5), 35% in the third year (DAFA = 0.75), 25% in the fourth year (DAFA = 0.875), 5% in the fifth year (DAFA = 0.9375), and in the sixth year after complete defoliation the mortality would be back to zero again. These figures are based on unpublished data of Benz on the mortality due to physiological weakening from the second larval instar till the adult stage.

The relative mortality rates are calculated as follows.
Since mortality is a continuous process, the rate of mortality RM can at any moment be expressed by the equation:

$$RM = RRM \times A$$

in which RRM is the relative rate of mortality and A is the amount of individuals.
In differential notation, this equation is written as:

$$dA/dt = RRM \times A$$

The integrated form of the equation is:

$$A = IA \times e^{RRM \times \Delta t}$$

in which IA is the amount of individuals before they begin to die,

and Δt is the time interval, i.e. the mean development duration of the larvae plus the pupae. If the total mortality is 75% within this time interval, the proper value of RRM would be:

$$RRM = (\ln 25 - \ln 100)/\Delta t$$

4.2.6 Mortality from lack of food

As feeding in the model is concentrated in the last larval age classes, LAU3 and LAP3, (see Section 4.2.2), mortality from lack of food is also assumed to be concentrated here. The relative rate of mortality from lack of food RSM is a function of WENE/NDTR, i.e. the quotient of the actual needle mass and the needle mass of a completely undamaged tree.

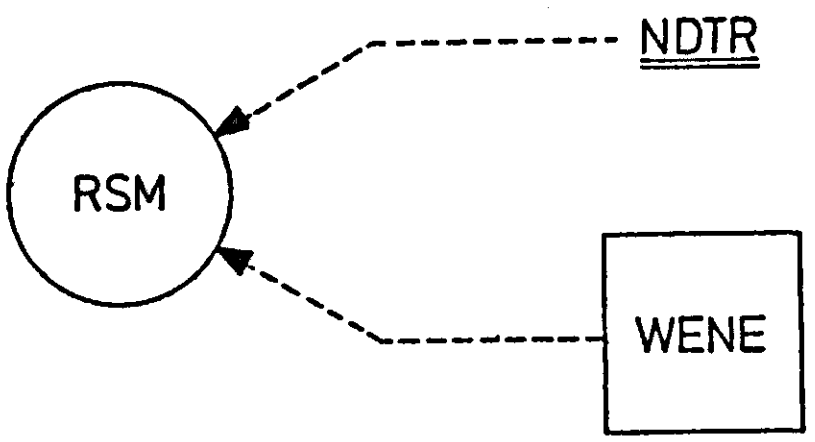

Fig. 14 | Relational diagram of the mortality by intraspecific competition of the larch bud moth.

Gerig (1967) mentioned that the factor 'space' apparently plays an important role for the intraspecific competition of the larch bud moth long before the factor 'lack of food', because the mean body weight decreases long before the food source is exhausted. As Gerig observed an increase of body weight with increasing age only till a density of 375 larvae per 7.5 kg larch branches, mortality by intraspecific competition is assumed to start at this density and to increase strongly as soon as 95% of the food source is exhausted. The more prematurely the food source becomes depleted within the larval feeding period, the longer RSM exerts its maximum influence and the larger the proportion of the larvae that die.

No quantitative data on the mortality from lack of food were available. Therefore the values of RSM as a function of WENE/NDTR had

to be found by trial and error. As soon as the values of all the other mortality factors were fixed, the values of RSM were varied until a realistic downswing of the population density in the first regression year resulted. RSM is zero until WENE/NDTR drops below 0.7, RSM is 0.01 when WENE/NDTR is 0.05 and increases to 0.4 when WENE/NDTR reaches zero.

4.2.7 Density-independent mortality

In the model a constant relative rate of density-independent mortality affects all the larval and pupal development classes. Of course this mortality is independent of the population density and of the damage to the tree. Hence the relative rate of mortality is represented by a fixed value in the model. This value was chosen in such a way that it results in a total mortality of 70% from the first larval instar till the adult stage, according to unpublished data of Benz.

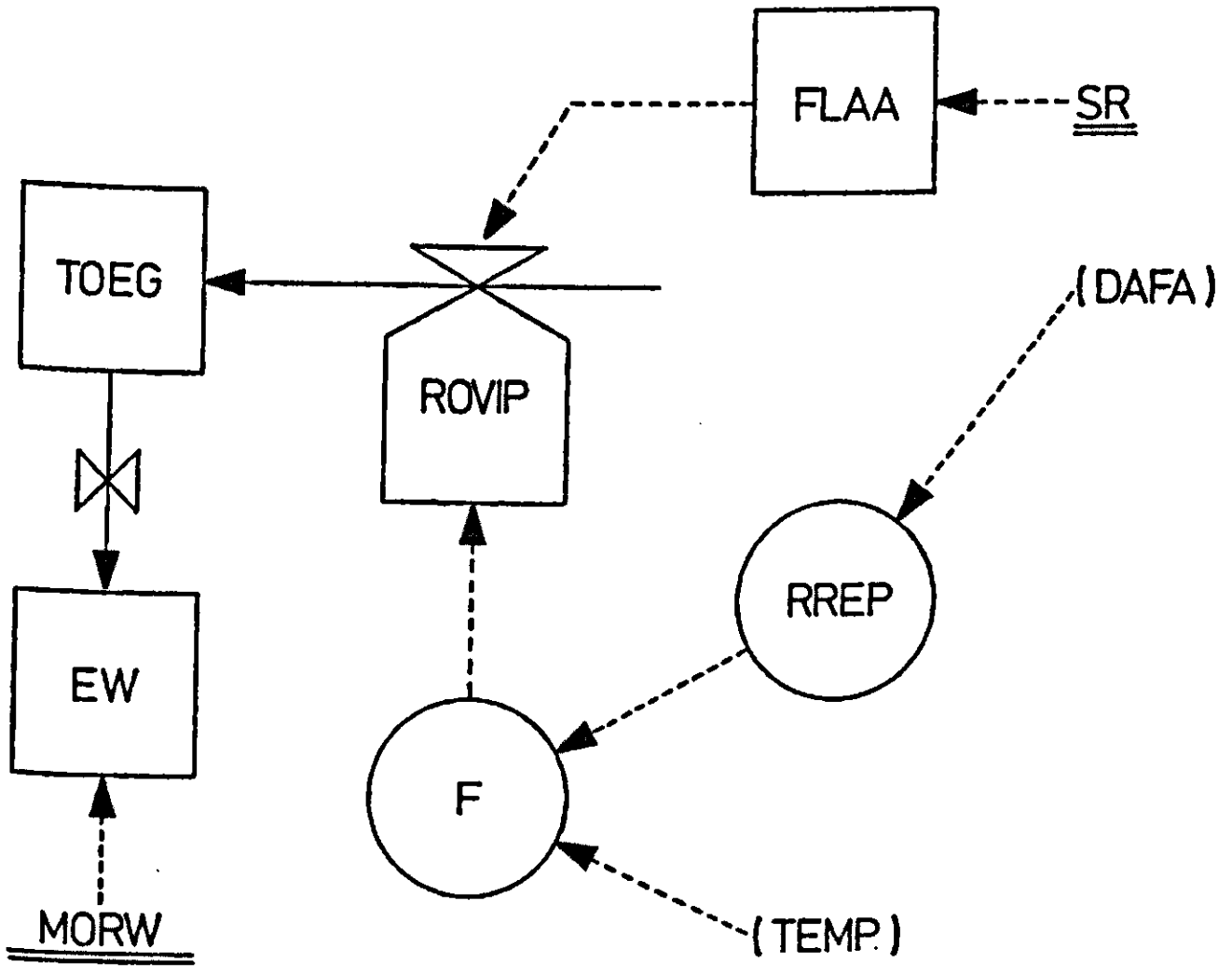

Fig. 15 | Relational diagram of the fecundity, oviposition and egg mortality of the larch bud moth.

4.2.8 Fecundity, oviposition and egg mortality

The rate of oviposition ROVIP is determined by the number of females present at a certain moment, and by the number of eggs laid per female per day. The number of eggs each female lays per day (F), is a function of the temperature. The values of this function were chosen in such a way that the females realize their full egg potential at any temperature, provided they do not die prematurely. The optimal fecundity was assumed to be 150 eggs per female, according to Baltensweiler (1968). Moreover the number of eggs laid per day, F, is modified by a reduction factor of reproduction, RREP. This reduction factor is a function of the damage factor DAFA. In the first year after complete defoliation (DAFA = 0), the fecundity of the females is assumed to be reduced by 70%. If after complete defoliation there is no more larval feeding in the following years, the recovery of the fecundity would take place as follows: a reduction of 40% in the second year after complete defoliation (DAFA = 0.5), 20% in the third year (DAFA = 0.75), and in the fourth year after complete defoliation (DAFA = 0.875) the fecundity would be back to normal again. These values were chosen according to unpublished data of Benz.

The number of females present at a certain moment (FLAA), is determined by the total number of adults present at that moment, and by the sex ratio SR which is assumed to be always 1:1 according to Maksymov (1959) and Benz (1974).

The total number of eggs that is laid during the season, TOEG, is found by integration of the rate of oviposition ROVIP. At the end of each year the number of eggs that will be ready to hatch at the beginning of the next year, EW, is calculated by reducing TOEG with the fraction MORW which represents the total egg mortality. It is assumed to have the value 0.4 every year, as the egg mortality ranges between 30% and 50% (Delucchi, pers. commun.). One of the main causes of this mortality seems to be the action of predatory mites.

4.2.9 The parasite complex

There are more than 70 different parasite species. Most of the species that are of real importance for the population dynamics of the larch bud moth in the Upper Engadin attack two or more larval instars, are univoltine and solitary and maintain themselves mainly on the larvae

of the larch bud moth (Baltensweiler, 1958; Auer *et al.*, 1959; Aeschlimann, 1969). Thus the parasite complex is simulated as if there was only one univoltine, solitary, monophageous species that attacks all larval instars. This parasite species must represent the whole parasite complex.

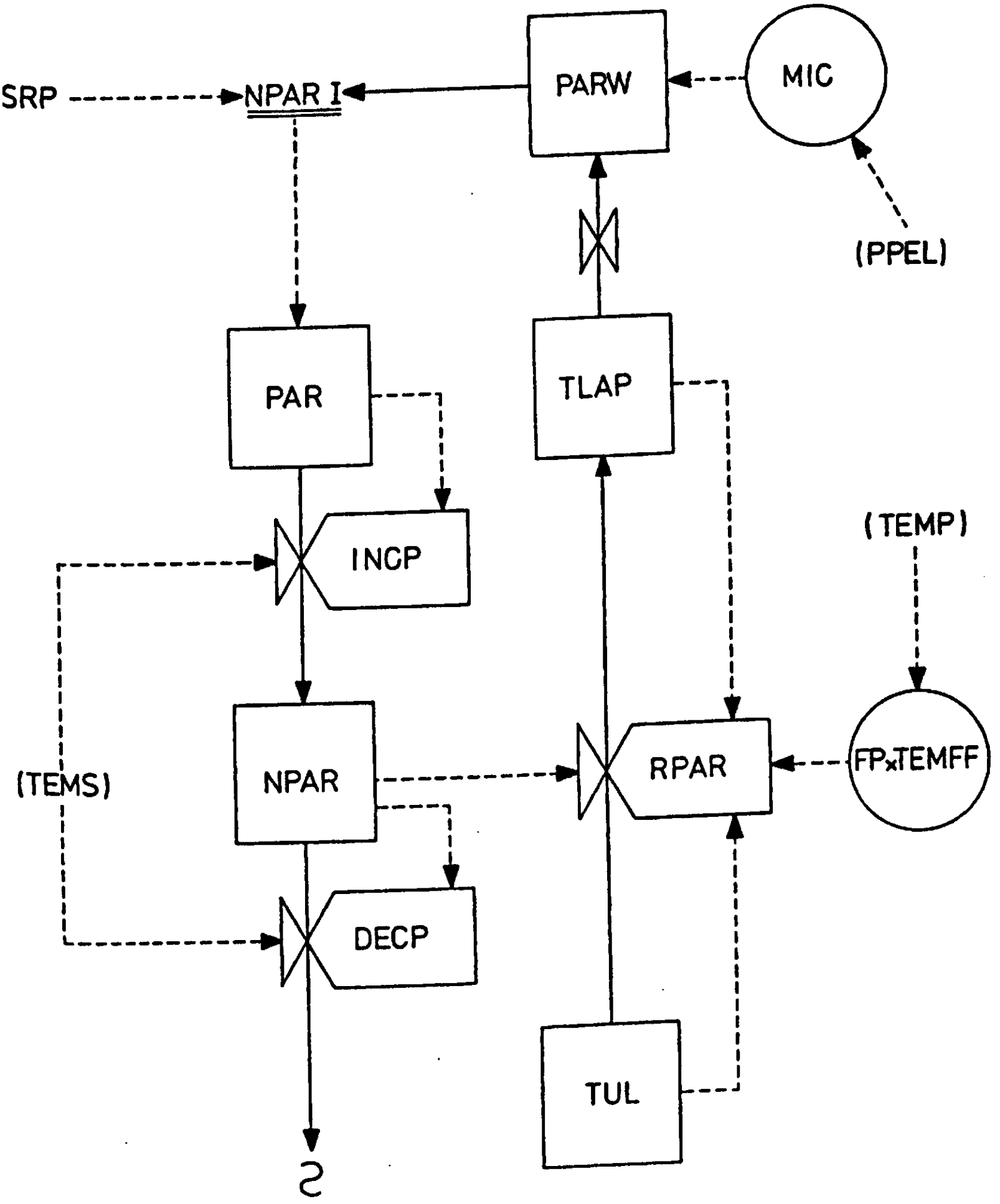

Fig. 16 | Relational diagram of the parasite complex (more detailed than Figure 8).

The beginning and the end of the reproductive period of the female parasites is determined in the model by the temperature sum TEMS. As soon as TEMS has passed the value 164, all female parasites start ovipositing within three days. As soon as the value of TEMS is more than 508, all parasites die within three days. As every year the same temperature data are given in the model, the reproductive period lasts from 30 May until 4 July every year. A period of 35 days was chosen in accordance with data on the parasite species *P. griseanae* (Baltensweiler, 1958).

During their reproductive period all female parasites can lay potentially a certain number of eggs FP per day at 15°C. This potential number of eggs is modified in the model by a temperature factor TEMFF. The values of this factor were chosen in accordance with information given by Aeschlimann. Thus below 5°C no parasitizing activity occurs, and at 7.5°C the female parasites can lay maximally 0.3 eggs per day, at 10°C 2.1 eggs per day, at 15°C 2.5 eggs per day, and at 20°C they can lay maximally 2.8 eggs per day. These values seem a realistic mean for the most important species of the parasite complex (see Baltensweiler, 1958; Aeschlimann, 1969; Baltensweiler & Moreau, 1957).

The number of eggs that the parasites lay per day is also dependent on the host density. In the model the total number of parasite eggs laid per day at low host densities is proportional to the product of the density of the ovipositing parasites NPAR and the host density TL ($= NPAR \times TL \times K \times TEMFA$). The factor K represents the 'area of discovery' of the parasites at 15°C. It is the number of eggs that is laid per parasite per host per day at low host densities at this temperature. In the model, K has the value 0.2. K is modified by a temperature factor TEMFA. For the time being it was assumed that TEMFA has the same values as the temperature factor TEMFF.

At a certain host density the maximum reproductive capacity of the parasites at the given temperature is reached. From then on the total number of parasite eggs laid per day amounts to $NPAR \times FP \times TEMFF$.

All this results in the functional response curve (for one parasite!) given in Figure 17. This curve is rather arbitrary, since the data were insufficient. It reflects however the strong searching capacity of the parasites, that are always able to build up a parasitism level of 10–20% during the progression phase, even when progression starts from an extremely low host density.

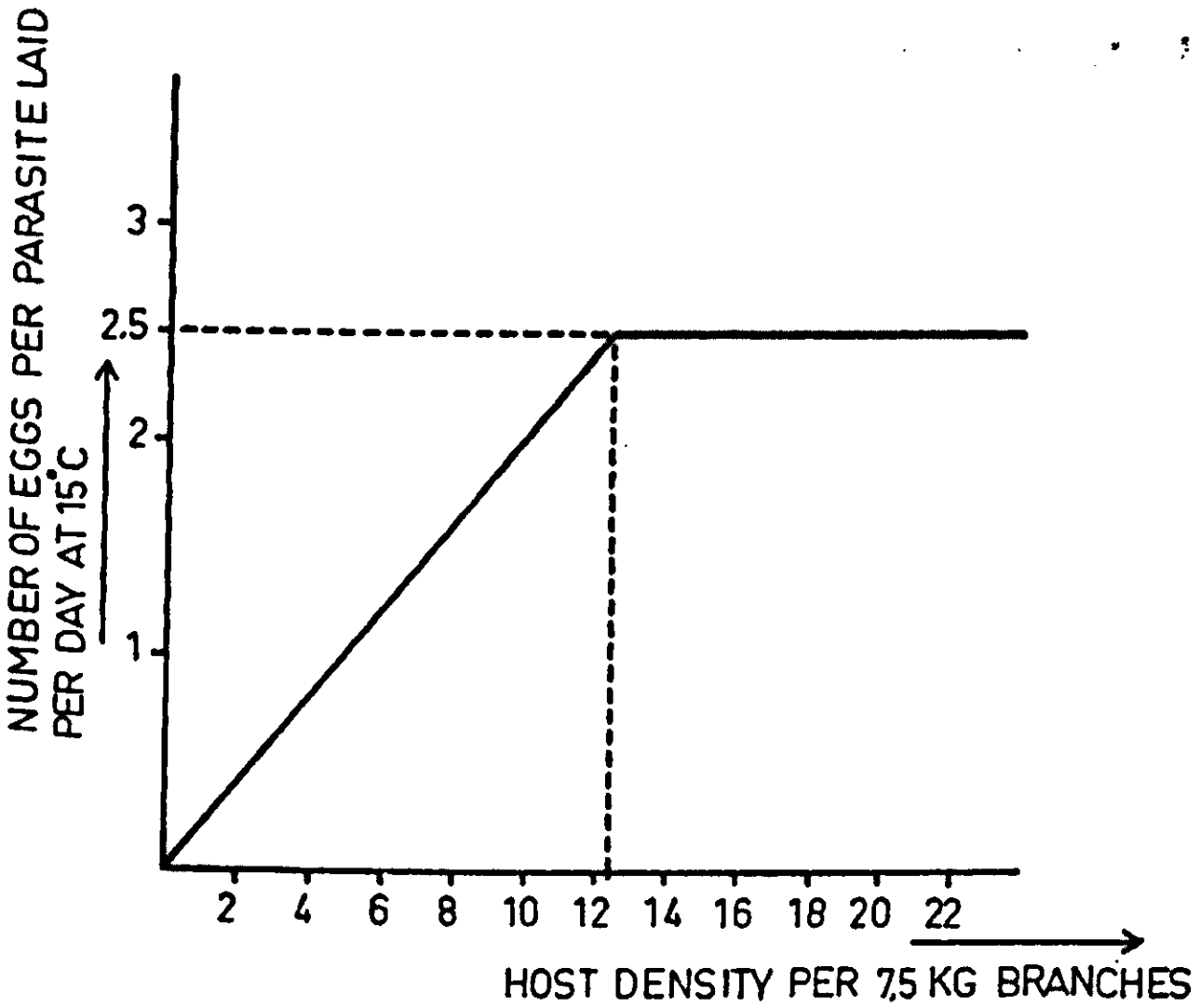

Fig. 17 | Functional response curve of the parasites to increasing density of larch bud moths.

Table 1 The relation between MIC and PPEL.

Percentage parasite eggs wasted by coparasitizing and superparasitizing (PPEL)	0	10	27	81	100
Percentage parasitized hosts from which no parasite emerges (MIC)	0	50	95	99.9	100

The maximum reproductive capacity of the parasites is already reached at a host density of 12.5 larvae per 7.5 kg larch branches at any temperature. Of course, in reality the slope of the functional response curve gradually declines with increasing host density, so that the maximum reproductive capacity gradually is reached at a higher density, but such details are hardly reflected in the end result.
Since the simulation concerns a complex of species, it is assumed that the parasites do not discriminate between unparasitized and already parasitized hosts and that they do not have any preference for one of

the larval development classes. Therefore the host density TL can simply be represented by the sum of the contents of all the development classes of parasitized and unparasitized larvae. The relative rate of parasitism RPAR is then found by dividing the total number of parasite eggs laid per day by the host density TL. The rate of parasitizing for each of the development classes of unparasitized larvae is found by multiplying RPAR with the contents of that development class. The parasitized larvae are kept in a separate series of development classes that run parallel to those of the unparasitized larvae, as can be seen in the relational diagram in Section 4.2.1. The parasitized larvae in the model show the same feeding capacity, density-independent mortality, development rate etc. as the unparasitized larvae. They die before they can pupate.

It is assumed that the parasites are solitary because Baltensweiler (1958) said that generally only one parasite larva per host can complete its development. Hence the proportion of parasite eggs that is wasted by coparasitizing and superparasitizing, PPEL, can be found by accumulating both the number of parasite eggs that is laid in already parasitized hosts, and the total number of parasite eggs laid, and dividing the former by the latter. So PPEL is an expression for the average level of coparasitizing and superparasitizing at a certain moment.

The total number of overwintering parasites (PARW) is found by accumulating the numbers of hosts that leave the last development class of parasitized larvae (LAP3). The rate of inflow of PARW is reduced by a factor MIC. This factor represents the proportion of parasitized hosts from which no parasite instead of one parasite emerges. MIC is a function of the level of coparasitizing and superparasitizing PPEL. The introduction of this factor seems justified as it is a general phenomenon in host-parasite relations that at high levels of coparasitizing and superparasitizing many parasitized hosts fail to produce a parasite because of the increased pressure of different forms of competition between the parasites. Frequent attacks or 'host feeding' by the adult parasites can cause premature death of the host and of the parasite larvae within it. Another possibility is that the competition between the parasite larvae within the host causes their collective death. So MIC represents a number of different processes that are only indirectly connected via the level of coparasitizing and superparasitizing.

No data were available. Therefore we had to determine the values of MIC as a function of PPEL by 'trial and error'. The gradation cycle was divided into three different parts: the progression, and the first and the second half of the regression. Each part of the gradation cycle has its characteristic level of coparasitizing and superparasitizing. The corresponding values of MIC were found by an iterative process. This process was done for the progression first. Then it was done for the first half of the regression, and finally it was done for the second half of the regression. The whole procedure was repeated until a realistic gradation curve resulted. The values of MIC as a function of PPEL are represented in Table 1.
The sex ratio of the parasites is assumed to be 1:1, so the initial number of female parasites for the next year, NPARI, is found by dividing the total number of overwintering parasites, PARW, by 2.0 at the end of the year.

4.3 Program description

4.3.1 Damage to the tree

The needle mass is simulated as an initial needle mass WENEI that decreases with the rate of damage RDAM:

```
WENEA=INTGRL(WENEI,-RDAM)
```

The actual needle mass, WENE, is kept at zero as soon as WENEA is zero or smaller. As long as WENEA is greater than zero, WENE equals WENEA:

```
WENE=WENEA*INSW(WENEA, 0.,1.)
```

The rate of damage RDAM depends on the number of feeding larvae and on their feeding capacity FEDR:

```
RDAM=(LAU3+LAP3)*FEDR
```

The feeding capacity FEDR is dependent on the quality of food:

```
FEDR=AFGEN(FEDRT,DAFA)
AFGEN FEDRT= -10.,.000075, 0.,.000075,...
  .93,.00015, 1.,. 00015
```

In the AFGEN, the first value of each pair of values represents the

damage factor DAFA, and the second value represents the feeding capacity FEDR.
The damage factor DAFA is calculated as follows:

```
DAFA=1.-(NDTR-WENEI)/(.5*NDTR)
```

The needle mass of a completely undamaged tree NDTR is a parameter with a constant value:

```
PARAM NDTR=3.314
```

At the end of the year, the initial needle mass for the next year is calculated as follows:

```
TERMINAL
PARAM X=.5
WENEI=(1.-X)*WENE+X*NDTR
```

4.3.2 Hatching of the eggs of the larch bud moth and mortality of hatching larvae

The number of eggs that has not yet hatched, NEG, is simulated as an initial number of eggs that is ready to hatch after winter, that decreases at a certain rate, the rate of hatching RHAT:

```
NEG=INTGRL(EW,-RHAT)
```

The rate of hatching RHAT is dependent on the number of unhatched eggs NEG, and the relative rate of hatching RRHAT that is a function of the temperature TEMP:

```
RHAT=NEG*AFGEN(RRHAT,TEMP)*
  INSW(TEMS-45.,0.,1.)
```

The statement 'INSW(--, --, --)' takes the value 0 as long as the temperature sum TEMS is smaller than 45. As soon as TEMS passes the value 45, the value of the statement changes into 1. At that moment the RHAT can proceed.

```
TEMS=INTGRL(0.,TEMP)
AFGEN RRHAT=0.,0., 4.,0., 6.,2.,
  10.7,.45
```

The rate of inflow of the first development class of unparasitized

larvae, LAUO, is formed by the reduced rate of hatching RHATR. This rate equals RHAT multiplied by a reduction factor RDM:

```
RHATR=RHAT*(1.-RDM)
```

RDM represents the mortality of larvae due to incoincidence of hatching with the sprouting of the larch, and is dependent on the quality of food:

```
RDM=AFGEN(RDMT,DAFA)
AFGEN RDMT=-10.,.65, 0.,.65, .96,0.,
 1.,0.
```

4.3.3 Development of the larch bud moth

For an explanation of the basic principles of the technique that were used to simulate the development of the larch bud moth (larvae, pupae, and adults), the reader is referred to Chapter 3. In this section only some additional remarks are made. The development classes of the larvae are the integrals:

```
LAUO=INTGRL(0.,RLAUO)
LAPO=INTGRL(0.,RLAPO)
LAU1=INTGRL(0.,RLAU1)
LAP1=INTGRL(0.,RLAP1)
LAU2=INTGRL(0.,RLAU2)
LAP2=INTGRL(0.,RLAP2)
LAU3=INTGRL(0.,RLAU3)
LAP3=INTGRL(0.,RLAP3)
```

The rates of change of all the development classes consist of a rate of inflow, a rate of outflow, a rate of mortality, and a rate of parasitizing that flows from each development class of unparasitized larvae (LAUO–LAU3) to the corresponding development class of parasitized larvae (LAPO–LAP3):

```
RLAUO=RHATR-LAUO*(RTEL+MRT+RPAR)
RLAPO=RPAR*LAUO-LAPO*(RTEL+MRT)
RLAU1=LAUO*RTEL-LAU1*(OUTU+MRT+RPAR)
RLAP1=LAPO*RTEL+RPAR*LAU1-LAP1*(OUTP+
  MRT)
RLAU2=LAU1*OUTU-LAU2*(OUTU+MRT+RPAR)
```

```
RLAP2=LAP1*OUTP+RPAR*LAU2-LAP2*(OUTP+
  MRT)
RLAU3=LAU2*OUTU-LAU3*(OUTU3+MRT3+RPAR)
RLAP3=LAP2*OUTP+RPAR*LAU3-LAP3*(OUTP3+
  MRT3)

RTEL=2.*RTL/FRL
RTL=AFGEN(RTLT,TEMP)
AFGEN RTL=-10.,0., 2.,0., 11.5,.0612,
  18.,.1334
FRL=AMAX1(DELT*RTL,1.-3.*KL)
KL=AFGEN(KLT,TEMP)
AFGEN KLT=0.,0., 2.,0., 11.5,.0017,
  18.,.0020, 24.5,.0055
OUTU=PUSHL*(FRL/DELT-MRT-RPAR)
OUTP=PUSHL*(FRL/DELT-MRT)
OUTU3=PUSHL*(FRL/DELT-MRT3-RPAR)
OUTP3=PUSHL*(FRL/DELT-MRT3)
PUSHL=INSW(GSL-1.,0.,1.)
GSL=INTGRL(.5,RTL/FRL-PUSHL/DELT)
```

RTL is the inverse of one third of the longevity of the larval stage, which is a function of the temperature. Only one third of the longevity was used to calculate RTL, as three development classes (plus one pre-class) were used for the simulation of the larval development. KL is the square of the quotient of the standard deviation of the longevity of the larval stage and the longevity itself. KL is a function of the temperature as well.
The relative rate of mortality MRT consists of density-independent mortality and mortality from physiological weakening due to decreased food quality:

```
MRT=.01486+RPHM
```

RPHM is a function of the damage factor DAFA:

```
RPHM=AFGEN(RPHMT,DAFA)
AFGEN RPHMT=-10.,.0198, 0.,.0198, ...
  .45,.0075, .75,.0062, .875,.0039, ...
  .937,.0009, .96,0., 1.,0.
```

In the last development class of parasitized and unparasitized larvae (LAP3 and LAU3), starvation mortality can also occur:

```
MRT3=MRT+RSM
```

The relative rate of starvation mortality RSM is a function of the depletion of the food source:

```
RSM=AFGEN(RSMT,WENE/NDTR)
AFGEN RSMT=-10.,.4, 0.,.4, .05.,01, ...
  .7,0., 1.,0.
```

4.3.4 Oviposition and egg mortality

The total number of eggs that is laid during the season (TOEG) is found by integration of the rate of oviposition ROVIP:

```
TOEG=INTGRL(0.,ROVIP)
```

ROVIP is determined by the total number of females FLAA, and by the number of eggs each female lays per day. This number is a function of the temperature, and is modified by a reduction factor RREP

```
ROVIP=AFGEN(FTB,TEMP)*(1.-RREP)
AFGEN FTB=0.,0., 6.,0., 11.,5.8, ...
  20.,10.1
```

FLAA is determined by the total number of adults and by the sex ratio:

```
FLAA=(AD0+AD1+AD2+AD3)*SR
PARAM SR=0.5
```

The factor RREP represents the reduction of fecundity due to decreased food quality:

```
RREP=AFGEN(RREPT,DAFA)
AFGEN RREPT=-10.,.67, 0.,.67, ...
  .45,.42, .75,.19, .875,0., 1.,0.
```

At the end of the year the number of eggs that will be ready to hatch at the beginning of the next year (EW), is found by multiplying TOEG by the factor (1 – MORW):

```
TERMINAL
EW=TOEG*(1.-MORW)
```

The reduction factor MORW represents the total winter mortality:

```
PARAM MORW=.4
```

4.3.5 The parasites

The potential relative rate of parasitism PRPA was formulated as follows:

```
PRPA=1./(TL+NOT(TL))*
  AMIN1(NPAR*TL*K*TEMFA,NPAR*FP*TEMFF)
```

The statement 'AMIN1(––, ––)' always takes the smallest of the two values between the brackets. The operation of this statement results in the functional response that was described in Section 4.2.9.
TL represents the total host density:

```
TL=TUL+TLAP
TUL=LAU0+LAU1+LAU2+LAU3
TLAP=LAP0+LAP1+LAP2+LAP3
```

K represents the 'area of discovery' of the parasites, which is the number of eggs that is laid per parasite per host per day at low host densities, K is modified by a temperature factor TEMFA:

```
PARAM K=.2
TEMFA=AFGEN(TEMFT,TEMP)
AFGEN TEMFT=0.,0., 5.,0., 7.5,.12, ...
  10.,.85, 15.,1.
```

FP represents the number of eggs one parasite potentially lays per day at 15°C, and is modified by a temperature factor TEMFF:

```
PARAM FP=2.5
TEMFF=AFGEN(TEMFT,TEMP)
```

NPAR represents the number of ovipositing parasites. At the beginning of the year, there is a certain number of female parasites that will start ovipositing later in the season (NPARI). The rate of increase of the number of ovipositing parasites (INCP) starts as soon as TEMS has increased to 85. The rate of decrease of the number of oviposition parasites (DECP) starts as soon as TEMS has increased to 404:

```
NPAR=INTGRL(0.,INCP-DECP)
INCP=PUSH*PAR*.8*INSW(TEMS-85.,0.,1.)
PAR =INTGRL(NPARI,-INCP)
DECP=PUSH*NPAR*.8*INSW(TEMS-404.,0.,1.)
PUSH=IMPULS(1.,1.)
```

The statement '*IMPULS*(1., 1.)' means that PUSH assumes the value 1. once a day and the rest of the time is zero.
The time step for integration DELT was fixed at 0.1 day. It is not excluded that an unparasitized larva can be parasitized twice (or even more) within this period of time when parasitism is divided randomly over the total number of larvae, parasitized and unparasitized. So the number of unparasitized larvae that will be parasitized within this period of time will be smaller than expected on the basis of the value of PRPA.
The proper way to solve this problem would be to make the time step for integration DELT so short that within this time step double parasitizing is excluded. We did not choose this solution because it would make the time step for integration too short. Instead we introduced a factor that corrects the value of PRPA for double parasitizing within the time step of integration:

```
RPAR=(1.-LOR)*PRPA
```

LOR represents the proportion of the number of parasite eggs that is laid in the unparasitized larvae within one time step of integration, and that are wasted by coparasitizing and superparasitizing. LOR was calculated according to Justesen & Tammes (1960). When r is the number of beetles (each beetle attacking randomly one grain seed), and n is the number of grain seeds, the proportion of seeds that is attacked will be $(1-e^{-r/n})$. As the expected proportion of attacked seeds was (r/n), the 'loss' ratio is $(r/n-(1-e^{-r/n})):(r/n)$. The quotient (r/n) being equivalent to PRPA × DELT, LOR equals:

```
LOR=(PRPA*DELT+EXP(-PRPA*DELT)-1.)/
  (PRPA*DELT+NOT(PRPA*DELT))
```

The total number of adult parasites that emerges from the parasitized hosts (PARW) during the season, is found by integration of the rate of outflow of the last development class of parasitized larvae (LAP3).

Since not every parasitized host will produce a parasite because of different forms of competition between the parasites, this rate was modified by a reduction factor MIC in the expression for PARW:

```
PARW=INTGRL(0.,LAP3*OUTP3*(1.-MIC))
```

MIC represents the proportion of parasitized hosts from which no parasite instead of one parasite emerges, and is a function of the level of coparasitizing and superparasitizing PPEL:

```
MIC=AFGEN(MICT,PPEL)
AFGEN MICT=-10.,0., 0.,0., .10,.5, ...
  .27,.95, .81,.999, 1.,1.,2.,1.,
```

PPEL is found by accumulating the total number of parasite eggs that is laid, and the total number of parasite eggs that is wasted by coparasitizing and superparasitizing, and dividing the latter by the former:

```
TPEG =INTGRL(0.,PRPA*TL)
TLPEG=INTGRL(0.,PRPA*(TLAP+LOR*TUL))
PPEL =TPEG/(TLPEG+NOT(TLPEG))
```

The total number of female parasites that will start ovipositing in the next season (NPARI), is found by dividing PARW by 2 at the end of the year:

```
TERMINAL
NPARI=PARW*.5
```

4.3.6 Larval density and parasitism level

The mean larval density TOLA during a certain year, and the parasitism level PEPL for a certain year, are output variables. They are needed by the user of the model, but are not necessary for the simulation of the system of the larch bud moth. Since the annual population census is done when the fourth and the fifth larval instar are predominant, TOLA is calculated by accumulating the numbers of larvae that leave the third development class of unparasitized larvae (LAU2), and the numbers of larvae that leave the third development class of parasitized larvae (LAP2):

```
TOLA=INTGRL(0.,LAU2*OUTU+LAP2*OUTP)
```

The parasitism level PEPL is calculated by accumulating the numbers of larvae that leave the last development class of parasitized larvae (LAP3), and the numbers of larvae that leave the last development class of unparasitized larvae (LAU3), and dividing the former amount by the sum of the two amounts:

```
TNPL=INTGRL(0.,LAP3*OUTP3)
TULA=INTGRL(0.,LAU3*OUTU3)
PEPL=TNPL/((TNPL+TULA)+NOT(TNPL+TULA))
```

5 Results and discussions

The mean longevity of the larvae, pupae and adults was determined by simulating the development according to the method of controlled artificial dispersion (see Chapter 3); all mortality factors were omitted (Section 4.1). The mean longevity of the larvae equals the time interval between the day when 50% of the eggs have hatched and the day when 50% of the pupae have appeared. The mean longevity of the pupae was similarly determined. The mean longevity of the adults equals the time interval between the day when 50% of the adults have appeared and the day when 50% of the adults have died. As the same temperature table is used every year, the development rates are the same every year. The results are given in Table 2. The simulated lengths of development are approximately the same as those observed by Maksymov (1959) at Punt Muragl (Upper Engadin) in 1953.

Table 2 Mean development duration (days) of the different stages of the larch bud moth in the model and in the field.

Stage	In the model	In the Upper Engadin (Maksymov, 1959)
Larvae	58	51
Pupae	22	30
Adults	46	35

The simulated hatching curve of the eggs of the larch bud moth is presented in Figure 18. This curve applies for every year, since the temperature fluctuations are nearly the same every year. All the eggs hatched within three weeks during the second half of May. This result certainly is realistic (Baltensweiler, 1972).
Four different runs were made with the computer program that was described in Chapter 4. One run was made including all the effects

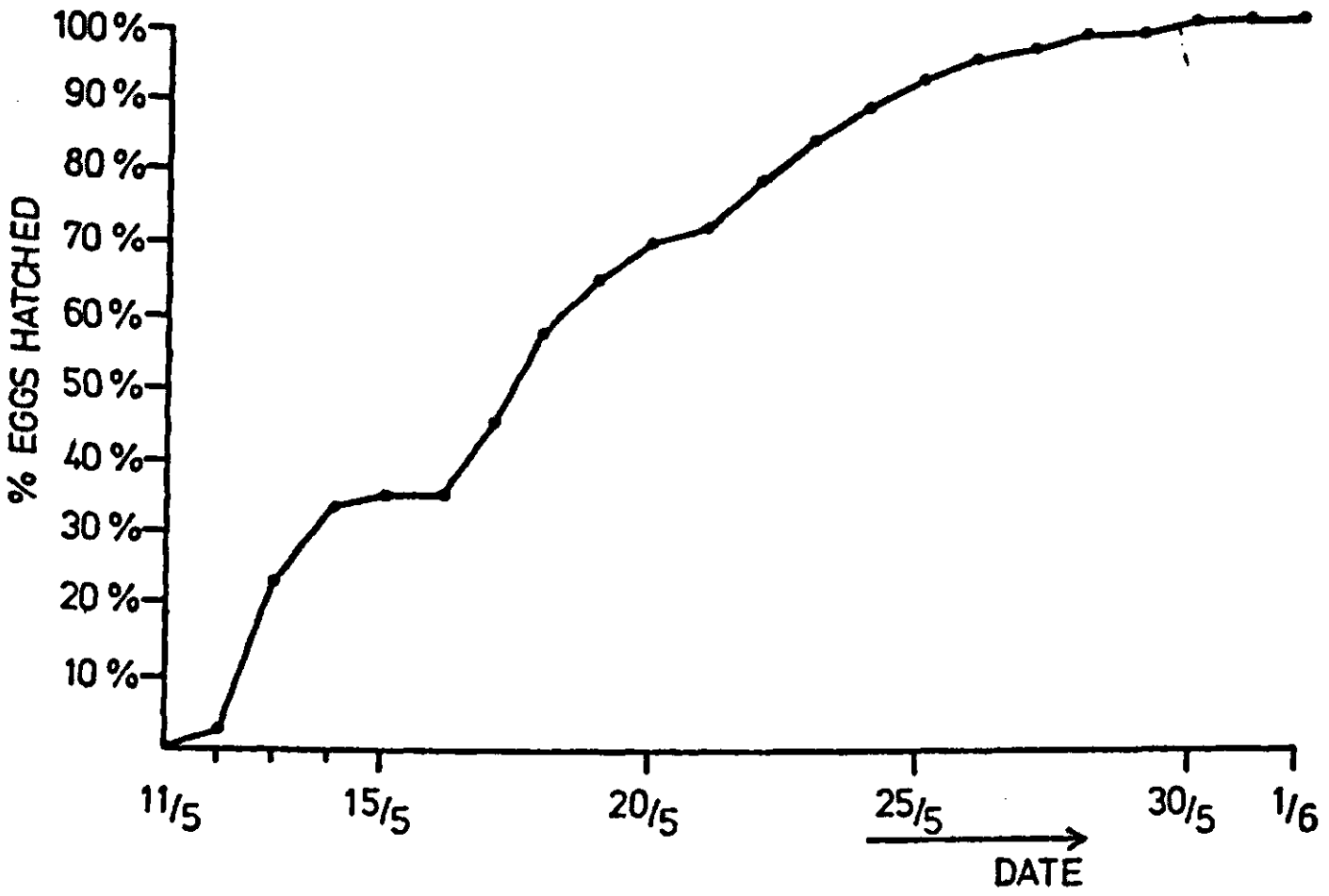

Fig. 18 | Simulated hatching curve for the eggs of the larch bud moth.

mentioned in Chapter 4. The results are given in Fig. 19 and Table 3. The gradation cycle and the connected phenomena that were observed in the field are presented in Fig. 19 and Table 4. The simulation including all effects resulted in an 8-year gradation cycle, the progression phase and the regression phase both lasting 4 years, as seen in Fig. 19 and Table 3.

The influence of a number of simulated mortality factors was calculated as a percentage of the total number of individuals, as can be seen in Table 3. These factors are the starvation mortality, the mortality by incoincidence, and the mortality by physiological weakening due to decreased food quality. As these mortality factors work simultaneously and so interact with each other, the percentages were calculated in such a way that the influence of each single mortality factor as such is expressed as clearly as possible. The mortality by incoincidence and the mortality by physiological weakening approximately lasted until six years after the culmination of the gradation. The starvation mortality was only important during the culmination year.

The simulated fecundity of the females (EPF) fluctuated within the same range as was observed in the field (compare Tables 3 and 4). The fecundity was reduced until five years after culmination of the gradation (see Table 3).

Table 3 The simulated population density fluctuations and connected phenomena. TOLA: number of larvae per 7.5 kg larch branches; PEPL: percentage of larvae parasitized; EPF: mean number of eggs laid per female; INM: mortality by incoincidence in % of EW; PHM: mortality by physiological weakening by decreased food quality in % of EW × (1-RDM); STM: starvation mortality in % of TOLA.

Year	TOLA	PEPL	EPF	INM	PHM	STM
1	0.197	21	149.8	0	0	0
2	2.01	3.4	149.5	0	0	0
3	24.9	4.6	149.6	0	0	0
4	305	6.6	149.8	0	0	0
5	1 519	53	52.7	65	50.8	6.6
6	298	98.9	68.3	56.9	43.7	3.3
7	4.64	98.0	95.3	33.1	24.0	0
8	0.361	8.0	120.8	15.3	24.2	0
9	2.13	3.4	148.9	6.3	16.9	0
10	20.9	5.5	150.0	1.9	5.2	0
11	240	8.0	150.0	0.4	1.2	0
12	2 125	10.9	158.7	8.5	16.9	45.9
13	1 459	57	52.9	65	50.6	6.5
14	271	97.0	68.6	55.9	43.1	3.1
15	11.9	98.8	98.7	32.1	23.8	0
16	0.589	15.3	121.4	15.0	23.9	0
17	3.22	8.3	149.4	6.2	16.6	0
18	30.3	12.2	150.3	1.9	4.9	0
19	319	15.3	150.6	0.8	2.0	0

The simulated parasitism level (PEPL) reached 98.8% during regression, while the observed parasitism level never exceeded 81% (compare Tables 3 and 4). However the maximum parasitism level in the field is probably higher than 81%. As only one population census per year is done, during the period of larval development, the parasitism level might be systematically underestimated (Baltensweiler, pers. commun.). Moreover it is difficult to measure the parasitism level reliably when the population density of the larch bud moth is low.

Table 4 The observed population density fluctuations and connected phenomena (Baltensweiler, 1968; Aeschlimann, 1969).

Year	Number of larvae per 7.5 kg larch branches	Percentage of larvae parasitized	Mean number of eggs laid per female
0	0.13		
1	0.62		
2	3.37		
3	31.3		
4	516		
5	2 488		
6	949		
7	160		
8	16.8	69	139
9	0.63	32	138
10	0.59	3	102
11	2.12	8	132
12	12.3	7	91
13	172	20	169
14	1 866	32	110
15	1 382	65	54
16	23.4	81	93
17	0.15	0	
18	0.015		
19	1.5		

A second run was made without parasites by giving the parameter NPARI the value zero:

PARAM NPARI = 0

The aim was to determine what influence the action of the parasites has on the course of the gradation cycle. The results are given in Fig. 20 and Table 5. In Fig. 20, besides the population density curve that resulted from the simulation without parasites, the curve that resulted from the simulation including all effects is presented. Of course the latter curve is the same as in Fig. 19. Without parasites, the population density of the larch bud moth fluctuated at a much higher level, since

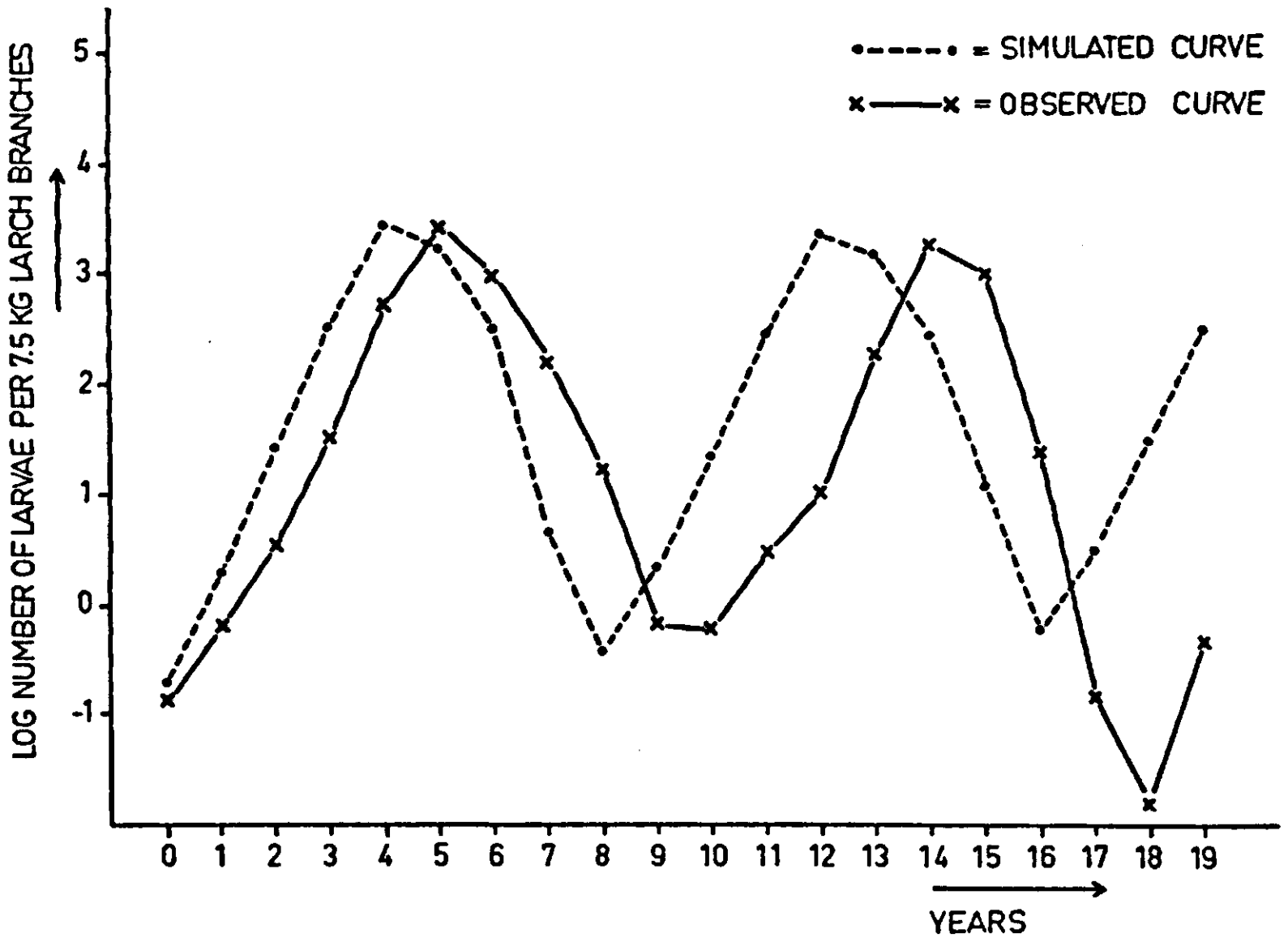

Fig. 19 | Simulated and observed population density curve for the larch bud moth in the Ober Engadin.

Table 5 The population density fluctuations simulated without parasites. Number of larvae per 7.5 kg larch branches (TOLA).

Year	TOLA	Year	TOLA
0	0.197	10	765
1	2.55	11	513
2	32.9	12	1 039
3	425	13	2 004
4	3 598	14	872
5	1 876	15	548
6	604	16	1 017
7	506	17	1 927
8	1 172	18	1 022
9	2 040		

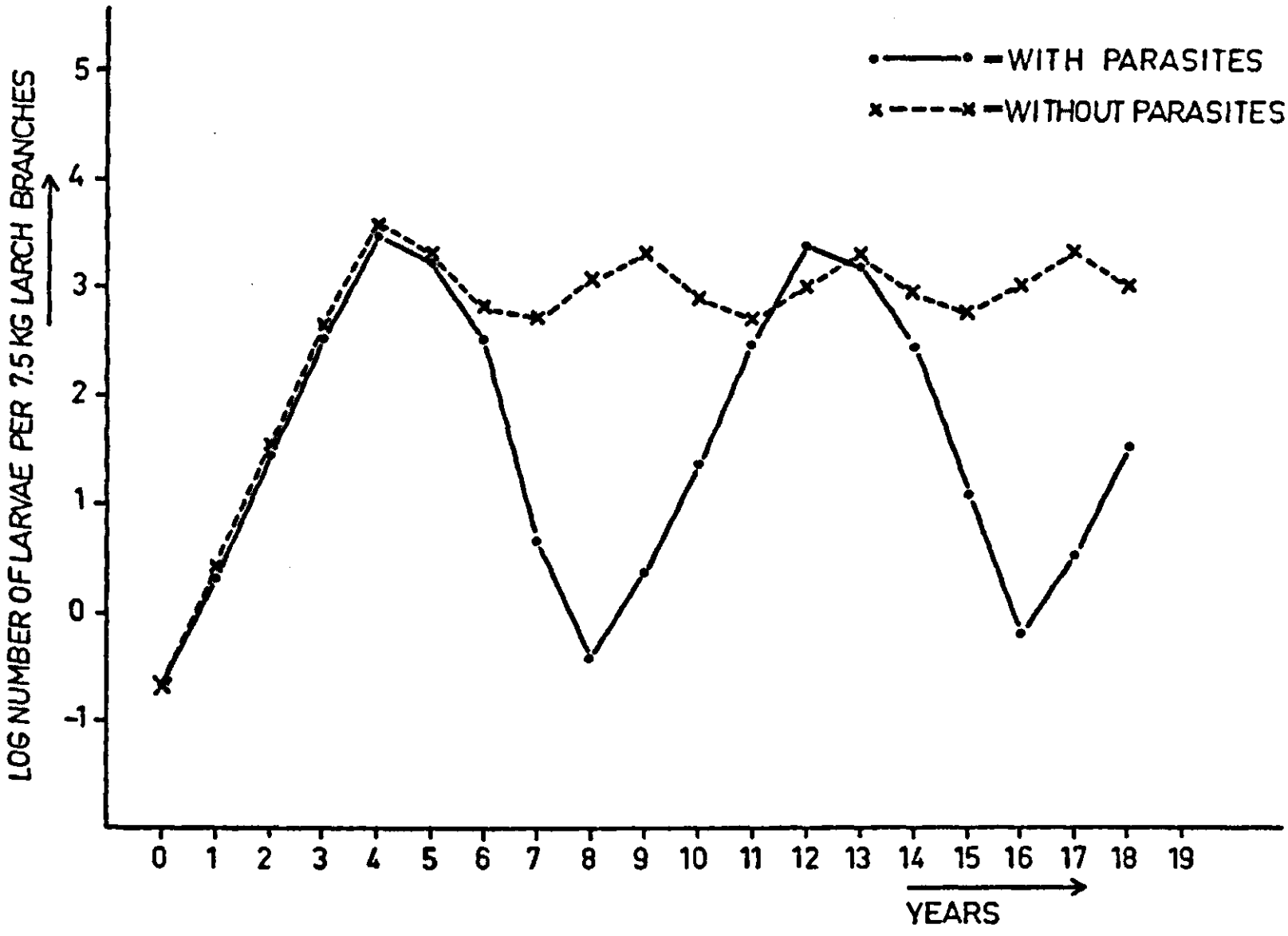

Fig. 20 | Simulated population density curve with and without effects of parasites.

the regression phase was not lengthened by the action of the parasites. The result was a 4-year cycle. The combined effects of food quality and quantity caused a regression of two years. Two years afterwards the culmination density was reached again. So according to the results of the simulations the action of the parasites lengthens regression by two years.

A third run was made without effects of food quality, i.e. under the assumption that there is no mortality of hatching larvae by incoincidence with the sprouting of the larch, no mortality by physiological weakening caused by decreased food quality, and no reduction of fecundity caused by decreased food quality. This was done by replacing the expressions: RDM = AFGEN(RDMT,DAFA), RPHM = AFGEN(RPHMT, DAFA), and RREP = AFGEN(RREPT, DAFA) by the following:

PARAM RDM = 0
PARAM RPHM = 0
PARAM RREP = 0

The aim was to determine the influence of the effects of food quality on regression. The results are given in Fig. 21 and Table 6. Without effects of food quality the population density of the larch bud moth fluctuated at an extremely high level. Apparently the combined effects of parasitism and food quantity were not sufficient to start the regression.
A fourth run was made without effects of food quantity, i.e. under the assumption that there was no starvation mortality. This was done by replacing the expression: RSM = AFGEN(RSMT, WENE/NDTR) by the following:

PARAM RSM = 0

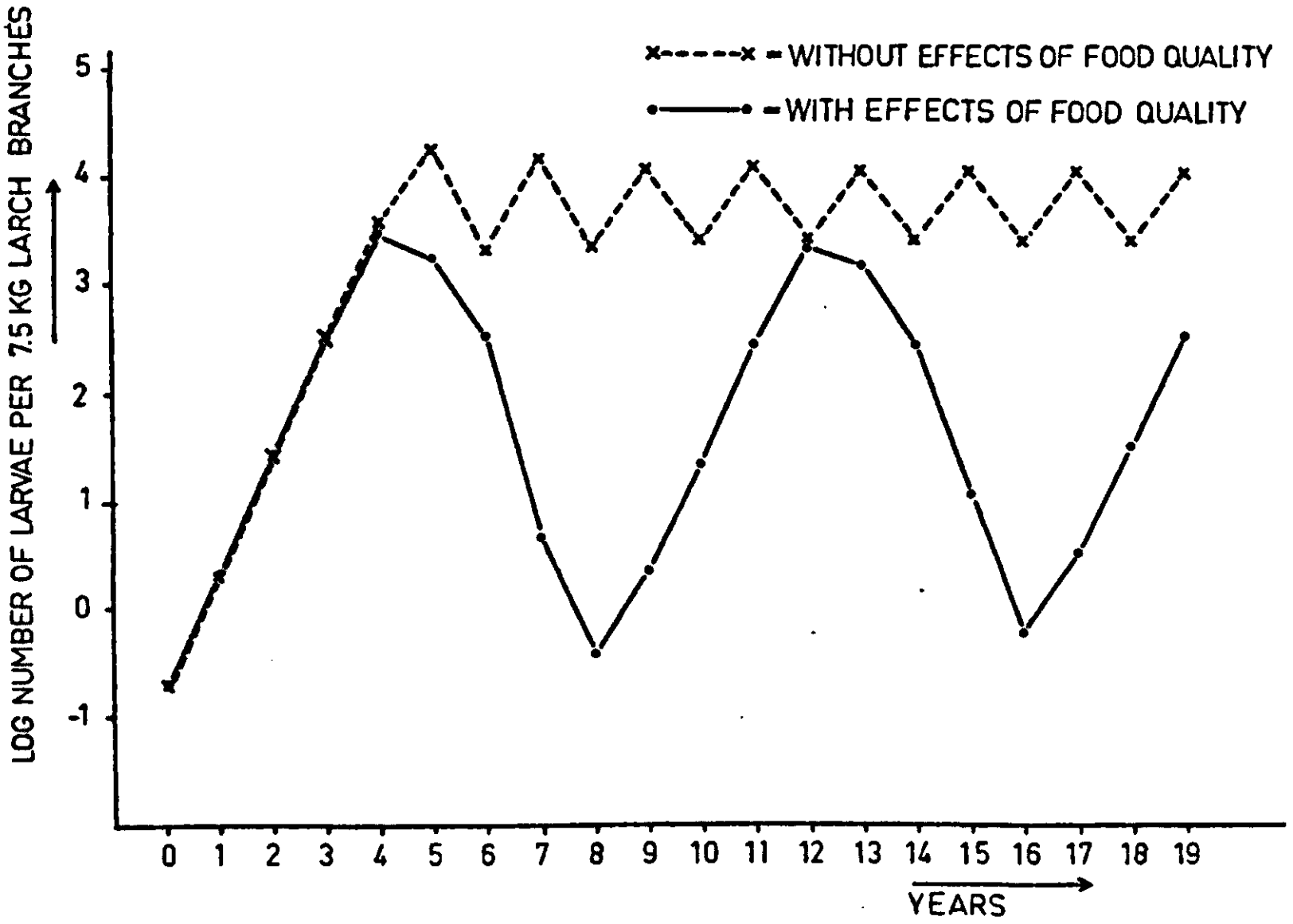

Fig. 21 | Simulated population density curve with and without effects of food quality.

Table 6 The population density fluctuations simulated without effects of food quality (i.e. no mortality by incoincidence, no mortality by physiological weakening by decreased food quality, no reduction of fecundity). TOLA: number of larvae per 7.5 kg larch branches; PEPL: percentage of larvae parasitized.

Year	TOLA	PEPL	Year	TOLA	PEPL
0	0.197	21.0	10	2 592	10.5
1	2.01	3.4	11	11 864	11.5
2	24.9	4.7	12	2 496	9.9
3	305	6.6	13	11 672	11.0
4	3 665	6.8	14	2 559	9.5
5	17 305	10.0	15	11 893	10.8
6	1 916	10.5	16	2 507	9.4
7	13 797	13.2	17	11 765	10.7
8	2 111	11.8	18	2 541	9.3
9	11 396	12.6	19	11 871	10.6

Table 7 The population density fluctuations simulated without effects of food quantity (i.e. no starvation mortality). TOLA: number of larvae per 7.5 kg larch branches; PEPL: percentage of larvae parasitized.

Year	TOLA	PEPL	Year	TOLA	PEPL
0	0.197	21.0	10	2.25	0.07
1	2.01	3.4	11	27.2	0.10
2	24.9	4.7	12	349	0.17
3	305	6.6	13	3 070	0.37
4	2 664	12.1	14	4 148	4.6
5	3 499	66.4	15	1 239	82.4
6	384	98.2	16	118	97.5
7	6.51	99.8	17	5.53	89.8
8	0.041	3.6	18	2.59	16.8
9	0.235	0.19	19	15.5	24.7

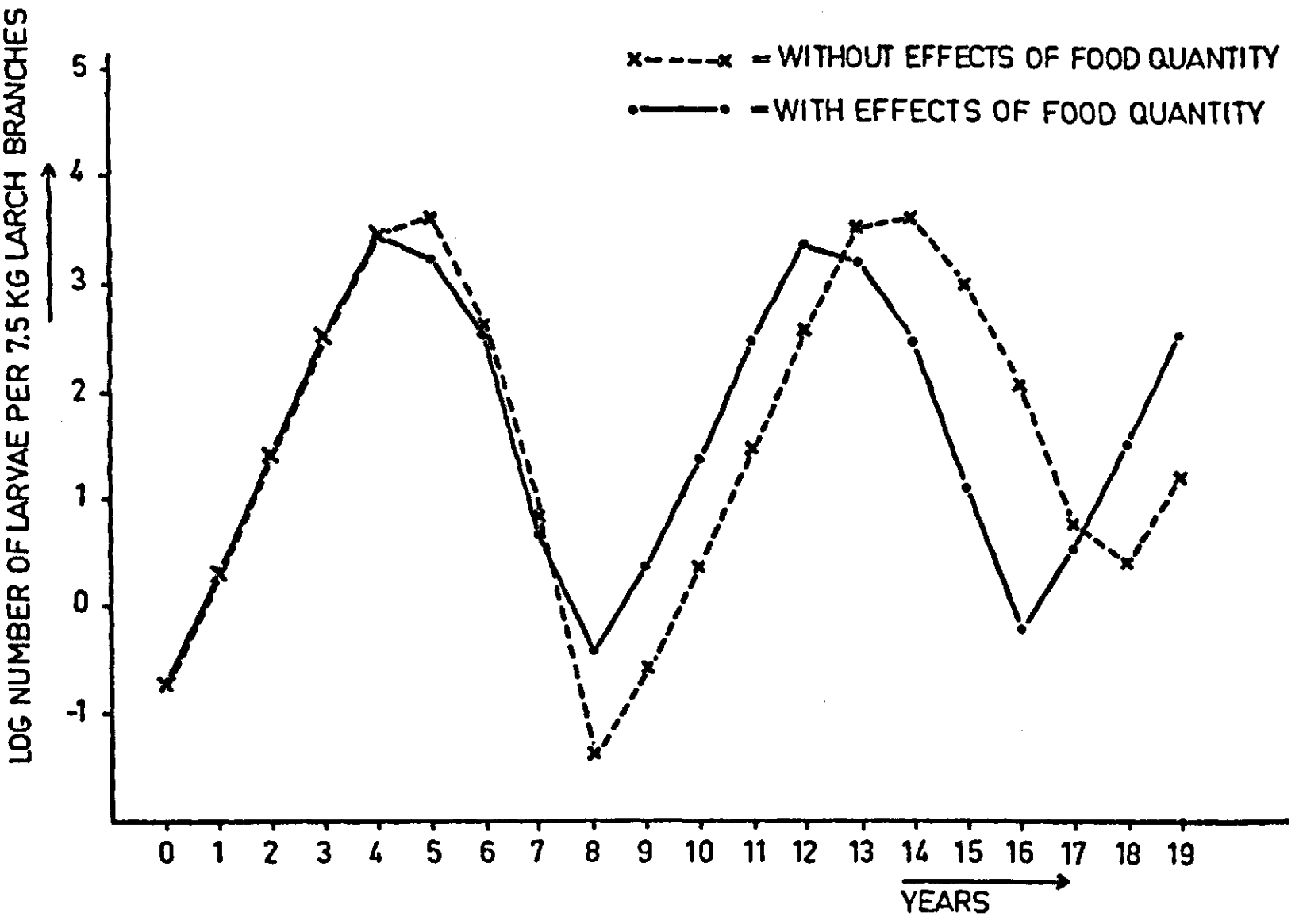

Fig. 22 | Simulated population density curve with and without effects of food quantity.

The aim was to determine the influence of the effects of food quantity on regression. The results are presented in Fig. 22 and Table 7. Without effects of food quantity the start of the regression phase was delayed by one year because the effects of food quality exerted their maximum influence only one year after complete defoliation. Since the rate of increase of the population density was strongly reduced during this last progression year because of the respective effects of food quality, parasitism could reach a very high level during this year. Thus the parasites reduced the population density of the larch bud moth to an extremely low level within three years. It took six years before the culmination density was reached again. As this progression started from an extremely low host density, the parasites were not able to build

up their populations sufficiently in time, so that the parasitism level remained very low during progression.

According to the results of the four runs mentioned, the basic factor that causes the start of the regression phase is formed by the combined effects of food quantity and food quality. The feedback from the larch to the larch bud moth, formed by the effects of food quality, permits a regression phase of sufficient length, so that death of the larch stands is prevented. Without this feedback mechanism the parasites would not be able to lengthen the regression. The population density of the larch bud moth would then fluctuate at a much higher level, and the trees would die. Changes in the genetic composition of the populations of the larch bud moth are probably not important for the regulation of numbers, as a reasonable explanation of the regular fluctuations can be deduced from the phenomena considered.

6 Sensitivity analysis

Sensitivity analysis is done to evaluate the relative weight of the rates and parameters in a model. The results can improve insight in the simulated system and should be a guide to further experiments and study. Sensitivity analysis consists of varying inputs and parameters over a certain range and comparing their influence on the end result. If the influence of a certain factor is relatively small, further analysis is not necessary, but if the influence is large, more work should be invested in a further analysis of the section of the model where this factor plays a role.
In order to obtain comparable results, sensitivity analysis may be applied to rates, parameters that act in the INITIAL and the TERMINAL part of the simulation program, and to parameters that act at more than one place in the model. Each factor listed below was multiplied by its own sensitivity factor SENA, SENB, etc.

1. Damage rate:

```
RDAM = (LAU3 + LAP3) * FEDR * SENA
```

2. Hatching rate:

```
RHATR = RHAT * (1.-RDM) * SENB
```

3. Development rate of the larvae:

```
RTL = AFGEN (RTLT,TEMP) * SENC
```

4. Development rate of the pupae:

```
RTP = AFGEN (RTPT,TEMP) * SEND
```

5. Rate of mortality by physiological weakening:

```
RPHM = AFGEN (RPHMT,DAFA) * SENE
```

6. Starvation mortality rate:

```
RSM = AFGEN (RSMT, WENE/NDTR) * SENF
```

7. Rate of parasitism:

```
PRPA = 1./(TL+NOT(TL))/AMIN1(NPAR*TL*
  K*TEMFA,NPAR*FP*TEMFF*SENG
```

8. Reproductive period of the parasites:

```
NPAR = INTGRL(0.,(INCP-DECP)*SENH)
```

9. Oviposition rate of the larch bud moth:

```
TOEG=INTGRL(0.,ROVIP*SENI)
```

10. Egg mortality in winter:

```
EW = TOEG * (1.-MORW * SENJ)
```

11. Winter mortality parasites:

```
PARW = INTGRL(0.,((1.-MIC)*LAP3*OUTP3)*
  SENK
```

The location of the respective sensitivity factors can also be read from the simulation program in Appendix C.
When all the sensitivity factors have the value 1., the originally simulated gradation cycle (see Table 3 and Figure 19) will result. For each single factor to be analysed two runs were made; one with SEN = 0.9, and one with SEN = 1.1, while all the other sensitivity factors were kept at the value 1. When SEN has a value other than 1, a gradation cycle will result that deviates from the original. The larger the deviation, the greater is the influence of the factor in question. Each sensitivity factor was given a value both above 1. and below 1., because the influence of some of the rates and parameters might be asymmetrically. If that is so, unilateral testing leads to false conclusions.
The deviating gradation cycles were compared with the original over a period of 30 years. The deviation was measured with three different criteria:
– the level of the gradation cycle. The level was calculated as the mean of the natural logarithm of the larval density of each successive year (Table 8, Column 1).

$$MNLL = (\ln(TOLA_0) + \ln(TOLA_1) + \ldots = \ln(TOLA_{29}))/30$$

The logarithm of the larval density was used because in principle the larch bud moth multiplies exponentially.

Table 8 Results of the sensitivity analyses.

Aspect	Factor	Column I	II	III	IV
		Mean number of larvae (natural logarithm 1–30 years)	Mean number of larvae (common logarithm 1–24 years)	Period in years	Amplitude
	SENA t/m K = 1	6.93	1.7171	8–9	3.381 −0.705
Damage rate	SENA = 0.9	7.282	1.6225	8–9	3.398 −0.721
	SENA = 1.1	8.09	1.717	7–8	3.476 −0.705
Hatching rate	SENB = .9	7.536	1.675	8	3.390 −0.705
	SENB = 1.1	6.5134	1.675	8	3.583 −0.705
Larval period	SENC = .9	2.366	1.5436	9–10	3.403 −0.982
	SENC = 1.1	6.69	1.735	8	3.66 −0.934
Pupal period	SEND = .9	7.941	1.677	8	3.399 −0.705
	SEND = 1.1	6.403	1.695	8–9	3.73 −1.09
Physiological mortality	SENE = .9	7.483	1.63	8	3.435 −0.705
	SENE = 1.1	1.725	1.725	7–8	3.416 −0.705

Table 8 Results of the sensitivity analyses *(contd.)*.

Aspect	Factor	Column			
		I	II	III	IV
		Mean number of larvae (natural logarithm 1–30 years)	Mean number of larvae (common logarithm 1–24 years)	Period in years	Amplitude
Starvation mortality	SENF = .9	7.701	1.665	8	3.425 −0.705
	SENF = 1.1	7.846	1.742	8	3.457 −0.705
Rate of parasitism	SENG = .9	7.584	1.62	8	3.444 −0.705
	SENG = 1.1	8.233	1.724	7–8	3.535 −0.705
Reproductive period of parasites	SENH = .9	8.11	1.706	8	3.439 −0.705
	SENH = 1.1	8.157	1.7376	8	3.532 −0.705
Oviposition rate larch bud moth	SENI = .9	7.6129	1.647	8	3.277 −0.705
	SENI = 1.1	6.865	1.645	8	3.556 −0.7659
Winter mortality	SENJ = .9	7.564	1.645	8	3.515 −0.705
	SENJ = 1.1	7.78	1.713	7–8	3.425 −0.705
Number of overwintering parasites	SENK = .9	7.57	1.62	7–8	3.44 −0.705
	SENK = 1.1	8.21	1.72	8	3.56 −0.705

– the period of the gradation cycle. The period was calculated as the number of years between two subsequent minima of the population density (Table 8, Column III).
– the amplitude of the gradation cycle. The amplitude was calculated as the range between the logarithm of the maximum population density and the logarithm of the minimum population density during the 30-year period. (Table 8, Column IV).

The results of the sensitivity analyses are presented in Table 8. There are only slight differences between the sensitivities of the factors considered. No particular key factor can be distinguished Apparently the gradation cycle of the larch bud moth is not determined by one single key factor, but can only be explained by the interaction of many different factors.

To apply these factors assumptions and estimations were made. These have been described in Chapter 4. Verifications of these could be one of the main subjects for further study.

7 Discussion on the structure of the model and research priorities

The development of the larch bud moth is simulated with the help of the mean daily temperatures. This simulation can lead to considerable deviations when the relationship between the development rate and the temperature is non-linear. Only for the egg stage it is certain that this relationship is linear (see Maksymov, 1959). Yet the simulated lengths of the different stages of the larch bud moth are similar to those observed by Maksymov (1959) at Punt Muragl (Upper Engadin) in 1953, as seen in Table 2.

The way the damage to the tree is simulated (see Section 4.2.2) might be oversimplified. The quality decrease of the needles was measured by the decrease of the initial needle weight WENEI. It was assumed that WENEI decreased by 50% in the first year after complete defoliation, and that the decrease was halved every year if no more larval fertility occurred. Furthermore it was assumed that the quality of the needles could be directly determined by the needle weight after larval feeding in the previous year. In reality the reaction of the tree after the second and the third years of damage might be different from the reaction after the first year.

Density-dependent changes of the behaviour of the larch bud moth, for instance of the copulation behaviour and the feeding behaviour, were not included. The differences between the northern and the southern slope of the Upper Engadin Valley were neglected.

It is not certain whether a parasite complex can be simulated as if it was only one species. Important interspecific relations might be neglected in this way, but with the data that were available there was no other choice.

The reproductive period of the parasites was simulated in an arbitrary way. For instance for Eulophids the reproductive period is not only determined by the temperature sum, but also by the presence of suitable hosts (see Aeschlimann, 1969).

Furthermore the parasites in the model were not able to discriminate between unparasitized and already parasitized hosts. In reality intraspecific discrimination ability is usually present, until this ability

breaks down for physiological reasons at low host densities at the end of regression (Baltensweiler, 1958). It depends on the species whether interspecific discrimination ability is present or not (Baltensweiler, 1958).

In cases where discrimination ability is present the simulation is not correct. However the reproduction of parasites can then be reduced as well, since the parasites lose time by frequently finding hosts that are already parasitized when the parasitism level is high.

Two aspects of the parasite-host relationship that are essential for the action of the parasites, the functional response and the mortality of parasite larvae from different sorts of competition at high levels of coparasitism and superparasitism(MIC), were simulated by trial and error as no literature data were available.

For many important relations in the model no reliable data were available. This lack of data is connected with the descriptive working method of the research team in Switzerland, and with the fact that a population census is done only once a year. Life-table research was initiated on a small scale only a few years ago. The measurements on the population density of the larch bud moth are very exact, but little is known about the quantitative importance of different mortality factors, and there is a marked lack of biological data that are needed to describe the processes that determine the gradation cycle of the larch bud moth. Hence the simulation model presented in this monograph certainly does not fully reproduce the gradation cycle. However it can be used to test the validity of the different explanations of the population dynamics of the larch bud moth, and to establish priorities for research.

Apparently the cyclic movement of the population densities is stable and seems to be described by a limit cycle. Whenever the limit cycle is disturbed, for example by structural changements in the model, the recovery is not reached, but within the limits accepted here (1.1–0.9), none of the factors involved has a decisive effect on the curve. This is not surprising as the long period during which this cyclic movement lasts is only reached when the system is stable. One important reason for the stability may be the isolated character of the considered region, therefore immigration and emigration seem negligible. Absence of these processes is stabilizing (May, 1973).

The effects of immigration and emigration can be evaluated by dividing the Upper Engadin in parts of reasonable size and studying

the population behaviour when different treatments are applied (for example, selective spraying, introduction of larch bud moths from other places).

As none of the considered factors proved to be decisive for the fluctuations there are no particular topics for research. Because there is still a marked lack of biological data needed to describe the relevant processes, the most effective way of continuing the research is to set up experiments to verify the structural relations that were put into the model.

The most important subjects are:

- Quantification of both the direct and the physiological damage to the tree.
- Quantification of the incoincidence between the sprouting of the larch and the hatching of the eggs of the larch bud moth.
- Quantification of the mortality and the reduction of fecundity caused by direct and physiological damage.
- Determination of the functional response curve of the parasites.
- Quantification of the mortality of parasite larvae due to different forms of competition between the parasites (MIC).
- Exact determination of the length of development and its standard deviation as a function of temperature, for each stage of the larch bud moth. Verification of the assumption of a momentaneous reaction of the development rates to temperature and the linear relationship between development rates and temperature.
- Estimations on the size of immigration and emigration in the Upper Engadin, and evaluation of these effects with the simulation model.
- Evaluation of the effects of immigration within the studied area by dividing the Upper Engadin in regions with different treatments.
- Further improvement of the simulation model and perhaps a sensitivity analysis over a wide range.

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Appendix A

List of abbreviations

AD0 = number of adults in development class zero
AD1 = number of adults in development class one
AD2 = number of adults in development class two
AD3 = number of adults in development class three
DAFA = damage factor, expressing the reduction of the food quality (dimensionless)
DECP = rate of decrease of the number of ovipositing parasites (number per day)
DELT = time step for integration (days)
EPF = mean total number of eggs laid per female (number per female)
EW = number of larch bud moth eggs after winter
FEDR = feeding capacity of the larvae of the larch bud moth (kg needles per larva per day)
FLAA = total number of female moths present at a certain moment
FP = egg-laying potential of the parasites (number of eggs per female parasite per day)
INCP = rate of increase of the number of ovipositing parasites (number per day)
K = area of discovery of the parasites (number of eggs per female parasite per larva per day)
KL = quotient of the square of the mean longevity and the square of the standard deviation of the longevity of the larvae of the larch bud moth (dimensionless)
KP = idem for the pupae
KA = idem for the adults
LAP0 = number of parasitized larvae in development class zero
LAP1 = number of parasitized larvae in development class one
LAP2 = number of parasitized larvae in development class two
LAP3 = number of parasitized larvae in development class three
LAU0 = number of unparasitized larvae in development class zero

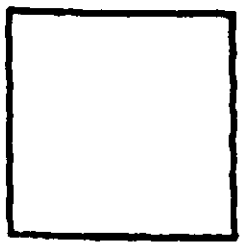
LAU1 = number of unparasitized larvae in development class one
LAU2 = number of unparasitized larvae in development class two
LAU3 = number of unparasitized larvae in development class three
LOR = proportion of the parasite eggs that is laid in the unparasitized larvae during one time step of integration, and that is wasted by coparasitizing and superparasitizing (dimensionless)
MIC = proportion of the parasitized larvae from which no parasite emerges at the time of pupation (dimensionless)
MORW = proportion of the total number of eggs that is laid by the larch bud moth that fails to produce a larva (dimensionless)
MRPU = relative rate of mortality of the pupae of the larch bud moth (day^{-1})
MRT = relative rate of mortality of the larvae in the development classes zero, one and two (day^{-1})
MRT3 = relative rate of mortality of the larvae in the development class three
NEG = number of larch bud moth eggs that have not yet hatched
NDTR = the needle mass of a completely undamaged tree (kg)
NPAR = number of ovipositing parasites
NPARI = number of female parasites at the beginning of the year
NUYE = number of years
PARW = total number of overwintering parasites
PEPL = proportion of the larvae that is parasitized (dimensionless)
PPEL = proportion of the parasite eggs that are wasted by coparasitizing and superparasitizing (dimensionless)
PRPA = potential relative rate of parasitizing (day^{-1})
PU0 = number of pupae in development class zero
PU1 = number of pupae in development class one
PU2 = number of pupae in development class two
PU3 = number of pupae in development class three
RDAM = damage rate (kg needles per day)
RDM = proportion of the hatching larvae that is not able to penetrate a short shoot (dimensionless)
RHAT = rate of hatching of the larch bud moth eggs (number of eggs per day)
ROVIP = rate of oviposition by the larch bud moth (number of eggs per day)

RPAR = relative rate of parasitism (day^{-1})
RPHM = relative rate of mortality by decreased food quality (day^{-1})
RREP = reduction factor of the egg-laying potential of the larch bud moth (dimensionless)
RRHAT = relative rate of hatching of the larch bud moth eggs (day^{-1})
RHATR = reduced rate of hatching of the larch bud moth eggs (rate of inflow of the first development class of unparasitized larvae) (number per day)
RSM = relative rate of mortality from lack of food (day^{-1})
RTL = the inverse of the duration of the larval stage per development class (day^{-1})
RTP = the inverse of the duration of the pupal stage per development class (day^{-1})
RTA = the inverse of the duration of the adult stage per development class (day^{-1})
SR = sex ratio of the larch bud moth (proportion of the adults that are females) (dimensionless)
TEMFA = temperature factor that modifies the 'area of discovery' of the parasites (dimensionless)
TEMFF = temperature factor that modifies the egg-laying potential of the parasites (dimensionless)
TEMP = temperature (°C)
TEMS = temperature sum (°C)
TL = total number of larvae, parasitized and unparasitized, that is present at a certain moment
TLAP = total number of parasitized larvae that are present at a certain moment.
TLPEG = the sum of the numbers of parasite eggs that are wasted by coparasitizing and superparasitizing
TNPL = the sum of the numbers of parasitized larvae that have left the last larval development class
TOEG = total number of larch bud moth eggs that are laid during the season
TOLA = the sum of the numbers of larvae that have reached the last larval development class
TPEG = sum of the numbers of parasite eggs that are laid during the season

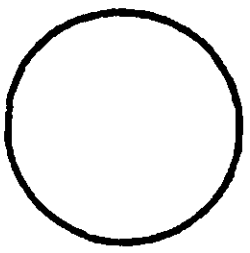
TRPHM = sum of the numbers of larvae and pupae that died from decreased food quality during the season
TRSM = sum of the numbers of larvae that died from lack of food during the season
TUL = total number of unparasitized larvae present at a certain moment
WENE = actual needle mass (kg)
WENEI = needle mass before larval feeding (kg)

Appendix B

Explanation of the symbols used in the relational diagrams



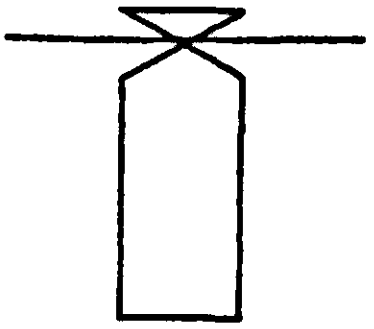
STATE VARIABLE OR VALUE OF AN INTEGRAL



AUXILIARY VARIABLE

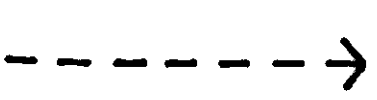
(ABCD)

DRIVING OR FORCING VARIABLE



RATE OF FLOW OF MATERIAL INTO OR FROM AN INTEGRAL

FLOW OF MATERIAL, INTO OR FROM AN INTEGRAL



FLOW OF INFORMATION

ABCD

PARAMETER

2

MORTALITY

Appendix C

```
      ***LISTING OF PROGRAM***

TITLE LARUMO
TITLE RABBINGE
FIXED NUYE
PARAM NUYE=1.
PARAM WENEI=3.314
PARAM EW=.37 ,NPARI=.06
INITIAL
INCON ILAU=0.
INCON ILAP=0.
      ILAU0=.5*ILAU
      ILAU1=.5*ILAU
      ILAP0=.5*ILAP
      ILAP1=.5*ILAP
      DELX=1./DELT
INCON NDTR=3.314
      DAFA=1.-(NDTR-WENEI)/(.5*NDTR)
DYNAMIC
      LAU0=INTGRL(ILAU0,RLAU0)
      LAP0=INTGRL(ILAP0,RLAP0)
      LAU1=INTGRL(ILAU1,RLAU1)
      LAP1=INTGRL(ILAP1,RLAP1)
      LAU2=INTGRL(0.,RLAU2)
      LAP2=INTGRL(0.,RLAP2)
      LAU3=INTGRL(0.,RLAU3)
      LAP3=INTGRL(0.,RLAP3)
      PU0=INTGRL(0.,RPU0)
      PU1=INTGRL(0.,RPU1)
      PU2=INTGRL(0.,RPU2)
      PU3=INTGRL(0.,RPU3)
      AD0=INTGRL(0.,RAD0)
      AD1=INTGRL(0.,RAD1)
      AD2=INTGRL(0.,RAD2)
      AD3=INTGRL(0.,RAD3)
      TOLA=INTGRL(0.,(LAU2*OUTU+LAP2*OUTP))
      AD=INTGRL(0.,PU3*OUTPU)
      TEMP=AFGEN(TEMPT,TIME)
      TEMS=INTGRL(0.,TEMP)
*
*  CALCULATION OF DAMAGE
*
      WENEA=INTGRL(WENEI,-RDAM)
      RDAM=(LAU3+LAP3)*FEDR*SENA
PARAM SENA=1.
      WENE=WENEA*INSW(WENEA,0.,1.)
      FEDR=AFGEN(FEDRT,DAFA)
*
*  HATCHING OF THE BUD MOTH EGGS
*
      NEG=INTGRL(EW,-RHAT)
      RHAT=NEG*AFGEN(RRHAT,TEMP)*INSW(TEMS-45.,0.,1.)
      RHATR=RHAT*(1.-RDM)*SENB
PARAM SENB=1.
*
*  LARVAE UNPARASITIZED
*
      RLAU0=RHATR-LAU0*(RTEL+MRTL+RPAR)
      RLAU1=LAU0*RTEL-LAU1*(OUTU+MRTL+RPAR)
      RLAU2=LAU1*OUTU-LAU2*(OUTU+MRTL+RPAR)
      RLAU3=LAU2*OUTU-LAU3*(OUTU3+MRTL3+RPAR)
      OUTU=PUSHL*(FRL*DELX-MRTL-RPAR)
      OUTU3=PUSHL*(FRL*DELX-MRTL3-RPAR)
      MRTL=RPHM+.01486
      MRTL3=MRTL+RSM
      RTEL=2.*RTL/FRL
      RTL=AFGEN(RTLT,TEMP)*SENC
PARAM SENC=1.
      PUSHL=INSW(GSL-1.,0.,1.)
      GSL=INTGRL(.5,RTL/FRL-PUSHL*DELX)
      FRL=AMAX1(DELT*RTL,1.-3.*KL)
      KL=AFGEN(KLT,TEMP)
```

```
*
*   LARVAE PARASITIZED
*
      RLAP0=RPAR*LAU0-LAP0*(RTEL+MRTL)
      RLAP1=LAP0*RTEL+RPAR*LAU1-LAP1*(OUTP+MRTL)
      RLAP2=LAP1*OUTP+RPAR*LAU2-LAP2*(OUTP+MRTL)
      RLAP3=LAP2*OUTP+RPAR*LAU3-LAP3*(OUTP3+MRTL3)
      OUTP=PUSHL*(FRL*DELX-MRTL)
      OUTP3=PUSHL*(FRL*DELX-MRTL3)
*
*   MORTALITY BY INCOINCIDENCE AND DECREASED FOOD QUALITY
*
      RDM=AFGEN(RDMT,DAFA)
      RPHM=AFGEN(RPHMT,DAFA)*SENE
PARAM SENE=1.
      TRPHM=INTGRL(0.,(TUL+TLAP+PU0+PU1+PU2+PU3)*RPHM*SENB)
*
*   STARVATION MORTALITY
*
      RSM=AFGEN(RSMT,WENE/NDTR)*SENF
PARAM SENF=1.
      TRSM=INTGRL(0.,(LAU3+LAP3)*RSM*SENC)
*
*   PUPAL STAGE
*
      RPU0=LAU3*OUTU3-PU0*(RTLP+MRPU)
      RPU1=PU0*RTLP-PU1*(OUTPU+MRPU)
      RPU2=PU1*OUTPU-PU2*(OUTPU+MRPU)
      RPU3=PU2*OUTPU-PU3*(OUTPU+MRPU)
      OUTPU=PUSHP*(FRP*DELX-MRPU)
      MRPU=.01486+RPHM
      RTLP=2.*RTP/FRP
      RTP=AFGEN(RTPT,TEMP)*SEND
PARAM SEND=1.
      PUSHP=INSW(GSP-1.,0.,1.)
      GSP=INTGRL(.5,RTP/FRP-PUSHP*DELX)
      FRP=AMAX1(DELT*RTP,1.-3.*KP)
      KP=AFGEN(KPT,TEMP)
*
*   ADULT STAGE
*
      RAD0=PU3*OUTPU-AD0*RTPA
      RAD1=AD0*RTPA-AD1*OUTA
      RAD2=(AD1-AD2)*OUTA
      RAD3=(AD2-AD3)*OUTA
      OUTA=PUSHA*FRA*DELX
      RTPA=2.*RTA/FRA
      RTA=AFGEN(RTAT,TEMP)
      PUSHA=INSW(GSA-1.,0.,1.)
      GSA=INTGRL(.5,RTA/FRA-PUSHA*DELX)
      FRA=AMAX1(DELT*RTA,1.-3.*KA)
      KA=AFGEN(KAT,TEMP)
*
*   CALCULATION OF PARASITIZING RATE
*
      RPAR=(1.-LOR)*PRPA
      PRPA=1./(TL+NOT(TL))*AMIN1(NPAR*TL*K*TEMFA, ...
      NPAR*FP*TEMFF)*SENG
PARAM SENG=1.
PARAM K=.2
PARAM FP=2.5
      LOR=(PRPA*DELT+EXP(-PRPA*DELT)-1.)/(PRPA*DELT+NOT(PRPA*DELT))
      TL=TUL+TLAP
      TUL=LAU0+LAU1+LAU2+LAU3
      TLAP=LAP0+LAP1+LAP2+LAP3
      TEMFA=TEMFF
      TEMFF=AFGEN(TEMFT,TEMP)
      NPAR=INTGRL(0.,(INCP-DECP)*SENH)
PARAM SENH=1.
      INCP=PUSH*PAR*.8*INSW(TEMS-85.,0.,1.)
      PAR=INTGRL(NPARI,-INCP)
      DECP=PUSH*NPAR*.8*INSW(TEMS-404.,0.,1.)
      PUSH=IMPULS(1.,1.)
```

```
*
*  PARASITIZING LEVEL
*
      TNPL=INTGRL(0.,LAP3*OUTP3)
      PARW=INTGRL(0.,(LAP3*OUTP3*(1.-MIC))*SENK)
      MIC=AFGEN(MICT,PPEL)
PARAM SENK=1.1
      TULA=INTGRL(0.,LAU3*OUTU3)
      PEPL=TNPL/((TNPL+TULA)+NOT(TNPL+TULA))
*
*  LOSS OF PARASITE EGGS BY CO- AND SUPERPARASITISING
*
      TPEG=INTGRL(0.,PRPA*TL)
      TLPEG=INTGRL(0.,(TLAP+LOR*TUL)*PRPA)
      PPEL=TLPEG/(TPEG+NOT(TPEG))
*
*  OVIPOSITION BY THE BUD MOTH
*
      ROVIP=AFGEN(FTB,TEMP)*FLAA*(1.-RREP)
      FLAA=(AD0+AD1+AD2+AD3)*SR
PARAM SR=.5
      RREP=AFGEN(RREPT,DAFA)
      TOEG=INTGRL(0.,ROVIP*SENI)
PARAM SENI=1.
      EPF=TOEG/(AD*SR+NOT(AD*SR))
*
*  FUNCTIONS
*
AFGEN RTLT=-10.,0., 2.,0., 11.5,.0612, 18.,.1334
AFGEN RTPT=-10.,0., 7.5,0., 12.5,.1154, 17.,.2041
AFGEN RTAT=-10.,0., 2.,0., 11.,.0857, 20.,.1429
AFGEN KLT=0.,0., 2.,0., 11.5,.0017, 18.,.0020, 24.5,.0055
AFGEN KPT=0.,0., 7.5,0., 12.5,.00027, 17.,.0015, 21.,.00060
AFGEN KAT=0.,0., 2.,0., 12.5,.00027, 17.,.0015, 21.,.00060
AFGEN RRHAT=0.,0., 4.,0., 6.,.2, 10.7,.45
AFGEN FEDRT=-10.,.000075, 0.,.000075, .93,.00015, 1.,.00015
AFGEN TEMFT=0.,0., 5.,0., 7.5,.12, 10.,.85, 15.,1.
AFGEN FTB=0.,0., 6.,0., 11.,5.8, 20.,10.1
AFGEN MICT=-10.,0., 0.,0., .10,.5, .27,.95, .81,.999,   ...
      1.,1., 2.,1.
AFGEN RDMT=-10.,.65, 0.,.65, .96,0., 1.,0.
AFGEN RPHMT=-10.,.0198, 0.,.0198, .45,.0075, .75,.0062,      ...
      .875,.0039, .937,.0009, .96,0., 1.,0.
AFGEN RSMT=-10.,.4, 0.,.4, .05,.01, .7,0., 1.,0.
AFGEN RREPT=-10.,.67, 0.,.67, .45,.42, .75,.19, .875,0., 1.,0.
AFGEN TEMPT=0.,7.0, 1.,4.6, 2.,3.7, 3.,-0.3, 4.,-0.9, 5.,0.6,   ...
      6.,2.3, 7.,5.4, 8.,6.1, 9.,7.3, 10.,5.9, 11.,4.7, 12.,5.9,   ...
      13.,7.2, 14.,2.9, 15.,0.7, 16.,3.7, 17.,6.5, 18.,6.8,   ...
      19.,5.4, 20.,2.9, 21.,5.2, 22.,8.1, 23.,8.7, 24.,6.9,   ...
      25.,9.2, 26.,8.7, 27.,9.6, 28.,8.8, 29.,10.1, 30.,8.4,   ...
      31.,7.9, 32.,8.2, 33.,7.1, 34.,8.4, 35.,6.9, 36.,6.1,   ...
      37.,7.5, 38.,3.3, 39.,8.0, 40.,9.1, 41.,9.1, 42.,9.7,   ...
      43.,10.9, 44.,9.4, 45.,2.8, 46.,4.8, 47.,6.9, 48.,8.3,   ...
      49.,11.7, 50.,12.7, 51.,10.7, 52.,14.8, 53.,15.8, 54.,12.9,   ...
      55.,11.9, 56.,6.9, 57.,11.3, 58.,14.4, 59.,13.1, 60.,13.2,   ...
      61.,12.5, 62.,14.3, 63.,12.5, 64.,11.1, 65.,11.6, 66.,8.4,   ...
      67.,11.0, 68.,14.1, 69.,10.4, 70.,11.0, 71.,8.9, 72.,11.0,   ...
      73.,9.7, 74.,9.4, 75.,9.7, 76.,12.0, 77.,14.1, 78.,15.4,   ...
      79.,12.6, 80.,13.2, 81.,14.1, 82.,15.6, 83.,15.7, 84.,12.8,   ...
      85.,14.4, 86.,14.3, 87.,12.1, 88.,13.7, 89.,12.9, 90.,11.6,   ...
      91.,13.9, 92.,13.3, 93.,13.5, 94.,14.1, 95.,15.8, 96.,14.2,   ...
      97.,14.4, 98.,14.2, 99.,11.3, 100.,10.9, 101.,9.8,   ...
      102.,9.7, 103.,12.1, 104.,12.8, 105.,11.9, 106.,13.9,   ...
      107.,12.4, 108.,10.8, 109.,9.9, 110.,5.4, 111.,7.3,   ...
      112.,8.7, 113.,3.8, 114.,7.5, 115.,10.5, 116.,11.3,   ...
      117.,12.5, 118.,12.5, 119.,10.8, 120.,5.1, 121.,5.0,   ...
      122.,5.8, 123.,8.1, 124.,9.6, 125.,10.1, 126.,10.5,   ...
      127.,10.0, 128.,7.0, 129.,5.5, 130.,5.9, 131.,8.2,   ...
      132.,7.4, 133.,7.7, 134.,8.0, 135.,7.9, 136.,8.1,   ...
      137.,10.2, 138.,9.7, 139.,10.7, 140.,10.0, 141.,10.6,   ...
      142.,9.0, 143.,9.7, 144.,10.9, 145.,10.6, 146.,10.2,   ...
      147.,7.9, 148.,7.3, 149.,4.6, 150.,9.9, 151.,5.3,   ...
      152.,4.1, 153.,6.3, 154.,6.6, 155.,6.1, 156.,6.7,   ...
      157.,8.2, 158.,3.7, 159.,3.7, 160.,3.2, 161.,3.5, 162.,2.7,   ...
      164.,2.2, 165.,3.9, 166.,4.0, 167.,4.1, 168.,3.8,   ...
      169.,2.5, 170.,2.2, 171.,4.2, 172.,3.3, 173.,2.3,   ...
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      174.,3.9, 175.,4.2, 176.,4.6, 177.,4.2, 178.,3.5, 179.,4.1,   ...
      180.,2.0, 181.,0.7, 182.,-1.9, 183.,-1.9, 184.,-1.4,   ...
      185.,0.3, 186.,1.1, 187.,1.2, 188.,2.3, 189.,2.8,   ...
      190.,3.5
METHOD RECT
TIMER DELT=.1,    FINTIM=190.,    PRDEL=190.
PRINT EW,TOLA,PEPL,PPEL,NPARI,EPF,TRSM,TRPHM,RDM,WENEI,MNLL,LOTOLA
      LOTOLA=ALOG10(TOLA)
TERMINAL
      ATOL(NUYE)=ALOG(TOLA)
      WENEI=.5*(WENE+WDTR)
PARAM MORW=.4
      EW=TOEG*(1.-MORW*SENJ)
PARAM SENJ=1.
      NPARI=PARW*.5
      NUYE=NUYE+1.
IF (NUYE.GT.30.) GOTO 99
      CALL RERUN
   99 CONTINUE
      ATOL'1,30'=ATOL('1,30')
      MNL=SUM1(ATOL'1,30')
      MNLL=MNL/NUYE
END
STOP
ENDJOB
```