

# 7

## Population Cycles of the Larch Budmoth in Switzerland

---

Peter Turchin, Cheryl J. Briggs, Stephen P. Ellner,  
Andreas Fischlin, Bruce E. Kendall, Edward McCauley,  
William W. Murdoch, and Simon N. Wood

### 7.1 Introduction

The population dynamics of the larch budmoth (LBM), *Zeiraphera diniana*, in the Swiss Alps are perhaps the best example of periodic oscillations in ecology (figure 7.1). These oscillations are characterized by a remarkably regular periodicity, and by an enormous range of densities experienced during a typical cycle (about 100,000-fold difference between peak and trough numbers). Furthermore, nonlinear time series analysis of LBM data (e.g., Turchin 1990, Turchin and Taylor 1992) indicates that LBM oscillations are definitely generated by a *second-order* dynamical process (in other words, there is a strong delayed density dependence—see also chapter 1). Analysis of time series data on LBM dynamics from five valleys in the Alps suggests that around 90% of variance in  $R_t$  is explained by the phenomenological time series model employing lagged LBM densities,  $R_t = f(N_{t-1}, N_{t-2})$  (Turchin 2002).

As discussed in the influential review by Baltensweiler and Fischlin (1988) about a decade ago, ecological theory suggests a number of candidate mechanisms that can produce the type of dynamics observed in the LBM (see also chapter 1). Baltensweiler and Fischlin concluded that changes in food quality induced by previous budmoth feeding was the most plausible explanation for the population cycles. During the last decade, the issue of larch budmoth oscillations was periodically revisited by various population ecologists looking for general insights about insect population cycles (e.g., Royama 1977, Bowers et al. 1993, Ginzburg and Taneyhill 1994, Den Boer and Reddingius 1996, Hunter and Dwyer 1998, Berryman 1999). These

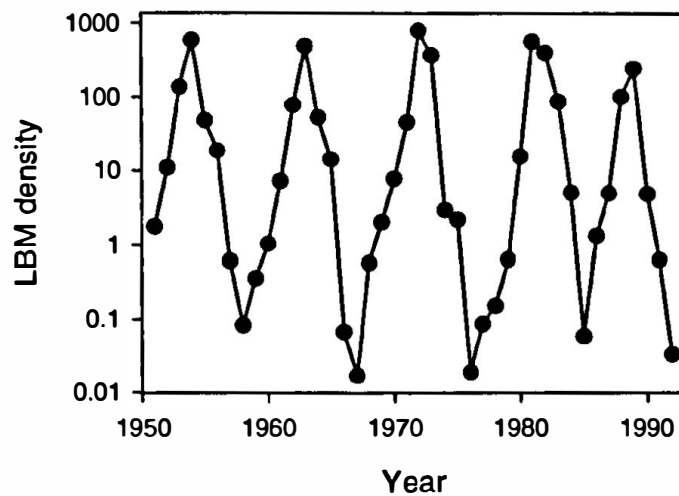


Figure 7.1 Population oscillations of the larch budmoth at Sils (Upper Engadine Valley, Switzerland). Moth density is the number of larvae per kilogram of larch branches (data from Baltensweiler 1993b).

authors generally concurred with the view that budmoth cycles are driven by the interaction with food quality. A recent reanalysis of the rich data set on budmoth population ecology collected by Swiss researchers over a period of several decades, however, suggested that the role of parasitism is underappreciated (Turchin et al. 2002).

## 7.2 General Overview of Hypotheses for LBM Cycles

Before focusing on the roles of food quality and parasitism in LBM dynamics, we briefly review the status of other hypotheses that were discussed in the literature on LBM cycles. First, the natural history of the LBM–larch system is such that *food quantity* is an unlikely factor to explain LBM oscillations. Mortality of the host trees due to defoliation is less than 1% (Baltensweiler and Fischlin 1988). Although the length of needles is reduced after a severe defoliation, the total amount of needle biomass is decreased only about two-fold. It is difficult to imagine how such small variations in food availability could drive a second-order population cycle in which the ratio of peak/trough densities is around 100,000. However, food quantity should act as a strong first-order mechanism regulating LBM density, since most LBM outbreaks are accompanied by widespread defoliation of host trees (Baltensweiler and Fischlin 1988), leading to mass starvation of larvae during peak years.

*Maternal effects* constitute a theoretically plausible intrinsic mechanism of second-order oscillations (Ginzburg and Taneyhill 1994). However, there is no evidence that this mechanism operates in the LBM. Even the proponents

of the maternal effect hypothesis admit that their model is not applicable to the LBM (Ginzburg and Taneyhill 1994).

Theory suggests that the interaction between *pathogens* and their hosts can exhibit oscillatory dynamics (e.g., Anderson and May 1980). In 1957, after the first cycle that was studied intensively, it seemed obvious to everybody that a granulosis virus disease played a critical role in suppressing the outbreak (Baltensweiler and Fischlin 1988). Unfortunately, the incidence of virus decreased during the next outbreak, and then disappeared completely. As a result, the pathogen hypothesis fell out of vogue, at least among field workers. Despite this, Anderson and May (1980) used LBM as their prime example of how an epidemiological model may explain population cycles in a forest insect.

There are two larch budmoth host races with distinct differences in color and ecological traits—a dark morph that feeds primarily on deciduous larch, and a light morph that feeds primarily on evergreens (*Pinus cembra* and *Picea abies*). The frequency of the dark morph tends to increase during outbreaks and decrease during declines (Baltensweiler 1993a, fig. 1). Baltensweiler (1977, 1993a) proposed the following explanation for this pattern: During population increases, the dark morphs become more abundant because they have faster development and higher survival than the light morphs. During population collapses, the dark morphs decrease faster than the light morphs, because they rely primarily on larch for food, and the quality of larch foliage is reduced by defoliation. Once the effects of defoliation on host quality dissipate, dark morphs begin increasing faster than light ones, and the cycle repeats itself.

Baltensweiler (1993a) argued that this polymorphism plays a key role in the LBM cycle. In particular, he suggested that it helps explain why low LBM populations switch immediately from the decline to the increase phase. However, as we shall see later, the abrupt switch from decline to increase is not a pattern that needs a special explanation because it arises naturally in several models considered later. Furthermore, the polymorphic fitness hypothesis is not an elemental mechanism, because it invokes plant quality as the primary factor causing population collapse (without prolonged decrease in plant quality the population density of dark morphs would not decrease, and no cycle would ensue). Thus, the polymorphic fitness hypothesis is not an explanation of the primary question (why LBM populations oscillate), but rather why morph frequencies change regularly during the LBM cycle. It is a consequence not a cause of the cycle.

The *food quality* hypothesis is currently the dominant explanation of LBM oscillations (Baltensweiler and Fischlin 1988). Larch trees suffering greater than 50% defoliation lack nutrient resources to grow high-quality needles during the following spring. Needles grown after the LBM peak are short (< 20 mm, compared with a normal length of > 30 mm) and have a high raw fiber content of about 18% (compared with the normal 12%), while the raw protein content falls from 6% to 4%. Low quality of food (as measured by high raw fiber, and indexed by low needle length) strongly

depresses larval survival and female fecundity (Benz 1974, Omlin 1977). Furthermore, poor needle quality persists for several years after an outbreak. This "quality transmission" effect imposes delayed density dependence on LBM population growth rates, and can theoretically lead to cycles, as shown by the model developed by Fischlin (1982; see also Fischlin and Baltensweiler 1979).

General theory suggests that *parasitoids* may play an important role in population dynamics of forest insects, and LBM parasitoids were intensively studied from the beginning of the systematic research program (e.g., Baltensweiler 1958). Once the data on parasitism rates became available, however, the initial enthusiasm for the parasitoid hypothesis waned. Parasitism rates at the population peak are typically low, around 10–20% (Baltensweiler and Fischlin 1988), suggesting that parasitoids play a minor role in *limiting* LBM densities; that is, in preventing further LBM increases. The parasitism rate reaches a high of around 90% during the collapse stage, but this high is reached only during the second (or even third) year after the peak. Accordingly, Delucchi (1982) concluded that control of LBM by parasitoids alone is not possible, and the current thinking is that parasites merely track the larch budmoth population; that is, budmoth fluctuations regulate the number of parasitoids and not vice versa. However, the observation that parasitoids do not play an important role in stopping LBM increases does not necessarily mean that they are a minor agent in LBM dynamics. This conclusion is erroneous because it confuses first- and second-order factors; that is, a mechanism imposing an upper bound on LBM population density may differ from one inducing oscillations.

In summary, there are two hypotheses about LBM cycles that require further examination—the plant quality hypothesis and the parasitism hypothesis. In the following sections we review the data, the models, and especially the cross-connections between empirical and theoretical approaches relevant to each of the hypotheses.

### 7.3 LBM–Plant Quality Interaction

Previous analyses of the interaction between plant quality and LBM dynamics emphasized the raw fiber content of larch needles as the main indicator of food quality (for example, the model of Fischlin was based on this index). However, there is no time series data available for this index, while we have an extensive data set for another index, the average needle length. Before using these data, however, we first need to check on how well needle length reflects the food quality from the point of view of LBM larvae. We can answer this question with the bioassay data of Benz (1974, table 8). Benz fed LBM larvae foliage from larch trees with known defoliation history, and measured larval survival and pupal weight. Because female pupal weight is linearly related to fecundity, we can translate the measured pupal weights into expected fecundity using the relationship estimated by Benz (1974, fig. 2).

Multiplying larval survival by the calculated fecundity we then obtain a measure related to the finite rate of population increase  $\lambda'$  (the prime is to remind us that this measure is not the true  $\lambda$  because it does not include egg and adult mortality). Plotting  $\lambda'$  against needle length index reveals a well-defined relationship between these two quantities, with a high coefficient of determination,  $r^2 = .86$  (fig. 7.2). Interestingly, the alternative index, raw fiber content, explains a somewhat lower percentage of variance in  $\lambda'$  ( $r^2 = .66$ ; analysis based on the same Benz data). Thus, the somewhat surprising conclusion is that needle length appears to be a better index of food quality than raw fiber content. Clearly, food quality is a complex variable, whose effect on LBM survival and fecundity is mediated by physical (e.g., toughness as measured by raw fiber content) and nutritional (e.g., protein content) properties of needles, as well as, perhaps, tree chemical defenses; for example, resin content (Benz 1974). However, the observation that the average length of needles is an accurate predictor of LBM rates of population change is encouraging.

We now consider the results of the analysis of time series data on LBM density and needle length during 1961–92 at Sils (Engadine Valley, Switzerland) (see figure 7.3a). Turchin et al. (2002) employed nonlinear regression to investigate the cross-effects of LBM density and needle length on each other. Although we tried a variety of functional forms for the general model  $R_t = f(N_{t-1}, Q_{t-1})$  (where  $R_t = \ln N_t/N_{t-1}$  is the realized per-capita rate of the budmoth population, and  $N_t$  and  $Q_t$  are LBM density and needle length in year  $t$ ), we could detect no strong effect of needle length (less than one third of the variance explained).

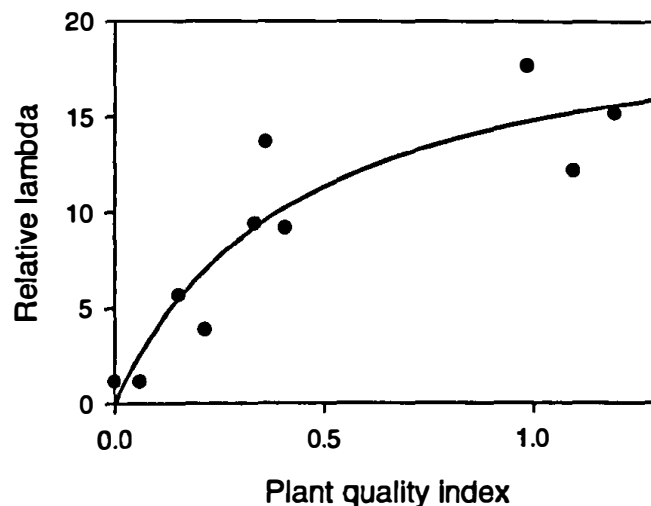


Figure 7.2 Effect of plant quality on the relative multiplication rate of the larch budmoth,  $k$  (calculations based on data from Benz 1974, table 8). Plant quality index is scaled by needle length:  $Q_t = (\text{needle length} - 15 \text{ mm})/15 \text{ mm}$  (this scales the index to the range of approximately 0–1).

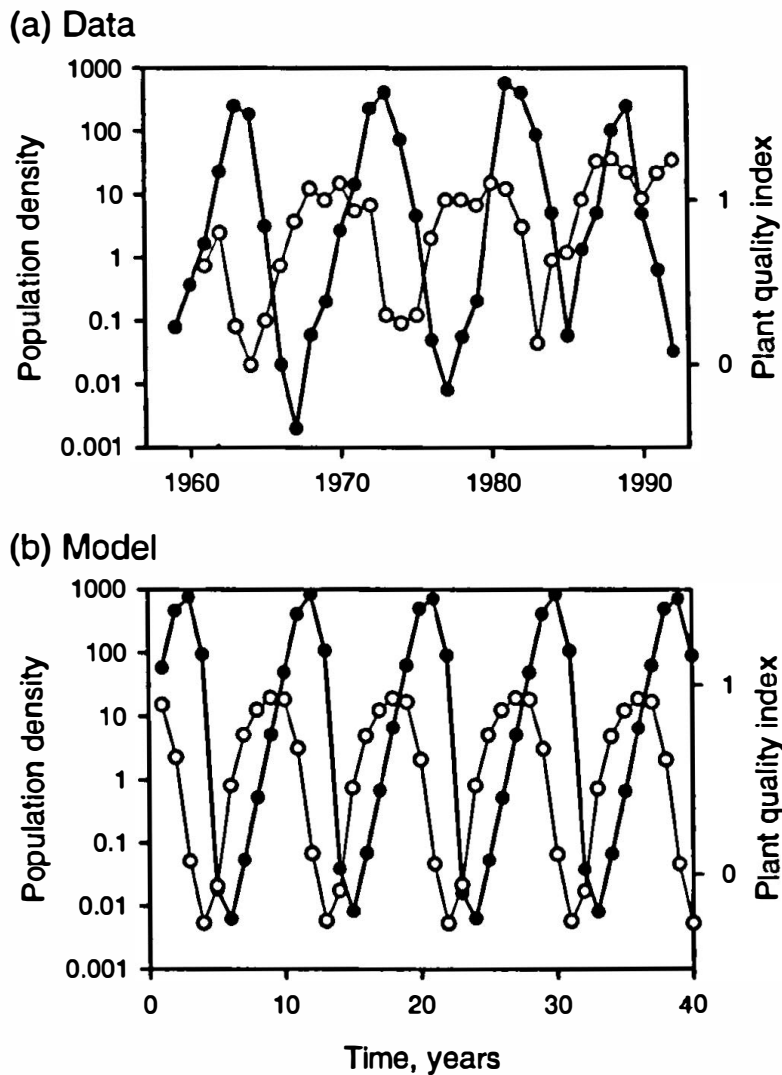


Figure 7.3 Dynamics of LBM density and food quality: (a) observed and (b) predicted by the model.

By contrast, the dynamics of needle length are strongly related to LBM density and the previous year's index. The following simple model (which is a discretization of Edelstein-Keshet and Rausher 1989; see Turchin 2002):

$$Q_t = (1 - \alpha) + \alpha Q_{t-1} + \frac{cN_{t-1}}{d + N_{t-1}} \quad (7.1)$$

explained around 75% of the variance in  $Q_t$ . The effect of “memory,” represented by the autoregressive parameter  $\alpha$ , is highly significant, and by itself explains about 47% of the variance.

The surprising result from these analyses is that an index of plant quality explains a very low proportion of variance in the LBM rate of change. Such a low level of predictability associated with plant quality contrasts unfavorably

with the  $r^2$  of around 90% suggested by phenomenological response-surface models, or regression analyses utilizing parasitism data (see section 7.4). While these regression analyses do not constitute a “proof” that plant quality is unimportant in LBM dynamics, they considerably weaken the case for it as the primary factor responsible for LBM oscillations. However, in order to pass the final verdict, we need to know whether a model based on the plant quality hypothesis is capable of mimicking the observed LBM dynamics.

In constructing the equation for LBM dynamics, we used the data depicted in figure 7.2. After trying several two-parameter relationships, we found that a negative exponential function fits the data best (this is a purely phenomenological approach, as we have no mechanistic basis for postulating a functional form). Using log-transformed  $\lambda'$  ( $R' = \log \lambda'$ ) as the response variable, the fitted curve was

$$R'_t = a[1 - \exp(Q_{t-1}\delta)], \quad (7.2)$$

where  $a = 3.8$  is the maximum rate of increase at the highest food quality, and  $\delta = 0.22$  is the parameter determining how fast the rate of change approaches its maximum. There are two things still missing from this model. First, it assumes that there is no mortality in the adult and small larva stages. We can remedy this by replacing the maximum rate  $a$  with the average per-capita rate of population change observed when plant quality is at its highest. A good choice for this parameter is  $R_0 = 2.5$ , corresponding to about a 10-fold increase in  $N_t$  per year (because this is the average rate at which the LBM density climbs out of the trough). Second, the model lacks a self-limitation term due to larvae overeating their food supply and starving as a result. One solution is to use the Ricker equation, which leads to the following model for LBM dynamics:

$$N_{t+1} = N_t \exp\{R_0[1 - \exp(Q_t/\delta)] - R_0 N_t/K\}. \quad (7.3)$$

For the dynamics of needle length,  $Q_t$ , we simply use the empirical equation (7.1). The regression-based parameter estimates (mean  $\pm$  SE) are  $\delta = 0.22 \pm 0.05$ ,  $\alpha = 0.5 \pm 0.1$ ,  $c = 0.7 \pm 0.2$ , and  $d = 150 \pm 150$ . Additionally, we have  $R_0 = 2.5 \pm 0.2$  and  $K = 500 \pm 200$ .

Numerical exploration of dynamics for parameters in the ranges defined by mean  $\pm$  SE indicated that this model is readily capable of generating population trajectories resembling the data (figure 7.3b). Trajectories predicted by the model match both the period and the amplitude of the observed LBM oscillations. Additionally, the model mimics the quantitative pattern of the quality index dynamics reasonably well, including the amplitude of variation and the timing of declines and increases (compare with figure 7.3a). However, the range of oscillations in  $Q_t$  predicted by the model is somewhat lower than that observed.

In summary, the model of LBM–plant quality interactions, with biologically plausible parameters, is capable of matching the empirically observed quantitative patterns in the time series data. Does it mean that we have found

the explanation for the LBM oscillations? Unfortunately, there remains one serious problem, the lack of detectable effect of  $Q_t$  on the LBM rate of change; that is, no negative feedback between  $Q_t$  and  $N_t$ .

Furthermore, if we examine the last documented LBM outbreak (peak in 1989), we notice that the plant quality index hardly declined at all, with needle lengths remaining at high levels through the whole period (figure 7.3a). As discussed by Baltensweiler (1993b), a sequence of unusual weather in 1989–91 caused high egg mortality. As a result, the budmoth population never reached the level at which widespread defoliation occurs (the 1989 peak density was only 240 larvae per kilogram of larch branches, while previous peak densities observed at Sils were 490, 590, 800, and 560 larvae/kg). Correspondingly, light defoliation resulted in no decline in plant quality. Yet, the LBM population collapsed during 1990–92. In other words, we have here a natural experiment suggesting that a large decrease in plant quality is not necessary for LBM cycles.

#### 7.4 Parasitism Hypothesis

Our investigation of the parasitism hypothesis employs an approach similar to that used in assessing the plant quality hypothesis. First, we subject time series data to nonlinear regression analyses. Then, we develop an empirically based model of LBM–parasitoid interaction that attempts to mimic the observed dynamics.

The general model that we used (Turchin et al. 2002) was based on the Nicholson–Bailey framework, to which we added a self-limitation term in the host and a Beddington-type functional response (this general form of functional response incorporates both the effects of handling time  $h$  and mutual interference between parasitoids, parameterized by wasted time  $w$ ). The equations were:

$$N_{t+1} = N_t \exp[R_0(1 - N_t/K) - aP_t/(1 + ahN_t + awP_t)], \quad (7.4a)$$

$$P_{t+1} = N_t S_t, \quad \text{where } S_t = 1 - \exp[-aP_t/(1 + ahN_t + awP_t)]. \quad (7.4b)$$

The parasitoid density,  $P_t$ , is not directly observed, and therefore, we need to estimate it by multiplying the host density during the previous year by that year's parasitism rate:  $P_t = N_{t-1} S_{t-1}$  ( $S_t$  is the proportion of hosts parasitized in year  $t$ ). Note that our estimate of  $P_t$  does not incorporate the (unknown) overwintering mortality. Thus,  $P_t$  is actually a relative index that is linearly related to the true parasitoid density, but with an unknown proportionality constant (this has no effect on the estimate of the proportion of variance resolved by parasitism).

Results of nonlinear regression suggest that the parasitism rate is quite well resolved by model (7.4). Thus, the simple three-parameter equation (7.4b) resolves 71% of the variance in the parasitism rate. The coefficient of deter-



mination for the LBM rate of change is even higher, with equation (7.4a) resolving 88% of the variance. What is particularly impressive is that a very simple three parameter model:

$$R_t = \ln(N_t/N_{t-1}) = R_0 - aP_{t-1}/(1 + awP_{t-1}) \quad (7.5)$$

manages to capture almost as high a proportion of variance,  $r^2 = .86$ .

To summarize, a simple, but theoretically sound, model based on the parasitism hypothesis resolves close to 90% of the variation in the LBM rate of change. The regression analysis suggests that model (7.4) can be simplified by setting parameter  $h$  to 0, because this procedure does not decrease the percentage of variance explained by the parasitism model.

The regression analysis also yields estimates of parameters  $a = 2.5 \pm 1$  and  $w = 0.17 \pm 0.02$  [means  $\pm$  SE estimated by fitting equation (7.5) to the data]. We have already estimated  $R_0$  and  $K$  above ( $R_0 = 2.5 \pm 0.2$  and  $K = 250 \pm 50$ ). Simulating the model within these parameter ranges shows that it produces high-amplitude oscillations for all reasonable values of parameters. For the median parameter values, however, the period is a bit short—7 years compared with the observed 8–9-year period. It is necessary to reduce  $w$  to 0.15 in order to lengthen the period to 8 years, and to 0.13 (2 SE from the point estimate and still within the realm of the possible) in order to lengthen the period further to 9 years. The model output matches well other characteristics of the data of that period, such as the amplitude and the cross-correlation function between LBM density and the proportion parasitized. In particular, the proportion parasitized peaks on average 2 years after the LBM peak, similarly to the pattern observed in the data.

## 7.5 Putting It All Together: A Parasitism-Quality Model

The preceding analyses of data and models suggest an interesting conclusion. On the one hand, the model with plant quality as the only mechanism driving second-order oscillation fails to match data patterns as well as the LBM–parasitoid model. On the other hand, short-term experiments suggest that there is a strong effect of changes in plant quality on LBM survival and reproduction. This raises an important question: Should we be satisfied with the parasitism-only explanation of the LBM dynamics, or do we instead need a multifactorial model, combining plant quality and parasitism? One way to address this issue is to investigate the dynamics predicted by the multifactorial model, and contrast its ability to match empirical patterns with the two simpler alternatives.

Combining the effects of plant quality and parasitism is quite straightforward, now that we have invested so much effort in building models for each component separately. The equations of this parasitism–quality model are:

$$Q_{t+1} = (1 - \alpha) + aQ_t - cN_t/(d + N_t), \tag{7.6a}$$

$$N_{t+1} = N_t \exp\{R_0[1 - \exp(Q_t/\delta)] - R_0N_t/K - aP_t/(1 + awP_t)\} \tag{7.6b}$$

$$P_{t+1} = N_t S_t, \quad \text{where } S_t = 1 - \exp[-aP_t/(1 + awP_t)]. \tag{7.6c}$$

Parameter estimates are the same as above. Simulating the model within these parameter ranges, we find that the model does very well for parameters at their median values (or very near to them). In particular, with slight modifications (specifically,  $R_0 = 2.3$ ,  $c = 0.9$ , and  $d = 100$ ; note that with each of these modifications we are staying within 1 SE of the median estimates), the model output matches the data patterns very well (figure 7.4). Quantitative measures of the observed time series pattern (periodicity, amplitude, and cross-correlations between LBM and parasitism or quality index) are also closely matched by the model-generated trajectories.

### 7.6 Discussion

Our theoretical and empirical analyses suggest the following conclusions. First, our reanalysis supports the previous efforts modeling the LBM–plant food quality interaction. A simple model with biologically plausible parameters (in fact, estimates based on experimental data) predicts population dynamics that are quite similar to the observed pattern (including matching such quantitative characteristics of observed fluctuations as order, periodicity, and amplitude). However, the plant quality hypothesis has weaknesses: Although the model predicts that there should be a strong feedback effect

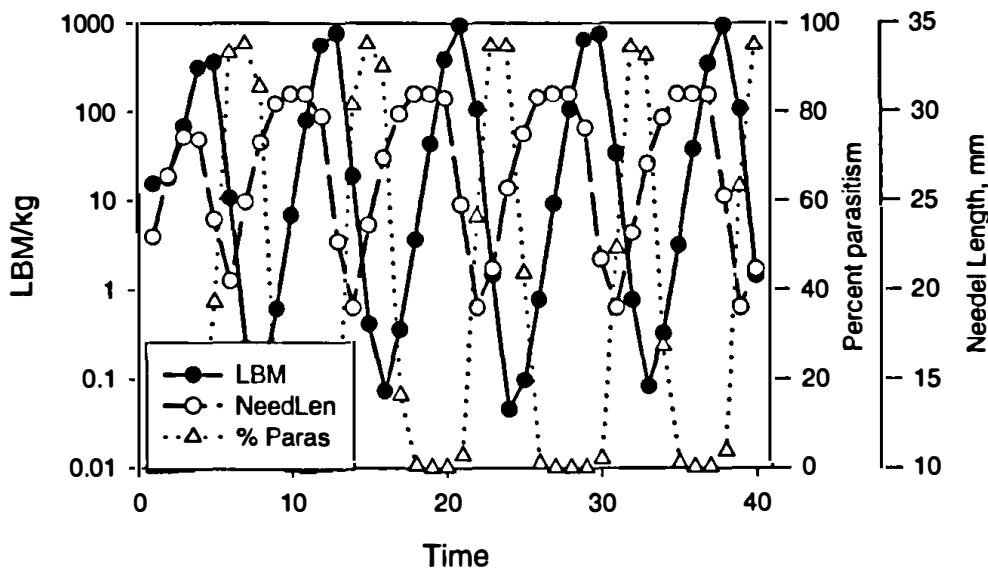


Figure 7.4 Dynamics of LBM density, food quality, and parasitism rate predicted by the tritrophic model.

from plant quality to the LBM rate of change, analysis of real data does not reveal it. Additionally, lack of quality decline during the last recorded cyclic collapse is hard to understand if plant quality is the main factor driving LBM oscillations.

Second, a model based on the parasitism hypothesis with empirical estimates of parameters is capable of mimicking the observed LBM dynamics. In this it is similar to the plant quality hypothesis. Unlike the rival explanation, however, the parasitism hypothesis is supported by regression analyses of the feedback relationship from parasitism rates to the LBM rate of change. However, to match the observed period, we have to “stretch” some parameter values. Additionally, the experimentally observed effect of plant quality is rather strong (at least 10-fold change in  $\lambda$  as a function of quality). It is generally a bad modeling approach to add a mechanism to the model simply because “it is there.” Having such a strong numerical effect, however, makes one wonder whether the explanation of LBM cycles should leave it out.

Finally, a tritrophic model combining both hypotheses does the best job at matching the observed dynamics for biologically reasonable parameter values. We have, thus, an interesting situation. On epistemological grounds, the tritrophic hypothesis suffers because it is more complex than either of the plant quality or parasitism hypotheses. However, while both simple hypotheses can reproduce the fluctuation pattern of the primary data (LBM density), they fail in some other ways, as discussed above. Therefore, given the present state of knowledge, we conclude that the currently best-supported hypothesis is that LBM cycles are driven by *both* parasitism and plant quality interactions.

If this conclusion is correct, then parasitoids and plant quality act as a *dynamical complex*. This means that if, for whatever reason, one factor fails to cause a prolonged LBM density collapse after peak, then the other factor ensures that the cycle will continue, as apparently happened in the early 1990s. Assuming that this example of multiple causation is not unique to larch budmoth, it raises an important methodological issue. It is possible that by experimentally manipulating each factor we may “prove” that it is not the “necessary condition” for sustained cycles, leading to an erroneous rejection of both hypotheses. Only an experiment that manipulates both factors together (ideally coupled with a modeling program) can, in principle, resolve the question of what mechanisms drive population oscillations (see, e.g., chapter 4).

## REFERENCES

- Anderson, R. M. and R. M. May. 1980. Infectious diseases and population cycles of forest insects. *Science* 210: 658–661.
- Baltensweiler, W. 1958. Zur Kenntniss der Parasiten des Grauen Larchenwichtlers (*Zeiraphera griseana* Hubner) in Oberengadin. *Mitt. Eidgen. Anst. forst. Versuch.* 34: 399–477.

- Baltensweiler, W. 1977. Colour-polymorphism and dynamics of larch budmoth populations (*Zeiraphera diniana* Gn., Lep. Tortricidae). *Mitt. Schweiz. Entomol. Ges.* 50: 15–23.
- Baltensweiler, W. 1993a. A contribution to the explanation of the larch bud moth cycle, the polymorphic fitness hypothesis. *Oecologia* 93: 251–255.
- Baltensweiler, W. 1993b. Why the larch bud-moth cycle collapsed in the subalpine larch–cembran pine forests in the year 1990 for the first time since 1850. *Oecologia* 94: 62–66.
- Baltensweiler, W. and A. Fischlin. 1988. The larch budmoth in the Alps. In A. A. Berryman (Ed.) *Dynamics of forest insect populations: patterns, causes, implications*. Plenum Press, New York, pp. 331–351.
- Benz, G. 1974. Negative Rückkopplung durch Raum- und Nahrungskonkurrenz sowie zyklische Veränderung der Nahrungsgrundlage als Regelsprinzip in der Populationsdynamik des Grauen Lärchenwicklers, *Zeiraphera diniana* (Guenee) (Lep. Tortricidae). *Z. Angew. Entomol.* 76: 196–228.
- Delucchi, V. 1982. Parasitoids and hyperparasitoids of *Zeiraphera diniana* (Lep. Tortricidae) and their role in population control in outbreak areas. *Entomophaga* 27: 77–92.
- Edelstein-Keshet, L. and M. D. Rausher. 1989. The effects of inducible plant defenses on herbivore populations. I. Mobile herbivores in continuous time. *Am. Nat.* 133: 787–810.
- Fischlin, A. 1982. *Analyse eines wald-insekten-systems: der subalpine Lärchenarvenwald und der graue Lärchenwickler Zeiraphera diniana Gn. (Lep. Tortricidae)*. Ph.D. thesis no. 6977, ETH, Zurich.
- Fischlin, A. and W. Baltensweiler. 1979. Systems analysis of the larch bud moth system. Part 1. the larch–larch bud moth relationship. *Mitt. Schweiz. Entomol. Ges.* 52: 273–289.
- Ginzburg, L. R. and D. E. Taneyhill. 1994. Population cycles of forest Lepidoptera: a maternal effect hypothesis. *J. Anim. Ecol.* 63: 79–92.
- Omlin, F. X. 1977. *Zur populationsdynamischen Wirkung der durch Raupenfrass und Dungung veränderten Nahrungsbasis auf den Grauen Lärchenwickler Zeiraphera diniana Gn. (Lep. Tortricidae)*. Ph.D. thesis no. 6064, ETH, Zurich.
- Turchin, P. 1990. Rarity of density dependence or population regulation with lags? *Nature* 344: 660–663.
- Turchin, P. 2002. *Complex population dynamics: a theoretical/empirical synthesis*. Princeton University Press, Princeton, N.J.
- Turchin, P. and A. D. Taylor. 1992. Complex dynamics in ecological time series. *Ecology* 73: 289–305.
- Turchin, P., S. P. Ellner, S. N. Wood, B. E. Kendall, W. W. Murdoch, A. Fischlin, J. Casas, E. McCauley, and C. J. Briggs. 2002. Dynamical effects of plant quality and parasitism on population cycles of larch budmoth. *Ecology* (accepted).