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Biology and Population Dynamics of the Common Pine Sawfly, *Diprion pini* L., in Russia

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I. Introduction

The common pine sawfly (*Diprion pini* L.) is one of the most serious pine pest insects in Russia, Ukraine, and Bielorussia. In Russia, its distribution comprises the European part (except northern regions) and southwest Siberia (Ilyinski and Tropin, 1965). Sawfly outbreaks occur mainly in the southern part of Russia (Rostov region), Ukraine, and Bielorussia, where the sawfly has two generations per year. During outbreaks, it causes severe defoliation of pines followed by retardation of tree growth and tree mortality (Kharlashina, 1984). Infestation of pines by secondary pests increases adverse effects of sawfly outbreaks.

Population ecology of *D. pini* was extensively studied in Western Europe (Eichhorn, 1977a,b,c, 1982; Dusaussoy and Geri, 1966; Geri and Goussard, 1984). Eichhorn (1977a) emphasized great flexibility of life cycle adaptations of this sawfly at different geographical locations; therefore, it is interesting to compare this information to studies of *D. pini* in Russia.

In this chapter, I present a review of the biology and population ecol-

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ogy of the common pine sawfly in Russia and discuss the role of different processes in its population dynamics. There is evidence that, at least in the Rostov region, parasitoids together with diapause mechanisms destabilize sawfly population dynamics and are responsible for its outbreak like pattern.

II. The Life Cycle and Diapause

In Russia, the common pine sawfly has a maximum of two generations per year. Females lay eggs into a split of a pine needle formed by the ovipositor. The female usually lays all the eggs in one cluster occupying about 10 adjacent needles. Larvae hatched from one egg cluster feed together and form a colony. Ultimate-instar larvae usually leave colonies and feed solitarily. When feeding is complete, they molt into eonymphs (prepupae), which spin cocoons either in the crown of trees or in the litter and soil. The place of cocooning depends on photoperiod: In long-day conditions eonymphs make cocoons in the crowns and develop without diapause, whereas in short-day conditions they spin cocoons in the litter or soil and go into diapause (Eichhorn, 1976). The next stage of the life cycle—a pronymph—differs from the eonymph by appearance of well-visible pupal eyes under the cuticula. There is no molt between the eonymph and pronymph stages. A pronymph pupates, and after a week or two an adult sawfly emerges from the cocoon. Adults do not feed and live only a few days.

The common pine sawfly hibernates as an eonymph in the cocoon. Some individuals hibernate as pronymphs. There are two waves of emergence of overwintered sawflies (1) at the end of April to the beginning of May and (2) at the end of July to the beginning of August (Fig. 15.1). More than half of the sawfly population remains in prolonged diapause. Sawflies emerging in the second wave are usually much more numerous than those emerging in the first wave (Avramenko, 1960; Sharov, 1982, 1983). The portion of population emerging in the first wave has two generations per year, whereas the portion emerging in the second wave has only one generation. In August and September, there is a mixture of sawflies of the first and second generations; therefore, the word *generation* may be confusing. In this case, I prefer to speak about two waves of development: one in spring and the other in fall. The wave of development is a set of synchronously developing organisms, no matter to what generation they belong (Sharov, 1984). The proportion of sawflies emerging in different waves differs considerably among years within one population (Eichhorn, 1977a, 1982). Individuals taken from one wave produce offspring that emerge in several waves. But the proportion of a population that has one generation, two generations, or prolonged diapause differs among geo-

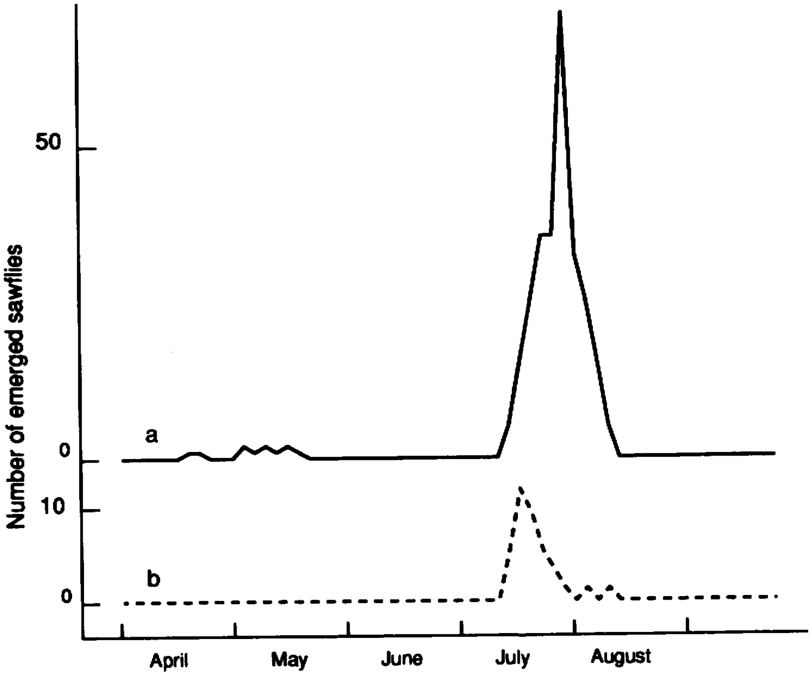

FIGURE 15.1 Seasonal pattern of *D. pini* L. emergence in 1978. (a) Hibernated generation. (b) Summer generation. Redrawn from Sharov (1983).

graphical populations and can be considered as an inherited trait (Eichhorn, 1977a, 1982).

Avramenko (1970) observed that the proportion of pronymphs among hibernating sawflies significantly correlated with the proportion of emergence in spring. He decided that pronymphs overwintered in the state of quiescence and all emerged in the first wave. This hypothesis corresponds well to the theory of Danilevskii (1965), that winter diapause breaks down very early—at the beginning or in the middle of winter—and after that insects remain in the state of quiescence.

Our results (Sharov and Safonkin, 1982) indicate that this hypothesis is only partially true. Sawfly cocoons used in the experiment were obtained by rearing larvae in screen bags in natural conditions in fall 1978, and then eonymphs were separated from pronymphs by dissecting cocoons. Dissected cocoons were closed and sealed with glue. After 6 months of chilling at 4°C, both eonymphs and pronymphs were transferred to different incubation conditions (temperatures of 12°C and 25°C and photoperiods of 14:10 and 18:06 hr L:D). Eonymphs reactivated only in the second wave in accordance with the hypothesis of Avramenko (1970), but not all pronymphs reactivated in the first wave; some of them reactivated only in the second wave synchronously with eonymphs (Fig. 15.2). Dissection of cocoons showed that between two waves of emergence, sawflies remained in the pronymph stage. This indicates that pronymphs

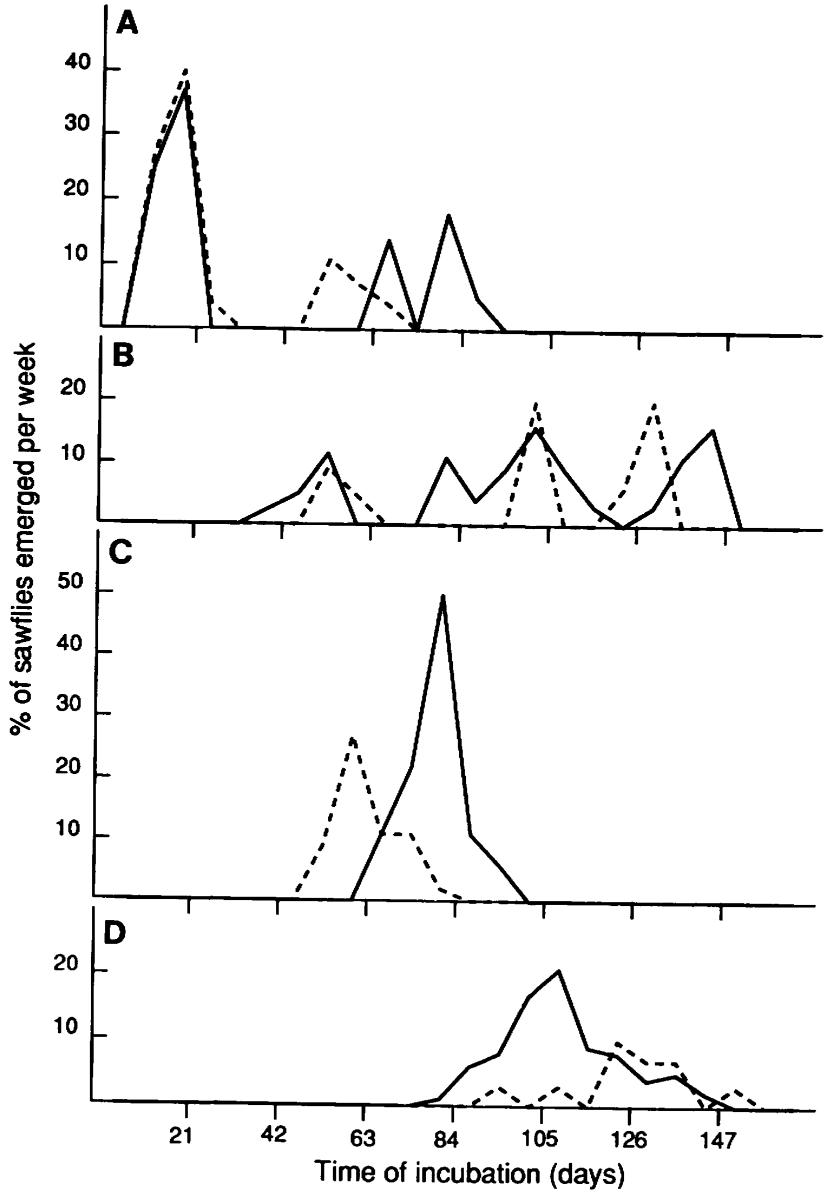

FIGURE 15.2 Percentage of emergence of *D. pini* L. in different incubation conditions after a 6-month diapause at 4°C. (A) Pronymph diapause, 25°C. (B) Pronymph diapause, 12°C. (C) Eonymph diapause, 25°C. (D) Eonymph diapause, 12°C. Photoperiods: 1 (—), 18:6 hr L:D, 2 (---), 14:10 hr L:D. Redrawn from Sharov (1980).

may diapause, but their diapause is not as strong as that of eonymphs. Pronymph diapause has already been observed in other sawfly species (Prebble, 1941; Novak, 1972) and is not unusual.

Another interesting finding is that the proportion of pronymphs reactivated in the first wave increased with temperature (Fig. 15.2 and Table

15.1). If some pronymphs were diapausing in winter and some were not, then the proportion of their emergence in the first wave would be the same at any incubation temperature. This assumption, however, contradicts our experiment. Thus, we suppose that all pronymphs were in diapause in winter; they reactivated only when being transferred to incubation conditions. The higher the incubation temperature, the greater proportion of pronymphs reactivated. Winter chilling does not cause reactivation itself; it only has sensibilization effect because, without a long period of chilling, no temperature change will cause reactivation. Thus, our study does not agree with Danilevskii's (1965) theory of diapause, but our data does correspond well to the new and more general theory of Zaslavski (1988), who introduced the term *sensibilization*.

Eonymph diapause is necessary for winter survival, but it may continue for up to 4 years (Eichhorn, 1977a). Thus, it may be useful for spreading of risk in variable environments. In the Rostov region of Russia, about 60% of the population has prolonged diapause (more than 1 year).

The proportion of eonymph reactivation (the second wave of emergence) depends on both temperature and photoperiod. At higher temperatures, more eonymphs are reactivated (Fig. 15.2 and Table 15.1). Short daylength decreases the proportion of emergence but shortens the time until adult emergence at 25°C (Fig. 15.2). The same effect of photoperiod on diapause duration is known for the European pine sawfly, *Neodiprion sertifer* Geoffr. (Sullivan and Wallace, 1965). It is obviously adaptive: If the summer is cold, then the date of sawfly emergence shifts toward autumn when days become short. This will cause a compensatory backward shift of emergence dates and reduce the number of emerging sawflies because a particular summer may not be favorable for larval development. We

TABLE 15.1 Reactivation Rate of the Common Pine Sawfly, *D. pini* L., in Different Incubation Conditions After a 6-Month Diapause at 4°C

	Incubation conditions			Reactivation rate (%)		
Diapausing stage	Temperature (°C)	Photoperiod (hr L:D)	Number of sawflies	First wave (±SE)	Second wave (±SE)	Prolonged diapause (%) (±SE)
Pronymph	25	18:6	35	63 ± 8	37 ± 8	0
Pronymph	25	14:10	35	71 ± 8	22 ± 7	7 ± 4
Pronymph	12	18:6	37	19 ± 7	81 ± 7	0
Pronymph	12	14:10	37	14 ± 6	46 ± 8	40 ± 8
Eonymph	25	18:6	19	0	100	0
Eonymph	25	14:10	83	0	59 ± 5	41 ± 5
Eonymph	12	18:6	73	0	82 ± 5	18 ± 5
Eonymph	12	14:10	29	0	34 ± 9	66 ± 9

Modified from Sharov and Safonkin (1982).

proposed a model of eonymph reactivation (Sharov and Safonkin, 1982) based on the theory of Zaslavski (1988).

According to Schwenke (1964), in cool summers larvae of the common pine sawfly largely stop feeding and developing and reamin in some form of diapause. Zavada (1969) also mentioned that in cool and wet summers sawflies that started their development in spring have only one long generation instead of two. In hot years, sawflies accumulate 500–600 degree-days during larval stage, whereas in cool years they require 1400 degree-days.

In 1978, we scheduled an experiment to check this information (Sharov and Safonkin, 1980). Sawflies were artificially reactivated in different dates of the season, and females were placed on pine branches in nature for oviposition. The number of larvae emerged from laid eggs, and their instars were visually checked at 3-day intervals. After the molt to the fifth instar, larvae were placed into screen bags hung on pine branches to prevent dispersion.

Individuals that hatched in May and June developed much faster than sawflies that hatched in July (Fig. 15.3). In the fall, the rate of sawfly development increased despite rather low temperature. Thus, fall cocooning dates appeared to be almost independent of the date of egg hatch. Therefore, our results confirmed the existence of larval diapause of *D. pini*.

The biological significance of this phenomenon is not clear. Apparently, it serves to synchronize fall cocooning and prevents the development of a second generation in cool years. Physiological mechanisms of this sort of diapause are not known. Larval diapause was not obtained in laboratory experiments with different temperatures and photoperiods (Eichhorn, 1977c; Dusaussoy and Geri, 1966). Diapause is probably induced by gradually decreasing photoperiods.

III. Parasitoids

The guild of egg parasitoids consists of four species, but only one species, *Chrysonotomyia ruforum* Krausse, is abundant (Sharov, 1983). The proportion of other parasitoid species is less than 1%.

Chrysonotomyia ruforum hibernates as an eonymph in host eggs in pine needles. Some needles with old sawfly eggs drop in autumn, but some remain in the crown. Sharov (1983) collected these needles in spring and reared adult parasitoids. To avoid autoparasitism, emerged parasitoids were removed from the cage. Two waves of emergence were observed, very similar to those of the host (Fig. 15.4). Only 8–22% of parasitoids emerged in spring, whereas the rest of the population emerged in July and August. Such two-wave emergence was not known previously, and the

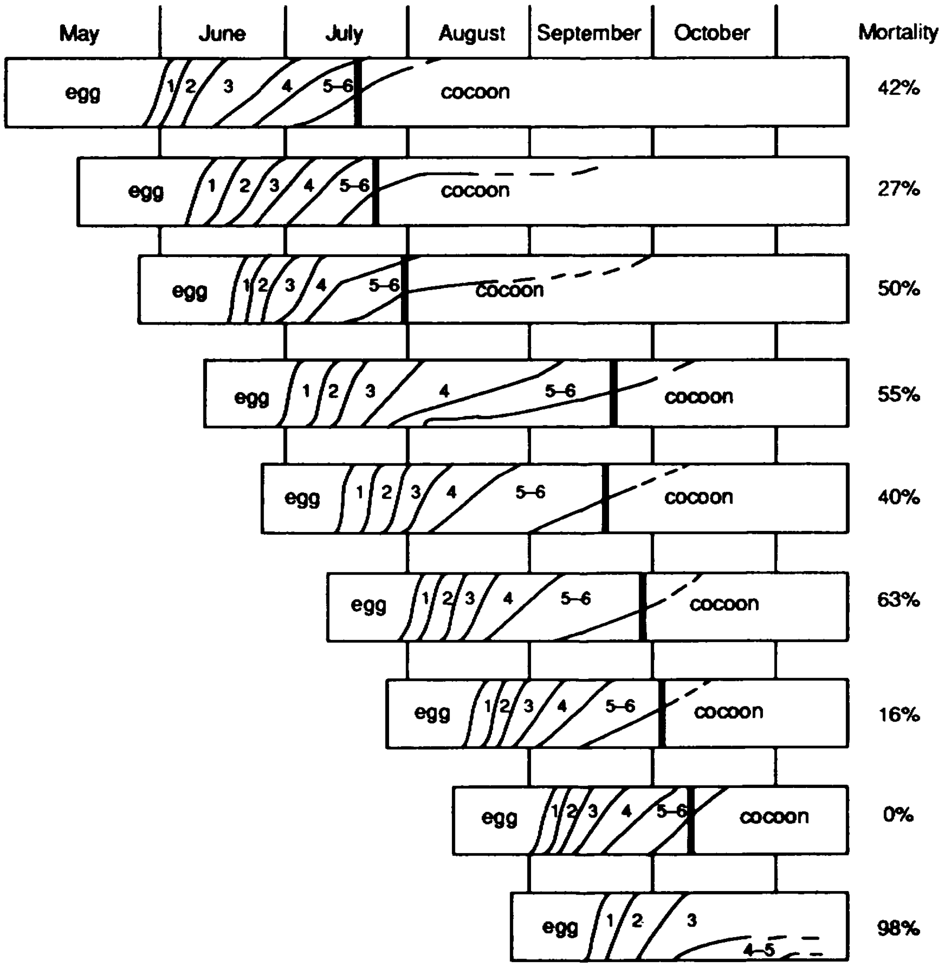

FIGURE 15.3 Development of *D. pini* L. in a natural experiment starting from eggs laid at different dates. Vertical bars indicate cocooning of 50% of sawflies. Redrawn from Sharov and Safonkin (1980).

second wave was originally considered a second generation (Zavada and Shvidenko, 1972).

The guild of larval parasitoids consists of two tachinid species (*Drino inconspicua* Meig. and *Diplostichus janithrix* Htg.) and two rare ichneumonid species (Sharov, 1983). In contrast, in Western Europe there are more larval ichneumonid parasitoids such as *Lamachus* spp. and *Olesicampe* spp. (Ecihhorn, 1977b). This is the main difference between parasitoid complexes of *D. pini* in Western and Eastern Europe.

The fly *D. inconspicua* is a polyphagous species that parasitizes various insect pests of pines (Herting, 1960). It has two generations per year and hibernates as a first-instar larva inside sawfly eonymphs. All overwintered individuals emerge in one wave in the end of May. *Diplostichus jan-*

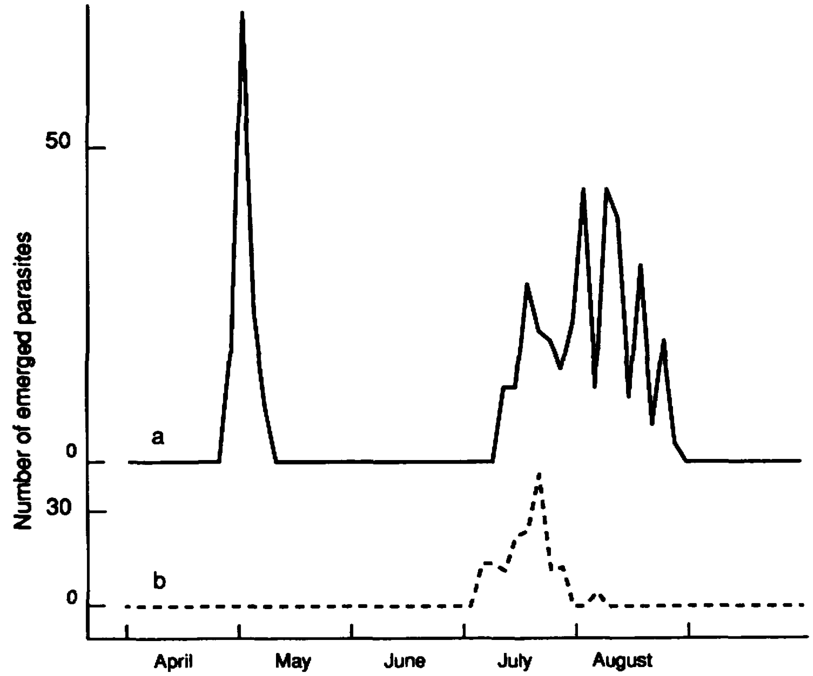

FIGURE 15.4 Seasonal pattern of *C. ruforum* Krausse emergence in 1978. (a) Hibernated generation. (b) Summer generation. Redrawn from Sharov (1983).

ithrix is a specialized parasitoid of *Diprion* (Herting, 1960). Preadult development takes about a month if there is no diapause. This parasitoid hibernates as a first-instar larve inside the sawfly eonymph. Ten to 15% of parasitoids emerged from the middle of May to the beginning of July and 50–73% in August to the beginning of September (Fig. 15.5), and the remaining 12–40% had prolonged diapause during the whole year.

Eichhorn (1977b) suggested that the termination of *D. janithrix* diapause is controlled by the host's hormonal system, because twice he observed reactivation of the parasite just after transition of the host from the eonymph to the pronymph stage. Sharov (1980) checked this phenomenon in a laboratory experiment in which parasites were provided with diapausing and nondiapausing sawfly eonymphs taken out of cocoons. Parasitized eonymphs were put back into cocoons, and the cocoons were then sealed with glue. The proportion of diapausing parasites was 0 on nondiapausing hosts and was 66% on diapausing hosts (Sharov, 1980). Thus, physiological states of the host and the parasitoid are obviously correlated. However, the physiological state of the host is not the only factor controlling parasitoid diapause because some parasitoid larvae continued their development even if the host remained in diapause.

The ichneumonid wasp *Exenterus oriolus* Htg. attacks sawfly eo-

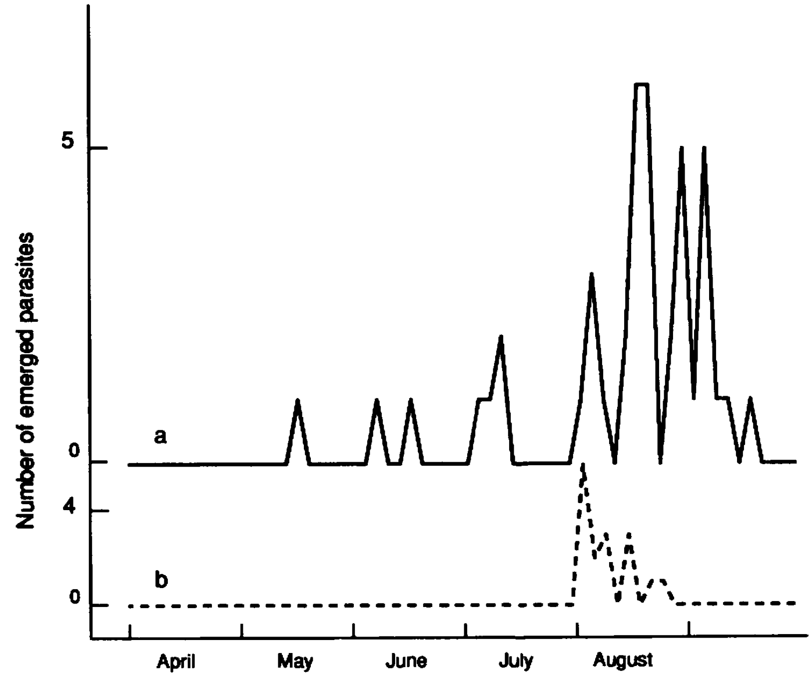

FIGURE 15.5 Seasonal pattern of *D. janithrix* Htg. emergence (pooled data from 1977 and 1978). (a) Hibernated generation. (b) Summer generation. Redrawn from Sharov (1983).

nymphs before they cocoon. The female attaches an egg to the eonymph integument, and this egg hatches after the host cocoons. The larvae are ectoparasitic. In the Rostov region, *E. oriolus* attacks only the common pine sawfly, although it is known as a parasite of some other diprionid species elsewhere (Oehlke, 1965).

Exenterus oriolus hibernates either as a second- to third-instar larva or as an eonymph in its own cocoon inside the host cocoon (Sharov, 1983). In the former case, the host is alive, and in the latter case it is already eaten. Parasitoid larvae exhibit a relatively weak diapause, which is stable only in cold wintertime. In spring they start growing, and many of them pupate and produce adults, but some of them can go into repeated diapause on the eonymph stage. This diapause is more stable and may continue for up to 3 years. *Exenterus oriolus* has two waves of emergence (1) the end of May to July and (2) August to September (Fig. 15.6). The proportion of parasitoid emergence in each wave strongly depends on the hibernating stage. Those that hibernated in the larval stage emerge mainly in the first wave, whereas the other parasitoids, which hibernated on the eonymph stage, emerge mainly in the second wave (Fig. 15.6).

Among cocoon parasitoids, three ichneumonid species predominate: *Pleolophus basizonus* Grav., *Oresbius subguttatus* Grav., and *Agrothereutes*

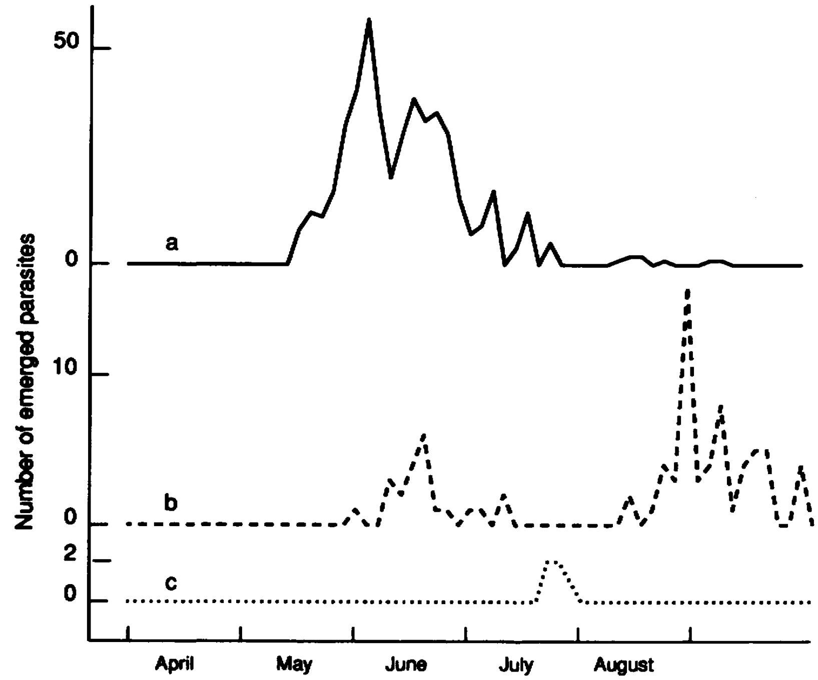

FIGURE 15.6 Seasonal pattern of *E. oriolus* Htg. emergence in 1977. (a) Parasitoids hibernated as larvae. (b) Parasitoids hibernated as eonymphs. (c) Summer generation. Redrawn from Sharov (1983).

adustus Grav. (Sharov, 1983). Female *P. basizonus* have short wings and search for hosts only in the litter; therefore, they rarely attack sawflies from the first wave of development, which spin their cocoons in tree crowns. *Oresbius subguttatus* search for hosts both in the litter and in the crown, whereas *A. adustus* prefer host cocoons in the crown. Thus, these parasitoids attacking the same stage of the host have differentiated their niches in space. *Pleolophus basizonus* and *O. subguttatus* have prolonged diapause and two waves of emergence, whereas *A. adustus* has only one wave of emergance (Fig.15.7) and no prolonged diapause.

Dynamics of these parasites are related to their strata preferences. During the outbreak, the first wave of development of the common pine sawfly is much greater than between outbreaks. Therefore, in outbreak periods there are many cocoons in tree crowns, and *A. adustus* becomes very abundant (Sharov, 1983). After the host population collapses, however, *A. adustus* almost disappears. *Pleolophus basizonus* densities are much more stable, because it can parasitize diapausing sawfly cocoons, which are numerous both in outbreak periods and in periods of population depression.

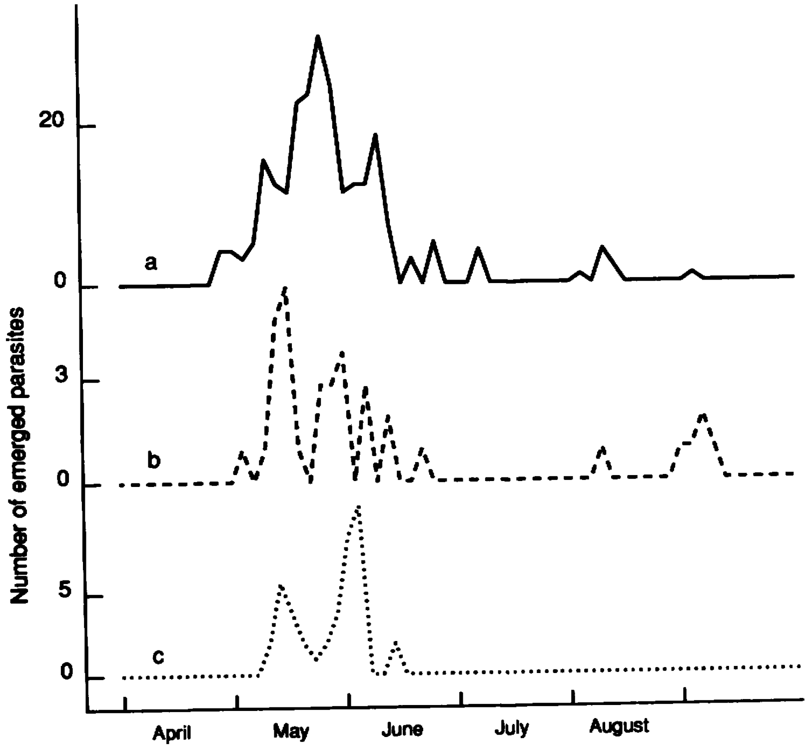

FIGURE 15.7 Emergence of hibernated cocoon parasitoids of the common pine sawfly (pooled data from 1977 and 1978). (a) *Pleolophus bisizonus* Grav. (b) *Oresbius subguttatus* Grav. (c) *Agrothereutes adustus* Grav. Redrawn from Sharov (1983).

IV. Population Dynamics of *Diprion pini* L.

In the steppe zone of the European part of Russia, the population dynamics of the common pine sawfly are pulse-eruptive, according to the classification of Isaev *et al.* (1984). Outbreaks typically occur after hot and dry summers within 3–6-year intervals (Kharlashina, 1984). Apparently, the primary trigger mechanism is linked with diapause regulation. According to Sharov and Safonkin (1982), proportion of reactivation increases with temperature. Thus, in hot summer greater reactivation is expected in the second wave. Unfortunately, there are no direct observations to support this hypothesis.

An outbreak is always accompanied by an increased proportion of sawfly reactivation in spring in the year following the drought (Ryvkin, 1963). This is the result of increased proportion of pronymphs among hibernating sawflies. The mechanism enhancing the proportion of hibernating pronymphs after drought is not clear. It may be the effect of the cocooning date (Zavada, 1969; Avramenko, 1970) or of the quality of the host plant.

In the year following the outbreak, the majority of sawflies remain in prolonged diapause. In spring, there is usually no emergence at all (Avramenko, 1960; Sharov, 1982). Diapause after an outbreak is very important for the population because almost all sawflies emerging in that year are killed by parasitoids, which are numerous (Avramenko, 1970).

Sharov (1980, 1987) studied populations of *D. pini* in the Rostov region, where great damage occurs due to sawfly outbreaks, Following an outbreak in 1976, my observations continued from spring 1977 to summer 1979. Sawfly cocoons spun in 1976 were analyzed as well. Proportion of parasitism was estimated without accounting for sawflies that died due to predation or disease, because whether or not they were parasitized previously was not known.

In 1977, just after the outbreak, the first wave of sawfly development was absent in the majority of locations, and it was impossible to find eggs. In the fall of the same year, the number of egg parasitoids was extremely high: On one egg cluster, there were sometimes more than 30 parasitoid females. Parasitization rate in the second wave of development was about 90% (Fig. 15.8B). Very high egg parasitism during the *D. pini* outbreak was also observed in Bielorussia (Ryvkin, 1963) and near Don River (Avramenko, 1960). As a result, a decreased number of sawfly larvae emerged from each egg cluster, and the colony size was small. The common pine sawfly has a group effect: Survival of larvae increases with the size of the colony (Sharov, 1988). According to my estimation, interaction of this effect with high egg parasitism will result in about 30% of additional mortality.

In subsequent years, egg parasitism declined at least in the second wave of development (Fig. 15.8). In general, egg mortality is greater in the second than in the first wave of development (Fig. 15.8).

Eonymph mortality due to parasitism was relatively low during the outbreak (in 1976) in the first wave of development (Fig. 15.9). This apparently indicates that sawflies were released from parasitoid regulation, but in the second wave of development in the same year, parasitism was very high—it was the start of population collapse. In spring 1977, there were plenty of parasitoids and only a few sawfly larvae, so the parasitism in the first wave of development was very high, but until autumn the number of parasitoids was sufficiently reduced because they had few hosts previously. Therefore, the eonymph mortality due to parasitism in the second wave of development appeared to be relatively low (Fig. 15.9). In 1978 the situation remained the same as in 1977, but in 1979, in several locations, parasitism in the first wave of development significantly decreased (Fig. 15.9). That summer was dry and hot, and this may have triggered a new

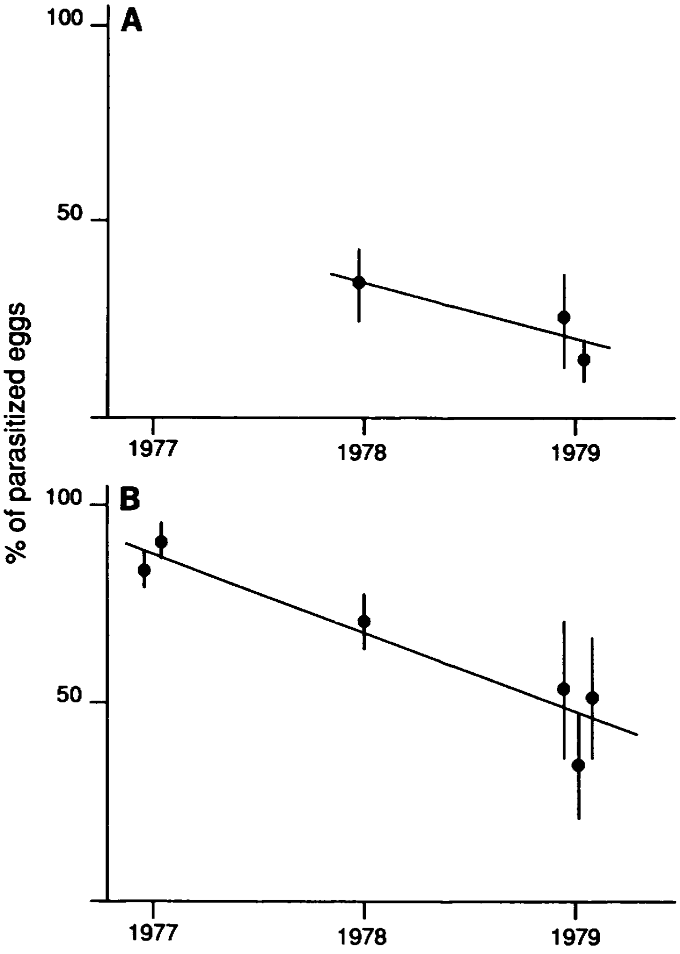

FIGURE 15.8 *Diprion pini* L. egg mortality due to parasitoids in 1977–1979. (A) First wave of development. (B) Second wave of development. Vertical lines indicate confidence intervals. $P = 0.05$. Redrawn from Sharov (1987).

outbreak in 1980. The outbreak possibly started at locations with reduced parasitism.

Eonymph mortality due to parasitism is usually greater in the first wave of development than in the second wave during the previous year. Thus, sawflies from the first wave of development died mainly due to larval and eonymph parasitism, whereas the second wave was affected mainly by egg parasitism. This can be explained on the basis of parasitoid phenology. Egg parasitoids emerged mainly in the fall (Fig. 15.4), whereas larval and eonymphal parasitoids emerged mainly in the spring (Figs. 15.6 and 15.7). Only *D. janithrix* (Fig. 15.5) and those *E. oriolus* that hibernated as eonymphs (Fig. 15.6b) had a significant wave of emergence in the fall,

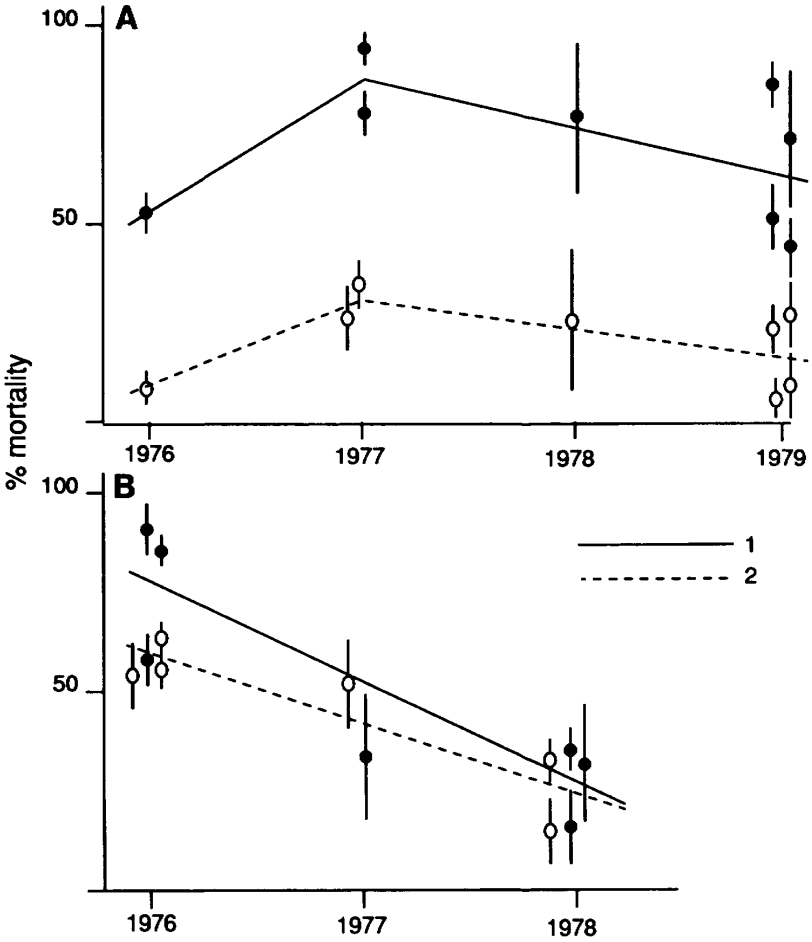

FIGURE 15.9 *Diprion pini* L. eonymph mortality due to parasitoids (—) and diseases (---) in 1976–1979. (A) First wave of development. (B) Second wave of development. Vertical lines indicate confidence intervals. $P = 0.05$. Solid circles correspond to solid line, and open circles correspond to dashed line. Cocoons that died due to diseases were not accounted for in the estimation of parasitism rate. Redrawn from Sharov (1987).

but these parasitoids were not numerous. The majority of *E. oriolus* overwintered as larvae, not eonymphs.

Dynamics of sawfly eonymph mortality due to diseases had the same pattern as mortality due to parasitism (Fig. 15.9). Cocoons of the second wave of development had greater mortality due to diseases than did cocoons of the first wave of development. The former are located in litter, whereas the latter are in tree crowns, where humidity is lower and, thus, the risk of becoming infected by fungus is less than in the litter. *Diprion pini* has no known viral pathogens.

The proportion of females in the sawfly population was as high as 64% during the outbreak in the first wave of development (Fig. 15.10). In 1977,

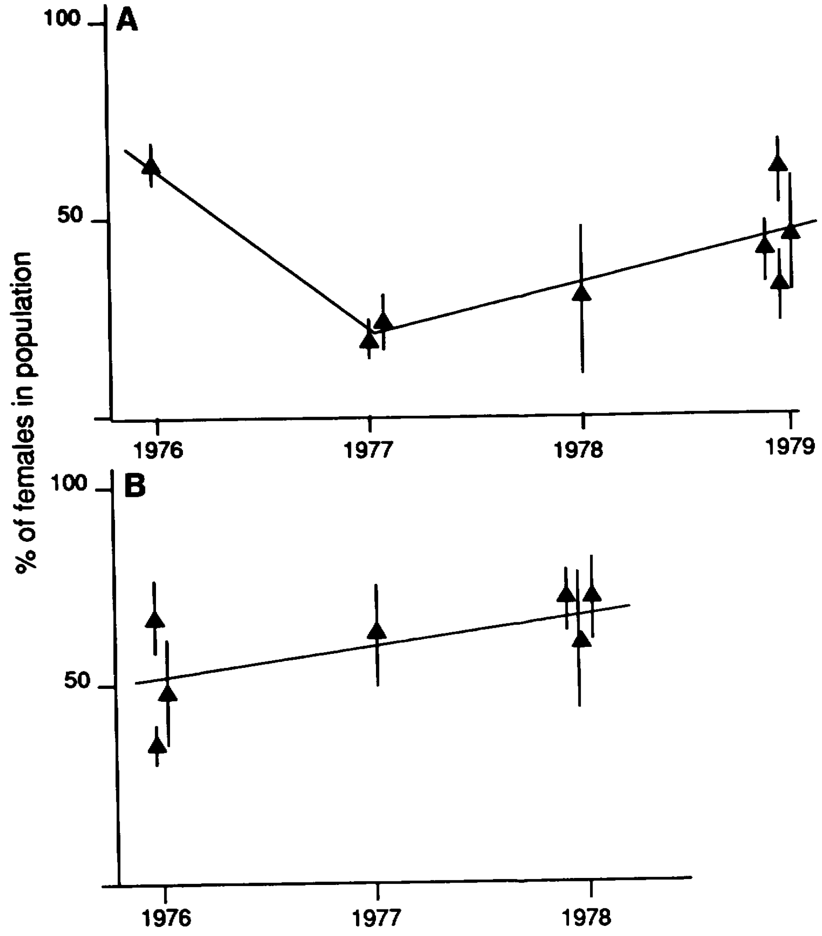

FIGURE 15.10 Proportion of females in the *D. pini* L. population in 1976–1979. (A) First wave of development. (B) Second wave of development. Vertical lines indicate confidence intervals. $P = 0.05$. Redrawn from Sharov (1987).

it decreased to 20–25%. Apparently, the number of females was reduced by disease because they have an additional instar, giving them more opportunity to become infected than males. In the second wave of development, the proportion of females was low in 1976 because the population collapse had already started. In subsequent years after the collapse of the outbreak, there was a trend of increase in the proportion of females in the population (Fig. 15.10), but it was not statistically significant in all locations. The proportion of females is usually lower in the first wave of development than in the second wave of the previous year (Fig. 15.10).

No significant change in sawfly fecundity was detected. In the second wave of development, egg clusters had on average 110–120 eggs (Sharov, 1980). In 1981–1983 in the same area, egg clusters were of similar size; 120–130 eggs (Kharlashina, 1984).

There are many common features of sawfly outbreaks in Russia and in Western and central Europe. Mass reactivation of sawflies and escape from parasitoids are the main factors releasing population density (Geri and Goussard, 1984). Outbreaks collapse mainly due to egg parasitism (Thalenhorst, 1953; Eichhorn, 1982). According to our data, these conclusions can be extrapolated to the European part of Russia. The outbreak frequency differs among geographical regions. In Finland intervals between outbreaks are 3–6 years (Kangas, 1963), whereas in France they are significantly greater, 18–27 years (Grison and Jacquiot, 1964; Geri and Goussard, 1984). The main difference in population biology of this pest in Eastern and Western Europe is the pattern of emergence of diapausing sawflies. In Western Europe, there are three waves of emergence (Eichhorn, 1977a) instead of two, observed in the European part of Russia, Ukraine, and Bielorussia. The additional wave occurs in June. In Russia, Ukraine, and Bielorussia the majority of the sawfly population emerges in July–August, whereas in Western Europe the most intensive flight is observed in June.

Zavada and Shvidenko (1972) developed a regression model for predicting common pine sawfly densities in the second wave of development, based on first wave density, egg mortality due to parasitoids, foliage quality, and weather. This model is good for planning control measures against the sawfly, but it does not help to understand the interaction of different ecological processes that drive the pest population. For this purpose, I developed a process-oriented simulation model (Sharov, 1986) based on experimental and field data obtained in the Rostov region (Sharov, 1983, 1987; Sharov and Safonkin, 1982). Some data were taken from the literature. The model simulates interaction of the sawfly with two guilds of parasitoids developing in eggs and eonymphs, respectively, and with the host plant (Fig. 15.11). All parasitoid species that develop in sawfly eonymphs are considered as eonymph parasitoids. They attack either larvae, free eonymphs, or cocoons. Diapause mechanisms and sawfly mortality due to predation and diseases were also considered. Weather was represented in the model by the mean air temperature in May–September for each year.

The model was validated using the records of population outbreaks in the Rostov region in 1956–1983. These data were not used for estimating model parameters. The model predicted five out of six real outbreaks (Sharov, 1986), so we consider this model to be valid enough on the qualitative level (unfortunately, no quantitative long-term data were available).

Analysis of the model showed that eruptive dynamics of the common pine sawfly was caused mainly by parasitoids, diapause mechansims, and, especially, the interaction of these factors (Sharov, 1991). The diapause is responsible for keeping the greater part of the population nonactive until drought and then inundating the forest with pests. Parasitoids cannot

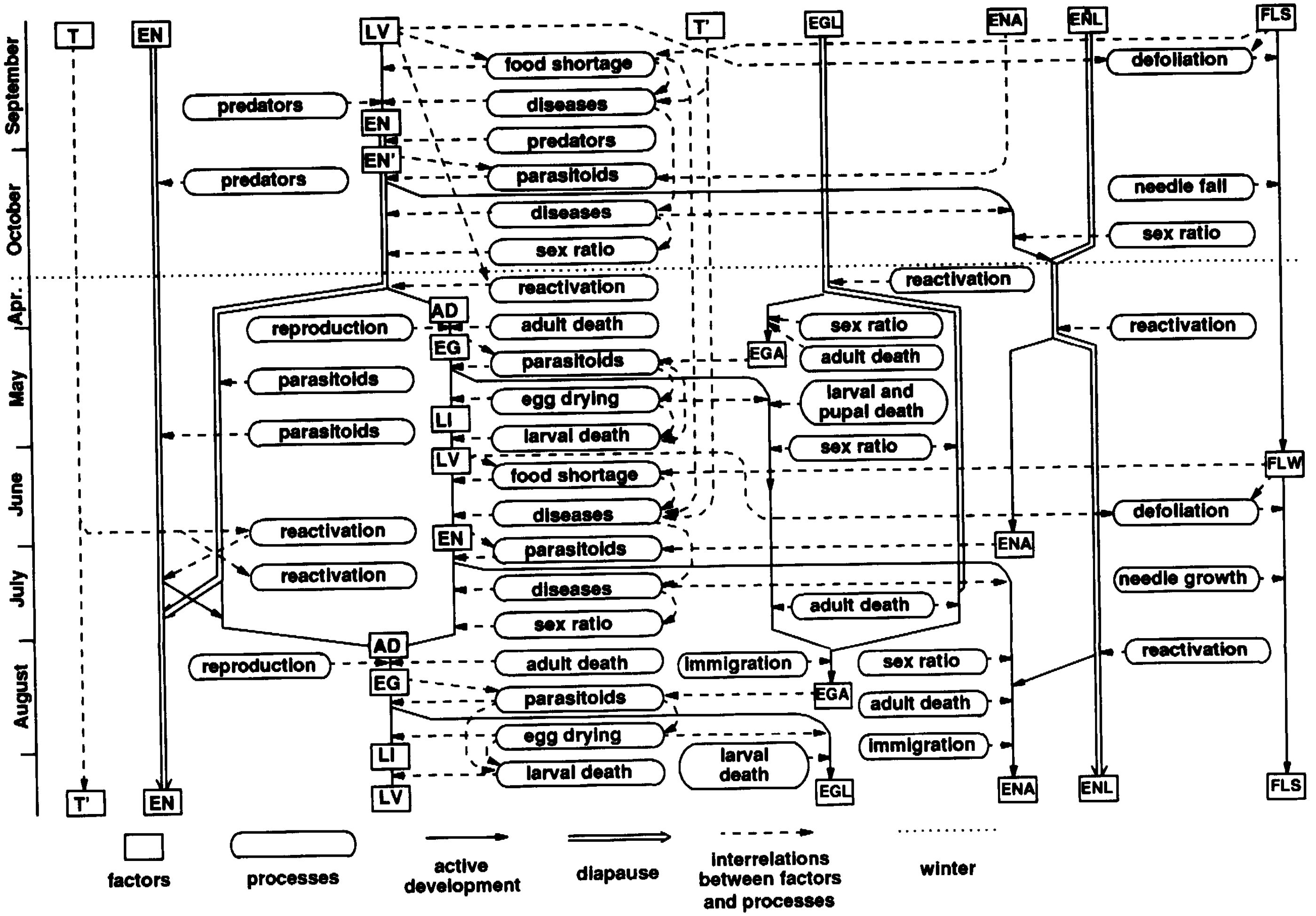

FIGURE 15.11 Scheme of the simulation model of the common pine sawfly. Density of populations: AD, sawfly adults; EG, sawfly eggs; EGA, adults of egg parasitoids; EGL, larvae of egg parasitoids; EN and EN′, sawfly eonymphs before and after their death, respectively, due to predation; ENA, adults of eonymph parasitoids; ENL, larvae of eonymph parasitoids; FLW and FLS, foliage biomass in winter and summer, respectively; LI and LV, sawfly larvae of the first and fifth instars, respectively; T and T′, air temperature in May–September in the current and previous years, respectively. From Sharov (1992).

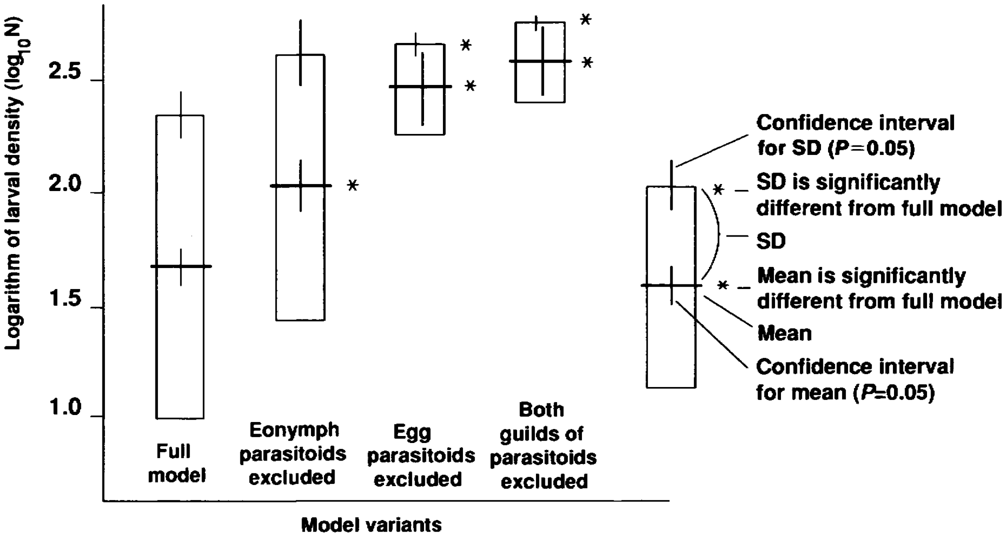

FIGURE 15.12 Consequences of parasitoid exclusion from the life system of the common pine sawfly (based on simulation). Mean values and standard deviations (SD) of log-transformed sawfly larval density in the second wave of development (per 1 m^2) characterize time series generated by the simulation model. Redrawn from Sharov (1991).

keep the pest population at the low-density level because their numbers have been sufficiently reduced during the multiyear host diapause. At the end of an outbreak, however, they are strong enough to suppress the sawfly population. Therefore, parasitoids destabilize the host population because the parasitism decreases at the beginning of an outbreak and rapidly increases at the end. The simulation model supports this hypothesis: Standard deviation of log-transformed population density becomes significantly greater after exclusion of egg parasitoids from the model (Fig. 15.12). This does not mean that parasitoids are harmful for the forest. They have double effect on the sawfly population: On one hand, they destabilize their dynamics and, on the other, they suppress the mean level of pest density (Fig. 15.12). The later effect is beneficial for the forest.

V. Summary of Life Cycle Adaptations

Parasitoids appear to be the most effective enemies of the common pine sawfly. The average predation rate on the cocoon stage is about 21% (Sharov, 1986). Larval mortality due to predation is unknown, but extrapolation of comparable data for the European pine sawfly (Sergeeva, 1978) suggests that it should be approximately the same as on the cocoon stage. Diseases cause extensive mortality only on the cocoon stage in the second wave of development, whereas the rate of parasitism is high in both waves of development, not only on the eonymph stage but on the egg stage as well.

Sawfly emergence in the second wave may be considered as a strategy to avoid parasitism. In late fall, larval and eonymph parasitoids are less numerous and, possibly, less active due to lower temperatures than in summer. Thus, it may be advantageous for the sawfly to shift emergence as late as possible.

Synchronization of larval development and cocooning are important in reducing the period of time when sawflies are available to predators and parasitoids attacking free eonymphs (*Exenterus* spp.). Larval diapause and photoperiod-dependent reactivation of eonymphs in the second wave improve synchronization of sawfly development.

Another mechanism of avoiding parasitism is prolonged diapause. Semevskii and Semenov (1982) showed that prolonged diapause is good for spreading of risk and reducing average density-independent mortality. Obviously, prolonged diapause will help to reduce average density-dependent mortality such as parasitism. In this case, the diapause must also be density-dependent: It must increase after outbreaks. A mathematical model is necessary to support this hypothesis.

Host adaptations are often followed by parasitoid counter-adaptations (the concept of coevolution). Common pine sawfly parasitoids show many such examples. Many parasitoids have developed the second wave of emergence to improve their coincidence with the host. *Chrysonotomyia ruforum* is the most well adapted to the seasonal cycle of the host (Sharov, 1982). This is the main reason for its great efficiency in suppressing sawfly populations. Several parasitoid species (*E. oriolus, D. janithrix,* and others) have prolonged diapause, which allows them to survive the years with a low proportion of host reactivation. Unfortunately, parasitoid counter-adaptations are not sufficient: *C. ruforum* has no prolonged diapause (more than 1 year), whereas many other species of parasitoids emerge mainly in the spring and, thus, the sawfly can escape from its natural enemies.

Thus, diapause regulation and parasitoids, the main factors of *D. pini* population dynamics, are links in one evolutionary chain. Together with weather instability (periodic droughts), they produce disastrous outbreaks of this pest.

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References

Avramenko, I. D. (1960). Needle-eating pests in forests of Kazansko-Veshenski sand region and their control. Thesis of the dissertation for degree of Candidate of Biological Sciences, Khrakovski Agric. Inst. Kharkov. (In Russian.)

Avramenko, I. D. (1970). Diapause and its significance in fluctuation of numbers of the pine sawfly. *Trans. Kharkovski Agric. Inst.* **138,** 109–121. (In Russian.)

Danilevskii, A. S. (1965). Photoperiodism and seasonal development of insects. Oliver & Boyd, Edinburgh and London.

Dusaussoy, G., and Geri, C. (1966). Étude d'une population de *Diprion pini* L. (Hym. Symphytes) en foret de Fontainebleau. I. Données biologiques sur *Diprion pini* et sur les principaux parasites. *Ann. Soc. Ent. Fr. (N.S.)* **2,** 503–534.

Eichhorn, O. (1976). Dauerzucht von *Diprion pini* L. (Hym.: Diprionidae) im Laboratorium unter Berucksichtigung der Fotoperiode. *Anz. Schaedlingskd. Pflanz Umweltschutz* **49** (3), 38–41.

Eichhorn, O. (1977a) Autökologische Untersuchungen an Populationen der gemeinen Kiefern-Buschhornblattwespe *Diprion pini* (L.) (Hym.: Diprionidae). I. Herkunftsbedingte Unterschiede im Schlüpfverlauf und Diapauseverhalten. *Z. Angew. Entomol.* **82,** 395–414.

Eichhorn, O. (1977b). Autökologische Untersuchungen an Populationen der gemeinen Kiefern-Buschhornblattwespe *Diprion pini* (L.) (Hym.: Diprionidae). II. Zur Kenntnis der Larvenparasiten und ihrer Synchronization mit der Wirt. *Z. Angew. Entomol.* **83,** 15–36.

Eichhorn, O. (1977c). Autökologische Untersuchungen an Populationen der gemeinen Kiefern-Buschhornblattwespe *Diprion pini* (L.))Hym.: Diprionidae). III. Laborzuchten. *Z. Angew. Entomol.* **84,** 264–282.

Eichhorn, O. (1982). Untersuchungen zur Ökologie der gemeinen Kiefern-Buschhornblattwespe *Diprion pini* (L.) (Hym., Diprionidae). VII. Populationsdynamische Faktoren. *Z. Angew. Entomol.* **94,** 271–300.

Geri, C., and Goussard, F. (1984). Evolution d'une nouvelle gradation de lophyre de pin (*Diprion pini* L.) dans le sud du Bassin parisien. I. Développement de la gradation jusqu'en 1982 et relation avec les facteurs de milieu. *Ann. Sci. For.* **41,** 375–404.

Grison, P., and Jacout, C. (1964). Observations sur une invasion de *Diprion pini* L. en forêt de Fontainebleau. *C.R. Acad. Agric. Fr.* **50,** 998–1006.

Herting, B. (1960). "Biologie der westpaläarktischen Raupenfligen *Dipt. Tachinidae*." Verlag Paul Parey, Berlin.

Isaev, A. S., Khlebopros, R. G., Nedorezov, L. V., Kondakov, U. P., and Kiselev, V. V. (1984). "Dynamics of Forest Insect Numbers." Nauka, Novosibirsk. (In Russian.)

Ilyinski, A. I., and Tropin, I. V. (eds.). (1965). "Monitoring, Registration and Prediction of Mass Reproductions of Needle- and Foliage-Eating Insects in the Forests of the USSR." Lesnaya promyshlennost, Moscow. (In Russian.)

Kangas, E. (1963). Über das schädliche Auftreten der *Diprion*—Arten (Hym., Diprionidae) in finnischen Kiefernbeständen in diesem Jahrhundert. *Z. Angew. Entomol.* **51,** 188–194.

Kharlashina, A. V. (1984). Ecology and silvicultural significance of the common pine sawfly (*Diprion pini* L.) in pine plantations in the steppe zone. Dissertation for degree of Candidate of Biological Sciences, Moscow Forest-Technical Inst. Moscow. (In Russian.)

Novak, V. Y. A. (1972). Hormonal base of insect diapause. In "Problems of Photoperiodism and Insect Diapause," Nauka, pp. 193–209. Nanka, Leningrad. (In Russian.)

Oehlke J. (1965). Die in europäischen Kiefernbuschhornblattwespen (Diprionidae) parasitierenden Ichneumonidae. *Beitr. Entomol.* **15,** 791–879.

Prebble, M. L. (1941). The diapause and related phenomena in *Gilpinia polytoma* (Hartig) in eastern Canada. *Can. J. Res. (D)* **19** (10), 295–322.

Ryvkin, B. V. (1963). "Entomophages and Forest Protection." Gosizdat selskohozyaistvennoi literatury BSSR, Minsk. (In Russian.)

Schwenke, W. (1964). Grandzüge der Populationsdynamik und Berkämpfung der gemeinen Kiefernbuschhornblattwespe, *Diprion pini* L. *Z. Angew. Entomol.* **54,** 101–107.

Semevskii, F. N., and Semenov, S. M. (1982). "Mathematical Modeling of Ecological Processes." Gidrometeoizdat, Leningrad. (In Russian.)

Sergeeva, T. K. (1978). Predator efficiency as a function of prey availability (for European pine sawfly, *Neodiprion sertifer,* as an example). *Zool. Zh.* **57,** 56–63. (In Russian.)

Sharov, A. A. (1980). Coincidence of seasonal cycles of parasites of the common pine sawfly (*Diprion pini* L.) with the seasonal cycle of the host. Dissertation for degree of Candidate of Biological Sciences, Moscow State Univ. Moscow. (In Russian.)

Sharov, A. A. (1982). Regulative role of seasonal cycling in popluation dynamics. *Zool. Zh.* **61,** 1339–1350. (In Russian.)

Sharov, A. A. (1983). Parasitoid complex of the common pine sawfly (*Diprion pini* L.) in Rostov region. *Entomol. Obozr.* **62,** 302–313. (In Russian.)

Sharov, A. A. (1984). Method for description of insect seasonal cycles. *Ekologiya* **1,** 51–57. (In Russian.)

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

Sharov, A. A. (1987). On the role of parasitoids and diseases in population dynamics of common pine sawfly *Diprion pini* L. (Hymenoptera, Diprionidae) in the Rostov region. *Zool. Zh.* **66,** 66–74. (In Russian.)

Sharov, A. A. (1988). Group effect of the larvae of the common pine sawfly *Diprion pini* L. (Hymenoptera, Diprionidae). *Ekologiya* **4,** 89–91. (In Russian.)

Sharov, A. A. (1991). Integrating host, natural enemy, and other processes in population models of the pine sawfly. *In* "Forest Insect Guilds: Patterns of Interaction with Host Trees." (Y. N. Baranchikov, W. J. Mattson, F. P. Hain, and T. L. Payne, eds.), pp. 187–198. USDA For. Ser. Gen. Tech. Rep. NE-153.

Sharov, A. A. (1992). The life-system approach: A system paradigm in population ecology. *Oikos* **63,** 485–494.

Sharov, A. A., and Safonkin, A. F. (1980). Seasonal dynamics of development of eggs and larvae of the common pine sawfly *Diprion pini* L. (Hymenoptera, Ddiprionidae). *Entomol. Obozr.* **59,** 73–78. (In Russian.)

Sharov, A. A., and Safonkin, A. F. (1982). Spontaneous and inductive processes in reactivation of common pine sawfly *Diprion pini* (Hymenoptera, Diprionidae). *Zool. Zh.* **61,** 1171–1179. (In Russian.)

Sullivan, C. R., and Wallace, D. R. (1965). Photoperiodism in the development of the European pine sawfly, *Neodiprion sertifer* (Geoffr.). *Can. J. Zool.* **43,** 233–245.

Thalenhorst, W. (1953). Vergleichende Betrachtungen über den Massenwechsels der Kiefernbuschhornblattwespen. *Z. Angew. Entomol.* **35,** 168–182.

Zaslavski, V. A. (1988). "Insect Development, Photoperiodic and Temperature Control." Springer-Verlag, Berlin e.a.

Zavada, N. M. (1969). Pine sawflies (Tenthredinidae: Diprionini) in forests of Ukrainian Polesie and their control. Thesis of dissertation for degree of Candidate of Biological Sciences, Kiev. (In Russian.)

Zavada, N. M., and Shvidenko, A. Z. (1972). Mathematical modeling and forecasting of pine sawflies reproduction. *In* "Questions of Indicational Phenology and Phenological Forecasting," pp. 20–26. Leningrad. (In Russian.)