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REDUCTION OF THE NUMBERS OF *OPEROPHTHERA BRUMATA* (L.)  
OVER THE OUTBREAK AND POST-OUTBREAK PERIOD  
IN THE "GRABOWY" RESERVE OF THE KAMPINOS NATIONAL PARK\*

**ABSTRACT:** Reduction of *Operophtera brumata* (L.) in larval and pupal stages over the outbreak and post-outbreak period has been estimated. Reduction of larvae in tree crowns is quite considerable and is much higher after outbreak than in the year of an outbreak. Mortality of pupae due to parasites increased in successive years following the outbreak, whereas mortality caused by non-specialized predators – decreased. As the outbreak is coming to the end the reduction of the larval stage in tree crowns increased, whereas that of the pupal stage in soil – decreased.

**KEY WORDS:** Forest (Pino-Quercetum), *Operophtera brumata*, phytophagous pests, outbreak, oak defoliation, pest reduction, reduction factors.

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1. INTRODUCTION

Studies on the outbreaks of leaf-eating insects point to a considerable influence of abiotic conditions which also influence the reduction of pest numbers. Lower mean values of precipita-

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tion and higher mean annual temperatures create proper conditions for an outbreak of pests. Under such conditions the trees are weaker because of drought, and the changes in biochemical processes, such as intense accumulation of saccharides in the leaves, provide for the development of leaf-eating entomofauna (M e r k e r 1962).

In the case, when the pest is a larva of early spring species *Operophtera brumata* (L.), synchronized opening of buds and hatching of larvae according to the weather is also quite important. Larvae of *O. brumata* feed on leaf tissues of oak and hornbeam and on leaves of other species of deciduous trees, but show preference to oak as the development conditions are there the best. The better synchronized the hatching of larvae with the opening of oak buds the lower the mortality of first larval stages (V a r l e y and G r a d w e l l 1968). Extremely high mortality in the egg stage, caused by severe frost, may result in a considerable decrease of the population numbers (M o r a v s k a j a 1960).

Still, assuming that the winter mortality is a key factor for changes in population numbers, it is known that fluctuations of the numbers of pest population over many years may be affected by the density-dependent activities of predators and parasites. According to model elaborations of many years' empirical data on the systems host-parasite or prey-predator both the type of density-dependent reactions and their intensity are important resulting either in a stable or unstable pest population (V a r l e y and G r a d w e l l 1970).

Here, we have investigated the reduction of *O. brumata* in the stages of larvae and pupae, mainly due to predators and parasites, without considering the winter reduction for which the weather is mainly responsible.

## 2. AREA AND METHODS

Material on the abundance of developmental stages of *O. brumata* was obtained from the reserve "Grabowy" which is a mixed forest of the Pino-Quercetum association (detailed description of the area and methods used are given by K a c z m a r e k and W a s i l e w s k i 1977). The material was obtained by several methods: (1) larvae were caught by a catcher sack for sampling in tree crowns (between 1968 and 1973) and the data were used for estimations of fluctuations in the numbers of larvae in different years and over the season; (2) larvae grazing on oak and hornbeam were picked up in order to determine their infestation; (3) larvae ready to pupate, falling from trees to the forest floor, were taken from leaf-fall catchers of a surface area  $0.1 \text{ m}^2$ , thus providing direct information about the number of larvae falling per  $1 \text{ m}^2$  of forest floor in the years 1971–1973; (4) the emergence of imagines was recorded in October by 25 isolators ( $50 \times 50 \times 50 \text{ cm}$ ) made of nylon net framed in metal and distributed at random in the area investigated.

The larvae were counted, measured and weighed in vivo or after fixing them in alcohol (according to D u n g e r (1968) the weight of moist larvae fixed in alcohol is almost the same as of live ones). During the measurements the number of larvae with traces of infestation was recorded.

## 3. RESULTS

On the area examined an outbreak of *O. brumata* was observed in 1971 (Table I).

Under conditions examined, similarly as in England (V a r l e y 1970), the development cycle of *O. brumata* begins at the end of April or beginning of May. Out of the eggs, laid at the

base of buds, the larvae hatch, enter the buds and start grazing. The density of larvae on particular trees may differ considerably (Morris and Reeks 1954). But the basic differences are between the oak and hornbeam. In some years of observation the density on oak is higher (Tables I and II) and the development of larvae much quicker (Table II, Fig. 1). Only in the year of outbreak (1971) the fluctuations of numbers and development of larvae are similar on oak and hornbeam, probably due to the migration of larvae from oak to hornbeam when the oak is defoliated.

Table I. Maximum numbers of larvae of *Operophtera brumata* in samples from tree crowns of oak and hornbeam, in particular years (numbers of larvae per 100 leaves)

| Species  | 1968 | 1969 | 1970 | 1971  | 1973  |
|----------|------|------|------|-------|-------|
| Oak      | 3.91 | 7.80 | —    | 40.94 | 2.25  |
| Hornbeam | 0.51 | 1.28 | 3.16 | 17.06 | 2.20* |

\*Data calculated from material picked by hand from hornbeam buds.

Table II. Changes in density of larvae of *Operophtera brumata* in crowns of oak (A) and hornbeam (B) over the seasons in different years (numbers of larvae per 100 leaves)

| Years  | Dates of observations |           |           |
|--------|-----------------------|-----------|-----------|
|        | 3–4 May               | 10–16 May | 22–24 May |
| 1968 A | 3.91                  | 0.85      | 0.29      |
| 1968 B | 0.25                  | 0.35      | 0.51      |
| 1969 A | 1.41                  | 7.80      | 1.29      |
| 1969 B | 0.00                  | 0.91      | 1.28      |
| 1971 A | 12.80                 | 33.52     | 2.76      |
| 1971 B | 3.30                  | 17.06     | 4.35      |

The material allows to estimate the reduction of numbers of *O. brumata* over the larval period till they descend on the ground, and over the pupal stage — between the moment the larvae fall onto the ground and the emergence of imagines in late autumn.

The larval period is only 1/12 of the entire developmental cycle of *O. brumata*. Still, over that period this insect is mostly endangered by predators, and especially parasites. Longer larval development increases the mortality due to parasites. An analysis of infestation of larvae from tree crowns shows that the infestation increases together with the time of grazing: on May 17, 1971, on oak there was 6.9% and on hornbeam 7.5% of larvae attacked by parasites, whereas on May 24 — 8.6% and 14.0%, respectively. This shows that the percentage of larvae attacked by parasites is also higher on the hornbeam, where they develop longer than on oak. Despite the fact that 2,338 larvae were analysed, the differences, although statistically not significant, confirm the relation between infestation and the duration of larval period. The data on the contribution of attacked by parasites larvae falling on the forest floor are very convincing (Table III). The larvae that had fallen the last were the lighter ones which probably grazed on the hornbeam. Also Hassel (1968) has observed higher survival of larvae of *O. brumata* developing on the oak.

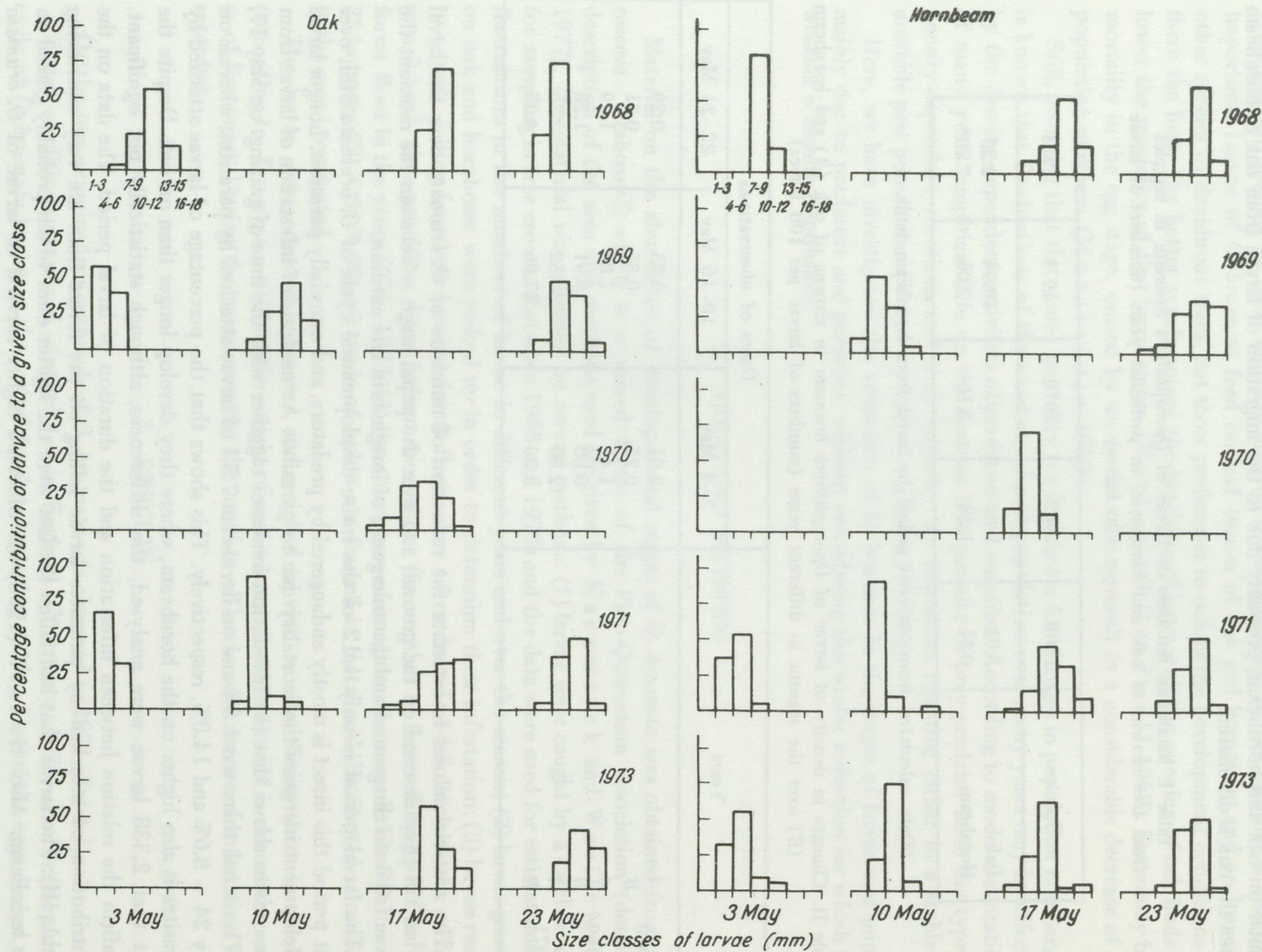


Fig. 1. Percentage of various size classes of larvae of *Operophtera brumata* over the season on the oak and hornbeam in different years

Table III. Infestation of larvae of *Operophtera brumata* falling on the forest floor

| Parameters                                 | 1971   |        | 1972   |        | 1973   |        |
|--|--------|--------|--------|--------|--------|--------|
|  | 22 May | 27 May | 26 May | 2 June | 30 May | 5 June |
| Number of analysed larvae                  | 317    | 199    | 70     | 9      | 49     | 14     |
| Weight of larvae (in mg)                   | 31.6   | 23.5   | 24.6   | 21.9   | 29.6   | 20.2   |
| Percentage of larvae attacked by parasites | 20     | 35     | 54     | 55     | 57     | 78     |
| Mean percentage of infested larvae         | 27.5   |        | 54.5   |        | 67.5   |        |

Although *O. brumata* is attacked by parasites in its larval stage, the individual mortality due to parasites occurs in the pupal stage. Therefore, the effect of parasites will be discussed when analysing the mortality of pupae.

Reduction of the numbers of larvae till the moment they descend on the forest floor has been estimated by comparing the maximum numbers of larvae in tree crowns with the number of larvae that fell on the forest floor. The latter was estimated according to larvae found in the leaf-fall catchers.

Table IV. Reduction of numbers of larvae of *Operophtera brumata* in crowns of oak (A) and hornbeam (B) in the year of outbreak (1971) and in the following years

| Parameters   | 1971  | 1972 | 1973 |
|--|-------|------|------|
| Maximum number of larvae per 1 m <sup>2</sup> of forest floor          |       |      |      |
| A  | 298.9 | —    | 18.9 |
| B  | 329.3 | —    | 52.4 |
| Total  | 628.2 | —    | 71.3 |
| Number of larvae that fell on the forest floor (per 1 m <sup>2</sup> ) | 172   | 47.2 | 1.2  |
| Reduction of larvae (per cent)   | 72.6  | —    | 98.3 |

The reduction of *O. brumata* in the larval stage is quite considerable (Table IV), but it is much higher in the year following the outbreak. Although we do not have direct data on the reduction of larvae in 1972, the increase of reduction since the outbreak is confirmed by the decrease in numbers of larvae falling into the leaf-fall catchers when comparing 1972 with 1971 and 1973 with 1972. In the first season following the outbreak the numbers of larvae in leaf-fall catchers decreased as compared to the previous year by 72.7%, and in the next season by 97.4%.

Data on the reduction of numbers of *O. brumata* in the pupal stage were obtained by comparing the number of larvae falling on the forest floor with the observed over successive years emergence of imagines. Simultaneously, the data on the infestation of larvae in particular years were used. Percentage of larvae attacked by parasites increased in successive years after

the outbreak (Table V) which is confirmed by data of Debach (1974). Total per cent of reduction of pupae increases in the first year after outbreak and decreases in the next year (Table V). At the same time, the mortality caused by parasites in the total reduction of pupae increases in successive years after the outbreak, whereas that due to other factors, probably non-specialized predators, decreases.

Table V. Reduction of *Operophtera brumata* in the pupal stage (in per cents)

| Parameters   | 1971 | 1972 | 1973 |
|--|------|------|------|
| Number of larvae that fell per 1 m <sup>2</sup>                    | 172  | 47.2 | 1.2  |
| Number of imagines that emerged from 1 m <sup>2</sup>              | 17   | 1.6  | 0.2  |
| Infestation of larvae that fell on the forest floor (in per cents) | 27.5 | 54.5 | 67.5 |
| Reduction due to parasites (in per cents)                          | 30.9 | 56.4 | 81.0 |
| Reduction due to factors acting in soil (in per cents)             | 69.1 | 43.6 | 19.0 |
| Total per cent of reduction in pupal stage                         | 90.1 | 96.6 | 83.3 |

Table VI. Contribution to total reduction of *Operophtera brumata* of: reduction in larval stage in tree crowns and reduction due to parasites and factors affecting the pupae (in per cents)

| Reduction                               | 1971 | 1973 |
|---|------|------|
| Of larval stage in tree crowns          | 74.6 | 98.6 |
| Due to parasites during pupal stage     | 7.7  | 1.1  |
| Due to other factors during pupal stage | 17.6 | 0.3  |

Total reduction in the larval and pupal stages till the emergence of imagines was 97.3% in the year of outbreak and 99.7% in the next year. But the contribution of particular factors to the total reduction changed: as the outbreak ends the reduction of larval stages in tree crowns increases, whereas the reduction due to parasites and other factors affecting the pupae in soil, decreases (Table VI). Thus, the mortality in the larval stage mostly contributes to the reduction of *O. brumata*, both in the year of outbreak and in the following one.

#### 4. DISCUSSION

Data on the reduction of numbers of *O. brumata*, obtained in various environmental conditions, show that in particular cases different groups of factors may be decisive for the control of population numbers. This concerns, first of all, predators and parasites. In Wytham (England), the non-specialized predators attacking the pupae were mainly responsible for the stability of population of *O. brumata*, whereas the influence of a specific parasite *Cyzenis albicans* (Fall.) was hardly noticeable, probably due to the occurrence of the hyperparasite

(Varley and Gradwell 1968). On the other hand, in Canada, *Cyzenis*, after the introduction, was an extremely efficient reducer, but the effect of soil predators on pupae was very small (Embre 1965). Studies on the reduction of numbers of *Operophtera* in the forest-steppe zone in the USSR (Moravskaja 1960) have shown that the degree of infestation of larvae was very low — on average 3.8%, and the infestation on areas of outbreak was lower than on areas with small numbers of the pest. It is an interesting fact that during the outbreak of *Ocneria dispar* L. in the same place, the species was greatly infested by parasites and the infestation increased from 72 to 82% as the pest numbers decreased. Still, the role of soil predators (Carabidae and Staphylinidae) in reducing the numbers of *O. brumata* was considerable, similarly as in England; they destroyed 66.2–89.6% of pupae.

As regards our investigations the reduction was the highest in the larval stage in tree crowns (Table VI), although in the year of outbreak there was also a considerable percentage of individuals reduced in the pupal stage. Still, the stabilizing effect on the population numbers is not so much due to the absolute reduction but to its relation towards the population density. Generally speaking, the directly proportional relation between the reducing factor and population density will be responsible for its stable numbers. The reversely proportional relation, strongly indicated, will increase the instability. Whereas the density-dependent relation with delayed action, typical for specific parasites, will intensify the cyclic fluctuations of the numbers of prey population (Varley and Gradwell 1970). The joint effect of all these relations will depend on the intensity of its components. In the case of population of *O. brumata* in the Wytham forest, the joint, reversely proportional to density, effect of non-specific parasites and density-dependent effect of non-specialized soil predators resulted in stable population numbers.

It is difficult to determine the character of predators and parasites considering the short period of our observations and lack of identification of the parasites and predators.

The increasing in successive years reduction of population by parasites (Table V) may be either due to directly proportional dependence on density with delayed effect or the reversely proportional dependence on density, typical for non-specific parasites. The latter seems to be the case here, because already in the outbreak year the percentage of infestation was considerably high (27.5). Whereas the reduction of pupae by other factors is obviously directly proportional to density, and similarly as in England, is probably due to the effect of non-specialized predators, and mainly of the Carabidae abundant in this area.

Reduction of numbers of larvae in tree crowns is also reversely proportional to density (Table IV). Nevertheless, it is an interesting fact that the contribution of this reduction is high (Table VI) when compared with data of other authors. Surely, the larvae of *O. brumata* were reduced by birds and larvae of *Calymnia trapezina* L., but the role of particular groups of other predatory invertebrates in the reduction of larvae in tree crowns is not clear. As regards birds, on the area examined there was an abundant and stable group consisting on average of 20 species and of a density about 20 individuals per 1 ha (A. Wasilewski —unpublished data). In the year of outbreak the contribution of larvae of Geometridae to the food of several species of birds increased, and also a large number of species, usually showing preference for other groups of insects, switched onto the larvae of Lepidoptera. Other Geometridae species, participating in the outbreak, were preferred to *O. brumata*. Approximate estimations show that reduction of larvae by birds in the year of outbreak was twice higher than at a small density of larvae (A. Wasilewski — unpublished data).

As regards the considerably small density range of pest the activity of birds is probably proportional to the prey density. This is confirmed by Tinbergen (1960) and Korol-

k o v a (1963). K o r o l k o v a (1963), in her experiments, has found that at densities of *Operophthera*: 34, 25 and 1 larvae per 100 leaves, the reduction by birds was 50, 88 and 54%, respectively, which proves the density-dependent effect of birds only to a certain level of prey density. Thus, it should be expected, that the high reduction of larvae (Tables IV, VI) is due to joint effect of non-specialized predators.

Although the authors do not have detailed data on several years' fluctuations of *O. brumata*, it is known that the previous outbreak of this species on the area examined took place in 1960. Considering the fact that the outbreak in 1971 came to an end due to biotic factors, we are dealing with a relatively stable pest population with something like a 10-years' cyclicity.

## 5. SUMMARY

The aim of the study was to estimate the reduction of numbers of *Operophthera brumata*, in its larval and pupal stages, caused mainly by predators and parasites. The material was obtained from the reserve "Grabowy" (mixed forest of the Pino-Quercetum association) in the Kampinos National Park. The material was obtained by four methods: (1) samples taken with a special catcher sack from tree crowns provided data on the fluctuations of numbers of larvae over the seasons in particular years; (2) separately picked up larvae which grazed on oak and hornbeam gave the percentage of individuals infested by parasites; (3) leaf-fall catchers provided material to estimate the number of larvae ready to pupate which were falling from trees on the forest floor; (4) isolators distributed in October recorded the emergence of imagines. Material on the fluctuations of numbers of *O. brumata* larvae was obtained in the years 1968–1973, other information was obtained in the years 1971–1973.

On the area examined, the outbreak of *O. brumata* took place in 1971 (Table I). Before the outbreak, the density of larvae on the oak was higher than on the hornbeam, and also the development of larvae was faster on the oak (Tables I, II, Fig. 1). In the year of outbreak the density of larvae and their development rate were similar on both tree species. Longer period of development results in a greater number of individuals being attacked by parasites: infestation of larvae grazing on the hornbeam was higher than on the oak, whereas, on the other hand, the early larval stages were much less infested than later stages.

The reduction of larvae till the moment they fell on the forest floor was estimated by comparing the maximal numbers of larvae in tree crowns with the number of larvae on the forest floor. This is a considerably high reduction (Table IV), and it is much higher a year after the outbreak (97.4%) than in the year of the outbreak (72.7%).

Data on the reduction of numbers of pupae of *O. brumata* were from a comparison of the number of larvae falling on the forest floor with the recorded over successive years emergence of imagines. Also, the data on the infestation of larvae in particular years, allowed to estimate the mortality of pupae due to parasites and other factors acting in soil.

The mortality of pupae due to parasites increases in successive years after the outbreak, but the reduction caused by other factors, probably by non-specialized predators, decreases (Table V).

Total reduction in the larval and pupal stages till the emergence of imagines was 97.3% in the year of outbreak and 99.7% in the year after it. Contribution of particular factors to this reduction changed: at the end of outbreak the reduction of larval stage in tree crowns increased, whereas the reduction caused by parasites and other factors influencing the pupae in soil decreased (Table VI). Mortality in the larval stage contributes mostly to the reduction of *O. brumata*, both during outbreak and afterwards.

## 6. POLISH SUMMARY

Celem pracy była ocena redukcji liczebności *Operophthera brumata* w stadiach larwalnych i w stadium poczwarki, spowodowanej głównie przez działanie drapieżców i pasożytów. Materiał zebrano na terenie rezerwatu „Grabowy” (bór mieszany zespołu *Pino-Quercetum*) w Puszczy Kampinoskiej. Materiał ten uzyskano za pomocą kilku metod: 1) na podstawie próbek pobranych specjalnym czerpakiem w koronach



drzew otrzymano dane o dynamice liczebności larw w ciągu sezonu w poszczególnych latach; 2) niezależne zbiory larw żerujących na dębie i grabie pozwoliły ocenić udział zaatakowanych przez pasożyty osobników; 3) przy użyciu chwytaczy opadu organicznego oceniono liczbę dojrzałych do przepoczwarczenia larw opadających z drzew na dno lasu; 4) ustawiane w październiku eklektory posłużyły do rejestracji wylotu imago. Materiały dotyczące dynamiki liczebności larw *O. brumata* zbierane były w okresie 1968–1973 r., pozostałe informacje uzyskano w okresie 1971–1973 r.

Masowy pojaw *O. brumata* nastąpił na badanym terenie w 1971 r. (tab. I). Poza rokiem masowego pojawu zagęszczenie larw na dębie było przy tym wyższe niż na grabie; rozwój larw na dębie przebiegał również szybciej niż na grabie (tab. I, II, rys. 1). W roku gradacji zagęszczenie larw i tempo ich rozwoju były podobne na obu gatunkach drzew. Stwierdzono, że przedłużenie okresu rozwojowego powoduje wzrost liczby osobników zaatakowanych przez pasożyty: opanowanie przez pasożyty larw żerujących na grabie było wyższe niż na dębie; z drugiej strony wczesne stadia larwalne są w mniejszym stopniu opanowane przez pasożyty niż stadia późniejsze.

Redukcję liczebności larw do momentu ich zejścia na dno lasu oszacowano przez porównanie maksymalnych liczebności larw w koronach drzew z liczbą larw, które zeszły na dno lasu. Redukcja ta osiąga znaczne wartości (tab. IV), przy tym na drugi rok po gradacji jest ona znacznie wyższa (97,4%) niż w roku masowego pojawu (72,7%).

Dane o redukcji liczebności poczwerek *O. brumata* uzyskano na podstawie zestawienia liczby larw opadających na dno lasu z zarejestrowanym w ciągu kolejnych lat wylotem imago. Jednocześnie wykorzystano tu dane o stopniu opanowania larw przez pasożyty w poszczególnych latach, co pozwoliło wyróżnić śmiertelność poczwerek spowodowaną przez pasożyty i przez inne czynniki działające w glebie.

Stwierdzono, że udział śmiertelności poczwerek spowodowany przez pasożyty narasta w kolejnych latach po gradacji, natomiast udział redukcji powodowanej przez inne czynniki – prawdopodobnie przez niewyspecjalizowane drapieżce – ulega zmniejszeniu (tab. V).

Całkowita redukcja w stadium larwy i poczwarki do wylotu imago stanowiła 97,3% w roku gradacji i 99,7% w drugim roku po gradacji. Udział poszczególnych czynników w tej redukcji ulegał przy tym zmianie: w miarę wygasania gradacji narastał udział redukcji w stadium larwalnym w koronach drzew, a ulegał zmniejszeniu udział redukcji powodowanej przez pasożyty i inne czynniki działające na poczwarki w glebie (tab. VI). Największy udział w redukcji *O. brumata* ma przy tym śmiertelność w stadium larwalnym, zarówno podczas gradacji jak i po gradacji.

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