

**Isolated populations of the winter moth, *Operophtera brumata*
(Lepidoptera: Geometridae), their heavy metal content and parasitism**

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Abstract. Ten dominant heavy metals were analyzed in adults of the winter moth, *Operophtera brumata* (L.), from six sites in four isolated localities in South Bohemia. At all of the sites, metal concentrations conformed to the order Zn > Fe > Cu > Mn > Ni > Pb > Co > Cd > Cr > Hg. The highest concentration of toxic metals (lead and cadmium) was found in moths associated with trees along the main road in Plástovice (3.1 and 1.1 ppm, respectively), while it was lowest in the Červené Blato peat bog (1.1 and 0.1 ppm, respectively). The main parasitoids were two tachinid flies, *Cyzenis albicans* Fall. and *Phorocera obscura* Fall., and one ichneumonid wasp, *Agrypon flaveolatum* Grav. Overall parasitism was low (2.8 and 5.9% in 1991 and 1992, respectively). The highest percentage of parasitism was on larvae in the unpolluted Červené Blato bog (4.8 and 28.3% in 1991 and in 1992, respectively), and the lowest on apple trees along the main road in Plástovice, which was the most polluted site of the four localities.

INTRODUCTION

The winter moth, *Operophtera brumata* (L.), is a univoltine geometrid moth, native to Europe and parts of western and eastern Asia (Kozhanchikov, 1950). It was accidentally introduced into North America in the early 1930's, but its presence not acknowledged until 1949, in Nova Scotia (Cuming, 1961). It is a serious defoliator of apple, cherry, oak, elm, maple and many other broadleaf species (Cuming, 1961; MacPhee, 1967).

Outbreaks of the winter moth have been recorded in England, in Scandinavian countries, and in Nova Scotia (Cuming, 1961; Varley & Gradwell, 1963; Embree, 1965; Tenow, 1972). During 1961–1964 there was a population explosion of the winter moth in the former Czechoslovakia, particularly in Moravia and Slovakia, causing extensive damage to oak and mixed forest stands (Mrkva, 1968). In recent years (from 1970), the winter moth has become the most important pest in southern Bohemia, and has seriously defoliated fruit trees, especially apple and cherry trees along the main road (Rejmánek & Spitzer, 1980).

The ecology of the winter moth has received much more attention than that of most other insects. During the past 30 years, the winter moth has been the subject of many studies to elucidate the fundamental principles of insect population dynamics and regulation (e.g. Embree, 1965; Varley & Gradwell, 1970; Varley et al., 1973; Holliday, 1977) and of biological control (Graham, 1958; Embree, 1966, 1971; Embree & Sisojevic, 1965; Hassell, 1980).

Although there is general knowledge about the parasitoids of *Operophtera brumata*, there exist no data concerning parasitoid incidence in isolated populations, nor metal levels in these populations. This study is an analysis of the heavy metal content and parasitism of the winter moth in some isolated localities, and an attempt to relate the occurrence of natural enemies to the level of metal contamination.

MATERIAL AND METHODS

Study sites

Four ecologically distinct localities in South Bohemia were selected (Fig. 1) for study in 1991–1992. Compared to other parts of Bohemia, South Bohemia has only slightly polluted air (see Novák & Spitzer, 1986). The places where the collections were made are as follows:

1. Horská Kvilda: located in the Šumava Mountains of southwestern Bohemia, situated 1058–1075 m A.S.L. This locality is a mountain spruce forest and a subalpine peat bog. Samples of the winter moth were collected on *Vaccinium myrtillus* L., an understory plant on the margins of the peat bog, where *Picea abies* L. is a dominant tree.

2. Červené Blato: This locality is a transient raised peat bog. The sampling site is situated near Šalmanovice in the Třebon Basin. The Červené Blato peat bog structurally resembles the peat bogs of the Šumava mountains, as a unique habitat island. However, the Červené Blato bog is more isolated within the landscape than the montane bogs of the Šumava Mountains. According to other extensive entomological surveys, Červené Blato is a significant biological area with the specific occurrence of a boreal and boreal-pine fauna and flora (Spitzer & Jaroš, 1983 and unpublished data). Winter moths were collected on *Vaccinium myrtillus* L. in various parts of the bog.

3. Plástovice: Plástovice has an environment similar to that of České Budějovice. Winter moth populations on apple trees along the main road were found at the same high levels as in the past (Rejmánek & Spitzer, 1980). Winter moths were sampled on apple trees along a main road and in the nearby oak forest.

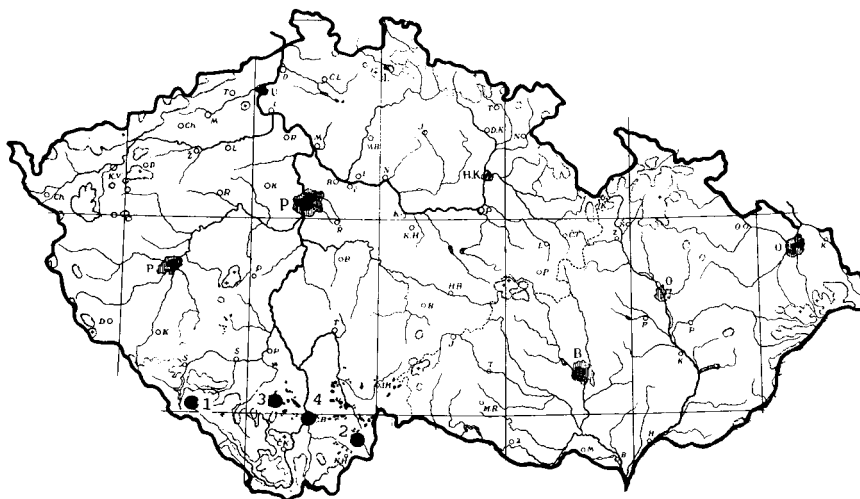


Fig. 1. Collection localities of the winter moth (*Operophtera brumata*) in South Bohemia: 1. Horská Kvilda; 2. Červené Blato; 3. Plástovice; 4. České Budějovice.

4. České Budějovice: Predominantly a cultivated landscape with small, wet hay meadows, fragments of deciduous forest, and large temporary agroecosystems and other anthropogenic vegetation. Winter moths were sampled in the oak forest and on fruit trees, chiefly on cherry and apple trees.

Sampling of adults

The sampling technique was a modification of the methods used by Cuming (1961) and Embree (1965). Accordingly, adults were collected in the field from October to December by torch, by net, by hand, and by shaking tree limbs at night. Both males and females were collected.

Sampling of larvae for parasitoids

Larvae were collected from clipped leaf clusters using beating sheets, by shaking tree limbs and by sweeping. Field collected specimens were identified according to Eidt & Embree (1968). A survey was conducted to determine whether there were significant local differences in the composition and incidence of winter moth parasitoids. Larvae were collected at all localities as the fourth and the fifth instars, the period after parasitoid attack on the larval stage. The criteria of instar determination were derived from Briggs (1957) and Cuming (1961).

Larvae were reared at 22°C and RH 70% in bottles containing host leaf clusters. After pupation of all larvae, the bottles were placed in an incubator at 13–15°C throughout the summer. These pupae were maintained in total darkness and constant humidity until the end of September or the beginning of October. The temperature was then reduced to 7°C for adult winter moth emergence by placing the pupae in a refrigerator. The pupae which did not eclose were kept at 7°C until the middle of April, when the temperature was raised to 15°C. Parasitoid emergence was monitored daily. Any pupal remains were dissected in the spring, to attempt to identify the cause of death.

Sampling for heavy metal analyses

The heavy metals zinc (Zn), iron (Fe), copper (Cu), manganese (Mn), nickel (Ni), lead (Pb), cobalt (Co), cadmium (Cd), chromium (Cr) and mercury (Hg) were analysed only in the adults (males and females mixed, 1 : 1). Samples of moths were kept separately for each site of a locality, and were later homogenized by grinding them in a laboratory rotor speed mill. The weight of each sample varied from 1.5 to 1.8 g according to the number of moths captured. Methods of heavy metal analysis followed, or were modified, from those described by Hunter et al. (1987); Heliövaara & Väisänen (1989, 1990a, 1990b) and Kroupa et al. (1990).

A part of the homogenized samples dried at room temperature was used for Hg analysis. Mercury concentration was measured with a total mercury analyser (TMA-254-Prague-Czechoslovakia), based on the cold vapour atomic absorption method.

The levels of Zn, Fe, Cu, Mn, Ni, Pb, Co, Cd and Cr were measured by Atomic Absorption Spectrophotometry using a Spectr AA 10- BQ. For complete details of this procedure see Middleton et al. (1973). The results were recalculated to the dry matter (DM), determined by the procedure mentioned above. All metal concentrations in this study are given in parts per million (ppm). The following basic statistics were calculated: mean, standard error ($n = 5$ for each treatment), and remarks on significant differences. Data were analyzed using the computer program ANOVA (Sokal & Rohlf, 1969).

RESULTS

Heavy metal content

The results and statistical evaluation of metal analyses on the adult winter moth are presented in Table 1. Concentrations of zinc were the highest and concentrations of mercury were the lowest among the metals examined in the entire analysed material.

Generally, the metal levels in the adults at all sites conformed to the order Zn > Fe > Cu > Mn > Ni > Pb > Co > Cd > Cr > Hg, except for cadmium concentrations lower than chromium concentrations in Červené Blato and in the apple and cherry gardens of České Budějovice (Table 1).

The highest and lowest concentrations of biogenic and less toxic metals Zn, Fe, Cu, Mn, Co, and Cr did not follow the same trend in the various localities. Levels of zinc, iron, and

copper were high and relatively constant in all localities (Fig. 2), but manganese, cobalt, and chromium did not follow this pattern. Except for manganese, these metals had low concentrations, and the differences between concentrations in various localities are significant (Fig. 3). Nickel concentrations were highest (4.1ppm) in Horská Kvilda, nearly three times higher than in Červené Blato and in the oak forest of České Budějovice (Table 1).

TABLE 1. Heavy metal concentration (ppm dry matter and standard error) in the winter moth adults at different sites in four ecologically distinct localities.

	H. Kvilda	Č. Blato	Plástovice (A)	Plástovice (B)	Č. Budějovice (A)	Č. Budějovice (B)
	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)
Zn	291.3 (3.0)	338.6 (3.2)	260.1 (4.0)	239.8 (4.1)	285.3 (4.1)	240.5 (2.8)
Fe	97.4 (3.5)	124.5 (4.3)	161.1 (3.7)	148.6 (5.5)	97.1 (4.3)	115.1 (4.2)
Cu	19.7 (0.6)	21.9 (0.9)	18.8 (0.6)	18.4 (0.5)	20.3 (0.7)	17.0 (1.2)
Mn	8.0 (0.4)	12.1 (0.7)	5.0 (0.4)	11.1 (0.7)	7.2 (0.3)	9.6 (0.6)
Ni	4.1 (0.1)	1.4 (0.1)	3.0 (0.1)	3.3 (0.1)	2.5 (0.1)	1.4 (0.1)
Pb	2.2 (0.1)	1.1 (0.1)	3.1 (0.1)	1.9 (0.3)	1.7 (0.2)	1.4 (0.1)
Co	1.1 (0.1)	0.5 (—)	1.1 (—)	1.5 (0.1)	0.7 (0.1)	0.9 (0.1)
Cd	0.3 (—)	0.1 (—)	1.0 (—)	0.5 (—)	0.3 (—)	0.4 (—)
Cr	0.3 (—)	0.1 (—)	0.2 (—)	0.4 (—)	0.6 (—)	0.3 (—)
Hg	0.11 (—)	0.08 (—)	0.09 (—)	0.09 (—)	0.04 (—)	0.05 (—)

Plástovice (A), along the main road.
Plástovice (B), in the oak forest.

Č. Budějovice (A), in the cherry and apple gardens.
Č. Budějovice (B), in the oak forest.

Among the toxic heavy metals (i.e. lead, cadmium and mercury), lead and cadmium concentrations reflected the general contamination of each site of a locality and the level of isolation of a locality, but mercury did not. Lead concentrations were highest (3.1ppm)

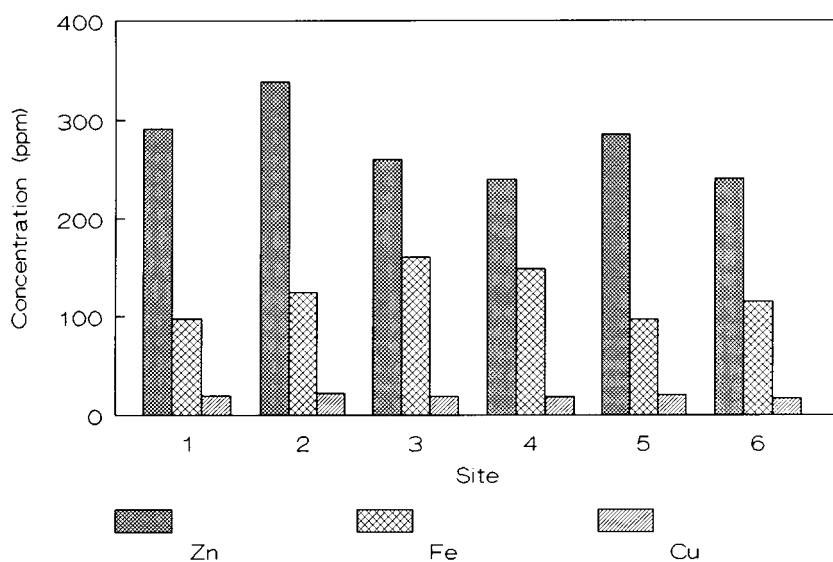


Fig. 2. Concentrations of zinc, iron and copper at different sites. For site, see Table 1.

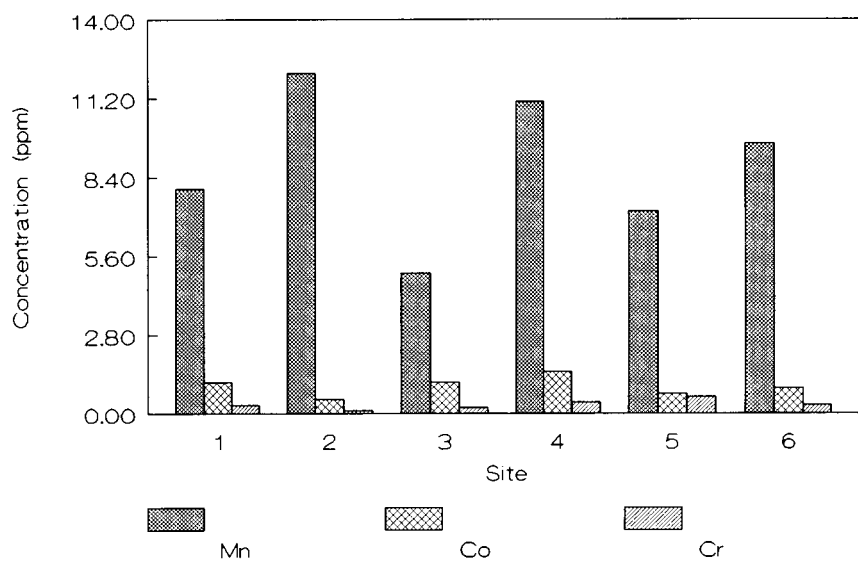


Fig. 3. Concentrations of manganese, cobalt and chromium at different sites. For site, see Table 1.

along the main road in Plástovice and lowest (1.1ppm) in Červené Blato. Compared to lead concentrations at Červené Blato, lead concentrations in the moth population along the main road in Plástovice were three times higher, and lead concentrations in Horská Kvilda

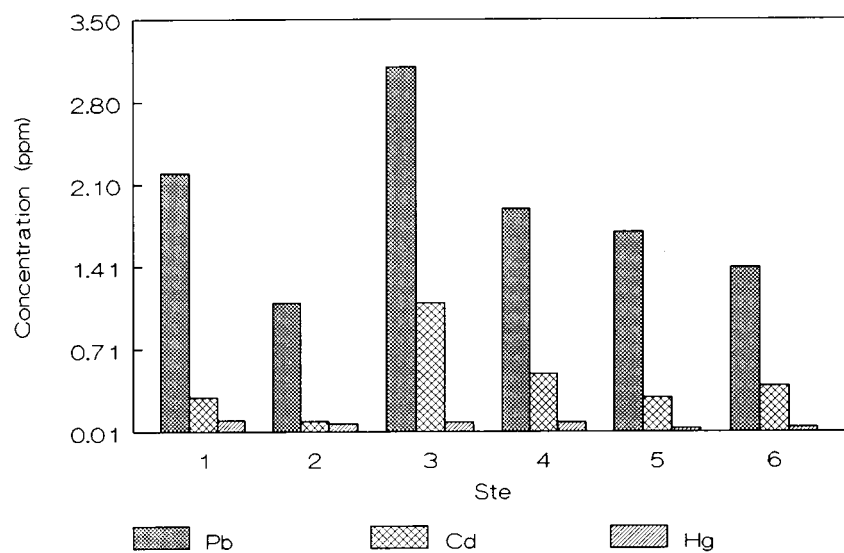


Fig. 4. Concentrations of lead, cadmium and mercury at different sites. For site, see Table 1.

in the Šumava Mts two times higher (Fig. 4). Concentrations of cadmium were the highest (1.1ppm) along the main road in Plástovice, eleven times higher than in Červené Blato, four times higher than in Horská Kvilda, and likewise four times higher in both the apple and cherry gardens and in the oak forest of České Budějovice (Fig. 4). By contrast, mercury concentrations were highest (0.1ppm) in moths of the Horská Kvilda population in the Šumava Mts and lowest (0.04ppm) in moths from the apple and cherry gardens in České Budějovice (Fig. 4).

Parasitism

The main parasitoids of winter moth larvae encountered in this study were the tachinid flies *Cyzenis albicans* (Fall.) and *Phorocera obscura* (Fall.), and the ichneumonid wasp *Agrypon flaveolatum* (Grav.). The proportion of *C. albicans*, *P. obscura* and *A. flaveolatum* was 38.3%, 53.3% and 8.3%, respectively, for both years. Overall parasitism was low, 2.8% (host n = 2,953) in 1991 and 5.9% (host n = 3,455) in 1992 (Table 2).

TABLE 2. Percentage of winter moth larvae parasitized by *Cyzenis albicans*, *Phorocera obscura* and *Agrypon flaveolatum*.

Locality	1991		1992	
	n	%	n	%
Horská Kvilda*	520	2.3	700	1.8
Červené Blato*	1,000	4.8	600	28.3
Plástovice**	800	0.7	1,385	0.6
Č. Budějovice***	633	2.7	770	1.5
Overall parasitism	2,953	2.8	3,455	5.9

* Larvae were collected on *Vaccinium myrtillus*

** Larvae were collected on apple trees along the main road

*** Larvae were collected in apple and cherry gardens

The highest percentage of parasitism was on larvae from Červené Blato, 4.8% in 1991 and 28.3% in 1992. The lowest was on larvae on apple trees along the main road in Plástovice, 0.7% in 1991 and 0.6% in 1992. Levels of parasitism in Horská Kvilda and in České Budějovice represent an average among the four localities (see Table 2). The diversity of parasitoids at the four localities studied is demonstrated in Table 3.

TABLE 3. Percentage of parasitoid species of winter moth larvae at four investigated localities in 1991–1992.

Species	Locality			
	H. Kvilda	Č. Blato	Plástovice	Č. Budějovice
<i>Cyzenis albicans</i>	13.5	28.0	8.0	9.0
<i>Phorocera obscura</i>	—	31.0	—	6.0
<i>Agrypon flaveolatum</i>	—	3.0	—	1.5

DISCUSSION AND CONCLUSIONS

Winter moth populations, with their wingless females, provide an opportunity to study locally bound populations in environments having different degrees of metal pollution.



Fig. 5. Apple trees defoliated by winter moth larvae (*Operophtera brumata*) along the main road near Plástovice.

At all sites, metal levels followed the order Zn > Fe > Cu > Mn > Ni > Pb > Co > Cd > Cr > Hg. The only exception was that cadmium concentrations at Červené Blato and in the apple and cherry gardens of České Budějovice were lower than concentrations of chromium. This order is about the same as that reported for other moths (Pihlajamäki et al., 1989; Rantataro et al., 1989; Nuorteva, 1990) and other insects (Beyer et al., 1985).

It has been shown that moths bioaccumulate Zn, Cu, Br and As, but not Al, Fe, Mn, Cd, Ni and Sr (Pihlajamäki et al., 1989; Rantataro et al., 1989; Heliövaara et al., 1990; Nuorteva, 1990; Lindqvist, 1992; Nuorteva et al., 1992). Levels of zinc, iron, copper and manganese were high in the winter moth, indicating that these moths play a role in the transfer of these metals to higher trophic levels. One possible transference is from the winter moth to shrews and other vertebrates feeding on winter moth pupae, and, further on, to birds of prey and predatory mammals (Frank 1967a, 1967b). The harmful transfer of metals from winter moth caterpillars to parasitoids is also possible, but has not yet been documented.

In contrast to copper, iron, and zinc; cadmium is not known to have any positive physiological function. It is, on the contrary, extremely toxic (Hunter & Johnson, 1982; Maroni & Watson, 1985). Concentrations of cadmium differ from those of zinc, iron, copper and manganese in that they are very low in the adult insects (Kroupa et al., 1990). The data in this study confirm this conclusion. Indeed, it is of theoretical interest to note that the degree of local Cd contamination showed itself in the Cd levels in winter moth adults. In boreal forests adult moths, with low Cd content, have no significant role in the transmission of this metal. Arthropods bearing high Cd contents (like spiders, ants and bark beetles) are

responsible for the danger of Cd accumulation (Nuorteva, 1990; Nuorteva et al., 1992). The same general trend was found with lead concentrations. The highest concentration was along the main road in Plástovice and the lowest was in Červené Blato. Compared to Červené Blato, concentrations of cadmium along the main road in Plástovice were 11 times higher, while in Horská Kvilda cadmium was three times higher (Table 1, and Fig. 4).

Most of the lead on plants is surface contamination, and is eaten by caterpillars. Roadside plants contain significantly more lead than control samples, and difference correlates to traffic volume (Beyer & Moore, 1980; Alstad et al., 1982; Dallinger et al., 1992). Price et al. (1974) found that lead is present at higher levels in insects near major highways and becomes more concentrated as it passes from herbivorous to carnivorous insects, thus posing a possible threat to beneficial predatory insects and insectivorous birds and mammals. The estimates of lead concentrations in the winter moth in this study agree with those of other insect studies (Giles et al., 1973; Gish & Christensen, 1973; Price et al., 1974) which found higher lead concentrations in insects of roadside environments. The highest lead concentration in the winter moth was found in those along the main road (3.1ppm) in Plástovice, while in Červené Blato lead concentration was lowest (1.1ppm). The concentration of lead in Horská Kvilda was 2.2ppm, almost twice as high as in Červené Blato. The higher concentration of lead at Horská Kvilda is associated with the proximity of the test site to relatively high traffic volume. The moths were collected here on *Vaccinium myrtillus* at the edge of a peat bog, approximately 100 m away from the main road. The results of estimates of levels of toxic heavy metals (i.e. lead and cadmium) and other trace metals confirmed that Červené Blato is ecologically much more isolated, and the least polluted by human activities of the four localities.

Compared to other studies (Giles et al., 1973; Price et al., 1974; Heliövaara & Väisänen, 1989, 1990b; Kroupa et al., 1990) made at highly polluted sites around industrial areas, lead and cadmium concentrations in the winter moth in South Bohemia can be considered low, except for those sites along the main road. The level of mercury in the winter moth was consistently very low and, in contrast to other elements studied, did not reflect the general contamination of a locality (see also Kroupa et al., 1990).

Although 60 different parasitoids attack winter moth larvae (Wylie, 1960), their impact on the population of the winter moth at Wytham Wood in England was small (Varley et al., 1973). The results on parasitism in this study confirm this conclusion. Three species of parasitoids were observed, and overall parasitism was found to be low (2.8% in 1991 and 5.9% in 1992). Holliday (1977) found that there was no significant reduction in the density of larvae on apple trees during the feeding period; parasitism in his study site at Wytham Wood, England never exceeded 1% (Holliday, 1975, cited after Holliday, 1985). Similar figures were obtained by Kimberling et al. (1986), who found a mean of 4.5% and 12.2% parasitism in 1979 and 1980, respectively, in western Oregon.

In this study the percentage of parasitism and parasitoid species (see Table 2 and Table 3) of winter moth larvae was highest in Červené Blato (4.8% in 1991 and 28.3% in 1992). The percentage of parasitism on larvae on apple trees along the main road in Plástovice was the lowest overall (0.7% and 0.6% in 1991 and 1992, respectively). These results might be explained by the effective bioaccumulation from winter moth larvae to parasitoids and by the susceptibility of winter moth parasitoids to the heavy metal pollutants

found in various localities. The results of metal analyses, especially those showing higher concentrations of toxic heavy metals in the winter moth on apple trees along the highway in Plástovice, could be used as evidence to link heavy metal pollutants with the population density increase of the winter moth on fruit trees, particularly on apple and cherry trees along the main roads in South Bohemia (Rejmánek & Spitzer, 1980). These results also support the idea (Price et al., 1974; Führer, 1975; Heliövaara et al., 1991) that parasitoids are less tolerant of pollutants than their host, which can thus escape parasitoid deprivation, and that the sensitivity of parasitoids and predators to contamination concentrated along the food chain could be involved with insect outbreaks.

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REFERENCES

- ALSTAD D.N., EDMUNDS G.F. JR., WEINSTEIN L.H. 1982: Effects of air pollutants on insect populations. *Annu. Rev. Entomol.* **27**: 369–384.
- BEYER W.N. & MOORE J. 1980: Lead residues in eastern tent caterpillars (*Malacosoma americanum*) and their host plant (*Prunus serotina*) close to major highway. *Envir. Entomol.* **9**: 10–12.
- BEYER W.N., PATTEE O.H., SILEO L., HOFFMAN D. J. & MULHERN B.M. 1985: Metal contamination in wildlife living near two zinc smelters. *Envir. Pollut. (Ser. A)* **38**: 63–86.
- BRIGGS J.B. 1957: Some features of the biology of the winter moth [*Operophtera brumata* (L.)] on the top fruits. *J. Hort. Sci.* **32**: 108–125.
- CUMING F.G. 1961: The distribution, life history, and economic importance of the winter moth, *Operophtera brumata* (L.) (Lepidoptera, Geometridae) in Nova Scotia. *Can. Entomol.* **93**: 135–142.
- DALLINGER R., BERGER B. & BIRKEL S. 1992: Terrestrial isopods: useful biological indicators of urban metal pollution. *Oecologia* **89**: 32–41.
- EIDT D.C. & EMBREE D.G. 1968: Distinguishing larvae and pupae of the winter moth, *Operophtera brumata*, and the bruce spanworm *O. bruceata* (Lepidoptera: Geometridae). *Can. Entomol.* **100**: 536–539.
- EMBREE D.G. 1965: The population dynamics of the winter moth in Nova Scotia, 1954–1962. *Mem. Entomol. Soc. Can.* **46**, 57 pp.
- EMBREE D.G. 1966: The role of introduced parasites in the control of the winter moth in Nova Scotia. *Can. Entomol.* **98**: 1159–1168.
- EMBREE D.G. 1971: The biological control of the winter moth in eastern Canada by introduced parasites. In Huffaker C.B. (ed.): *Biological Control*. Plenum Press, New York, pp. 217–226.
- EMBREE D.G. & SISOJEVIC P. 1965: The bionomics and population density of *Cyzenis albicans* (Fall.) (Tachinidae: Diptera) in Nova Scotia. *Can. Entomol.* **97**: 631–639.
- FRANK J.H. 1967a: The insect predators of the pupal stage of the winter moth, *Operophtera brumata* (L.) (Lepidoptera: Hydrionomidae). *J. Anim. Ecol.* **36**: 375–389.
- FRANK J.H. 1967b: The effect of pupal predators on a population of winter moth, *Operophtera brumata* (L.) (Hydrionomidae). *J. Anim. Ecol.* **36**: 611–621.
- FÜHRER E. 1985: Air pollution and the incidence of forest insect problems. *Z. Angew. Entomol.* **99**: 371–377.
- GILES F.E., MIDDLETON S.G. & GRAU J.G. 1973: Evidence for the accumulations of atmospheric lead by insects in areas of high traffic density. *Envir. Entomol.* **2**: 299–300.
- GISH C.D. & CHRISTENSEN R.E. 1973: Cadmium, nickel, lead, and zinc in earthworms from roadside soil. *Envir. Sci. Tech.* **7**: 1060–1062.
- GRAHAM A.R. 1958: Recoveries of introduced species of parasites of winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae), in Nova Scotia. *Can. Entomol.* **90**: 595–596.

- HASSELL M.P. 1980: Foraging strategies, population models and biological control: a case study. *J. Anim. Ecol.* **49**: 603–628.
- HELIÖVAARA K. & VÄISÄNEN R. 1989: Between-species differences in heavy metal levels in four pine diprionids (Hymenoptera) along an air pollutant gradient. *Envir. Pollut.* **62**: 253–261.
- HELIÖVAARA K. & VÄISÄNEN R. 1990a: Concentrations of heavy metals in the food, faeces, adults, and empty cocoons of *Neodiprion sertifer* (Hymenoptera, Diprionidae). *Bull. Envir. Contam. Toxicol.* **45**: 13–18.
- HELIÖVAARA K. & VÄISÄNEN R. 1990b: Heavy-metal contents in pupae of *Bupalus piniarius* (Lepidoptera: Geometridae) near an industrial source. *Envir. Entomol.* **19**: 481–485.
- HELIÖVAARA K. & VÄISÄNEN R., KEMPPİ E. & LODENIUS M. 1990: Heavy metal concentrations in males and females of three pine diprionids (Hymenoptera). *Entomol. Fennica*. **1**: 175–179.
- HELIÖVAARA K. & VÄISÄNEN R. & VARAMA M. 1991: Larval mortality of pine sawflies (Hymenoptera: Diprionidae) in relation to pollution level: a field experiment. *Entomophaga* **36**: 315–321.
- HOLLIDAY N.J. 1977: Population ecology of winter moth (*Operophtera brumata*) on apple in relation to larval dispersal and time of bud burst. *J. Appl. Ecol.* **14**: 803–813.
- HOLLIDAY N.J. 1985: Maintenance of the phenology of the winter moth (Lepidoptera: Geometridae). *Biol. J. Linn. Soc.* **25**: 221–234.
- HUNTER B.A. & JOHNSON M.S. 1982: Food chain relationships of copper and cadmium in contaminated grassland ecosystem. *Oikos* **38**: 108–117.
- HUNTER B.A., JOHNSON M.S. & THOMPSON D.J. 1987: Ecotoxicology of copper and cadmium in a contaminated grassland ecosystem. II. Invertebrates. *J. Appl. Ecol.* **24**: 587–599.
- KIMBERLING D., MILLER J.C. & PENROSE R.L. 1986: Distribution and parasitism of winter moth, *Operophtera brumata* (Lepidoptera: Geometridae) in western Oregon. *Envir. Entomol.* **15**: 1042–1046.
- KOZHANCHIKOV I.V. 1950: Life cycle development and geographical distribution of the frost spanworm, *Operophtera brumata* L. *Entomol. Obozr.* **31**: 178–197 (in Russian).
- KROUPA M., SPITZER K. & NOVÁK I. 1990: The heavy metal content in melanic and typical forms of *Biston betularia* (Lepidoptera, Geometridae) and its bioindicator significance. *Acta Entomol. Bohemoslov.* **87**: 248–252.
- LINDQVIST L. 1992: Accumulation of cadmium, copper, and zinc in five species of phytophagous insects. *Envir. Entomol.* **21**: 160–163.
- MACPHEE A.W. 1967: The winter moth, *Operophtera brumata* (Lepidoptera: Geometridae), a new pest attacking apple orchards in Nova Scotia and its coldhardiness. *Can. Entomol.* **99**: 829–834.
- MARONI G. & WATSON D. 1985: Uptake and binding of cadmium, copper and zinc by *Drosophila melanogaster* larvae. *Insect Biochem.* **15**: 55–63.
- MIDDLETON S.G., GILES F.E. & GRAU J.G. 1973: Preparation of insect specimens for analysis by means of atomic-absorption spectrophotometry. *Ann. Entomol. Soc. Am.* **66**: 226–227.
- MRKVA R. 1968: Embryogenesis of the winter moth (*Operophtera brumata* L.). *Acta Entomol. Bohemoslov.* **65**: 403–408.
- NOVÁK I. & SPITZER K. 1986: Industrial melanism in *Biston betularia* (Lepidoptera, Geometridae) in Czechoslovakia. *Acta Entomol. Bohemoslov.* **83**: 185–191.
- NUORTEVA P. 1990: *Metal Distribution Patterns and Forest Decline. Seeking Achilles' Heels for Metals in Finnish Forest Biocoenoses*. Publ. Dept. Envir. Conservation Univ. Helsinki II: 1–77.
- NUORTEVA P., NUORTEVA SIRKKA-L. & MATHUR B. 1992: Excretory inhibition of bioaccumulation in Lepidoptera. *Proc. Vth Int. Conf. Bioindicators Deteriorationis Regionis*. Inst. Landscape Ecol., Czechoslovak Academy of Sciences, Čes. Budějovice, pp. 362–367.
- PIHLAJAMÄKI J., VÄÄNÄNEN V.-M., KOSKINEN P. & NUORTEVA P. 1989: Metal levels in *Lothoe populi* and *Sphinx pinastri* (Lepidoptera, Sphingidae) in Finland. *Ann. Entomol. Fenn.* **55**: 17–21.
- PRICE P.W., RATHCKE B.J. & GENTRY D.A. 1974: Lead in terrestrial arthropods: evidence for biological concentration. *Envir. Entomol.* **3**: 370–372.
- RANTATARO M., LAINE J., KOSKINEN P. & NUORTEVA P. 1989: Metal contents in the scots pine feeding moths *Dendrolinus pini* L. (Lep., Lasiocampidae), *Bupalus piniarius* L. and *Thera obeliscata* L. (Lep., Geometridae). *Proc. Vth Int. Conf. Bioindicators Deteriorationis Regionis*. Inst. Landscape Ecol., Czechoslovak Academy of Sciences, Čes. Budějovice, pp. 322–326.

- REJMANEK M. & SPITZER K. 1980: Insecticides favour outbreaks of the winter moth. *Živa* **28**: 62–63 (in Czech).
- SOKAL R.R. & ROHLF J.F. 1969: *Biometry: The Principles and Practice of Statistics in Biological Research*. Freeman, San Francisco, 776 pp.
- SPITZER K. & JAROŠ J. 1983: *Eupithecia gelidata* Mosch. ssp. *Hyperboreata* Stgr. (Lepidoptera) recorded from the peat bog Červené Blato in South Bohemia. *Sbor. Jihočes. Mus. Čes. Budějovicích (Přír. Vědy)* **23**: 95–98.
- TENOW O. 1972: The outbreaks of *Oporinia autumnata* Bkh. and *Operophtera* Spp. (Lep., Geometridae) in Scandinavian mountain chain and northern Finland 1862–1968. *Zool. Bidr. Uppsala, Suppl. 2*, 107 pp.
- VARLEY G.C. & GRADWELL G.R. 1963: The interpretation of insect population changes. *Proc. Ceylon Ass. Advmt Sci. (D)* **18**: 142–156.
- VARLEY G.C. & GRADWELL G.R. 1970: Recent advances in insect population dynamics. *Annu. Rev. Entomol.* **15**: 1–24.
- VARLEY G.C., GRADWELL G.R. & HASSELL M.P. 1973: *Insect Population Ecology: An Analytical Approach*. Blackwell Scientific Publication, Oxford, 210 pp.
- WYLIE H.G. 1960: Insect parasites of the winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae) in western Europe. *Entomophaga* **5**: 111–129.

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