

What Moths Fly in Winter? The Assemblage of Moths Active in a Temperate Deciduous Forest During the Cold Season in Central Poland

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ABSTRACT

The composition and seasonal dynamics of the moth assemblage active in a temperate deciduous forest of Central Poland in autumn and spring was studied in two seasons 2007/2008 and 2008/2009. The standard light trapping method was used and, in addition, tree trunks were searched for resting moths. 42 species of moths from six families were found using both methods. The family Geometridae was predominant in terms of the numbers of individuals collected. Two geometrid species - *Alsophila aescularia* and *Operophtera brumata* - were defined as characteristic of the assemblage investigated. Late autumn and spring were richest in the numbers of species, whereas the species diversity was the lowest in mid-winter. Regression analysis showed that a temperature rise increased the species diversity of Geometridae but that rising air pressure negatively affected the abundance of Noctuidae.

Key words: Lepidoptera, Geometridae, Noctuidae, autumn-spring activity, winter, phenology, atmospheric conditions, regression, Central Poland.

INTRODUCTION

The seasonal weather changes in a temperate climate have a great impact on poikilothermic animals, as they have a limited ability to regulate their body temperature. Thus, the earliest and most easily detectable response to climate change is an adjustment of species phenology (Huntley, 2007). In recent years, global climate change has become an important scientific topic, and its impact on insects is widely and intensively investigated (e.g. Jepsen *et al.*, 2008; Kiritani, 2013; Nooten *et al.*, 2014; Williams and Hellmann, 2012a, b). Invertebrates active from autumn through early spring are strongly dependent on weather and snow cover (Moerkens *et al.*, 2012; Legault and Weis, 2013; Williams *et al.*, 2014). Thus, this fauna is well suited for observing changes in annual cycles, seasonal changes in composition and the impact of atmospheric factors on activity (Martin-Vega and Baz, 2013; Mikova *et al.*, 2013; Soszyńska-Maj and Jaskuła, 2013; Soszyńska-Maj *et al.*, in press).

In a temperate climate most invertebrates are inactive during the cold part of the year, i.e. late autumn, winter and early spring. However, some insects remain active, fly or swarm in winter despite the low temperatures. During hard frosts they look for shelter and enter quiescence. Some of those species are regularly recorded on the snow surface, while a great number of invertebrates remain active for almost the whole

winter in the leaf litter and soil using the excellent insulation capacity of the snow to prevent freezing (Aitchison, 2001). Flies (Diptera), snow scorpion flies (Mecoptera), spiders (Araneida), springtails (Collembola), beetles (Coleoptera) and even earwigs (Dermaptera) are well-known for winter phenology. These insects could be either multivoltine (e.g. Chironomidae, Diptera), some spend the warmer part of the year in larval (e.g. Plecoptera) or pupal (Boreidae, Trichoceridae) stages or even long-lived as some Coleoptera (e.g. Itämies and Lindgren, 1989; Aitchison, 2001; Soszyńska, 2004; Hågvar, 2010; Hågvar and Hågvar 2011; Jaskuła and Soszyńska-Maj, 2011; Soszyńska-Maj and Jaskuła, 2013; Soszyńska-Maj *et al.*, in press).

Some moths are adapted to remain active during winter even when the temperature falls below 0°C; they belong to the small number of Lepidoptera that overwinter as an imago (about 100 species in Poland). This strategy is supported by morphological (brachypterous or apterous forms), physiological (accumulation of antifreeze agents) and behavioural adaptations (with standing cold periods in suitable places with a higher temperature, supplementary feeding, dispersion) (e.g. Buszko and Nowacki, 1990, 1991; Sattler, 1991; Leather *et al.*, 1993; Soszyńska-Maj and Buszko, 2011).

The main aims of this study were to describe the composition and seasonal dynamics of the moth assemblage active during the cold period in a deciduous forest in Central Poland and to assess the influence of atmospheric factors on their activity.

MATERIAL AND METHODS

The study area is located in Central Poland in the Las Łagiewnicki forest complex (51°50'30"N, 19°28'13"E, UTM CC94), which lies within the administrative borders of the city of Łódź. It covers an area of 1200 hectares and is one of the largest urban forests in Europe. With its higher elevation (highest peak 260 m above sea level) the average air temperatures are lower, the humidity higher and the duration of snow cover longer than in the areas of surrounding lowlands. The dominant tree species in the Łagiewniki Forest are oaks (*Quercus* spp.), which make up 42% of the entire tree stand. The study site was located on the edge of a dry-ground forest (*Tilio-Carpinetum typicum*) with a proportion of riverside carr *Fraxino-Alnetum* and near a small pond (*Molinio-Arrhenatheretea*) (Kurowski, 1998).

The investigation was carried out from October to April in two consecutive autumn-spring seasons 2007/08 and 2008/09. The autumn-spring active moths were light-trapped using a 250W mercury-vapour lamp. Trapping started at dusk and lasted until the end of the moths' activity; this was done at intervals of 7-10 days. Light trapping was not done when the temperature dropped below -10°C. During the research, temperature and humidity were recorded daily; the corresponding data from the local weather station were also noted. During the first season, resting moths were also taken from tree trunks. All the moths collected were killed with ethyl acetate. The moths were identified to species level. The material is deposited in the collection of the Department of Invertebrate Zoology and Hydrobiology, University of Łódź, Poland.

In order to analyse the biocoenotic structure of the moth assemblage, dominance (D), frequency (F) and ecological significance (Q) were calculated. Index classes

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were used according to Kasprzak and Niedbała (1981) and modified to account for the specificity of the assemblage: D_5 , eudominants: $\geq 10.1\%$, D_4 , dominants: 5.1-10%, D_3 , subdominants: 2.1-5.0%, D_2 , recedents: 1.1-2.0%, D_1 , subrecedents: $\leq 1.0\%$; Frequency: F_5 , very common: 40.1-100%, F_4 , frequent: 20.1-40%, F_3 , frequent average: 10.1-20%, F_2 , rare: 5.1-10%, F_1 , very rare: $\leq 5.0\%$. The ecological significance (Q index) is the geometric mean of frequency and dominance: Q_4 , taxa characteristic, exclusive and selective: $>15.1\%$, Q_3 , associated taxa: 7.1-15%, Q_2 , less associated taxa: 3.1-7%, Q_1 , random taxa: $<3.0\%$.

To find out whether there is any relationship between weather conditions and the number of moths flying, Pearson's correlation coefficients were calculated at the significance level $p < 0.05$. Variables including the number of individuals and the number of species caught by light trapping in two seasons in a particular ten-day period of a month and the average value of each of the weather parameters at that time were taken into account for the calculation. The null hypothesis of no correlation between weather conditions and moth activity was tested. Regression analysis was carried out to find out if weather conditions had any impact on the winter activity of moths. All the statistical calculations were done in Statistica 10.0 (StatSoft, 2011).

RESULTS

42 species of moths from six families were found as a result of autumn-spring investigations. Light trapping in two autumn-spring seasons 2007/08 and 2008/09 yielded 442 specimens of moths from five families and 34 species. During that time no apterous females were found. Fig. 1 shows the percentages of moth families in the material. Two species belonging to the family Geometridae, *Alsophila aescularia* (Denis and Schiffermüller) and *Operophtera brumata* (Linnaeus), clearly predominated in the material from light trapping. Based on the Q index, the species characteristic of the autumn-spring moths assemblage were *A. aescularia* and *O. brumata*. Most of the species could be regarded as rare and very rare. Table 1 lists all the species collected by light-trapping and their biocoenotic indices. Tree trunk searches yielded 40 moths from three families and 15 species. Table 2 lists these species including sampling dates.

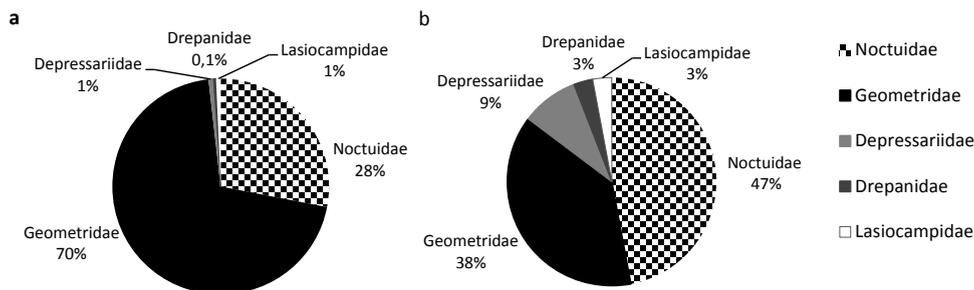


Fig. 1. Percentage of moth families collected in a temperate deciduous forest of Central Poland in two winter seasons 2007/2008 and 2008/2009: a. with respect to the number of specimens, b. with respect to the number of species.

Table 1. Moths collected using a light trap in two winters 2007/2008, and 2008/2009 in Central Poland in systematic order with classes of biocoenotic factors: No. number of specimens collected, D. dominance, F. frequency, Q. ecological significance.

Family	Species	No. of specimens	D	F	Q
Depressariidae	<i>Agonopterix ocellana</i> (Fabricius, 1775)	1	D ₁	F ₁	Q ₁
	<i>Semioscopis avellanella</i> (Hübner, 1793)	1	D ₁	F ₁	Q ₁
	<i>Semioscopis steinkellneriana</i> (Denis and Schiffermüller, 1775)	1	D ₁	F ₁	Q ₁
Drepanidae	<i>Achlya flavicornis</i> (Linnaeus, 1758)	2	D ₁	F ₁	Q ₁
Geometridae	<i>Agriopsis leucophaearia</i> (Denis and Schiffermüller, 1775)	6	D ₂	F ₂	Q ₂
	<i>Agriopsis marginaria</i> (Fabricius, 1776)	10	D ₃	F ₃	Q ₂
	<i>Alsophila aceraria</i> (Denis and Schiffermüller, 1775)	14	D ₃	F ₂	Q ₂
	<i>Alsophila aescularia</i> (Denis and Schiffermüller, 1775)	141	D ₅	F ₃	Q ₄
	<i>Apocheima hispidaria</i> (Denis and Schiffermüller, 1775)	3	D ₁	F ₂	Q ₁
	<i>Biston strataria</i> (Hufnagel, 1767)	1	D ₁	F ₁	Q ₁
	<i>Chloroclysta siterata</i> (Hufnagel, 1767)	1	D ₁	F ₁	Q ₁
	<i>Ectropis crepuscularia</i> (Denis and Schiffermüller, 1775)	2	D ₁	F ₂	Q ₁
	<i>Epirrita</i> sp.	1	D ₁	F ₁	Q ₁
	<i>Erannis defoliaria</i> (Clerck, 1759)	2	D ₁	F ₂	Q ₁
	<i>Operophtera brumata</i> (Linnaeus, 1758)	102	D ₅	F ₃	Q ₄
	<i>Operophtera fagata</i> (Scharfenberg, 1805)	1	D ₁	F ₁	Q ₁
	<i>Operophtera</i> sp.	2	D ₁	F ₂	Q ₁
	<i>Phigalia pilosaria</i> (Denis and Schiffermüller, 1775)	23	D ₄	F ₂	Q ₂
<i>Thera juniperata</i> (Linnaeus, 1758)	1	D ₁	F ₁	Q ₁	
Lasiocampidae	<i>Poecilocampa populi</i> (Linnaeus, 1758)	3	D ₁	F ₂	Q ₁
Noctuidae	<i>Agrochola circellaris</i> (Hufnagel, 1766)	2	D ₁	F ₁	Q ₁
	<i>Agrochola macilenta</i> (Hübner, 1809)	3	D ₁	F ₂	Q ₁
	<i>Anorthoa munda</i> (Denis and Schiffermüller, 1775)	3	D ₁	F ₂	Q ₁
	<i>Brachionycha nubeculosa</i> (Esper, 1785)	1	D ₁	F ₁	Q ₁
	<i>Cerastis rubricosa</i> (Denis and Schiffermüller, 1775)	1	D ₁	F ₁	Q ₁
	<i>Conistra ligula</i> (Esper, 1791)	1	D ₁	F ₁	Q ₁
	<i>Conistra rubiginea</i> (Denis and Schiffermüller, 1775)	2	D ₁	F ₂	Q ₁
	<i>Conistra rubiginosa</i> (Scopoli, 1763)	6	D ₁	F ₂	Q ₂
	<i>Conistra vaccinii</i> (Linnaeus, 1761)	23	D ₄	F ₃	Q ₃
	<i>Eupsilia transversa</i> (Hufnagel, 1766)	22	D ₃	F ₃	Q ₃
	<i>Lithophane omitopus</i> (Hufnagel, 1766)	1	D ₁	F ₁	Q ₁
	<i>Orthosia cerasi</i> (Fabricius, 1775)	4	D ₁	F ₂	Q ₁
	<i>Orthosia cruda</i> (Denis and Schiffermüller, 1775)	31	D ₄	F ₂	Q ₃
	<i>Orthosia gothica</i> (Linnaeus, 1758)	4	D ₁	F ₂	Q ₁
	<i>Orthosia incerta</i> (Hufnagel, 1766)	18	D ₃	F ₃	Q ₂
<i>Orthosia populeti</i> (Fabricius, 1775)	2	D ₁	F ₂	Q ₁	

Two peaks were observed in the seasonal dynamics of autumn-spring active moths (Fig. 2). The first peak consisted of 20 species, but the activity of five was limited to the end of October; ten were active in November but only four of these

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survived to the end of autumn. The dominant species in this period, with the largest numbers of individuals, were *Operophtera brumata* and *Alsophila aceraria* (Denis and Schiffermüller). The former displayed the longest uninterrupted period of activity. These two species were recorded from late-October / early-November until the end of December and then, after about a two-month break, from the end of February to the end of the study period. In mid-winter the moths' activity ceased. The second peak consisted of 25 species. It started at the end of February, when a small number of species was observed. Most of them became active in late February and early March. The dominant species in spring, with the largest abundance, were *A. aescularia* and *Orthosia cruda* (Denis and Schiffermüller, 1775). *Conistra vaccinii* (Linnaeus, 1761) had the longest uninterrupted period of activity during this time.

Table 2. Moths found on tree trunks in winter 2007-2008 - species which were only caught

Family	Species	No. of speciemem	Date
Geometridae	<i>Agriopis aurantiaria</i> (Hübner, 1799)	4	29.10.2007 14.11.2007
	<i>Agriopis marginaria</i> (Fabricius, 1776)	1	25.03.2008
	<i>Alsophila aceraria</i> (Denis and Schiffermüller, 1775)	7	14.11.2007 21.11.2007 28.11.2007
	<i>Colotois pennaria</i> (Linnaeus, 1761)	1	29.10.2007
	<i>Epirrita christyi</i> (Allen, 1906)	1	26.10.2007
	<i>Epirrita dilutata</i> (Denis and Schiffermüller, 1775)	2	14.11.2007 21.11.2007
	<i>Epirrita</i> sp.	3	14.11.2007
	<i>Erannis defoliaria</i> (Clerck, 1759)	2	29.10.2007
	<i>Operophtera brumata</i> (Linnaeus, 1758)	7	26.10.2007 14.11.2007 21.11.2007 28.11.2007
	<i>Operophtera fagata</i> (Scharfenberg, 1805)	1	14.11.2007
	<i>Operophtera</i> sp.	2	21.11.2007
	<i>Pennithera firmata</i> (Hübner, 1822)	1	23.10.2007
	Noctuidae	<i>Asteroscopus sphinx</i> (Hufnagel, 1766)	1
<i>Conistra erythrocephala</i> (Denis and Schiffermüller, 1775)		2	26.10.2007
<i>Conistra vaccinii</i> (Linnaeus, 1761)		1	29.10.2007
<i>Eupsilia transversa</i> (Hufnagel, 1766)		1	29.12.2007 29.12.2007
Pterophoridae	<i>Emmelina monodactyla</i> (Linnaeus, 1758)	3	14.11.2007

Geometrids were collected at a minimal temperature of -4°C. Temperatures above 0°C stimulated the moths to greater activity; this is expressed by the higher number of individuals and species. Above this temperature, the moths' activity levels varied. The humidity, measured daily during the study, ranged between 70 and 100%. Most individuals and species were collected at humidities of 80-89%. The relationship between weather conditions and the species diversity and number of individuals is presented in Fig. 3.

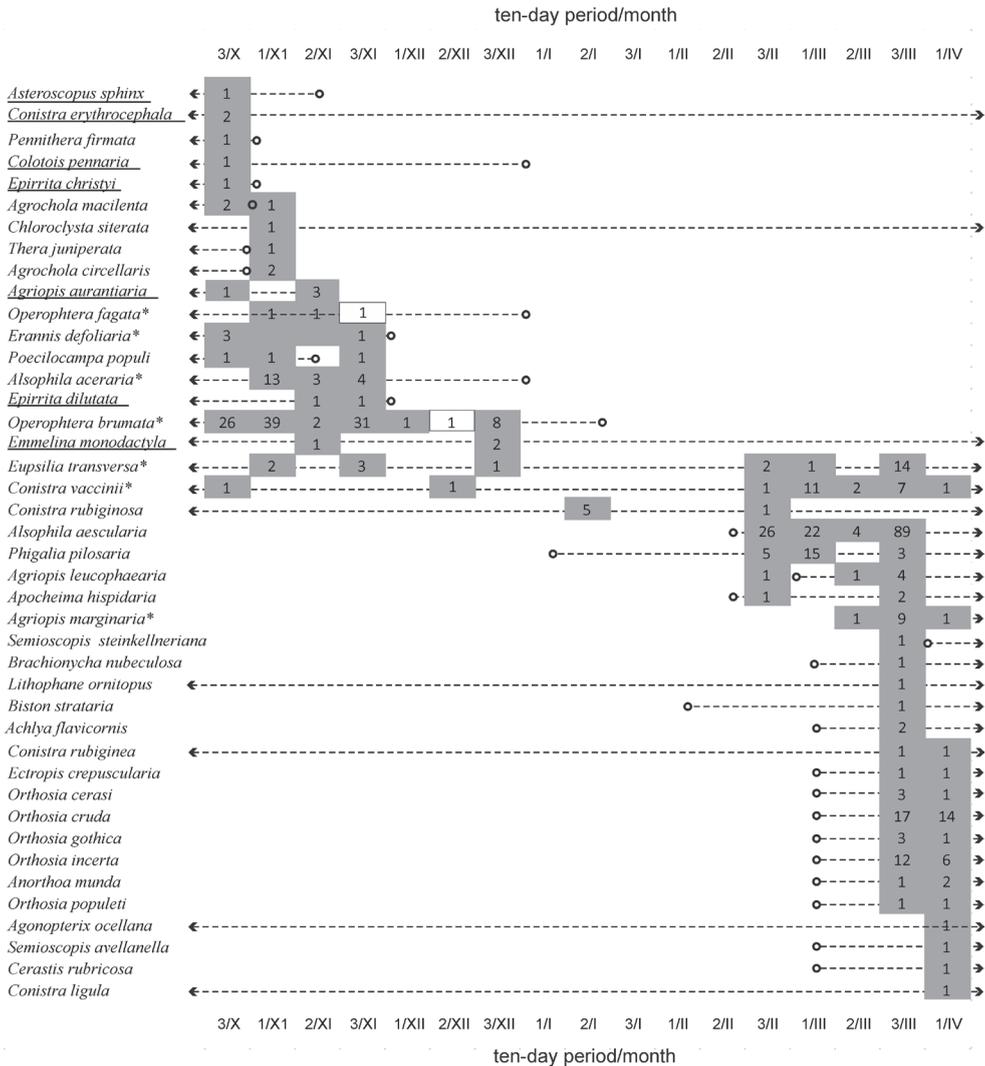


Fig. 2. Seasonal dynamics of moths in a temperate deciduous forest of Central Poland in two winter seasons 2007/2008 and 2008/2009: ◀ - - arrows inform about phenology in Poland, ○ circle points beginning or end of activity, both based on literature (Jonko 2014); species - moths caught only by searching tree trunks; * moths caught using both methods, □ - additional data according to Soszyńska-Maj and Buszko (2011). The first, second and third ten-day periods of months are given in Arabic numerals, the months in Roman numerals.

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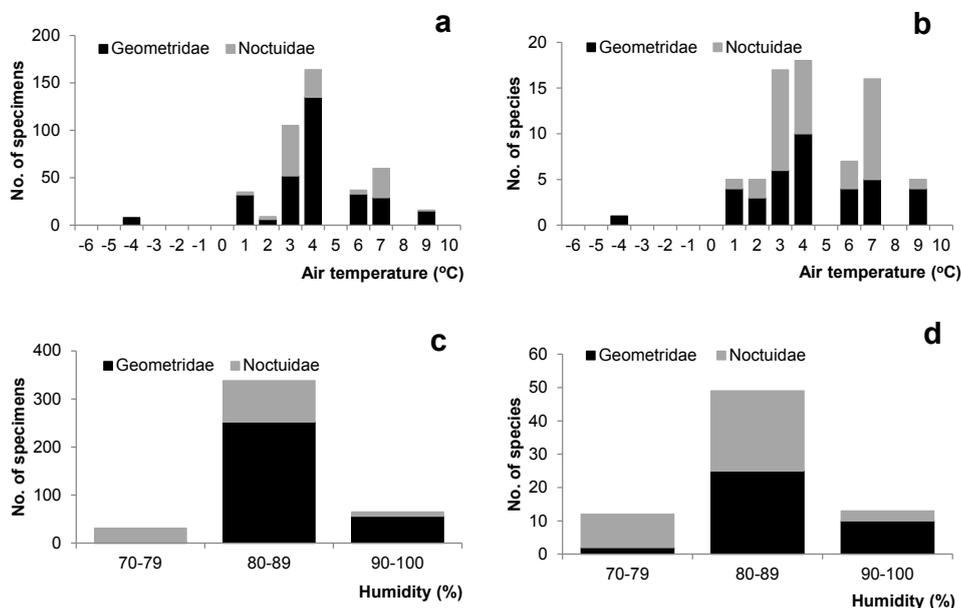


Fig. 3. Number of moth specimens and species in relation to atmospheric factors: a. Number of specimens in relation to air temperature; b. Number of species in relation to air temperature; c. Number of specimens in relation to humidity; d. Number of species in relation to humidity.

The correlations between temperature and the number of geometrids species was positive ($r=0.344$) while between air pressure and the number of noctuids was negative ($r=0.358$). The correlation with humidity was not statistically significant. Detailed data on Pearson's correlation coefficient are listed in Table 3. Regression analysis showed that a rise in temperature had a positive effect on the number of geometrid species ($r^2=0.1186$, $p=0.046$) whereas a rise in air pressure negatively affected the abundance of Noctuidae ($r^2=0.1283$, $p=0.0375$) (Fig. 4).

Table 3. Pearson's correlation (seasons 2007-2009), depending on environmental variables (air temperature and pressure). Correlations are significant at $p<0.05$.

	AM	SD	$r(X,Y)$	r^2	t	p
Average temperature	2.2	3.8				
Number of Geometridae species	1.1	1.7	0.344	0.119	2.075	0.046
Pressure	1015.9	8.7				
Abundance of Noctuidae	3.6	8.8	-0.358	0.128	-2.17	0.038

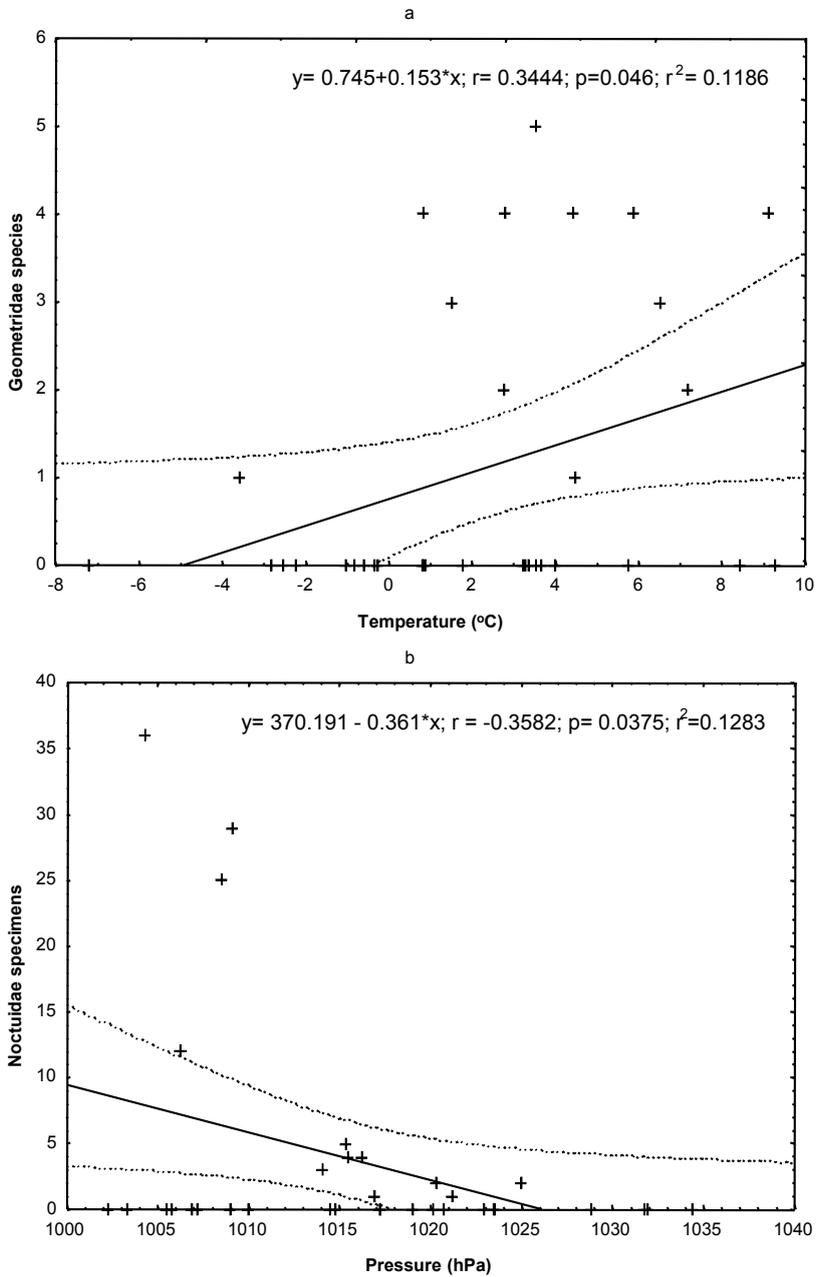


Fig. 4. Linear regression analysis displaying Geometridae species vs. temperature, a. Noctuidae specimens vs. pressure b. at $p < 0.05$.

DISCUSSION

Until recently, studies of winter active moths focused mainly on one species - the forest geometrid pest *Operophtera brumata* (e.g. Jepsen *et al.*, 2012; Nowinszky *et al.*, 2012). Our study is the first systematic research into the assemblage of autumn-spring active moths to have been undertaken. As expected, the investigated community consisted mainly of representatives of two families: Geometridae and Noctuidae. However, the former family are characteristic mainly of the autumn and early winter, while the latter of late winter and early spring, what is directly associated with their biology (Buszko and Nowacki, 1991; Majerus, 2002).

Autumn-spring active moths had two peaks of activity. The first was observed in autumn and consisted mainly of Geometridae. This part of investigated assemblage is classified by Majerus (2002) as a group hatching, breeding and egg-laying in winter and dying soon after, often represented by flightless females. Their eggs survive the wintertime and early hatched larvae have unlimited food resources and no competition (Majerus, 2002). This type of life strategy is typical of the following geometrid species we collected: *Colotois pennaria* (Linnaeus, 1761), *Epirrita christyi* (Allen, 1906), *E. dilutata* (Denis and Schiffermüller, 1775), *Thera juniperata* (Linnaeus, 1758), *A. aurantiaria* (Hübner, 1799), *O. brumata*, *O. fagata* (Scharfenberg, 1805), *Erranis defoliaria* (Clerck, 1759), as well as of the noctuids *Asteroscopus sphinx* (Hufnagel, 1766), *Agrochola macilenta* (Hübner, 1809), *A. circellaris* (Hufnagel, 1766) and the lasiocampid *Poecilocampa populi* (Linnaeus, 1758). Males of Winter Moth (*O. brumata*) made up a large proportion (over 23%) of the total number of moths collected in the two seasons. Besides *O. brumata*, males of 10 other winter-active geometrid species of flightless females were collected during our light trapping. This group accounted for over 67% of the total number of moths captured, which reflects their large proportion in the assemblage investigated. Males attracted to light were highly active, even in a few degrees of frost. They perched on nearby trees and on the white screen. Brachypterous females were not attracted to light; but a previous study had shown them to be winter-active. Soszyńska-Maj and Buszko (2011) found large numbers of brachypterous females of *O. brumata* on the snow in the same area. The wingless or micropterous females of some geometrids lost their ability to fly through evolutionary adaptation to minimise heat loss in an environment experiencing reduced predatory pressure during the winter (Barbosa and Krischik, 1989; Roff, 1990; Sattler, 1991; Snäll *et al.*, 2007).

Noctuidae, second most abundant family in our study were active mainly in early spring, less so in late autumn, while in mid-winter were practically inactive. We observed that arriving at the light, noctuids were not very active, often falling into the litter and remaining there. After landing on the screen they remained motionless. At lower temperatures noctuids are hidden under fallen leaves, snow cover and tree bark. It is slightly warmer in such sites, which allows the moths to withstand the unfavourable conditions in quiescence (Heinrich, 1987). Invertebrate hibernation and activity in the litter during winter is possible owing to the snow cover, which insulates the ground

from temperature changes (Coulianos and Johnels, 1962). The behaviour we observed could have been an attempt to find a suitable hiding place for overwintering. In contrary to Geometridae, only two noctuid specimens were found on the snow (Soszyńska-Maj and Buszko, 2011). Buszko and Nowacki (1991) reported two noctuids - *Eupsilia transversa* (Hufnagel, 1766) and *C. vaccinii* as being dominants in winter investigations, accompanied by congeners like *C. rubiginosa* (Scopoli, 1763). In our study, these species occurred also most often during light trapping at night. The differences in numbers and frequency of mentioned taxa are undoubtedly the result of different method used (liquid baits) by Buszko and Nowacki (1991), what have influenced the structure of this assemblage. Buszko and Nowacki (1991) pointed out that this activity results from the biology of the Noctuidae. As imagines, these moths live up to nine months and in favourable conditions during winter, part of their population suspends diapause for supplementary feeding. A good example confirming this type of behaviour is the activity of *C. vaccinii* in our study. This species is present as an imago for most of the year (www.lepidoptera.eu) and was caught mostly in spring, but also in small numbers in autumn and winter. Majerus (2002) classified these moths into groups hatching in autumn, surviving winter as imagines (usually in diapause) and then laying eggs in the spring. Other examples given by this author include other noctuids found in our study: *C. vaccinii*, *C. ligula* (Esper, 1791) and *E. transversa*. Typical early-spring noctuids (overwintering as pupae, frequently concealed under the leaf litter, under bark or in the soil) also take advantage of the limited competition for food resources such as nectar (Majerus, 2002). A good example is the genus *Orthosia*, of which we found four species *O. cruda* (Denis and Schiffermüller, 1775), *O. gothica* (Linnaeus, 1758), *O. incerta* (Hufnagel, 1766), *O. populeti* (Fabricius, 1775) and *Anorthoa munda* (Denis and Schiffermüller, 1775). It was observed that Noctuidae were less active when the temperature was about 0°C. They were looking for a place to conceal themselves, dropping into the leaf litter and resting there.

As it was mentioned previously the winter activity of all insects is related to the lower predatory pressure insectivorous mammals hibernate, and birds have either migrated or change their diet from insects to seeds. However, autumn-spring active invertebrate fall victim to small insectivorous mammals from the family Soricidae as well as bats. Shrew do not hibernate and remain active throughout the winter, feeding on invertebrates active in the leaf litter and associated with snow cover (Itâmieș and Lindgren, 1989) including flightless female geometrids as well as some other lepidopterans hibernating in the litter. According to the findings of Kaňuch *et al.* (2005), Lepidoptera, and particularly the Noctuoidea, are also the most important winter food component for the noctule bat *Nyctalus noctula* Schreber, which is active and hunts even at a minimum temperature of +2°C, while the geometrid *Colotois pennaria* is a prey item for the hibernating *Rhinolophus euryale* (Miková *et al.*, 2013). Among the collected moths, the two closely related geometrid species were active at the lowest temperatures. *Operophtera brumata* was attracted to light at -4°C and recorded on snow at -3°C (Soszyńska-Maj and Buszko, 2011), while *O. fagata* was found on snow at -6°C. Below this temperature, no other Lepidoptera species was active. During

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our research, the activity of Noctuidae was observed to increase only when the temperature was above 0°C, although *C. vaccinii* was collected on snow even below 0°C (Soszyńska-Maj and Buszko, 2011). Buszko and Nowacki (1990) demonstrated that an increase in air temperature affects their activity and can as a result interrupt or terminates quiescence. Their observations showed that the number of individuals of this family collected increased in proportion to the growth in temperature. We found that a rise in air temperature positively influenced the number of active Geometridae species in the cold period of the year and also that rising air pressure has a negative effect on the abundance of Noctuidae. In winter, high pressure is often accompanied by a decrease in air temperature. The influence of humidity on moth activity was not confirmed statistically. Previously Buszko and Nowacki (1990) had shown that humidity had an indirect influence on the activity of Noctuidae. High humidity slows down the decrease in temperature because of the heat generated by the condensation of the humidity in the air. Slower temperature drops at night lead to higher noctuid activity. Those authors also observed that a rapid drop in humidity limits moth activity, even if there is a small temperature increase.

Recent studies have shown that winters have become milder not only in Poland (Kožuchowski and Degirmendžič, 2005) but also around the world (Williams *et al.*, 2014) with alternate cold periods and thaws. Végvári *et al.* (2014) found that Noctuidae species hibernating as adults are able to react on changing climate faster than species overwintering in less developed stages, as they either prolong their autumn activity or can emerge right after hibernation. Moths from investigated assemblage will undoubtedly increase their winter activity as a consequence of more periods with higher temperatures, as compared to insects in which dormancy is controlled hormonally and depends on the photoperiod. It must affect their reproductive success, as warmer winters reduce the energy reserves needed for post-winter reproduction (Hahn and Denlinger, 2011; Williams *et al.*, 2012).

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